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# Le développement de la perception des expressions faciales

## The development of facial expressions perception

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# Le développement de la perception des expressions faciales

1er octobre 2015

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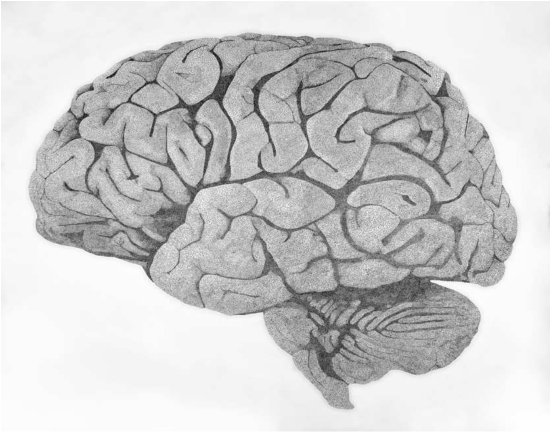

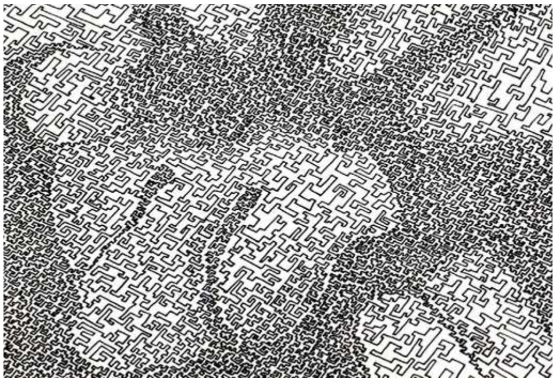

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Un index alphabétique de ces remerciements est disponible sur demande.

# RÉSUMÉ

Cette thèse se propose d'examiner le développement de la perception des expressions faciales émotionnelles en le replaçant dans le cadre théorique de la perception des visages : séparation entre aspects variants (expression, regard) et invariants (genre, type), rôle de l'expérience, attention sociale. Plus spécifiquement, nous avons cherché à mettre en évidence l'existence, tant chez l'enfant que chez le nourrisson, d'interactions réciproques entre la perception d'expressions faciales de colère, de sourire ou de peur et la perception du genre (Études 1-2), la perception du regard (Étude 3), et la détection des visages (Étude 4).

Dans un premier temps, nous avons montré que les adultes et les enfants de 5 à 12 ans tendent à catégoriser les visages en colère comme masculins (Étude 1). Comparer les performances humaines avec celles de classifieurs automatique suggère que ce biais reflète l'utilisation de certains traits et relations de second-ordre des visages pour en déterminer le genre. Le biais est identique à tous les âges étudiés ainsi que pour les visages de types non-familiers. Dans un second temps, nous avons testé si, chez le nourrisson, la perception du sourire dépend de dimensions invariantes du visage sensibles à l'expérience - le genre et le type (Étude 2). Les nourrissons ont généralement plus d'expérience avec les visages féminins d'un seul type. Les nourrissons de 3.5 mois montrent une préférence visuelle pour les visages souriants (dents visibles, versus neutre, de type familier) lorsque ceux-ci sont féminins ; l'inverse est observé lorsqu'ils sont masculins. L'effet n'est pas répliqué lorsque les dents des visages souriants (d'un type familier ou non) ne sont pas visibles. Nous avons cherché à généraliser ces résultats à une tâche de référencement d'objet chez des nourrissons de 3.5, 9 et 12 mois (Étude 3). Les objets préalablement référencés par des visages souriants étaient autant regardés que les objets préalablement référencés par des visages neutres, quel que soit le groupe d'âge ou le genre du visage, et ce malgré des différences en terme de suivi du regard. Enfin, en employant une mesure univariée (préférence visuelle pour le visage) et une mesure multivariée (évidence globale distinguant le visage du bruit) de la détection du visage à chaque essai, associées à une modélisation des courbes psychométriques par modèles non-linéaire mixtes, nous mettons en évidence une meilleure détection des visages de peur (comparés aux visages souriants) dans le bruit phasique chez les nourrissons à 3.5, 6 et 12 mois (Étude 4).

Ces résultats éclairent le développement précoce et le mécanisme des relations entre genre et émotion dans la perception des visages ainsi que de la sensibilité à la peur.

**Mots-clés :** nourrisson, enfant, perception, visage, émotion, expression faciale

# ABSTRACT

This thesis addressed the question of how the perception of emotional facial expressions develops, reframing it in the theoretical framework of face perception: the separation of variant (expression, gaze) and invariant (gender, race) streams, the role of experience, and social attention. More specifically, we investigated how in infants and children the perception of angry, smiling, or fearful facial expressions interacts with gender perception (Studies 1-2), gaze perception (Study 3), and face detection (Study 4).

In a first study, we found that adults and 5-12 year-old children tend to categorize angry faces as male (Study 1). Comparing human performance with that of several automatic classifiers suggested that this reflects a strategy of using specific features and second-order relationships in the face to categorize gender. The bias was constant over all ages studied and extended to other-race faces, further suggesting that it doesn't require extensive experience. A second set of studies examined whether, in infants, the perception of smiling depends on experience-sensitive, invariant dimensions of the face such as gender and race (Study 2). Indeed, infants are typically most familiar with own-race female faces. The visual preference of 3.5 month-old infants for open-mouth, own-race smiling (versus neutral) faces was restricted to female faces and reversed in male faces. The effect did not replicate with own- or other-race closed-mouth smiles. We attempted to extend these results to an object-referencing task in 3.5-, 9- and 12-month-olds (Study 3). Objects previously referenced by smiling faces attracted similar attention as objects previously cued by neutral faces, regardless of age group and face gender, and despite differences in gaze following. Finally, we used univariate (face side preference) and multivariate (face versus noise side decoding evidence) trial-level measures of face detection, coupled with non-linear mixed modeling of psychometric curves, to reveal the detection advantage of fearful faces (compared to smiling faces) embedded in phase-scrambled noise in 3.5-, 6-, and 12-month-old infants (Study 4). The advantage was as or more evident in the youngest group than in the two older age groups.

Taken together, these results provide insights into the early ontogeny and underlying cause of gender-emotion relationships in face perception and the sensitivity to fear.

**Keywords:** infant, children, perception, face, emotion, facial expression

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# PUBLICATIONS OF THE CANDIDATE

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## Publications included in the thesis

The experimental chapters of this thesis contain several working or published papers, slightly edited for consistency.

### Forthcoming

CHAPTER 4 **Bayet L.**, Quinn P. C., Tanaka J., Lee K., Gentaz E., & Pascalis O. (in preparation) Experience-dependent and experience-independent contributions to the visual preference for smiling at 3.5 months.

CHAPTER 5 **Bayet L.**, Quinn P. C., Tanaka J., Lee K., Gentaz E., & Pascalis O. (in preparation) Who to follow, what to learn: Face gender and positive emotion effects on gaze referencing in infancy.

CHAPTER 6 **Bayet L.**, Quinn P. C., Laboissiere R. , Caldara R., Lee K., & Pascalis O. (in preparation) Facilitated detection of fear faces from early infancy.

### Published or in press

CHAPTER 3 **Bayet L.**, Pascalis O., Quinn P. C., Lee K., Gentaz E., & Tanaka J. (2015) Angry facial expressions bias gender categorization in children and adults: behavioral and computational evidence. *Frontiers in Psychology* 6, 346 doi: 10.3389/fpsyg.2015.00346

CHAPTER 4 **Bayet L.**, Quinn P. C., Tanaka J., Lee K., Gentaz E., & Pascalis O. (2015) Face gender influences the looking preference for smiling expressions in 3.5-month-old human infants. *PLOS ONE* 10: e0129812 doi: 10.1371/journal.pone.0129812

## Other publications

### Forthcoming

submitted Damon F., Méary D., Quinn P. C., **Bayet L.**, Heron-Delaney M, Lee K., & Pascalis O. (under review) A preference for adult faces in newborns that is modulated by face race.

**Bayet L.**, Damon F., Méary D., Porcheron A., Russell R., & Pascalis O. (under review) Sensitivity to contrast-enhanced facial features in human infants.

### Published or in press

2015 Damon F., **Bayet L.**, Hillairet de Boisferon A., Méary D., Dupierrix E., Quinn P. C., Lee K., & Pascalis O. (2015) Can human eyes prevent perceptual narrowing for monkey faces? *Developmental Psychobiology* 57, 637-642 doi: 10.1002/dev.21319

Marti S., **Bayet L.**, & Dehaene S. (2015) Subjective report of eye fixations during serial search. *Consciousness and Cognition* 33, 1-15 doi: 10.1016/j.concog.2014.11.007

2014 **Bayet L**., Pascalis O. & Gentaz E. (2014) Le développement de la discrimination des expressions faciales émotionnelles chez les nourrissons dans la première année. *L'Année Psychologique* 114, 469-500 doi: 10.4074/S0003503314003030

# INTRODUCTION

When we think broadly about human communication, language is usually the first channel to come to mind. And yet, a slightly raised brow, a little grin, even from a stranger or on a photograph, triggers attributions of feelings and complex mental states. Humans live surrounded by the faces of other humans; Silent face-to-face communication is so deeply engrained in our everyday experience that we easily overlook it. Faces have been around for hundreds of millions of years, ever since the first "heads", the concentration of nervous tissue, sensory receptors and a mouth on an anterior body part. Thus, it is after all not surprising that some amount of face processing exists in social species as diverse as sheep, wasps, and of course humans - with deep connections between social and perceptual learning processes in ontogeny. Facial expressions, on the other hand, are relatively recent in phylogeny, being present in all mammals but particularly developed in primates. The perception of emotional facial expressions lies at the intersection of three broad questions in cognitive science: perception, social cognition, and emotion processes. The complex nature of this ability is perhaps best reflected by its sensitivity to a very broad range of conditions and developmental circumstances: Autism, emotion disorders, violence or neglect have all been linked to variations in the perception of emotional faces.

During the course of the present thesis, we address the question of how this ability develops in childhood and infancy. This is not a new question as it was already raised by Darwin more than a hundred years ago. After providing a brief review of the literature on this subject in CHAPTER 1, and outlining some outstanding questions and general methods in CHAPTER 2, we will attempt to further the current understanding of this old question in a series of four experimental chapters. In CHAPTER 3, we report the existence in children and adults of a bias that causes angry faces to be categorized as male more often than smiling or neutral faces, and use computational models of gender categorization to research the underlying representations responsible. In CHAPTER 4, we focus on the visual preference for smiling that has been found in infants younger than 5 months and test the hypothesis that it is experience-driven. In CHAPTER 5, we ask whether smiling expressions modulate gaze following and referential object learning in infants from 3.5 to 12-months of age. In CHAPTER 6, we report the higher detection of fearful faces embedded in phase-scrambled noise compared to smiling faces. Finally, in CHAPTER 7 we will briefly summarize and discuss these findings.

## Chapter 1

# LITERATURE REVIEW

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## 1.1 PERCEPTION OF FACES AND FACIAL EXPRESSIONS BY ADULTS

Box 1: Résumé de la revue de littérature

- La perception des visages relève de la vision dite de haut-niveau, c'est-à-dire de la perception des objets et des formes. Plus particulièrement, la perception visuelle des visages implique des mécanismes spécialisés permettant la reconnaissance de visages individuels présentés selon différents points de vue (reconnaissance invariante) et traitant en continu les variations d'expression faciale.
- Les expressions faciales déclenchées par l'expérience émotionnelle ont une longue histoire évolutive et participent de la communication humaine au sens large. Au niveau neurophysiologique, percevoir ces expressions met en jeu une multitude de voies visuelles et affectives, ainsi que des voies plus spécifiques dédiées à la détection de stimuli pertinents pour l'organisme.
- Les différentes dimensions des visages (expression, genre, type, ...) interagissent dans leur perception. Par exemple, la perception de l'identité et la perception de l'expression des visages apparaissent relativement indépendantes, alors que le type (caucasian, chinois, ...) du visage affecte profondément la perception de son identité ou de son genre.
- Des compétences spécifiques à la perception des visages peuvent être mises en évidence dès la naissance. La perception des visages se développe durant la petite enfance sous l'influence de l'environnement, n'atteignant la maturité qu'à la fin de l'adolescence chez l'humain. Les stéréotypes raciaux influencent la perception des visages dès l'enfance.
- Les nourrissons montrent une certaine sensibilité aux expressions émotionnelles (visages et yeux de peur en particulier) vers l'âge de 6-7 mois. Les nourrissons plus jeunes semblent plus sensibles aux sourires, tandis que les nourrissons plus grands montrent l'émergence d'une compréhension plus fine, en contexte, des expressions émotionnelles et des situations sociales.
- Le développement de la perception des expressions faciales émotionnelles semble relativement robuste aux variations anormales de l'environnement social. Cette robustesse n'est que relative, et ménage une certaine plasticité. Les contributions respectives de l'expérience, de la maturation, et d'autres facteurs restent discutées.

## 1.1.1 Decoding the face space: How the brain represents faces

### 1.1.1.1 A rough guide to the ventral stream

“What does it mean, to see?” asked Marr in the introduction of his 1982’s book, *Vision*. Five centuries of research in vision have led to the characterization of vision first and foremost as an information-processing task, as a web of divergent and convergent streams carrying out a collection of representational strategies related to a whole range of different tasks from the guiding of eye movements to the detection of moving flies (Barlow, 1953) or the recognition of one’s own grand-mother (Quiroga, Kreiman, Koch, & Fried, 2008). Here, we briefly describe the functional organization of a portion of the visual system known as the ventral or occipito-temporal stream. The stream is a branch of the retinothalamic (or geniculostriate) pathway that runs through area V4 to infero-temporal areas (IT) subtending conscious object perception and recognition (FIGURE 1.1A). It represents only a portion of all the pathways and areas that process visual information such as the pulvinar nuclei of the thalamus, the dorsal or occipito-parietal stream (Ungerleider & Haxby, 1994), with which it is heavily connected (FIGURE 1.1B), and non-retinothalamic visual pathways such as the retinohypothalamic or the retinotectal tract.

**Primitives of object representation: Volumes and surfaces.** Inputs relevant to the ventral stream mainly originate from foveal cone photoreceptors. Those inputs are distributed in the primary visual cortex V1 in a highly organized manner that preserves binocularity and retinotopy and gives rise to V1’s prototypical orientation selectivity (FIGURE 1.2A; Hubel & Wiesel, 1959). Other basic selectivities are already apparent such as color, length or direction of motion. Contour segmentation occurs in V2-V4 from discontinuities in luminance, texture, or motion direction (FIGURE 1.2C). Contours may be extrapolated (illusory), such as in the famous Kanizsa triangle (FIGURE 1.2B; Kanizsa, 1955; Von der Heydt, Peterhans, & Baumgartner, 1984). Such representations are typically referred to as low- or mid-level vision as opposed to higher-order representations of entire objects. Basic depth-ordering is evident although receptive fields remain relatively local and complete figure-ground segmentation does not occur until later stages in inferior temporal areas (Orban, 2008) where the size-invariant coding of 3-D shape from convexity or binocular disparity is also evident (FIGURE 1.2D; Orban, 2008). It should be noted that while the hierarchical taxonomy of low-, mid-, and high-level vision is useful to interpret visual representations functionally in a computational light (Marr, 1982), feedback, top-down, and predictive processes dominate vision even at the level of V1 (e.g. Bullier, 2001; Mamassian, Landy, & Maloney, 2002; Rao & Ballard, 1999).

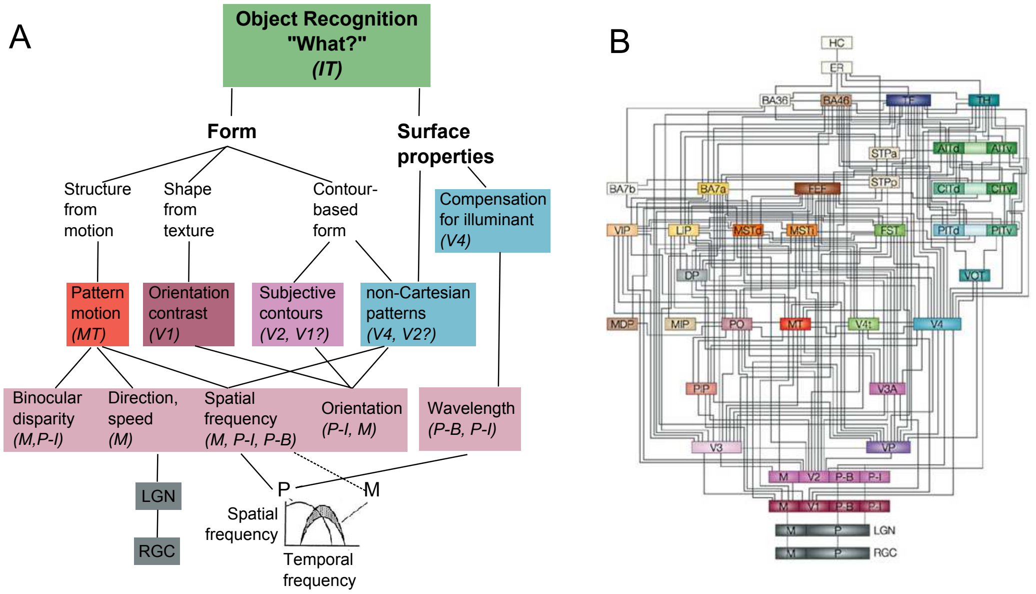

Figure 1.1: **Functional organization of the visual system. (A) Low and middle levels of processing leading to human object recognition according to Van Essen and Deyoe (1995).** Far from showing a parallel processing of isolated streams from the retina to the extrastriate cortex, human object recognition show patterns of convergence and divergence of representational streams. Adapted from Van Essen and Deyoe (1995). **(B) Organization of visual areas in the macaque brain.** Thirty-two visual cortical areas, two sub-cortical visual stages and several non-visual areas are shown, connected by 187 anatomically demonstrated links, most of which are reciprocal. Green and blue areas are traditionally referred to as belonging to the ventral stream. Note that they are heavily connected with other areas that belong to the dorsal stream (e.g., MT) or subtend the control of eye movements (e.g. LIP, FEF). Reprinted from Rees et al. (2002). AIT, anterior inferotemporal cortex; BA, Brodmann area; CIT, central inferotemporal cortex; d, dorsal; DP, dorsal prelunate area; ER, entorhinal cortex; FEF, frontal eye fields; FST, floor of superior temporal cortex; HC, hippocampus; LGN, lateral geniculate nucleus; LIP, lateral intraparietal area; M, magnocellular regions; MDP, mediodorsal parietal area; MIP, medial intraparietal area; MSTd, dorsal part of the medial superior parietal area; MSTi, inferior part of the medial superior parietal area; MT, middle temporal cortex (visual area 5); P, parvocellular regions; P-B, parvo-blob; P-I, parvo-interblob; PIP, posterior intraparietal area; PIT, posterior inferotemporal cortex; PO, parieto-occipital area (visual area 6); RGC, retinal ganglion cells; STPa, anterior superior temporal polysensory cortex; STPp, posterior temporal polysensory cotex; TF–TH, temporal areas; v, ventral; V1–V4t, visual areas; VIP, ventral intraparietal area; VOT, visual occipitotemporal cortex; VP, ventroposterior visual area. M, blob and interblob regions are subdivisions of V1, characterized by cytochrome oxidase staining. Non-Cartesian patterns are concentric, radial, or hyperbolic patterns.

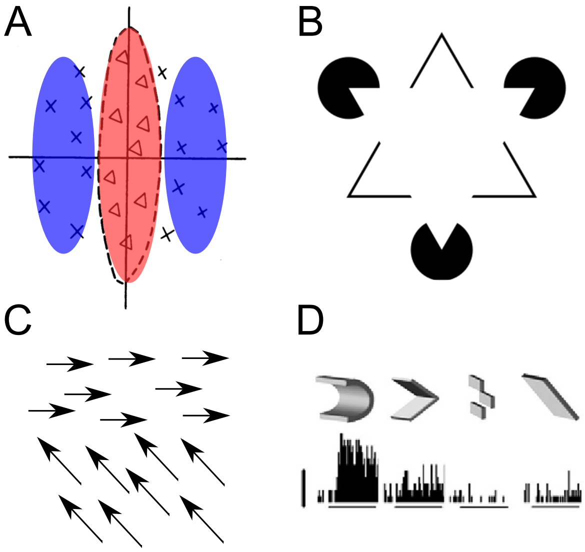

Figure 1.2: **Building blocks of high-level vision.** **(A)** Classical Receptive Field as exhibited from simple cells in V1. The receptive field displays parallel areas of excitation (triangles, red) and inhibition (crosses, blue) in a given orientation. Only bars of this orientation passing through the excitation region will elicit a maximal response. Adapted from Hubel and Wiesel (1959). **(B)** Kanizsa triangle (Kanizsa, 1955). Contours of the triangle are illusory. Neurons in V2 are selective to the orientation of such illusory contours (Orban, 2008). Adapted from Von der Heydt et al. (1984). **(C)** A kinetic boundary arising from a difference in the direction of motion of dots. Neurons in V4 readily detect such contours (Orban, 2008). **(D)** Selectivity to 3-D shape derived from binocular disparity in infero-temporal neurons, as evidenced by single-cell recordings in macaques (*Macaca sp.*). Horizontal lines indicate stimulus duration. Vertical line indicates a firing rate of 30 spikes/s. Adapted from Orban (2008).

**Explaining object and face recognition.** Selective responses to complex shapes or features, such as upright faces or gaze direction, is evident in infero-temporal neurons particularly in the Superior Temporal Sulcus (e.g. (Perrett et al., 1985; K. Tanaka, Saito, Fukada, & Moriya, 1991)). The IT cortex projects to the medial temporal lobe, where neurons display exquisitely abstract, integrated, sparse selectivities possibly subtending long-term semantic memory (Quiroga et al., 2008). But is selectivity sufficient to explain recognition? As noted by Marr (1982), the ability to recognize objects (or faces) implies the existence of object-centered representations, i.e., representations that are expressed in a coordinate-system independent of viewpoint (FIGURE 1.3). These representations should be reasonably easy to compute, appropriate to the targeted shapes, and based on information readily accessible in the lower-order representations (volumes, surfaces) from which they derive. Further, Marr noted that representations that are useful for recognition should ignore non-essential variations (i.e., *stable* or *invariant* representations) which should nonetheless remain expressible (i.e., *sensitivity* to these variations should remain). The tension between sensitivity and invariance means that representations of both variant and invariant aspects have to coexist and could possibly be organized in a hierarchic, modular fashion of increasing invariance. Marr's ideas were critical in inspiring Bruce and Young's model of face recognition (SECTION 1.1.1.2; Bruce & Young, 1986), and object-centered selectivities have indeed been found in the antero-temporal neurons of awake rhesus macaques (*Macaca mulatta*; FIGURE 1.3B; Freiwald & Tsao, 2010; Perrett et al., 1991). Although Marr's model has been critized and new models have been proposed (e.g. see Biederman, 1987; Donnadieu, Edouard, & Marendaz, 2006; Hummel & Stankiewicz, 1996; Tarr & Bülthoff, 1995), the idea remains that invariance is a fundamental property of object recognition. Strikingly, the invariant object recognition performance of hierarchical models has been shown to correlate strongly with how such models could predict the activity of infero-temporal neurons in awake rhesus macaques, which suggests that the organization of higher visual cortex is shaped, evolutionary or through development and plasticity, by the functional constraint of invariant recognition performance (Yamins et al., 2014). In fact, such constraint may be tuned dynamically by task demands (McKee, Riesenhuber, Miller, & Freedman, 2014). The "meta-modal" hypothesis of brain organization even suggests that what functionally and structurally defines the visual cortex is not the visual nature of its input, but its support of invariant recognition (Hannagan, Amedi, Cohen, Dehaene-Lambertz, & Dehaene, 2015); The hypothesis is supported by the cortical regionalization of sensory-substituted visual input processing in blind subjects (Hannagan et al., 2015).

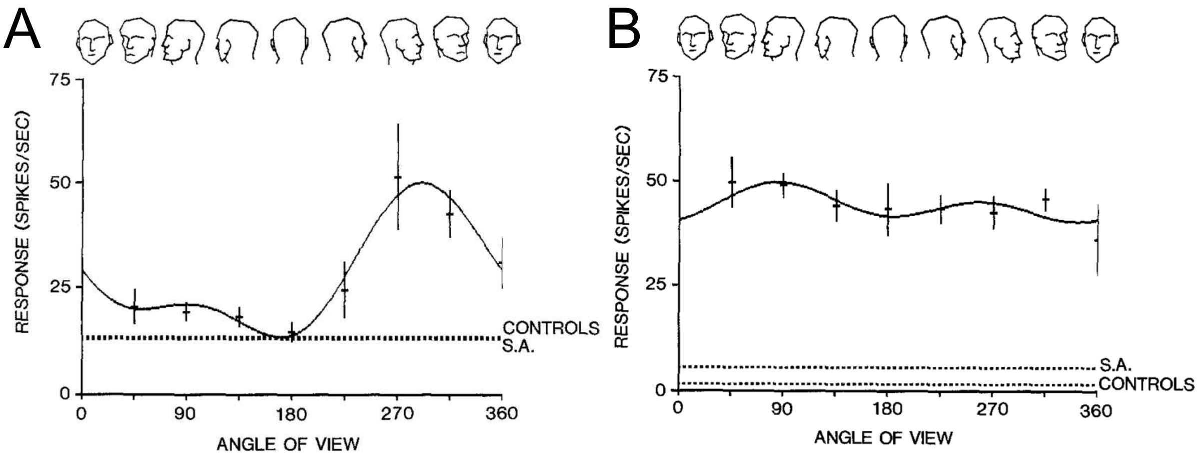

Figure 1.3: **Viewer- versus object-centered representations.** Perrett et al. (1991) recorded single-cell activity of neurons in the Superior Temporal Sulcus of awake rhesus macaques. **(A)** Among the cells that responded to faces, most demonstrated a view-dependent, i.e., viewer-centered coding. Here, the cell responds maximally (solid line) to the right profile view, whereas its response to other views does not differ from spontaneous activity or response to control stimuli (dashed line). **(B)** Some cells, on the contrary, demonstrated view-independent, i.e., object-centered, tuning. Adapted from Perrett et al. (1991).

#### 1.1.1.2 Behavioral approaches to human face perception

While high-level vision in general is concerned with all kinds of objects and scenes, the perception of faces engages specific mechanisms that cannot be reduced to expertise or subordinate-level recognition (Kanwisher, 2000; McKone & Kanwisher, 2005; Mckone, Kanwisher, & Duchaine, 2007). Fully functional face processing in adulthood requires early visual experience with faces (Le Grand, Mondloch, Maurer, & Brent, 2003), but the distinction between face and object processing may already be observed in infancy (de Haan & Nelson, 1999; Otsuka et al., 2007). The debate on face specificity (Mckone et al., 2007) versus general expertise (e.g., Gauthier & Tarr, 1997) falls outside of the scope of this thesis and will not be developed further.

**The Bruce & Young model.** Drawing from Marr's 1982 model of object recognition, Bruce and Young sought to present a model of face recognition that would explain the wealth of behavioral results that had been collected from typical adults as well as lesion patients (R. J. Baron, 1981), and summarize the cognitive models that had already been proposed (e.g. Ellis, 1975).

The model was based on three main ideas:

1. Face processing generates different "codes" (representations, information) that coexist. Such codes include purely perceptual codes (pictorial or invariant), semantic information that may be either perception-based (e.g., age, gender, personality traits...) or identity-

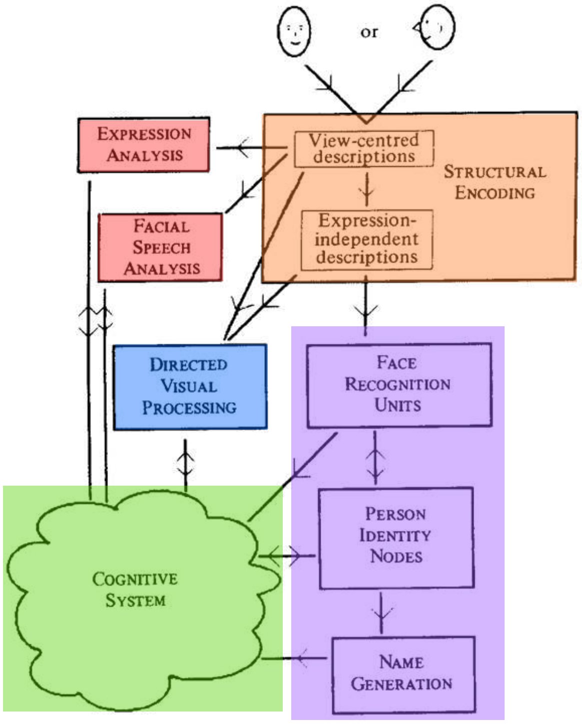

Figure 1.4: **Bruce and Young's model of face recognition.** Face processing starts from view-centered pictorial codes. In a common stage called structural encoding (orange box), variant and invariant aspects are segregated. This stage generates (1) a stream of variant information that may support the analysis of speech movement and facial expressions (red boxes); and (2) structural, invariant, object-centered codes that allow the recognition of face identity (purple boxes). Invariant dimensions such as gender or race are derived from directing visual attention (blue box) to specific, relevant features under cognitive control (green box). Adapted from Bruce and Young (1986).

based (e.g. familiarity, relationships, context, non-perceptual attributes), and streams of variant information relating to facial expressions and speech movements.

2. Starting from view-centered codes, an invariant (structural) code is generated in a stage called structural encoding (FIGURE 1.4, orange). The structural code is an object-centered, expression-independent representation that includes configural and featural information, internal and external traits. From this common stage, variant (expressions or speech; FIGURE 1.4, red) and invariant (identity; FIGURE 1.4, purple) information are segregated and streamlined into two parallel modules, resolving the tension between the requirements of sensitivity and invariance (Marr, 1982). Judgment on invariant dimensions (e.g. race, gender) occurs at a later stage.

3. Face recognition itself involves three serial steps (FIGURE 1.4, purple). First, the structural (invariant) code of the face is compared to the faces in memory (*"Person Identity Nodes"*) and a perceptual decision is made. If a match is found, a feeling of familiarity arises and identity-based semantic information may be accessed (*"Person Identity Nodes"*). Finally, the name of the person is accessed (*"Name Generation"*).

It should be noted that the model is not purely unidirectional, as multimodal or semantic priming may occur from the generic "*Cognitive System*" or more specifically from the *"Person Identity Nodes*" (e.g. a contextual cue facilitating the recognition of a face). Thus, the model leaves open the possibility that stereotypes or generic social knowledge (FIGURE 1.4, green) may, for example, steer visual attention (FIGURE 1.4, blue) towards certain features that are deemed to be diagnostic to a given invariant dimension such as gender or race. In other words, it opens a door to top-down, non-perceptual influences on face processing.

**A "face space" in the human brain?** Adults show superior recognition of distinctive faces, but poorer recognition of inverted or other-race faces (see SECTION 1.1.3.3 for a more detailed description of the Other-Race Effect). Based on these observations, Valentine proposed a general framework in which it is assumed that faces are represented by a point in a multidimensional space or "face space" (Valentine, 1991). Each encountered face could be mapped on that space, and points corresponding to (local) maxima of density in the face space would correspond to a norm, or prototype, which may be metaphorically described as the center of the face space (FIGURE 1.5C). In other words, the face space would be functionally centered on the average face (in the case of a single local maximum density). Two possible implementations of the face space have been proposed, with very similar predictions, where a given

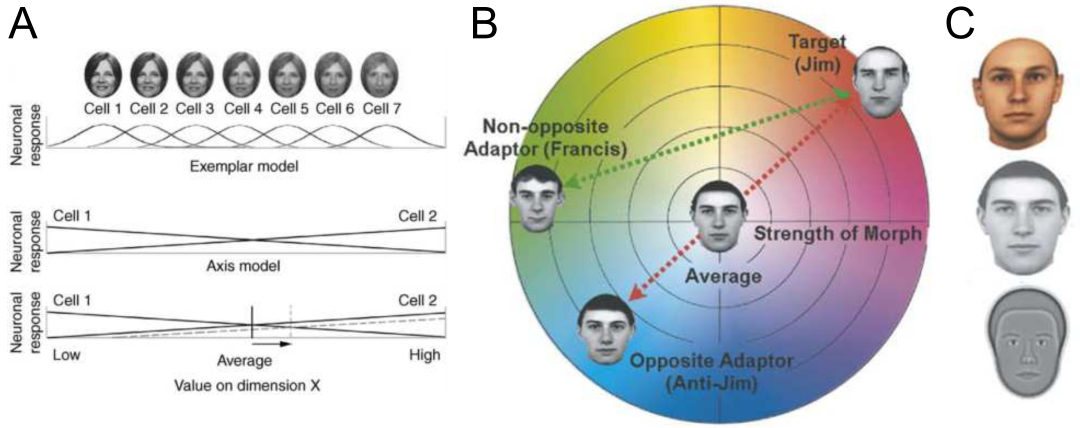

Figure 1.5: **The face space model.** **(A)** Exemplar-based (top) and norm-based (middle) accounts of the face space. In the latter, faces on a given dimension that crosses the average face would be coded by the relative firing of two cells corresponding to each extreme of that dimension; in the case of adaptation (bottom), the response to the adapted extreme face is depleted in Cell 2 (gray line) so that the true average face (black vertical line) now appears shifted in the opposite direction, in regards to the new apparent average face (gray vertical line). **(B)** A successful prediction of norm-based coding is that the recognition of a particular target face ("Jim") versus an adapted face will be enhanced if the adapted face is opposite to the target with respect to the average face ("Anti-Jim"), but not otherwise ("Francis"). **(C)** Average faces from different experiments. These average faces were noticeably different, evidencing a dynamic encoding of "the average face" that may change with learning and task requirements. Adapted from Tsao and Freiwald (2006).

face would be coded either with regards to its own properties (exemplar-based, FIGURE 1.5A, top) or with regards to its properties relative to the average face (norm-based, FIGURE 1.5A, middle). Both accounts make very similar predictions, although it has been argued that norm-based coding provides a better explanation for the phenomenon of after-effects (FIGURE 1.5B; Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes & Jeffery, 2006 but see Ross, Deroche, & Palmeri, 2014). Norm-based coding also found some support from single-unit recordings in the anterior infero-temporal cortex of rhesus macaques (Leopold, Bondar, & Giese, 2006) as well as fMRI studies in humans (Loffler, Yourganov, Wilkinson, & Wilson, 2005). Interestingly, it is suggested that norm-based coding provides an efficient solution to the invariance problem: common transformations would only need to be learned with respect to the prototype, or norm, whereas all the other faces (whatever the view-angle, expression, or other transformation) would only have to be coded with respect to one invariant norm. This means that there is no need to learn how all faces look from all possible angles, etc.

The "face space" model is agnostic to the actual aspects of faces that the dimensions of the face-space represent (Valentine, 1991). A first line of argument, informed by single unit recordings of awake rhesus macaques, suggests that the dimensions represent particular features in isolation or combination (Freiwald, Tsao, & Livingstone, 2009). In addition to fea-

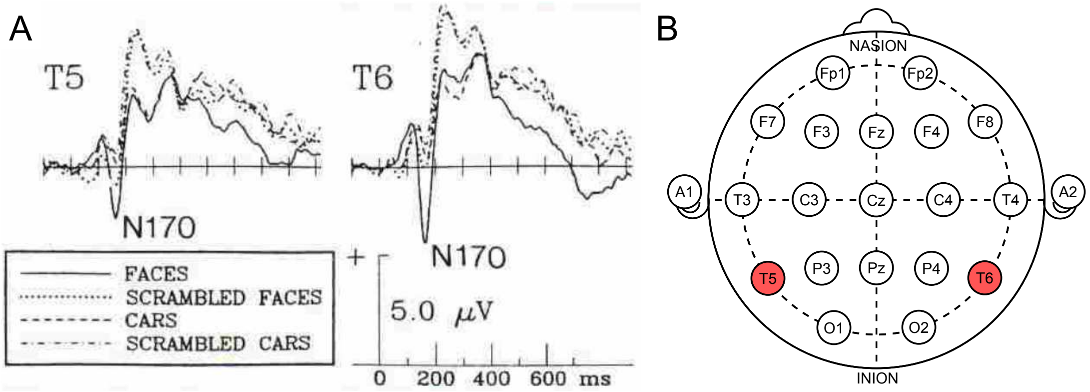

Figure 1.6: **Face-sensitive components of scalp EEG recording.** **(A)** Recordings of the face-sensitive N170 at occipito-temporal electrodes T5 (left hemisphere) and T6 (right hemisphere), re-referenced to the tip of the nose, showing a higher amplitude for faces especially on the right hemisphere. Reprinted from Bentin et al. (1996) **(B)** Sensor locations in the standard 10-20 system, with electrodes T5-6 colored in red.

tures, studies in humans have emphasized the role of 2-D and 3-D second order relations (Burton, Bruce, & Dench, 1993), and configural encoding (Renzi et al., 2013). A second line of argument has been advanced for a role of unsupervised representation analogs to Principal Component Analysis (Calder & Young, 2005), Principal Component Analysis combined with multi-dimensional scaling (X. Gao & Wilson, 2013) or Gabor filters (Kaminski, Méary, Mermillod, & Gentaz, 2011). Note that both accounts are not diametrically opposite because representations of facial features may be learned without supervision or priors.

#### 1.1.1.3 Neurophysiological approaches to human and non-human primate face perception

A rich body of work has been accumulated on the neural underpinnings of face perception in humans as well as macaques. Because the experimental contribution of the present thesis is exclusively based on behavioral paradigms, this literature will be touched only briefly.

**Time course of face perception in humans.** Intracranial (iEEG), electroencephalographical (EEG), and magnetoencephalographical (MEG) recordings of the time-resolved electrical activity of the brain concur to show an onset of face-selective activity that is time-locked at around 170 ms (EEG or MEG; Bentin et al., 1996, 2007; Z. Gao et al., 2013) to 200 ms (iEEG; Allison, McCarthy, Nobre, Puce, & Belger, 1994; Allison, Puce, Spencer, & McCarthy, 1999) post-stimulus presentation. This time-window corresponds to the EEG component N170 (MEG, iEEG components M170, N200, respectively), the second component that may be measured on averaged ERPs following visual stimulation and directly follows the component P1

(MEG, iEEG components M100, P120, respectively). The face-sensitive N200 may be observed from intracranial electrodes implanted in the fusiform gyrus (Allison et al., 1999), while the face-sensitive N170 may be maximally observed on temporal electrodes T5-6 with maximal amplitude on the right hemisphere (FIGURE 1.6, Bentin et al., 1996). The M170 has been estimated to originate from cortical sources in the right inferior occipital, inferior temporal, or fusiform gyri (Z. Gao et al., 2013) - although activity in the amygdala (a group of nuclei in the middle temporal lobe) may also contribute to it (Dumas et al., 2013). Both the N200 and the N170 are sensitive to inversion and other gross manipulations of configuration such as the presentation of isolated face parts (Bentin et al., 1996; McCarthy, Puce, Belger, & Allison, 1999), although a normal N170 may be observed when faces are not consciously perceived (Vuilleumier et al., 2001) or when configuration is only subtly perturbed (Halit, de Haan, & Johnson, 2000). Such automaticity, early latency, and complex sensitivities suggest that configural face processing precedes featural face processing in humans (McCarthy et al., 1999). The reverse has been suggested in rhesus macaques (Perrett, Mistlin, & Chitty, 1987). Overall, the higher amplitude of the EEG component N170 in response to faces, along with similar modulations of related components in MEG or iEEG, reflect the early detection and structural encoding of faces by temporal-occipital cortical structures in the right hemisphere. Later components (290-700 ms) and gamma bursts, on the other hand, are sensitive to a number of higher-level properties such as identity, familiarity, or perceptual integration (Z. Gao et al., 2013; Puce, Allison, & McCarthy, 1999).

**The face processing network in humans and macaques.** Cortical areas responding selectively to faces have been described in the ventral stream and superior temporal sulcus (STS) of humans using PET or fMRI (FIGURE 1.7A; Grill-Spector, Knouf, & Kanwisher, 2004; Kanwisher, McDermott, & Chun, 1997; Sergent, Shinsuke, & Macdonald, 1992). The clear anterior-posterior organization of these areas (Deen, Koldewyn, Kanwisher, & Saxe, 2015; Puce et al., 1999) strikingly resembles that which is found in face-selective areas of rhesus macaques using fMRI or single-unit recordings (FIGURE 1.7B; Freiwald et al., 2009; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003; Tsao, Freiwald, Tootell, & Livingstone, 2006). However, face-selective areas of humans are found more ventrally, whereas those of rhesus macaques are found more dorsally along the STS (Tsao, Moeller, & Freiwald, 2008). While a clear homology between macaque and human face selective regions hasn't been demonstrated yet, fMRI studies in awake macaques remain of particular interest because they allow direct comparisons with fMRI studies in humans and with single unit recordings in macaques (Or-

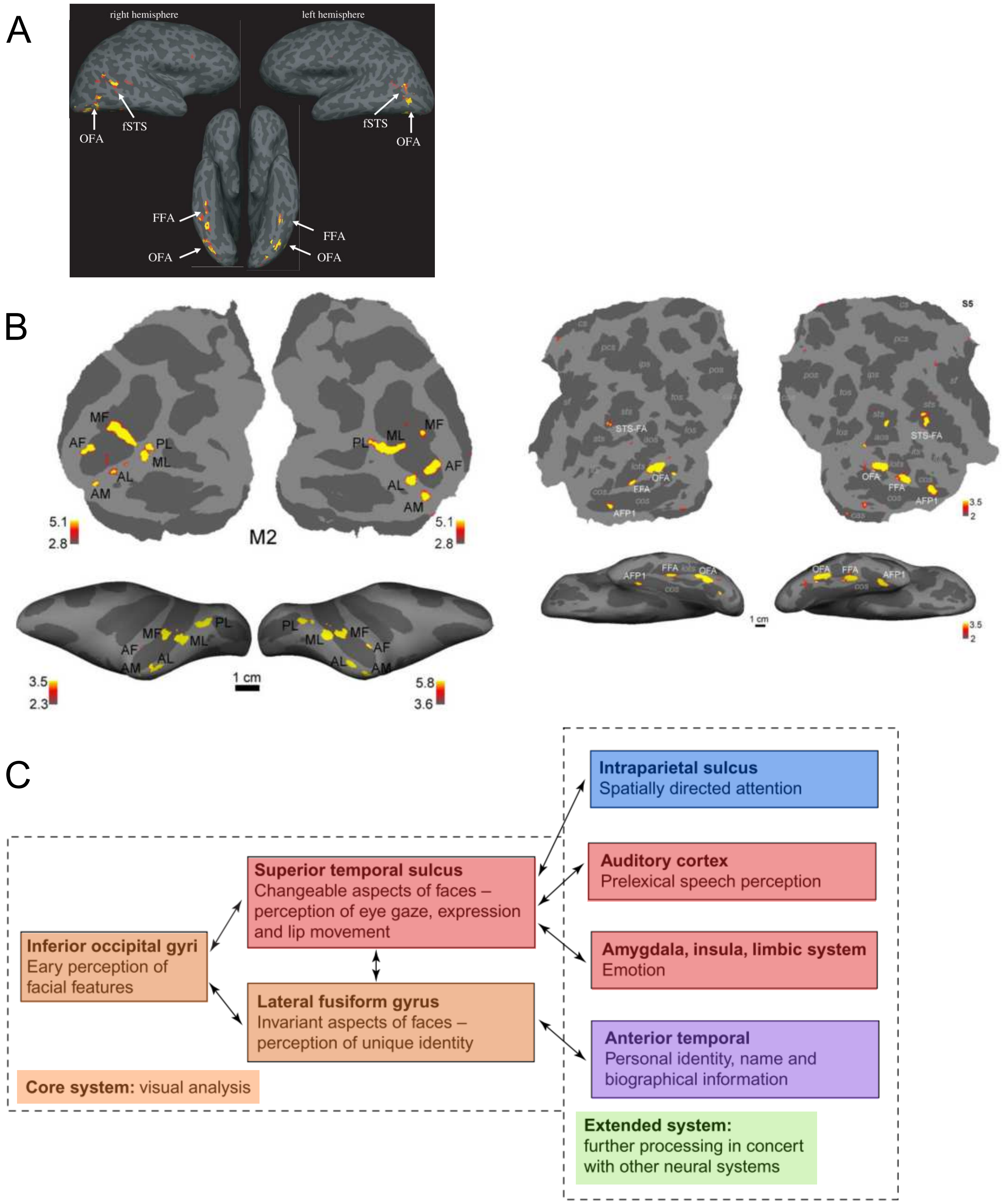

Figure 1.7: **Face selective cortical regions in humans and macaques.** **(A)** Main face selective regions in the human brain. Reprinted from Kanwisher and Yovel (2006). **(B)** A comparison of face selective patches in rhesus macaques (left) and humans (right). Reprinted from Tsao, Moeller, and Freiwald (2008). **(C)** The distributed model of face perception. Colors map each region to the Bruce and Young model reprinted on FIGURE 1.4. Adapted from Haxby et al. (2000). AFP1, anterior face patch 1; AL/AF, ML/MF, and PL/PF, anterior, middle, and posterior face patches in the Superior Temporal Sulcus lower lip/fundus (situated in TEa, TEm, and TEO, respectively); AM, anterior face patch on the ventral surface of the Infero-Temporal cortex (situated in anterior ventral TE); FFA, Fusiform Face Area; OFA, Occipital Face Area; fSTS/STS-FA, face-selective Superior Temporal Sulcus. TEO and TE are defined cytoarchitecturally with reference to von Economo's nomenclature (Von Bonin & Bailey, 1947).

ban, 2008). In both groups the interconnected face-selective areas form a network (Moeller, Freiwald, & Tsao, 2008; Rossion et al., 2003) that is differentially implicated by each particular aspect of face processing (FIGURE 1.7C; Haxby et al., 2000; Hoffman & Haxby, 2000).

In particular, the human fusiform face area (FFA) has been implicated in the structural encoding of faces (Caldara et al., 2006; Haxby et al., 2000; but see Grill-Spector, Sayres, & Ress, 2006), as well as in the retrieval of invariant information such as gender or race (Contreras, Banaji, & Mitchell, 2013), and is heavily connected to inferior and superior temporal cortices (Saygin et al., 2011). Critically, its fMRI activity is sensitive to face inversion, a major behavioral marker of specialized face processing (Yovel & Kanwisher, 2005), and correlates with trial-by-trial performance of face recognition (Grill-Spector et al., 2004). However, fMRI activity may not be necessarily causal. Evidence for a causal involvement of the right fusiform gyrus in conscious face perception in humans has recently been obtained by using a combination of electrocorticography and electrical brain stimulation in epileptic patients (Rangarajan et al., 2014). When the right face-selective fusiform gyrus was stimulated, face distortions or illusions were experienced. By contrast, stimulation of the left face-selective fusiform gyrus merely produced unspecific visual changes such as speckles. Interestingly, while the right-hemisphere dominance of face activations in the FFA may already be present in infancy well before the onset of language production (de Heering & Rossion, 2015; Tzourio-Mazoyer et al., 2002), in adults it increases with reading performance as well as with the left-hemisphere dominance for language (Pinel et al., 2014).

Selectivity for emotional faces has been found in face-selective patches of the orbito-frontal cortex in rhesus macaques (FIGURE 1.8 A-B; Tsao, Schweers, Moeller, & Freiwald, 2008). Such selectivity had also been observed with single unit recordings in the temporal neurons of rhesus (*Macaca mulatta*) and cynomolgus (*M. fascicularis*) macaques (Hasselmo, Rolls, & Baylis, 1989). We will see next that the human perception of emotional faces relies on partly similar pathways, implicating the face-selective STS as well as cortical and sub-cortical regions linked to the processing of emotions (FIGURE 1.7C; Haxby et al., 2000).

### 1.1.2 Facial expressions: from subjective experience to biological relevance

#### 1.1.2.1 Emotions as part of the subjective landscape

Ever since Ekman posited the existence of a limited number of basic, pure emotions that are constrained by physiology and provoke specific responses of the facial musculature and

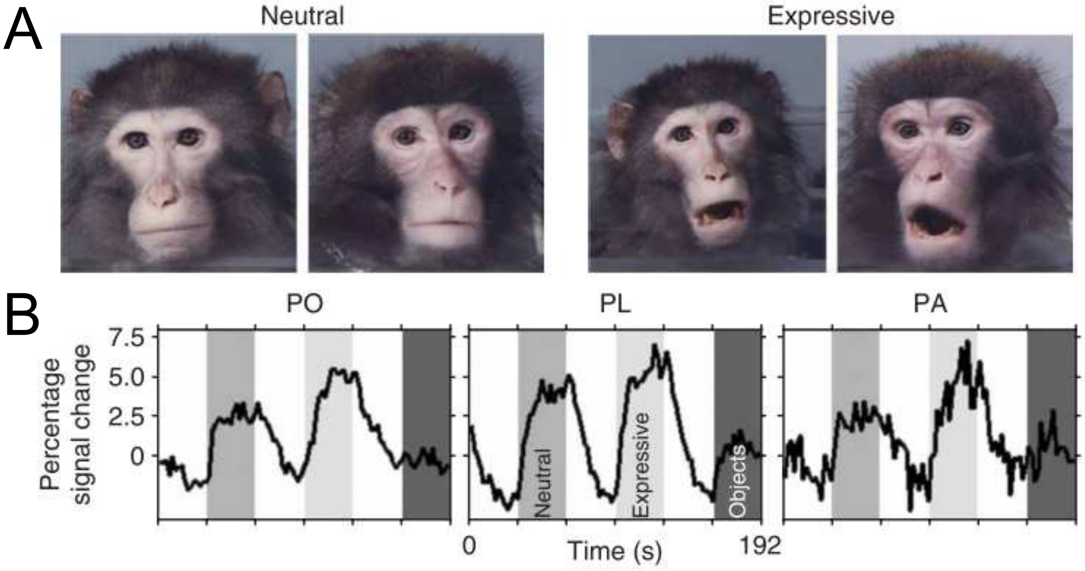

Figure 1.8: **Face-selective patches in the macaque orbito-frontal cortex respond to emotional expressions.** **(A)** Example of the stimuli used. **(B)** Average BOLD response of three prefrontal, face-selective patches (PO, PL and PA) averaged over three rhesus macaques. Adapted from Tsao, Schweers, et al. (2008).

autonomic system (Ekman, 1980, 1992; Ekman & Friesen, 1971; Ekman, Levenson, & Friesen, 1983; Ekman & Oster, 1979; Ekman, Sorenson, & Friesen, 1969), it has become common to limit the experimental investigation of emotion to the cases of joy, sadness, fear, and anger, possibly supplemented by disgust, surprise, interest or contempt. The present thesis does follow this practice and restrains itself to smiling (SECTION 3, 4, 5 and 6), fear (SECTION 6), and anger (SECTION 3). It is clear that a small number of robust emotional experiences and expressions dominate the emotional landscape; They do not cover the entire landscape and their discreteness, universality, and function all remain debated. Only a few of the recent developments on these issues will be covered here, but for a historical review see for example Gendron and Barrett (2009).

**Are there emotion-specific areas in the brain?** Is there a single mechanism, area, process, mental state, which causally triggers one specific emotion but no other, ie., are emotions natural kinds (Barrett, 2006)? Of course emotions may evoke distinct, recognizable physiological responses (although even that is debated; Barrett, 2006), but that doesn't settle the question of their causes. One way to tackle this problem is to abandon subjective self-reports and look for specific mechanisms or brain activation patterns which may account for a particular emotion (LeDoux, 1995). There is indeed evidence for cross-modal, emotion-specific fMRI activity in the amygdala, precuneus, posterior cingulate cortex, superior temporal sulcus, and medial prefrontal cortex (Kim et al., 2015; Klasen, Kenworthy, Mathiak, Kircher,

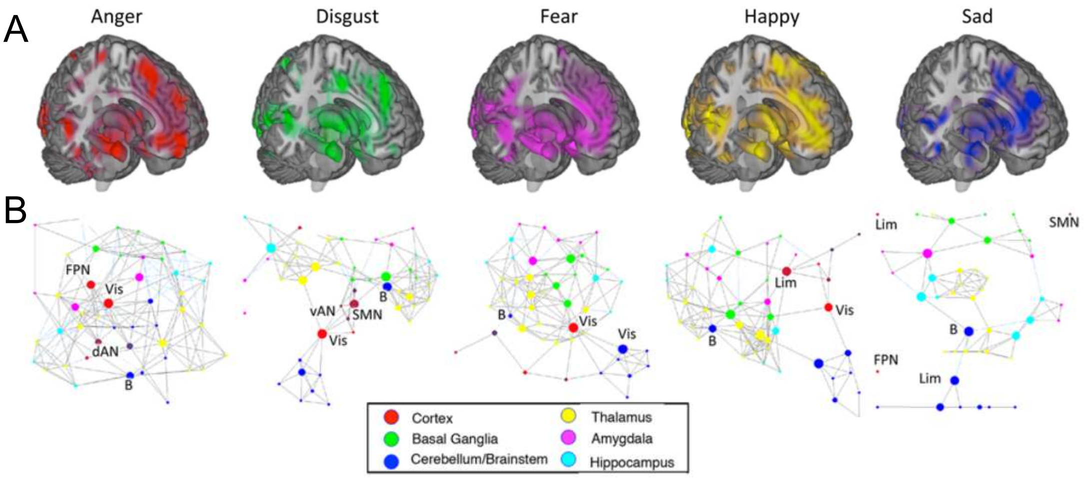

Figure 1.9: **Emotions in the brain.** **(A)** Derived intensity maps for each emotion estimated from meta-analysis, thresholded at 0.001. The unit is such that the integral of the intensity over any volume of the brain gives the predicted number of peak activation centers for all studies evoking that particular emotion. **(B)** Co-activation patterns for each emotion category. Lines reflect co-activation assessed based on the joint distribution of activation intensity in the model. The size of each circle reflects its centrality, i.e. how strongly it connects disparate networks. B, brainstem; dAN, dorsal attention network; Def, default mode network; FPN, fronto-parietal network; Lim, limbic network; SMN, somatomotor network; vAN, ventral attention (salience) network ; Vis, visual network. Reprinted from Wager et al. (2015)

& Mathiak, 2011; Peelen, Atkinson, & Vuilleumier, 2010; Saarimaki et al., 2015; S. Wang et al., 2014). However, most of those regions respond to multiple emotion categories, possibly because emotion-specificity occurs at the level of single neurons or network connectivity patterns (see Namburi et al., 2015, for a remarkable demonstration of single-neuron level dissociation of negative versus positive valence associations in the basolateral nucleus of the amygdala in mice). A meta-analysis of 148 studies (Wager et al., 2015) attempted to solve this problem by using Bayesian statistics to estimate, for each of five basic emotions, the joint posterior probabilities of peak activation locations in the brain given the emotion category that is evoked by the task (i.e. a forward model that accounts for co-activation patterns). Results showed that all emotions typically engaged a variety of cortical and subcortical areas, including the amygdala, ventral striatum, orbitofrontal cortex, anterior and posterior cingulate cortices, brainstem, insula, prefrontal cortices, hippocampus and medial temporal lobes, and even occipital regions (FIGURE 1.9A). While no particular area distinguished between all emotions, patterns of activation and co-activation between broad cortical and subcortical systems did (FIGURE 1.9B). Emotion categorization accuracy was maximal for fear at 86% (66% overall). Interestingly, the most pronounced distinction between clusters of emotions was not valence but the engagement of networks related to “external” attention (dorsal attention, fronto-parietal, default-mode) during fear and anger versus the engagement of networks

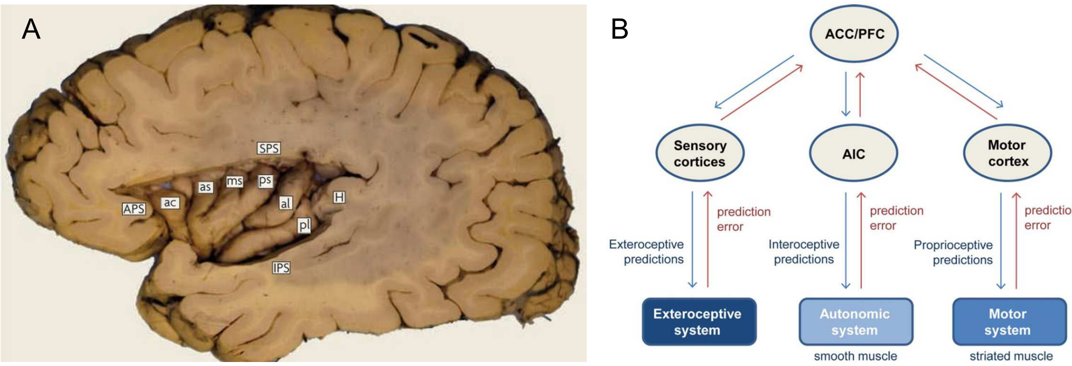

Figure 1.10: **Interoceptive theory of conscious emotional states. (A) Insular cortex.** View on the left hemisphere. Anterior insular cortex: ac, accessory gyrus; as, ms, and ps, anterior, middle, and posterior short gyri. Posterior insular cortex: al, ml, and pl, anterior, middle, and posterior long gyri. APS, SPS, and IPS, anterior, superior, and inferior peri-insular sulci; H, Heschl's gyrus. Reprinted from Craig (2009). **(B) Interoceptive inferences in the anterior insula.** An analogy is drawn with the predictive processes occurring in exteroception and motor control. Reprinted from Gu et al. (2013).

related to "internal" attention (salience, somatosensory) during happiness, sadness and disgust. It is possible that this was due to the method which gave access to global patterns of connectivity between regions but not to fine-grained networks at the level of individual neurons. See also Chang, Gianaros, Manuck, Krishnan, and Wager (2015) for a similar decoding study targeting the intensity of negative affect using physical pain as a control condition.

**Anatomy of a feeling.** One issue that is left unresolved when focusing on the neural correlates of different kinds of emotion is that of emotional awareness in general. How do we consciously experience emotions? The question appears tightly linked to the notion of appraisal; the interplay between visceral, autonomous reactions and cognitive, cortical processes has been emphasized for years in the "appraisal" framework of emotion theory (James, 1994). A modern twist of this idea links predictive inferences of interoception computed in the anterior insular cortex (FIGURE 1.10A-B) with the conscious experience (awareness) of emotion (Gu et al., 2013; Seth, 2013). An argument for a role of interoception in emotional appraisal and experience is that a *false* cardiac feedback has been shown to enhance both subjective ratings of emotional intensity and fMRI activity in the anterior insula (Gray, Harrison, Wiens, & Critchley, 2007). Of note is that the question of whether bodily reactions are causes or consequences of emotions is immediately resolved by predictive accounts which allow for causality to flow top-down as well as bottom-up. The theory is rooted in predictive accounts of exteroperception (Friston, 2009; Kanai et al., 2015) and makes sense with regards to the idea of self, body ownership, and first-person perceptual experience as rooted in enteroceptive awareness (Faivre, Salomon, & Blanke, 2015; Park & Tallon-baudry, 2014), as well as with regards to the known implication of the anterior insula in subjective salience (Critchley, 2004; Uddin, 2014).

**Probing emotional experience in nonverbal subjects.** There are no emotion-specific areas of the brain; Emotions and emotional awareness arise from reproducible states of mind characterized by patterns of behavioral, cognitive and physiological responses that may be distinguished but only up to a point as emotion pervades all subjective experience. A converging argument has been made in the field of linguistics based on the observation that almost no language has developed emotion-specific grammar structures, although the expression of emotions seems to follow some identifiable rules; For example, the expression of some affect may borrow from the expression of action, possession of an affected body part, being acted upon, etc. showing remarkable parsimony in expressing complex subjective phenomena (Hagège, 2006). A practical consequence for the purpose of this thesis is that no unambiguous (i.e. necessary and sufficient) marker of emotional experience, let alone emotion categories, exists besides that of subjective report which cannot be obtained from animals or nonverbal infants. This is a general problem for all kinds of subjective phenomenon including metacognition, aesthetic judgment, and consciousness (but see Sitt et al., 2014), for which subjective reports are gold standards. An alternative framework has been proposed that defines "emotion" by testable properties (scalability, valence, persistence and generalization; Anderson & Adolphs, 2014) rather than subjective reports; Reverse inference has also been used to conclude on the possibility of various affective experiences in nonverbal subjects e.g. regret in rats (A. P. Steiner & Redish, 2014), anxiety in crayfish (Fossat, Bacqué-Cazenave, De Deurwaerdère, Delbecque, & Cattaert, 2014), stress in Drosophila ("persistent state of defensive arousal"; Gibson et al., 2015), pain in infants (Goksan et al., 2015; Trapanotto et al., 2004). Both approaches have considerable merit, but in the absence of testable predictions of outcome or subjective reports neither is entirely satisfactory.

### 1.1.2.2 A natural history of facial expressions?

While internal, subjective states may not be observed, they are often expressed, or communicated, for example by facial expressions such as a smile. Emotions may be expressed, or ostensively communicated, through a range of other channels including nonverbal vocalizations (Sauter, Eisner, Ekman, & Scott, 2010), posture (Aviezer, Trope, & Todorov, 2012; de Gelder, 2006), prosody (Adolphs, Damasio, & Tranel, 2002; Frick, 1985), chemicosensory signals (Mujica-Parodi et al., 2009), music (Sievers, Polansky, Casey, & Wheatley, 2013), and language (Rimé, Corsini, & Herbette, 2002). For the purpose of this thesis we will focus on

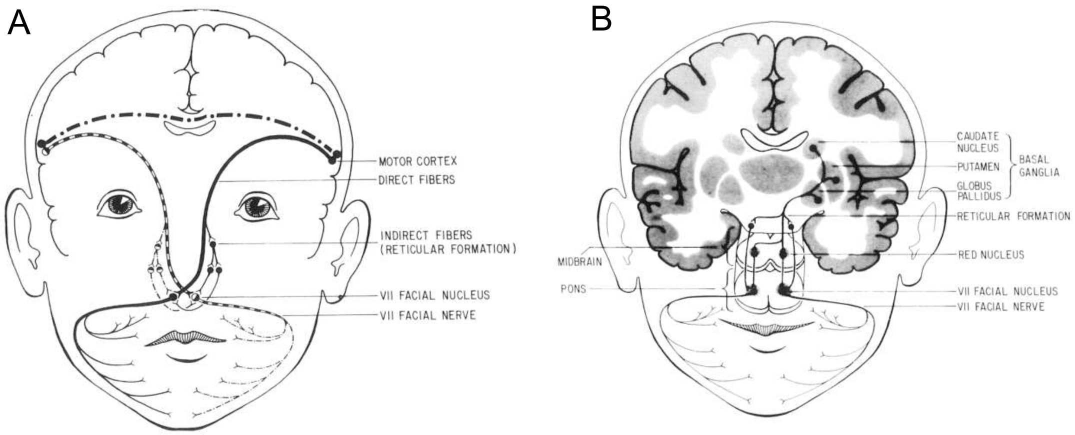

Figure 1.11: **Pathways controlling facial musculature. A.** Pyramidal control. **B.** Extra-pyramidal control. Reprinted from Gazzaniga and Smylie (1990).

facial expressions.

**The origin of smiles.** The ability to read even subtle, fleeting emotions on a man's face as if through a natural language has fascinated many. Among those was Duchenne, who famously explored the mechanisms of facial expressions using electrical stimulations of the facial muscles (Duchenne, 1862). Mechanistically, facial expressions arise under the control of the facial nerve (cranial nerve VII) originating from the facial nucleus in the brainstem (Gazzaniga & Smylie, 1990; Rinn, 1984). Five branches (temporal, zygomatic, buccal, mandibular, and cervical branches) of the facial nerve contact different facial muscles; For example the temporal branch contacts the corrugator supercilii muscles which are involved in many emotional expressions in a way that is related to valence (Larsen, Norris, & Cacioppo, 2003; Magnée, Stekelenburg, Kemner, & de Gelder, 2007; Neta, Norris, & Whalen, 2009; Tottenham, Phuong, & Flannery, 2013). The facial nucleus receives "voluntary" inputs from the primary motor cortex through the pyramidal corticobulbar tract, both directly and indirectly through the reticular formation (Figure 1.11A). It also receives "spontaneous" inputs from the basal ganglia through the extra-pyramidal rubrospinal tract passing through the reticular formation and red nucleus (Figure 1.11B). The latter extra-pyramidal tract provides a basis for spontaneous (involuntary) displays of emotion. But how, and why, do different emotions cause different expressions? Duchenne attributed this emotional language of facial expressions to a "divine fantasy" (Duchenne, 1862). Darwin, however, noted that some non-human mammals also display emotions through facial, body, and vocal expressions (Darwin, 1872). This led him to formulate the hypothesis that the behavior is evolutionary ancient. In fact, facial expressions are shared by all mammals (last common ancestor estimated at 160 million years), although all species have different repertoires and the ability appears especially developed in primates (Burrows, 2008). Spontaneous facial expressions have been observed in blind persons (Freedman, 1964; Galati, Sini, Schmidt, & Tinti, 2003; Tracy & Matsumoto, 2008) and individual differences in expressions seem partly heritable (Peleg et al., 2006). Facial expressions appear early in development; Newborns and even fetuses produce some although with a limited repertoire (Reissland, Francis, Mason, & Lincoln, 2011; J. E. Steiner, 1979). Overall, the evidence is extremely strong that facial expression production represents an evolutionary ancient and developmentally robust human attribute. What remains controversial is the amount of variations that exist in the specific expressions that are produced and their relation to the different emotions. Early cross-cultural studies have suggested a partial universality, with a few "basic" emotions being displayed in similar ways across very different cultures (Ekman, 1980, 1992; Ekman & Friesen, 1971; Ekman & Oster, 1979; Ekman et al., 1969). However, data-driven methods suggest significant cultural variations when subjects are asked to label random facial expressions displayed on artificial faces; these variations do not support the "basic emotion" hypothesis in all cultures at least in the case of labelling tasks (Jack, Garrod, Yu, Caldara, & Schyns, 2012). Similar observations have been made regarding the scanning of emotional faces by Western versus Eastern observers (Jack, Blais, Scheepers, Schyns, & Caldara, 2009). Thus, while there is a universal propensity to express emotions through facial movements, the precise decoding and possibly encoding strategies differ across cultures.

**Adaptive functions of emotional expressions.** The mechanistic exploration of how emotional facial expressions may be produced (proximal cause) leaves open the question of why such system exists (ultimate cause), i.e., describing the evolutionary history that led to its maintenance or selection (Dezecache, Mercier, & Scott-Phillips, 2013). Such a history probably was complex because emotional expressions production (i.e. transmission) and perception (i.e. reception) likely co-evolved (Aoki & Feldman, 1987; McComb & Semple, 2005). Let's assume that emotional expressions are not neutral characteristics and have some adaptive function for receivers, transmitters, or both. In the terminology of Scott-Phillips (2008) these functions correspond to cuing, coercion, or true communication (i.e. signal), respectively (FIGURE 1.12A). For example, a threatening angry expression may be interpreted as coercion rather than communication in the sense that it has the practical function of forcing the receiver to retreat quickly rather than communicating with him (Dezecache, Mercier, & Scott-Phillips, 2013). It has also been argued that the expressions of fear and disgust may be incidental cues

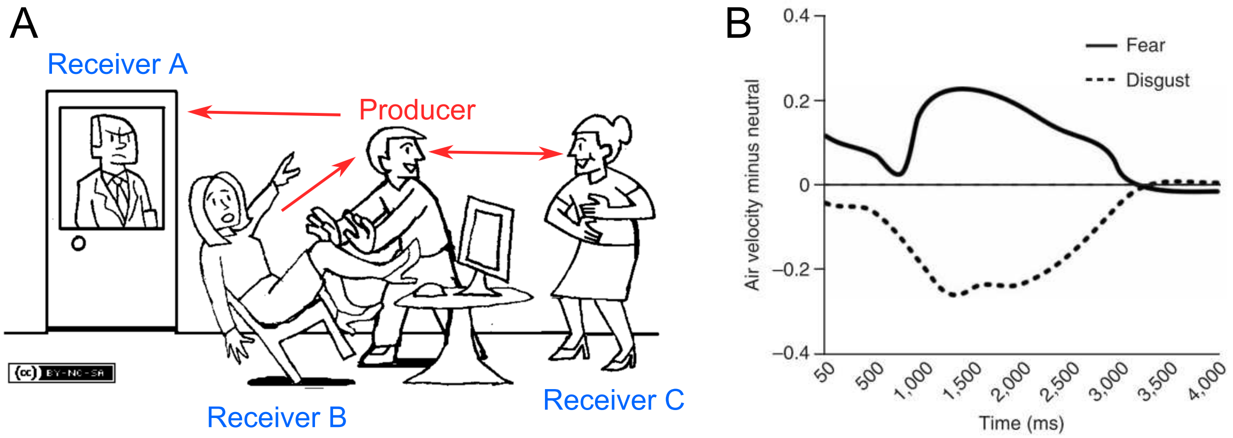

Figure 1.12: **Possible functions of emotional expressions.** **(A)** Analogy for the different types of functions. Each line represents one interaction going on as a result of the Producer's action. The arrows point to who benefits from the specific interaction. Here, the Producer forces Receiver B to fall from her chair (benefits the Producer only) and shows it to Receiver C; The action is observed by Receiver A although the Producer only intended for Receiver C to see it (benefits Receiver A only). Receiver C sees the Producer's intent to show her the action, and laughs in response (genuine communication). It is coercion for Receiver B, a cue for Receiver A, and true communication (i.e. a signal) for Receiver C. Adapted from Scott-Phillips and Kirby (2013). **(B)** Are fear and disgust expressions non-communicative cues? Nasal air flow is increased during the expression of fear and reduced during disgust, with functional advantages when exposed to threat or noxious contaminants, respectively. Reprinted from Susskind et al. (2008).

rather than signals; they may serve a primary function for the producer that is independent on the expression being actually perceived. For example, fear enhances nasal air flow and promotes the detection of targets by widening the eye's aperture while disgust reduces nasal air flow and enhances focal acuity by reducing the eye's aperture (Figure 1.12B; D. H. Lee, Mirza, Flanagan, & Anderson, 2014; Susskind et al., 2008). This closely relates to the idea of emotions as "action preparedness". Finally, facial expressions of emotions may be genuinely communicated, i.e. produced with the intent on being perceived and interpreted as signals by receivers (Dezecache, Pierre, Marie, & Dezecache, 2013). Many facial expressions of emotions may have been selected first as cues or coercive displays and became communicative only at later stages (Darwin, 1872), an example of exaptation. But how would this communication work, and how automatic, implicit is it (Frith & Frith, 2008)? It has been argued that emotional communications through facial expressions occurs by mirroring, mimicking, or affect-sharing: The receiver involuntarily mimics or mirrors the producer's expression, leading to his or her own change in emotional state; alternatively, somatosensory representations linked to that emotion may be directly activated by-passing the facial musculature (Grèzes & Dezecache, 2014). Such mechanisms may account for the sharing of fear and joy, a phenomenon known as emotional contagion (Dezecache, Jacob, & Grèzes, 2015). However, they can't explain why, for example, one would react with fear, rather than anger, in the face of an angry individual; some amount of appraisal (regarding self-relevance in particular) is needed to explain the production of appropriate responses to facial expressions of emotion (Grèzes & Dezecache, 2014).

The production of facial expressions of emotion has an ancient phylogenetic history, marked with (1) the ability of facial muscles to be triggered involuntarily and voluntarily and (2) possible non-communicative functions of some expressions or their primitives (e.g. possible function of fear in enhancing peripheral threat detection). However, these expressions may be controlled voluntarily and vary across cultures; they are, in most cases, insufficient to establish genuine communication without the additional occurrence of appraisal. This complex cultural behavior probably took roots in pre-existing biases (Hannagan et al., 2015) acting as "guides", "scaffolds", or "gutters".

#### 1.1.2.3 Low, high, and multiple roads to perceiving emotional faces

The precise mechanisms and representations involved in the perception of facial emotions remain disputed (Said, Haxby, & Todorov, 2011), and perception without appraisal and engagement of motor cortices is insufficient to account for the production of most adaptive responses to the emotional expressions of others (SECTION 1.1.2.2; Grèzes & Dezecache, 2014). For the purpose of this thesis we will however limit ourselves to outlining a few general principles regarding the perception of emotional facial expressions.

**Broad and intricate roles of perceptual, emotional, and sensorimotor systems.** The perception of facial expressions of emotions may be understood first and foremost as a branch of variant face perception, i.e. the perception of facial movements, engaging the most dorsal (STS) sections of the distributed face processing network (Haxby et al., 2000; FIGURE 1.7C and FIGURE 1.13A). However, both the FFA and the STS respond to static facial expressions (anger, disgust, fear, surprise) more than to neutral faces, showing sensitivity to specific configurations of the face rather than facial movements (Said et al., 2011). The case of facial expressions demonstrates the importance of the interplay between ventral (e.g., FFA) and dorsal (e.g., STS) regions during perceptual processing.

Second, lesion as well as functional imaging studies point towards the implication of emotion-specific though not necessarily modality-specific mechanisms for recognizing different facial expressions of emotion such as fear, anger, or disgust (for a review, see Calder & Young, 2005; FIGURE 1.13B); This is in keeping with the idea that normal recognition of facial expressions

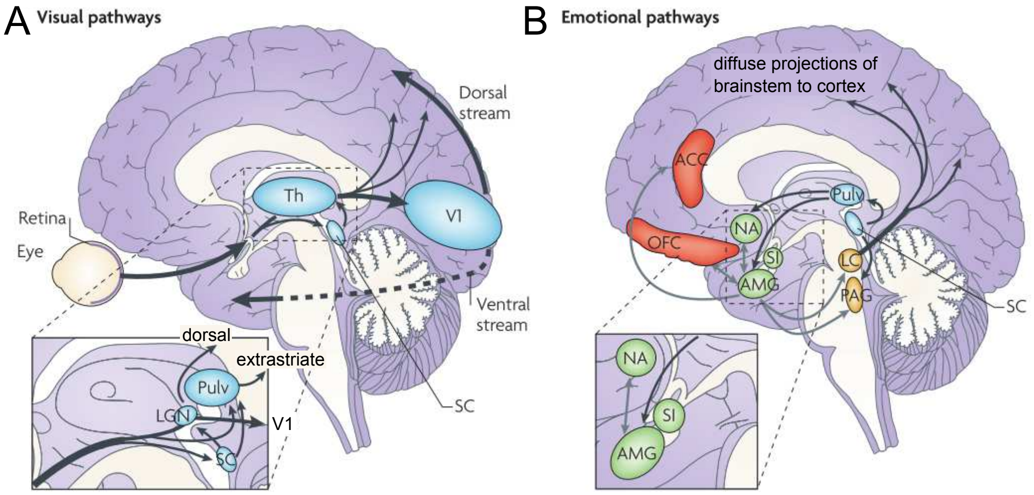

Figure 1.13: **Visual and emotional systems.** **(A)** Visual pathways, showing the ventral and dorsal branches of the retinogeniculostriate pathway through V1 (bold and dotted arrows) along with additional projections to extrastriate areas bypassing V1 (fine arrows). **(B)** "Emotional" pathways, here defined as the circuits formed by visual (blue), cortical limbic (red), subcortical limbic (green) and modulatory midbrain (yellow) structures. Black arrows in panel (B) denote visual inputs to subcortical and midbrain structures. Grey arrows denote projections within the limbic system. ACC, anterior cingulate cortex; AMG, amygdala; LC, locus coerelus; LGN, lateral geniculate nucleus; NA, nucleus accumbens; OFC, orbitofrontal cortex; PAG, periaqueducal gray; Pulv, pulvinar; Th, thalamus; SC, superior colliculi; SI, substantia innominata. Adapted from Tamietto and de Gelder (2010).

of emotion necessitates intact multimodal emotion processing which itself engages distributed cortical and subcortical regions areas in emotion-specific ways (Section 1.1.2.1). For example, the amygdala receives extensive inputs from IT and STS regions in rhesus macaques (Aggleton, Burton, & Passingham, 1980; not shown on Figure 1.13B), providing a pathway for the engagement of emotional networks during face processing. In fact, the implication of the STS itself in the perception of emotional expressions may reflect multimodal emotion as well as visual processing (Hein & Knight, 2008; Said et al., 2011).

Finally, the production or mere planning of facial expressions in response to perceived expressions (overt non-conscious mimicking or covert implicit initiation of motor commands) does appear to play a role in the perception of facial expressions of emotions (Bate, Cook, Mole, & Cole, 2013). The hypothesis is supported by activations in the frontal operculum (a possible homologue to the macaque "mirror" area F5) in response to facial expressions that are specific to emotion category (Said, Moore, Engell, & Haxby, 2010), as well as by the disruption of facial expression recognition by inhibitory trans-magnetic stimulation of the facial somatosensory cortices (Pitcher, Garrido, Walsh, & Duchaine, 2008).

**Subcortical contributions in question.** Face and facial emotions are emotionally and biologically relevant stimuli whose processing evokes responses in cortical as well as in subcor-

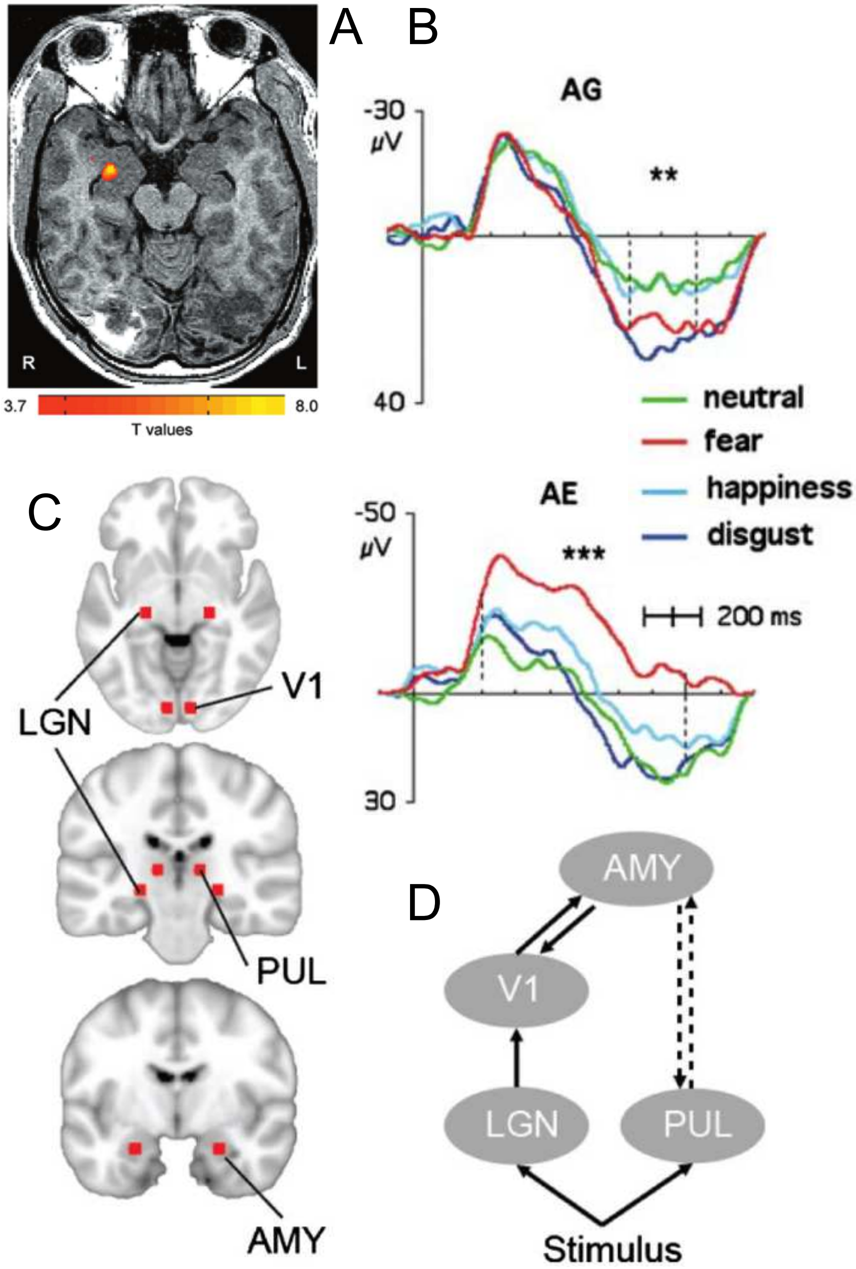

Figure 1.14: **Latency and origin of the sensitivity of the amygdala to emotional faces. (A)** Amygdala activation to emotional faces in a patient with blindsight. The lesion to the primary visual cortex is clearly visible. *t*-values for the emotional versus neutral contrast, uncorrected. Reprinted from Pegna et al. (2005) **(B)** Intracranial EEG recording of amygdala in response to consciously perceived emotional faces showing evidence against the existence of a pre-attentive fast track for the perception of emotional faces. Amygdala response to facial expressions was modulated by attention with emotional modulation occurring earlier when attention was directed to the emotional expressions (AE) than to the faces gender (AG). Reprinted from Krolak-Salmon et al. (2004) **(C-D)** Dynamic Causal Modelling of MEG responses to conscious, task-irrelevant emotional faces. **(C)** Sources and **(D)** causal models. All models included a geniculostriate pathway through V1 and the LGN (full arrows). Models that included a direct pathway (dotted arrows) from the pulvinar (PUL) to the amygdala (AMY) were compared to models that did not include this pathway, with more evidence in favor of the former. Reprinted from Garvert et al. (2014)

tical areas such as the superior colliculi, amygdala and pulvinar (FIGURE 1.13A-B). Do subcortical activations to emotionally salient stimuli and faces in general, and emotional faces in particular, provide a fast, parallel, route to facial emotion perception which may by-pass and modulate higher visual cortices (Morris, DeBonis, & Dolan, 2002; Morris et al., 1998; Senju & Johnson, 2009; Vuilleumier, 2005), or do they mostly receive their inputs from the visual cortex? A pre-attentive ("fast", "automatic") route from superior colliculi and pulvinar to amygdala, functioning independently of consciousness and attention, may be sustained by magno-cellular pathways carrying mostly low-frequency visual information (Vuilleumier, Armony, Driver, & Dolan, 2003) and may come to modulate later cortical conscious processing, attention, and memory (M. H. Johnson, 2005).

There is indeed evidence in favor of a subcortical pathway to the amygdala in humans that is operating during non-conscious perception (de Gelder, van Honk, & Tamietto, 2011; Tamietto & de Gelder, 2010). For example, amygdala activations and implicit emotional reactions to non-consciously perceived fearful faces have been observed in several patients with blindsight (lesions of the visual cortex resulting in residual processing despite cortical blindness; FIGURE 1.14A; Pegna et al., 2005; Tamietto et al., 2009; Tamietto & de Gelder, 2010), although these results may in principle reflect direct connections from the LGN to extrastriate areas (Pessoa & Adolphs, 2010). Similarly, masked fearful (Liddell et al., 2005) or aversive Morris, Ohman, and Dolan (1999) faces evoke correlated responses in the superior colliculi, pulvinar, and amygdala. Both the pulvinar, through its projections to the cortex and the amygdala, and the amygdala itself, through its direct and indirect (through the prefrontal) connectivity to the visual cortex, may functionally amplify weak or brief visual stimuli of emotional, biological or task-related relevance (Pessoa & Adolphs, 2010). Emotional expressions, most particularly negative expressions such as fear, seem to not only recruit enhanced processing but also hold attention involuntarily (Stroop-like) which results in counter-intuitively delayed reaction times for labeling or judgment tasks even when emotion is irrelevant (e.g., Calder, Young, Keane, & Dean, 2000). The effect contrasts with the facilitation of detection of various kinds of emotional faces (e.g. smiling, angry or fearful) in visual search (E. Fox et al., 2000; Hansen & Hansen, 1988; Lobue, 2009; Ohman, Lundqvist, & Esteves, 2001), dot-probe (Mogg & Bradley, 1999), or masking (Esteves & Öhman, 1993; Milders, Sahraie, & Logan, 2008) paradigms.

However, the functional importance of the pulvinar-amygdala route with respect to other routes during conscious and non-conscious processing of emotional faces, and its interpretation as a "fast-track", have been challenged on the basis that cortical processing already allows for multiple bypass connections alongside its hierarchy ("multiple waves"); this observation renders inadequate the characterization of cortical vision as a unique and slow "high road" (Pessoa & Adolphs, 2010, 2011). Pessoa and Adolphs (2010; 2011) further question the characterization of amygdala and pulvinar as forming an uninterrupted and isolated "low road", and argue that both areas heavily connect bidirectionally to a large number of cortical areas. Finally, whether these pathways reflect specialization for emotional perception (de Gelder et al., 2011; Tamietto & de Gelder, 2010) or broad relevance (Garrido, Barnes, Sahani, & Dolan, 2012; Pessoa & Adolphs, 2010, 2011) remains debated as well.

Time-resolved electrophysiological signals (iEEG, EEG or MEG) have led to very conflicting results regarding the existence of a "fast-track" to emotion perception; some studies have reported emotional modulation of face-evoked signals occurring at latencies of 200-800 ms (iEEG in amygdala; FIGURE 1.14B; Krolak-Salmon et al., 2004) or 170 ms (MEG with source reconstructed in middle occipital and fusiform; Japee, Crocker, Carver, Pessoa, & Ungerleider, 2009), coincident or posterior to the time-window of the cortical N170 (SECTION 1.1.1.3) while other have reported earlier latencies around 100 ms (EEG, emotion operationalized as self-reported pleasant versus unpleasant judgments; Pizzagalli, Regard, & Lehmann, 1999). A recent study using Dynamic Causal Modelling (DCM) of MEG signals evoked by neutral, smiling or fearful faces found evidence for a "fast", bidirectional, direct connection from the pulvinar to the amygdala that is independent of the LGN and functions at short latencies (<180 ms) post-stimulus (FIGURE 1.14C; Garvert et al., 2014); No evidence was found for a modulation of this connection by emotional valence possibly due to insufficient power. Crucially, in this experiment the emotional faces were consciously perceived, although the participants were engaging in a gender categorization task and had to ignore an uncorrelated auditory oddball. This result of a pulvinar-amygdala connectivity at shorter latencies only is in keeping with the finding by Williams et al. (2006) that fMRI functional connectivity of the amygdala with thalamic and cortical areas depends on stimuli duration and/or conscious access (short, subliminal versus long, conscious). Finally, tentative evidence exists in favor of a feature-based coding of emotional faces (eyebrow position, eye size) in the amygdala (Ahs, Davis, Gorka, & Hariri, 2014). This observation is in favor of a genuine role for this structure in face processing as opposed to a unidimensional "emotional salience".

In this section we reviewed mechanisms engaged in the production and perception of emotional faces as if these occurred, so to speak, in isolation. Next, we will briefly review how dimensions such as emotion, race, or gender, may interact during face perception.

### 1.1.3 Interactions between face dimensions

#### 1.1.3.1 Multiple sources of interaction

Numerous studies report finding that a given facial dimension (for example, race) influences the perception of another facial dimension (for example, emotional expression) to a certain level. However, such interactions between facial dimensions may have vastly different causes, ranging from the lowest to the highest level of processing.

1. The effect of one facial dimension may be mostly or entirely stimulus-driven if cues for one dimension (e.g., age) differ according to another (e.g., race). Such mechanism may underlie the observation that estimations of age are affected by face race, so that for example Caucasian observers will systematically underestimate the age of Asian faces (Porcheron, Mauger, Soppelsa, Pascalis, & Morizot, 2014).

2. Neurons may be selective to a given conjunction of facial dimension, driving subsequent responses. For example, single unit recordings in face-selective patches from the STS of rhesus macaques have revealed selectivities to expression-identity, gaze-identity, and expression-gaze conjunctions, particularly in the anterior portion of the STS (Morin, Hadj-Bouziane, Stokes, Ungerleider, & Bell, 2014). Such data is consistent with the general idea that face processing in macaques operates by increasing integration of features (Perrett et al., 1987) and view-invariance (Freiwald & Tsao, 2010) along the posterior-to-anterior axis of the temporal cortex. EEG studies in humans point to an early (170 ms) sensitivity to facial expressions that is followed by a sensitivity to gaze direction (190 ms) and finally (200-300 ms) the conjunction of both cues (Conty, Dezecache, Hugueville, & Grezes, 2012). The amygdala is involved in this integrative process, although the temporal dynamics of the process appear task-dependent (Dumas et al., 2013) and it is not known whether the interaction is driven at the level of single units or population dynamics.

3. Perceptual narrowing for faces, the developmental process by which discrimination abilities decreases for unfamiliar or irrelevant face types (e.g. other-race faces) but increases for familiar or relevant face types (e.g. own race faces) during the first year of life, is known to affect not only facial identity discrimination but a range of face processing abilities such as gender categorization (O'Toole, Peterson, & Deffenbacher, 1996; Quinn, Uttley, et al., 2008). This will cause interactions between the narrowed dimension (e.g. race) and the affected dimension (e.g. gender) that may not necessarily be stimulus-

driven. See SECTIONS 1.1.3.3 and 1.2.1.2 for a more detailed discussion of perceptual narrowing and the "Other-Race Effect".

4. Inferences rooted in perceptual experience could, theoretically, cause interactions between face dimensions. For example, if one dimension (e.g. smiling) is systematically associated to another (e.g. familiarity, since social exchanges between familiar people typically include smiling), then one could act as a cue to the other simply by way of inference. It has been observed that, indeed, smiles cue familiarity (Baudouin, Gilibert, Sansone, & Tiberghien, 2000) - but the underlying mechanism is unknown.

5. Social stereotypes as well as more typical forms of semantic knowledge (Amodio, 2014; Contreras, Banaji, & Mitchell, 2012) may be the source of belief-based inferences made during face perception. For example, Caucasian participants typically associate Black faces with the emotion of anger, an association that is rooted in stereotype rather than low-level resemblance or actual experience (Hehman, Ingbretsen, & Freeman, 2014). This association causes the perception of race to influence the perception of emotion, and vice-versa (Hehman et al., 2014).

We next review two specific cases where such interactions have been reported or, conversely, debated. Many other examples of interactions may be cited, among which two will be approached in the present thesis: the interaction of facial dimensions attributable to stereotypes in CHAPTER 3 and 4, and the effect of emotional expression during gaze cuing in CHAPTER 5.

#### 1.1.3.2 The case of identity and expression

Segregated processing of identity and expression is a main prediction of the Bruce and Young model (1986), at least under the assumption that structural encoding always succeeds. A similar claim was made by Haxby et al. (2000). Therefore, integration or segregation of identity and expression have been subject to intense scrutiny. Overall, evidence suggests that facial identity and expression are supported by different types of information e.g. different spatial frequencies mapping the segregation of magno- and parvo-cellular pathways (Vuilleumier et al., 2003). For example, relatively preserved recognition of dynamic, but not static, facial expressions have been reported in a patient with acquired prosopagnosia from extensive occipitotemporal lesions (although the patient showed a clear deficit in the recognition of dynamic fear); such dissociation supports the idea that the recognition of dynamic expressions may be carried out in the more dorsal STS independently from the processing of facial identity (Richoz, Jack, Garrod, Schyns, & Caldara, 2015), in accord with the close connections of this region with the dorsal stream (FIGURE 1.1B; Ungerleider & Haxby, 1994). However, the extent to which identity and expression are segregated has been questioned on the basis that cases of prosopagnosia with preserved facial expression recognition are rare, and that relative separation of identity and expression in the statistical regularities (as captured by unsupervised learning methods such as the Principal Component Analysis) of the faces themselves may suffice to explain their relative segregation in processing and behavioral effects (Calder & Young, 2005; Tiberghien, Baudouin, Guillaume, & Montoute, 2003).

In any case, despite observations that emotional expressions may influence face recognition and vice-versa (Baudouin, Gilibert, et al., 2000; Baudouin, Sansone, & Tiberghien, 2000; Brenna, Proietti, Montirosso, & Turati, 2012; Turati, Montirosso, Brenna, Ferrara, & Borgatti, 2011) and debates regarding the underlying mechanism (i.e. complete "explicit" segregation through distinct representations or pathways after structural encoding, or relative "implicit" statistical segregation possibly occurring at later stages), the idea remains that identity and expression engage different mechanisms and cortical areas even though they cannot be regarded as *entirely* independent.

#### 1.1.3.3 The case of the "Other-Race Effect"

The "Other-Race Effect" (ORE) refers to the highly robust observation that adults are typically impaired when recognizing faces from an unfamiliar race (Brigham & Malpass, 1985; Feingold, 1914; Malpass & Kravitz, 1969). In other words, the dimension of race affects the dimension of identity during recognition. Interestingly, identity recognition isn't the only dimension for which performance is impaired: similar deficits have been described for gender categorization (O'Toole et al., 1996) or age (Porcheron et al., 2014) recognition, although it is unclear whether a unique mechanism is responsible. Emotion recognition appears largely spared (Ekman, 1980; Ekman & Friesen, 1971; Ekman & Oster, 1979; Ekman et al., 1969 but see Amodio, 2014). The ORE has been described in a wide range of ages, races, and cultural groups (for a review see Kelly, 2007). However, it is not irreversible and may be alleviated by perceptual training (Goldstein & Chance, 1985).

**Mechanism of the "Other-Race" Effect: Why do they "all look the same"?** The universality of the other-race effect implies that it does not arise from actual differences in resemblances between faces of different races. This is confirmed by anthropometric studies (Goldstein, 1979). Thus, the ORE arises from a differential ability to represent other-race compared to own-race faces. It has been argued that the deficit arises from the nature of

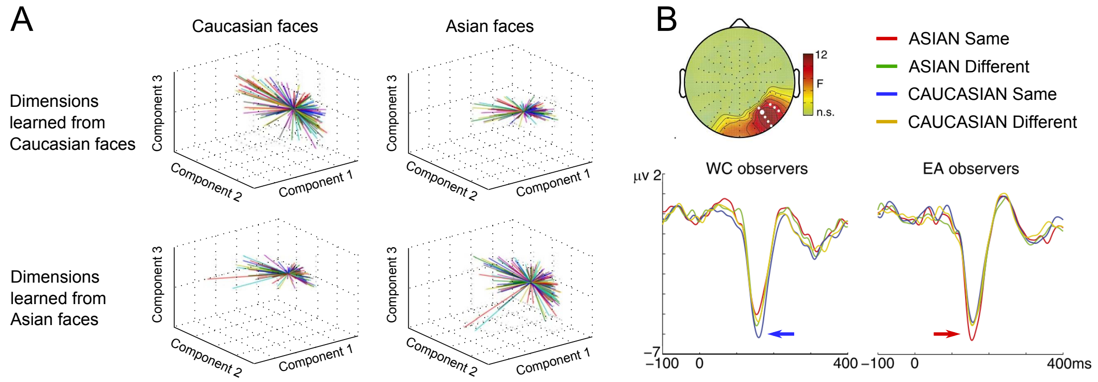

Figure 1.15: **Computational and neuroimaging investigation of the Other-Race Effect. (A) Computational model.** A Principal Component Analysis (PCA) is run on Caucasian or Asian faces, then Caucasian and Asian faces are expressed along the obtained dimensions. Only the first three components are represented, with faces plotted as a line going from to the barycenter of all faces to their location in the space (i.e. norm-based coding). Faces that are "other-race" (with regards to the faces used to run the PCA) show reduced variations (reduced mean distance from barycenter) compared to "own-race" with regards to dimensions extracted from the original set using for PCA. Such dimensions obtained by PCA have been suggested as statistical analogs of the dimensions of the face-space (Calder & Young, 2005). Adapted from Caldara and Abdi (2006). **(B) Neuroimaging investigation using repetition suppression.** Subjects saw two faces per trial: an adaptor face, followed by a target face of the same race (Asian or Caucasian) and gender but with same or different identity. The graph shows the subtraction of scalp EEG signal obtained for target versus adaptor at electrode PO8 (between O2 and T6 on FIGURE 1.6B). The more negative, the greater the repetition suppression. Greater suppression was observed around 170 ms for own-race, but not other-race, targets with same rather than different identity (blue and red arrows), i.e. repetition suppression for identity in the time-window of the N170. The scalp map shows the area where a significant interaction of race and target condition for repetition suppression was observed (*F*-statistic). WC, Western Caucasian subjects; EA, East Asian subjects. Adapted from Vizioli et al. (2010).

face representations, namely, that the face-space (Valentine, 1991; Valentine & Endo, 1992) is heavily biased towards discriminating own-race faces, which form the vast majority of visual experience: thus, its dimensions will be tuned to maximize the discriminability of faces in the familiar population while other-race faces will cluster away from the prototype (average face) and remain poorly discriminable. In other words, the cues that individuate familiar faces drive the construction of the face-space but differ from that which individuate other-race faces, so that other-race faces will look similar relative to the "average face". This hypothesis has found support from computational models using PCA dimensions as features of the face-space (FIGURE 1.15A; Caldara & Abdi, 2006). In addition, the processing of other-race faces relies less on configural processing as measured by the composite effect (Michel, Rossion, Han, Chung, & Caldara, 2006) or the inversion effect (Rhodes, Tan, Brake, & Taylor, 1989). Because adults are also typically faster at classifying the race of other-race faces, it has also been proposed that race might be directly coded as a feature that is present for out-group races but absent for the in-group race; the tendency to consider members of out-group as more homogeneous than members of one's in-group means that out-group membership is considered more informative than in-group membership (Levin, 1996, 2000; Linville, Fischer, & Salovey, 1989). Thus, the other-race classification advantage would arise because it takes longer to assess the absence than the presence of a target feature, and the ORE would be a consequence of race information taking precedence over individuation information. Neuroimaging studies show lesser fMRI activity of the FFA for other-race than own-race faces (Golby, Gabrieli, Chiao, & Eberhardt, 2001) and similar N170 amplitude for single faces (Caldara, Rossion, Bover, & Hauert, 2004; Caldara et al., 2003) but reduced repetition-suppression (Grill-Spector, Henson, & Martin, 2006) for identity in the N170 time-window (FIGURE 1.15B; Vizioli et al., 2010). This suggests that other-race faces may recruit face-processing areas less, and that their individual identities are not efficiently encoded, stored, or retrieved. The development of the ORE is attributed to the phenomenon of perceptual narrowing which will be reviewed in the next section (SECTION 1.2.1.2).

## Key points

- Face processing, a branch of high-level vision, evokes specific mechanisms that appear specialized for the invariant recognition of individual faces and stream variations of facial expression.
- Facial movements elicited by emotions have deep phylogenetic roots and belong to human communication. Perceiving these expressions engages a multiplicity of visual, af-

fective, and relevance-tracking pathways.

- Facial dimensions interact with one another in specific ways. For example, identity and emotion appear largely segregated in face processing, while race profoundly affects the perception of identity, gender, and age.

## 1.2 DEVELOPMENT OF FACES AND FACIAL EXPRESSIONS PERCEPTION

### 1.2.1 Overview of face perception in development

While it is now know that visual processing exists in fetuses (Dunn, Reissland, & Reid, 2015), birth usually marks the onset of visual experience with the light, objects, faces and scenes of the outside world. Because of this, early investigations of the visual abilities of newborns reflected a long-standing debate opposing nativists to empiricists (Fantz, 1961) as experimentalists tried to understand whether newborns could see as adults (correcting for acuity) despite their limited experience, or whether they had to learn to see lights, colors or shapes by trial and error. Empirical results refuted both of these extreme views, revealing a complex interplay of core assumptions and abilities (Spelke & Kinzler, 2007), maturation, and learning from visual experience i.e. an activity-dependent process guided by initial biases (M. H. Johnson, 2001).

There is a considerable literature on the development of low-level vision, mid-level vision and object individuation in infancy (Wilcox & Biondi, 2015), but for the purpose of this thesis we will focus exclusively on face perception (Pascalis & Kelly, 2009).

#### 1.2.1.1 Newborns

Newborn vision, though limited in acuity (Dobson & Teller, 1978; Norcia, 2013; Teller, 1997; von Hofsten et al., 2014) due to retina configuration and difficulties in convergence, carries out significant functions related to face perception.

**Visual preference for faces.** A striking feature of newborns' vision is their preference for face and face-like stimuli. This was incidentally noted by Fantz (1961) in a preferential looking paradigm (FIGURE 2.1; see also SECTION 2.3.1.1 for a definition and discussion of this paradigm), and tested for the first time by Goren, Sarty, and Wu (1975) in a tracking paradigm. Newborns made more eye and head movements towards the face stimuli than to-

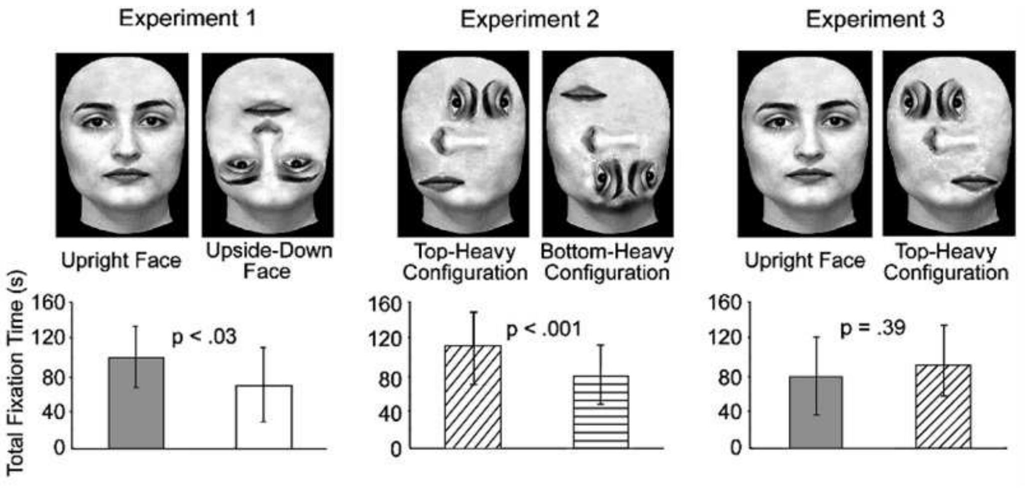

Figure 1.16: **A visual preference for faces at birth.** Newborn show a preference for upright rather than inverted faces (Experiment 1) and for "top-heavy" rather than "bottom-heavy" scrambled faces (Experiment 2). No preference is observed between normal and "top-heavy" scrambled face. Of note, however, is that geometry isn't the only parameter being manipulated; the "top-heavy" scrambled face is closer to the natural configuration of an upright face than the "bottom-heavy" scrambled face (for example, the eyes are located on the top part of the face). Reprinted from Macchi Cassia et al. (2004).

wards the control stimuli. These impressive results, replicated several times (e.g. M. H. Johnson, Dziurawiec, Ellis, & Morton, 1991), are unlikely to reflect prior experience with faces since the median age of newborns tested in the original study by Goren et al. (1975) was of just 9 minutes post-partum (3-27 minutes). In fact, the preference for faces actually declines with age, with equivocal evidence for a preference at 3 months and no evidence at 5 months (M. H. Johnson et al., 1991). Careful controls revealed that the face preference is unlikely to arise from stimulus energy (M. H. Johnson et al., 1991; Morton & Johnson, 1990), but which structural elements trigger the preference remains unclear. While the geometry of the elements in the face plays a role, and in particular the increased number of elements on the top rather than the bottom part (Simion, Cassia, Turati, & Valenza, 2001), it is unclear whether this reflects a preference for the geometry alone (a "top-heavy" bias; Macchi Cassia et al., 2004) or for a more elaborate face configuration pattern which may for example include the positioning of two eyes at the top of the face (FIGURE 1.16; Macchi Cassia et al., 2004). In fact, preferential tracking of upright versus inverted face-like patterns is not always reported (e.g. it was not observed in Easterbrook, Kisilevsky, Hains, & Muir, 1999; however it should be noted that the viewing distance for this study was 80 cm, as compared to a 15-30 cm viewing distance as used in Goren et al., 1975).

Functionally, the visual preference of newborns for faces may act as a scaffold, directing their attention towards faces and thus boosting their ability to learn and recognize (see below) conspecifics or caregivers. Alternatively, it may be vestigial. Interestingly, a "top-heavy" bias has also been found in the right FFA activations of adults (Caldara et al., 2006), in line with the argument that newborn face preference shapes face perception.

What mechanism is driving the face preference in newborns? A visual preference is insufficient to conclude to the involvement of the visual cortex, as other independent visual pathways exist in addition to the geniculostriate pathway (SECTION 1.1.1.1) that control eye movements. In particular, the retinotectal pathway, which runs from the retina to the superior colliculi, directly controls eye movements without the need to pass through the thalamus or visual cortex. A convincing "signature" of a retinotectal origin for the face preference of newborns is that it is sensitive to the nasal-temporal asymmetry: the superior colliculi, but neither the LGN nor V1-V3, show greater activation to stimuli presented in the temporal rather than nasal hemifield of each eye during monocular presentation (Sylvester, Josephs, Driver, & Rees, 2007); newborns will indeed track faces longer only when presented in the temporal field during monocular presentation (Simion, Valenza, Umiltà, & Dalla Barba, 1998). Surprisingly, a reverse face preference (increased orientation to an inverted face-like pattern) was found when stimuli were presented in the nasal hemifield. Interestingly, comparable preferences for faces have been observed in infants of non-human primates such as closely related agile gibbons (*Hylobates agilis*; Myowa-Yamakoshi & Tomonaga, 2001) as well as several macaque species including Sunda pigtail (*Macaca nemestrina*; Lutz, Lockard, Gunderson, & Grant, 1998), Japanese (*M. fuscata*; Kuwahata, Adachi, Fujita, Tomonaga, & Matsuzawa, 2004), and rhesus (*M. mulatta*; Kuwahata et al., 2004) macaques. However, the face preference of newborns appears sensitive to the contrast between the iris and the sclera (Farroni et al., 2005). This suggests possible divergence from non-human primates and co-evolution between specifically human newborn face-preference and sclera-iris contrast, as the contrast between iris and sclera and amount of exposed sclera are maximal in humans compared to other primates (H. Kobayashi & Kohshima, 1997). Contributions of subcortical structures to face processing (but not cars or letters processing; Gabay, Nestor, Dundas, & Behrmann, 2014), including the superior colliculi, have been documented in adult face processing (see also SECTION 1.1.2.3) and are also sensitive to the amount of white sclera in the eyes (Whalen et al., 2004); this suggests comparable mechanisms. Finally, even though sclera-iris contrast seems to play a role in the visual preference for faces, it cannot explain the preference away since newborns will not look longer to a monkey face with human eyes (i.e. with high sclera-iris contrast) than to a regular monkey face (although 3-month-olds will; Dupierrix et al., 2014).

Earlier suggestions had emphasized that newborns, due to immaturity of their cortical

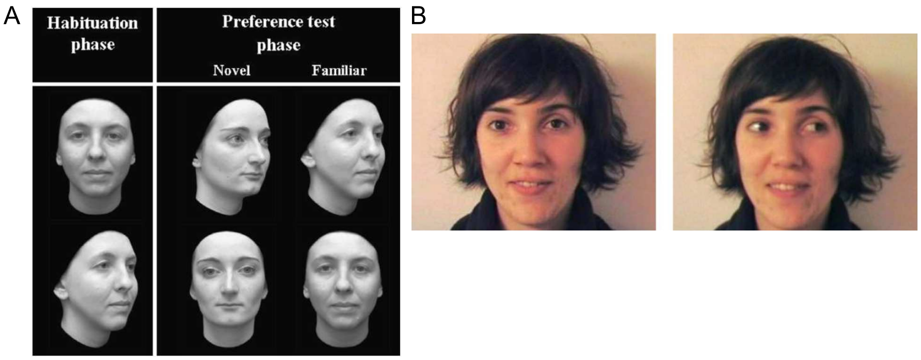

Figure 1.17: **Face recognition at birth. (A) Partial invariance.** Newborns demonstrated evidence of recognition over a change in viewpoint between full front and 3/4 pose; No evidence of recognition was found for other changes in viewpoint such as full front to profile. Reprinted from Turati et al. (2008). **(B) Moderation by speech and gaze direction.** Newborns showed evidence of face recognition when the face was talking with a direct (left) gaze, but not when the gaze was averted (right). Reprinted from Guellai and Streri (2011).

pathways, could show a (subcortically-driven) face preference but not the (cortically-driven) recognition of individual faces (M. H. Johnson et al., 1991). However, it is now clearly established that newborns do possess some ability to recognize individual faces.

**Face recognition.** A first demonstration of face recognition abilities in newborns comes from the observation that they recognize the real face of their own mother after 2-3 days (Bushnell, Sai, & Mullin, 1989; Pascalis, de Schonen, Morton, Deruelle, & Fabre-Grenet, 1995). It has also been found that newborns learn to recognize a novel face presented on picture after habituation, even after a 2 min delay (Pascalis & de Schonen, 1994) or if the face is presented at a slightly different angle at test (full front versus 3/4 pose; Figure 1.17A; Turati et al., 2008). The latter observation is important as a demonstration of burgeoning invariant recognition, a hallmark of high-level vision (see Section 1.1.1.1). Additional evidence in favor of configural processing of inner features (Turati, Macchi Cassia, Simion, & Leo, 2006), but not holistic processing (Turati, Di Giorgio, Bardi, & Simion, 2010), have also been reported. Recognition is enhanced when the face is talking (Guellaï, Coulon, & Streri, 2011; Sai, 2005) during habituation, possibly because it enhances face detection and processing or because face-voice are already represented cross-modally at birth. Recognition abilities extend to non-face objects even when presented in a different eye (Slater, Morison, & Rose, 1983) or modality (touch to vision; Streri & Gentaz, 2004) during familiarization and test. Together, these impressive results demonstrate without ambiguity that the recognition abilities of the newborn may not be reduced to mere retinal adaptation., and make it extremely improbable that newborn vision and eye movement control are *purely* subcortical. This doesn't mean, of course, that newborns rely on the same visual cues or processing strategies than adults for face processing. For example, newborns tend to rely more on the outer (e.g. hairline) features of faces when available (Pascalis et al., 1995; Turati et al., 2006; but see Slater et al., 2000) as well as on low spatial frequency information (0-0.5 cycles/degree; de Heering et al., 2008), with low visual acuity acting as a "low pass filter" (de Heering et al., 2008; von Hofsten et al., 2014). Finally, newborns also show visual preferences for faces rated as attractive by adults when those faces are presented upright, but not when they are inverted (Slater et al., 2000, 1998). The mechanism for this preference is unknown, but the inversion effect suggests that domain-specific face processing is indeed involved (Yovel & Kanwisher, 2005).

**Gaze and speech movements processing.** The above results give clear evidence for face detection and face identity recognition at birth. Another aspect of face processing is the processing of variant information, including gaze. Newborns prefer looking to faces with direct (versus averted) gaze (Farroni, Csibra, Simion, & Johnson, 2002), and it moderates their ability to recognize faces learned from a video (FIGURE 1.17B; Guellai & Streri, 2011). It is possible that the preference and recognition advantage for faces with direct gaze comes from their closer resemblance to the "face schema" that is responsible for face detection, attention, and streamlining of face processing resources (see above, SECTION 1.2.1.1). It is also possible that gaze, face and voice are already processed together as they are in adults (Pascalis et al., 2014). An effect of early experience also cannot be ruled out because the newborns tested were several days old. In any case, gaze processing abilities in newborns appear relatively limited, with no evidence of gaze following or gaze cuing reported.

There is however some evidence that newborns process speech movements cross-modally (Coulon, Hemimou, & Streri, 2013), and in SECTION 1.2.2.1 we will see that they demonstrate a basic ability to process some facial expressions.

#### 1.2.1.2 Infants

**Face scanning and the structural encoding of faces in infancy.** Configural (Maurer, Le Grand, & Mondloch, 2002) and invariant processing of faces emerge early in infancy. 3-4 month-olds recognize the normal configuration of faces (Gliga & Dehaene-Lambertz, 2005) and show greater invariant recognition of upright versus inverted faces (i.e. an inversion effect diagnostic of configural processing in general; Farah, Tanaka, & Drain, 1995; Maurer et al., 2002; Turati, Sangrigoli, Ruel, & de Schonen, 2004; Yovel & Kanwisher, 2005) although they do not connect profile to full-view faces unless specifically trained to do so (Gliga & Dehaene-Lambertz, 2007). Evidence of a composite effect also exist at 3-4 months (Turati et al., 2010),

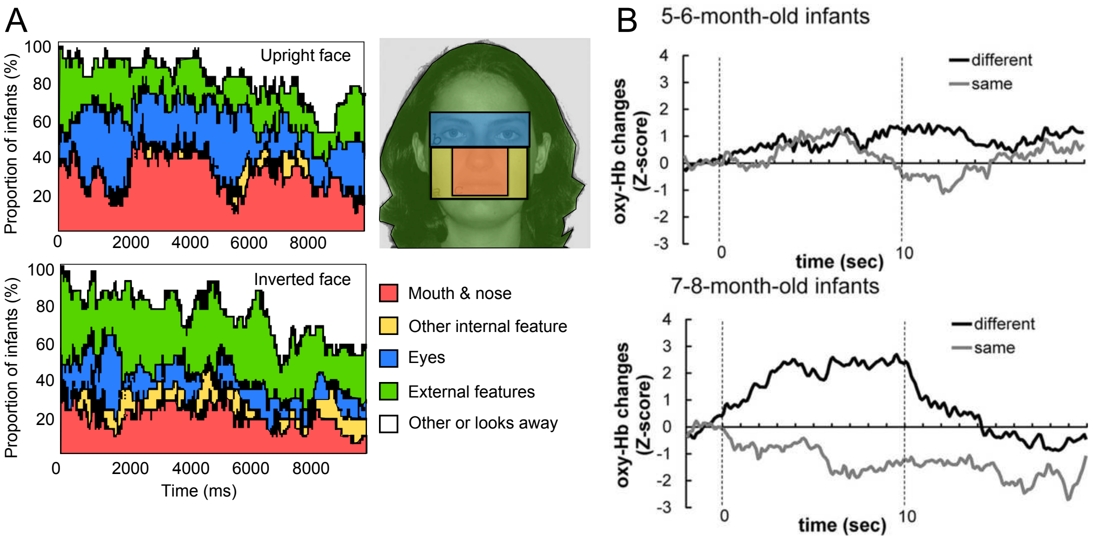

Figure 1.18: **Face processing strategies develop in infancy.** **(A)** Scanning patterns of upright and inverted faces, showing the proportion of 4-month-old infants looking at different parts of the face stimuli during the first trial. Infants tend to look back and forth towards internal features when faces are upright, but look more towards external features when faces are inverted. Adapted from Gallay et al. (2006). **(B)** Adaptation to faces showing different facial expressions. Z-scores of oxygenated hemoglobin (oxy-Hb) concentration are computed with respect to a baseline period on right temporal channels. During each 10 s trial, faces of same (gray line) or different (black line) identities were repeatedly flashed and had varying facial expressions. The results show a difference between the same and different conditions (i.e. an expression-independent identity repetition suppression effect) in 7-8 but not 5-6 month-olds. Reproduced from M. Kobayashi et al. (2014).

a clear signature of holistic processing (i.e. the "gestalt", a subtype of configural processing, Maurer et al., 2002). Finally, 5- but not 3-month-olds show sensitivity to second order relationships between facial features (a type of configural information e.g., eye-nose distance) in upright but not inverted face (Bhatt, Bertin, Hayden, & Reed, 2005). Finally, eye-tracking studies reveal that 4-month-old infants begin to show increased fixation towards the eye, nose and mouth regions of upright but not inverted faces, as adults do (FIGURE 1.18A; Gallay et al., 2006; Maurer & Salapatek, 1976; Turati, Valenza, Leo, & Simion, 2005); this is also the age at which face gaze starts to direct the infant's attention (Hood, Willen, & Driver, 1998). 3-4 month-old infants also show a visual preference for faces that have been rated as attractive by adults, including the faces of non-domesticated animals (Quinn, Kelly, Lee, Pascalis, & Slater, 2008). The causes of this effect, however, remain much disputed. In short, at 3-5 months faces represent a "special" category of stimuli leading to face-specific processing and scanning strategies. All things considered, 3-5 months is an extremely short time to learn these dedicated strategies especially considering that infants of that age sleep for extended periods of time; this is suggestive of an experience-expectant process (see also Le Grand et al., 2003, for evidence of a critical period of early visual experience for learning these strategies later).

Full-blown structural encoding, characterized by mostly independent processing of face identity and expression (see SECTIONS 1.1.1.2 and 1.1.3.2), emerges later at around 7 months. Infants older, but not younger, than 7 months readily habituate to expressions portrayed by different identities (R. F. Caron, Caron, & Myers, 1985); symmetrical evidence for an expression-independent encoding of identity was found in a functional near-infrared spectroscopy (fNIRS; Aslin, Shukla, & Emberson, 2015; Ferrari & Quaresima, 2012; Gervain et al., 2011; Lloyd-Fox, Blasi, & Elwell, 2010; Minagawa-Kawai, Mori, Hebden, & Dupoux, 2008; Wilcox & Biondi, 2015) repetition suppression paradigm (FIGURE 1.18B; M. Kobayashi et al., 2014). Thus, partial invariance and configural, holistic processing emerge earlier than the functional segregation between expression and identity that is observed in adults. It is possible that partial invariant face recognition serves as a building block for processing expressions independently of the invariant face dimensions, as the Bruce and Young (1986) model would perhaps predict. Complete invariance isn't achieved until the end of the first year, when infants begin to recognize faces shown in a profile view (Rose, Jankowski, & Feldman, 2002).

**Building a face-space: Experience-based effects and perceptual narrowing.** Before the age of 10-12 months, infants are able to discriminate between phonemes from languages

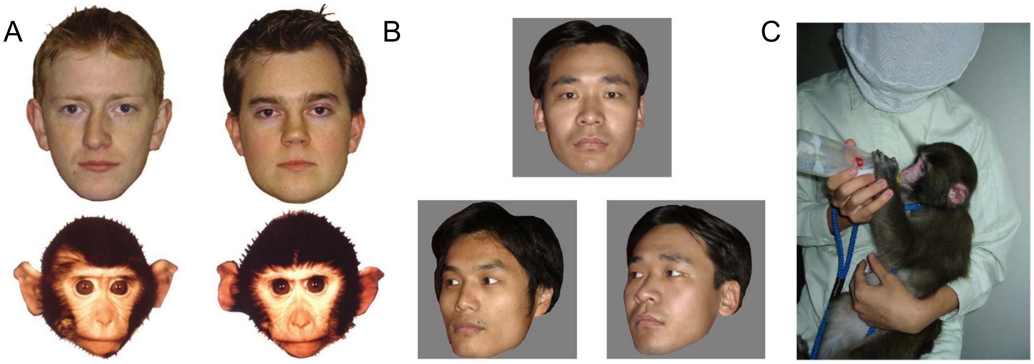

Figure 1.19: **Perceptual narrowing for faces in infancy.** **(A)** Example human (top row) and monkey (bottom tow) faces used in Pascalis et al. (2002). Following habituation, the familiar face and a novel face were presented as a pair for 5 s (adults) or 10 s (6 and 9 month-olds). Recognition is assessed by longer looking times to the novel face. **(B)** Example face stimuli used with infants from a Caucasian environment ("other-race") in Kelly et al. (2007) and with infants from a Chinese environment ("own-race") in Kelly et al. (2009). Following habituation with one face (top), the familiar face (bottom, right) and a novel face (bottom, left) face were shown for two 5 s test trials in a different orientation (full-front or 3/4 pose). The habituation face is at the top, while the test faces (novel, familiar) are at the bottom. In both environments 3-month-olds looked longer to novel own-race and other-race faces while 9-month-olds looked longer to novel own-race but not to novel other-race faces. Reprinted from Kelly et al. (2009). **(C)** Infant macaque being reared in a laboratory setting without exposure to faces. The caregiver is wearing a face-mask. Toys and decorations provided rich visual stimulation in the absence of face exposure. Reprinted from Sugita (2008).

other than the one in which they are being reared, however at 10-12 months of age they become better at discriminating phonemes which are native to the language which is predominant in their environment. Their ability to discriminate non-native phonemes, which they don't experience, decreases. This phenomenon is known as perceptual narrowing and functionally corresponds to an early specialization of perceptual abilities for the infant's linguistic environment (Nelson, 2001; Scott, Pascalis, & Nelson, 2007). By analogy, it has been suggested (Nelson, 2001) that perceptual narrowing may occur in the face domain also, and leading for example to a lesser ability to discriminate between faces of other-race individuals (the Other-Race Effect, SECTION 1.1.3.3). Interpreted in terms of face-space (SECTION 1.1.1.2) this means that during infancy the face space would be shaped by experience, gradually acquiring meaningful (generalizable, robust) dimensions as experience with different faces accumulates (Pascalis & Kelly, 2009), and leading to increasing specification (parcellation) of face-processing neural circuitry (Nelson, 2001).

Considerable evidence exists now to support the notion of perceptual narrowing in the domain of face perception. For example, 6 month-olds readily discriminate between different individual monkey faces, but 9-month-old infants and adults will not unless trained to individualize monkey faces from the age of 6 months (FIGURE 1.19A; Pascalis et al., 2002, 2005).

The effects appear driven by a lack of holistic and second-order configuration processing for other race faces (K. Lee, Quinn, Pascalis, & Slater, 2013). That individuation, not mere exposure, may overcome narrowing is additional evidence that individuation and sociality are key evolutionary constraints shaping face processing in primates (Pascalis & Kelly, 2009). The effect is delayed to 12 months, but not abolished, if human eyes are added to the monkey faces (Damon et al., 2015). Similarly, 3 month-olds discriminate between the faces of different other-race individuals, but 6-12 month-olds gradually loose this ability and demonstrate an "Other-Race Effect" (FIGURE 1.19B; Kelly et al., 2009, 2007). Infants younger than 6-months do not show the effect of perceptual narrowing, but are already sensitive to visual experience. For example, 3-month-old infants will visually prefer own-race to other-race faces (Kelly, Quinn, & Slater, 2005), or human faces to monkey faces (Heron-Delaney, Wirth, & Pascalis, 2011). Experience may also reverse perceptual narrowing past infancy as observed for "other-race" faces in adopted cohorts (Sangrigoli, Pallier, Argenti, Ventureyra, & de Schonen, 2005). It is less clear whether perceptual narrowing is reversible for other-species faces (it was found to be irreversible in Japanese macaques; Sugita, 2008). Finally, perceptual narrowing may open the door to the formation of race-based social categories. In recent, striking studies it has been observed that between the age of 6 and 9 months infants switch from categorizing face race based on perceptual cues to categorizing face race as "us versus them" (Quinn, Lee, Pascalis, & Tanaka, 2015).

The effect of experience on the development of face perception in infancy extends beyond perceptual narrowing for race and species. For example, 3-4 month-old infants typically show a visual preference for female versus male faces, as well as a deficit in recognizing male faces (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002; Ramsey-Rennels & Langlois, 2006). The preference is thought to originate in the predominance of female faces in most infants' visual experience (Sugden, Mohamed-Ali, & Moulson, 2014), is reversed in infants with a male primary caregiver (Quinn et al., 2002), and is absent for female faces of other races (Quinn, Uttley, et al., 2008). Interestingly, the preference also reverses in older infants as a function of accumulated experience with male faces (Liu et al., 2015). Face gender also appears to influence the timing of the other-race effect (Tham, Bremner, & Hay, 2015). Infants aged of 5-10 months readily form exclusive categories of faces based on their gender, although the precise age at which this ability emerges remains unclear (Cornell, 1974; Younger & Fearing, 1999).

**Critical periods for expert face processing in infancy?** The extensive effect of visual experience in shaping face processing in infancy suggests the possible existence of critical periods for acquiring dedicated face processing strategies in infancy. Because the entire visual environment of infants can't typically be manipulated experimentally, much attention has been devoted to (1) adult subjects with a history of abnormal visual experience in infancy and (2) animal studies.

Studies of adults that were deprived of patterned visual experience during the first 1-5 months of life due to a congenital cataract reveal that a lack of visual input to the right hemisphere (i.e. dense cataract in left eye) in early infancy impairs the processing of holistic and second-order relationships up to adulthood in a critical-period manner (Le Grand et al., 2003; Maurer, Lewis, & Mondloch, 2005). This is suggestive of a role for the face preference (SECTION 1.2.1.1) in securing visual experience with faces during this critical period. However, studies in Japanese macaques deprived of experience with faces but preserved visual experience indicate that, at least in this species, face experience in early infancy *per se* isn't necessary to develop face-specific processing strategies later on (Sugita, 2008). If the result can be generalized to humans, then what is causing face processing deficits in congenital cataract patients may be a lack of patterned visual input in a critical period of infancy rather than a lack of early visual experience with faces specifically.

The study by Sugita (2008) also provides insight into the existence of perceptual narrowing in non-human primates. In the study, Japanese macaques were initially reared for 6-24 months without exposition to faces (deprivation period; FIGURE 1.19C). Importantly, the infant macaques were exposed to a rich visual environment so that the deprivation was restricted to faces. During the deprivation period, the macaques had a visual preference for human and macaque faces versus objects and discriminated between individual human and macaque faces equally well (Sugita, 2008). The macaques were then exposed to either human or macaque faces for a month, developing selective discrimination abilities for the exposed face type but perceptual narrowing for the other face type and preferring to look to the exposed face type, without any effect of deprivation length (Sugita, 2008). These results clearly demonstrate that, at least in macaques, face perception develops through both experience-independent (face preference) and experience-dependent (specialization, narrowing) mechanisms. No evidence for a critical period was found (i.e. the effect of the initial deprivation was independent of its length) as macaques appeared to gain normal face processing abilities once the deprivation was ended.

**Emergence of the face processing network in infants.** Face-specific activity in the infant brain appears in the lateral occipital, STS and fusiform areas with a right hemisphere

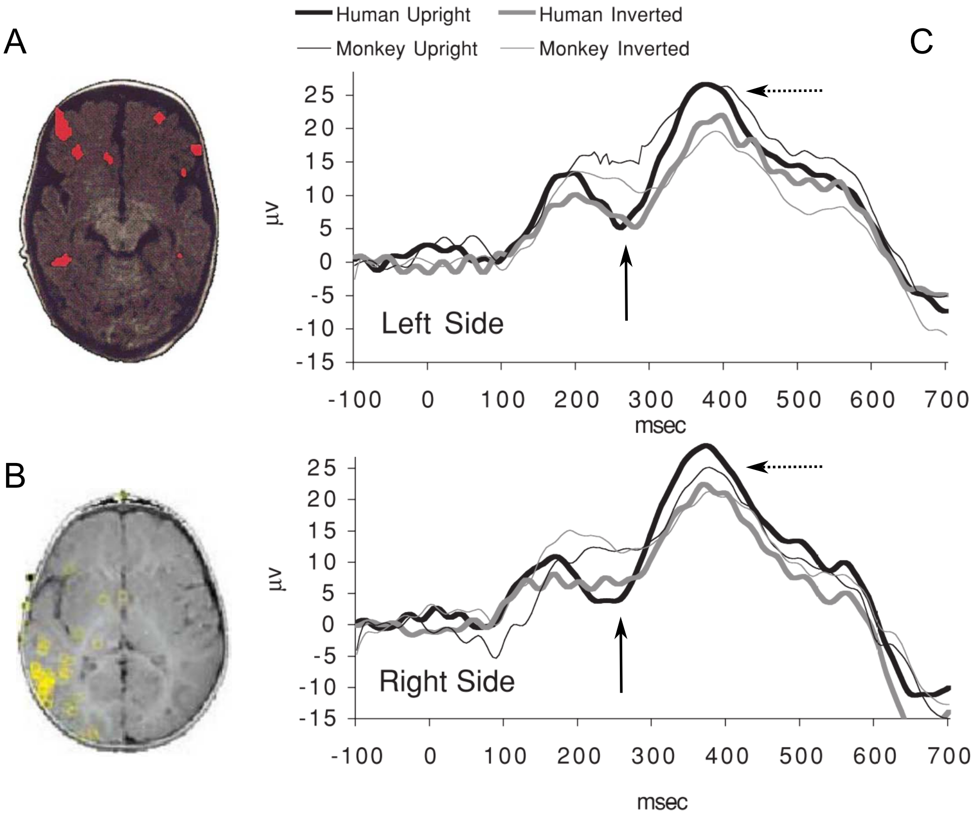

Figure 1.20: **Emergence of the face processing network in infancy.** **(A)** Face-specific activations in a 2-month-old subject as measured by Positron Emission Tomography (PET). The baseline was an abstract moving object which may explain the lack of activation in the STS for the face stimuli compared to baseline. Bilateral clusters in the fusiform region are visible, with a larger response in the right hemisphere. Frontal clusters are clearly visible. Reprinted from Tzourio-Mazoyer et al. (2002). **(B)** Estimated temporal sources of face-sensitive ERPs in 4-month-old subjects, showing higher activity for upright than inverted faces. Reprinted from M. H. Johnson et al. (2005). **(C)** Face sensitive ERPs in 6-month-old infants recorded from posterior temporal electrodes (T5-6). On both sides the N290 window shows sensitivity to the face species (full arrow), while the P400 window shows sensitivity to the face orientation (dotted arrow). Adapted from de Haan et al. (2002).

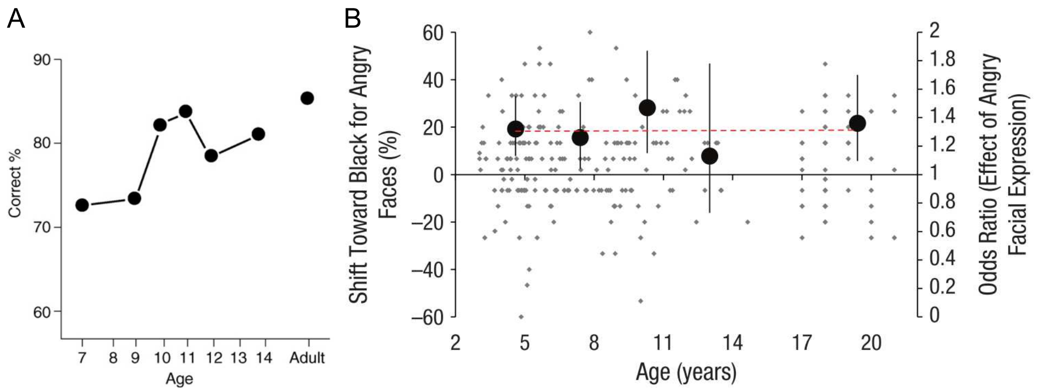

Figure 1.21: **Stability and variation in face processing abilities during childhood and adolescence. (A)** Recognition accuracy for unfamiliar face improves with age, except for a dip at the onset of puberty. Reprinted from Grill-Spector et al. (2008), data from Carey et al. (1980). **(B)** White participants tend to categorize ambiguous Black-White artificial faces as “Black” rather than “White” when the faces are angry (compared to smiling; gray dots, individual data points, % categorization difference; black dots, group level, odds-ratios). The effect is surprisingly stable with age (red dotted line) from childhood (3-14 years) to adulthood (17-20 years). Reprinted from Dunham et al. (2013).

advantage (FIGURE 1.20A-B; de Heering & Rossion, 2015; M. H. Johnson et al., 2005; Tzourio-Mazoyer et al., 2002) from 2-months onwards, the earliest group tested. Converging evidence for a right-hemisphere advantage has been found in 4-10 months in a behavioral task (de Schonen & Mathivet, 1990). Additional frontal clusters (e.g. Broca’s area) are recruited, possibly corresponding to automatic face-speech linkage (M. H. Johnson et al., 2005; Tzourio-Mazoyer et al., 2002). Electrophysiological evidence points to a development of face perception across infancy which shortens processing time, reduces the number of serial steps involved, and renders early components sensitive to higher level properties: 6-month-old ERP responses to faces include an early N290 that is insensitive to inversion but species-specific, and a late P400 component that is sensitive to inversion (de Haan et al., 2002; Halit, de Haan, & Johnson, 2003). By contrast, ERPs from adults and 12-month-olds show an early component (N170/N290) that is species-specific and sensitive to inversion (Halit et al., 2003; Rossion et al., 2000). Of note is that the functional role of the STS may change during development, with the STS being more involved in face perception and less involved in gaze perception in infants than adults, with fusiform regions participating in gaze processing in infants (Calder, Rhodes, Johnson, & Haxby, 2010). In line with this idea, the STS has different connectivity patterns in infants compared to adults at least in cynomolgus macaques (*Macaca fascicularis*; Kennedy, Bullier, & Dehay, 1989).

#### 1.2.1.3 Children and young adolescents

**Quantitative or qualitative developmental changes in face processing strategies?** Overall performance in face processing tasks generally increases with age from infancy to adulthood, but it remains unclear whether the changes which face processing undergoes during childhood are (1) qualitative, as opposed to quantitative, and (2) face-specific, as opposed to solely driven by other cognitive factors such as attention or explicit memory (K. Lee et al., 2013; McKone, Crookes, Jeffery, & Dilks, 2012; Weigelt et al., 2014). The question is difficult to address as most tasks will result in floor effects in the performance of younger groups (e.g. 3-6 year-olds) or ceiling effects in the performance of adolescent or adult groups, making it hard to assess effect sizes across age groups (Crookes & McKone, 2009). Some robust findings emerge despite these methodological difficulties (for a review see K. Lee et al., 2013; McKone et al., 2012). For example, holistic processing appears adult-like from 4-6 years of age onwards (Carey & Diamond, 1994; de Heering, Houthuys, & Rossion, 2007; Maurer et al., 2002; J. W. Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998). Sensitivity to second-order relationships between facial features is present from infancy (SECTION 1.2.1.2), but children may rely less on second-order relationships and more on individual features, external features, or irrelevant paraphernalia, and the sensitivity to second-order relationships increases during childhood until at least 10 years of age (Baudouin, Gallay, Durand, & Robichon, 2010; Maurer et al., 2002; Mondloch, Geldart, Maurer, & Grand, 2003; Mondloch, Le Grand, Maurer, & Grand, 2002; but see McKone & Boyer, 2006). Face-space encoding strategies are also evident from 4-7 years of age onward as shown by distinctiveness effects (McKone & Boyer, 2006), false recall of the average and principal components of a set of learned faces (X. Gao, Maurer, & Wilson, 2015), and after-effects (Anzures, Mondloch, & Lackner, 2009; Nishimura, Maurer, Jeffery, Pellicano, & Rhodes, 2008). However, it is unclear at what age the face-space may be considered "adult-like", i.e. at what age does any additional experience with faces in the same environment cease to significantly affect face-space structure and face processing performance. False recall of the principal components of a set of learned faces increases from 9 years to adulthood (X. Gao et al., 2015), but the relatively small number of faces (about 100) that is necessary to built an adult-like computational model of face-space suggests that maturity could be reached earlier at least in theory (McKone & Boyer, 2006). It is possible that the exact age at which the face-space may be considered "adult-like" depends on the variety of faces that is found in the environment (e.g. see Balas & Saville, 2015, for an effect of hometown size on face processing abilities in adulthood). Finally, performance on a variety of face processing tasks presents a "dip" at age 12-15 years which is locked to pubertal status (FIGURE 1.21A; Carey et al., 1980; Diamond, Carey, & Back, 1983). More generally, an important reorganization of the social brain occurs during adolescence (Blakemore, 2008; Cohen Kadosh, Johnson, Dick, Cohen Kadosh, & Blakemore, 2013).

In sharp contrast with the somewhat protracted development of face processing from infancy to adolescence, the effects of social stereotypes on face perception emerge early. For example, Dunham et al. (2013) evidenced racial stereotyping from 3 years of age using a race categorization task with ambiguous face stimuli (FIGURE 1.21B). Similar findings were reported on social judgments of character based on facial features (Cogsdill, Todorov, Spelke, & Banaji, 2014). Children as young as 4 years old infer the behavior of individuals based on social group membership (A. S. Baron, Dunham, Banaji, & Carey, 2014), and tentative evidence exists that perceptual biases emerging in infancy may cause implicit, but not explicit, social stereotypes (W. S. Xiao et al., 2015).

**Functional and structural changes in the face processing network during childhood.** It has been suggested that face-selective regions continue to develop well into adolescence, taking more time than other high-level vision regions to reach maturity (Grill-Spector et al., 2008; Scherf, Behrmann, Humphreys, & Luna, 2007; Scherf, Luna, Avidan, & Behrmann, 2011). However, similar methodological problems apply for neuroimaging and behavioral paradigms, e.g. the difficulty in separating face-specific from other developmental trends. Increased inter-participant variability and artifacts (e.g. movement-related) in the children groups as well as variations in head size complicate the direct comparison of children, adolescent, and adult face processing in neuroimaging paradigms (e.g., Kuefner et al., 2010).

Children show a N170 but its amplitude, latency, morphology, laterality and sensitivity to inversion change across childhood and adolescence (Taylor et al., 2004). Additionally, younger children (4-12 year-olds) often appear to show a bifid N170 instead of one single component (FIGURE 1.22A; Taylor et al., 2004). However, visual ERPs (P1, N170, N250) show variations in childhood and adolescence that are not specific to face stimuli, and controlling for these changes (notably, the larger P1 in children) using a phase-scrambled control condition eliminates most developmental changes in the face-evoked N170 (FIGURE 1.22B; Kuefner et al., 2010). Kuefner et al. (2010) further suggest that the apparent second deflection of the N170 in children corresponds to a different component (the N250), with both deflections appearing to merge due to group averaging. Independent-Component Analysis (ICA) methods of EEG analysis may clarify these issues by disentangling independent but temporally overlapping ERP components.

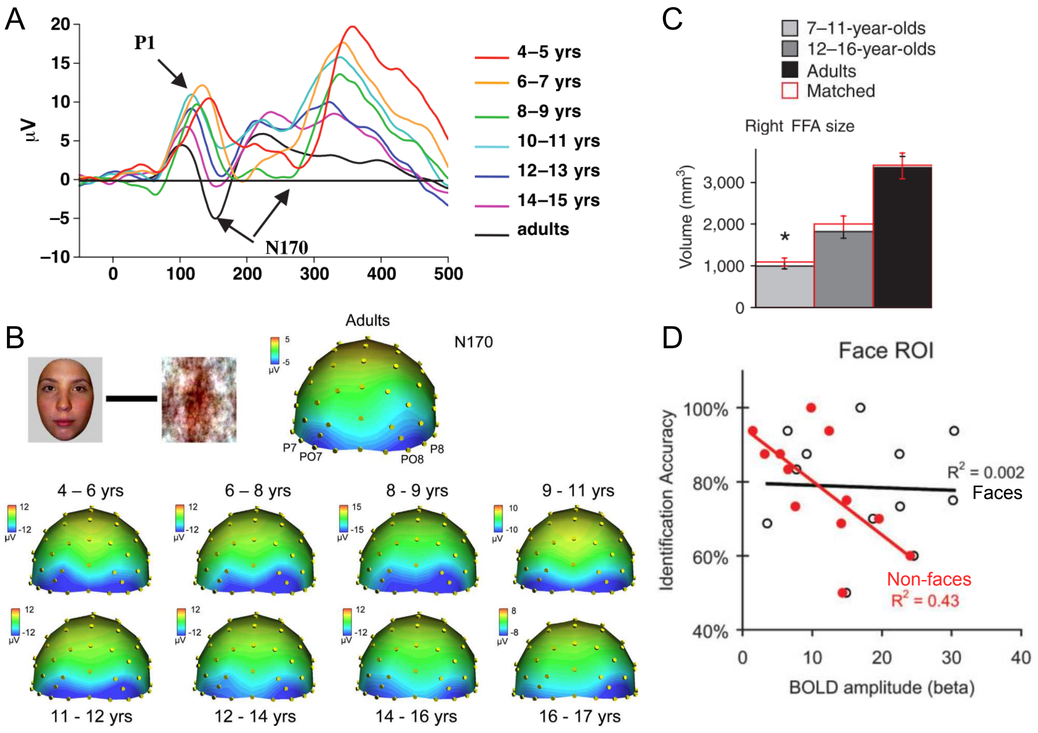

Figure 1.22: **Face-specific networks develop in childhood and adolescence. (A)** Bifid N170 in children (arrows), measured over right posterior temporal electrodes (P8-P10) during a passive face viewing task. The N170 is more negative in adults than children. Reprinted from Taylor et al. (2004). **(B)** Similar N170 (defined as the first negative peak following the P1) topography and amplitude in children and adults, controlling for developmental changes in low-level visual ERPs (phase-scrambled stimuli). Pearson's correlation coefficients between children maps and the adult map were 0.87-0.96, maximal in the oldest age group. Adapted from Kuefner et al. (2010). **(C)** Volume of the functionally defined right FFA (faces > objects, $p$ <0.001) in children and adults. Red bars show data from a smaller subset of subjects matched for noise and motion confounds. Of note is that while there was a difference in the size of the functionally-defined FFA across age groups, there was no difference in its intensity of activation to faces. Adapted from Golarai et al. (2007). **(D)** Negative correlation between the behavioral performance of 4-year-olds in a face recognition task (3 s delay match-to-sample, chance level 50%) and the fMRI activation of fusiform areas in response to non-face objects (shoes, red circles). Behavioral performance did not correlate with fMRI activations in response to faces (black and white circles). A single age group is represented here (4-year olds) so the trend in itself does not imply a developmental mechanism. Adapted from Cantlon et al. (2011).

Conflicting evidence exists on the development of focal versus extended activity in fusiform areas from late childhood to adulthood (Aylward et al., 2005; Passarotti et al., 2003; Scherf et al., 2011), but recent studies linking fMRI responses to behavioral measures of face recognition performance in children and adults suggest that the size of the (functionally-defined) right FFA increases while its activity in response to non-face stimuli decreases, i.e., an increase in size and selectivity of the face-selective areas during development (FIGURE 1.22C-D; Cantlon et al., 2011; Cohen Kadosh & Johnson, 2007; Golarai et al., 2007; Grill-Spector et al., 2008; Scherf et al., 2007). While children tend to have more inter-individual variability in the exact location of the functionally-defined FFA, the finding of a smaller FFA volume still holds when it is individually defined - but the magnitude of activation in children and adults FFA is similar (Golarai et al., 2007; Scherf et al., 2007), and activated volume outside the FFA region results in the total number of active voxels being equivalent in children and adults (Cohen Kadosh, Cohen Kadosh, Dick, & Johnson, 2011; Scherf et al., 2007). The exact location of the functionally-defined FFA also seems to change, becoming more anterior and lateral between childhood and adulthood (Scherf et al., 2007). The effective connectivity between face-selective occipital regions and the fusiform gyrus increases in adolescence and does not appear to be modulated by top-down task demands in children, although compensatory connections outside of this network may exist in this population (Cohen Kadosh et al., 2011). Data on the extended face processing network further reveal that the STS is among the last regions to attain adult-level cortical thickness (Gogtay & Giedd, 2004; Lenroot & Giedd, 2006) and is activated by gaze shifts as early as 7 years of age (Mosconi, Mack, McCarthy, & Pelphrey, 2005) but shows less face-selectivity in children than adults (Scherf et al., 2007). Amygdala volume increases with age but more so in girls than boys (Giedd et al., 2006). Further, the effective connectivity between face-selective occipital regions and the STS appears to emerge in late adolescence (Cohen Kadosh et al., 2011).

### 1.2.2 Facial expression perception by infants and children

In parallel with the development of face processing, facial expression processing develops steeply in infancy. Basic building blocks of this ability are evident at birth or even before.

#### 1.2.2.1 Newborns

**Spontaneous production of facial expressions by newborns.** Spontaneous facial expressions emerge before birth and have even been observed in 24-34 week fetuses using 4-D ultrasound (FIGURE 1.23A; Reissland et al., 2011). Are these expressions produced randomly,

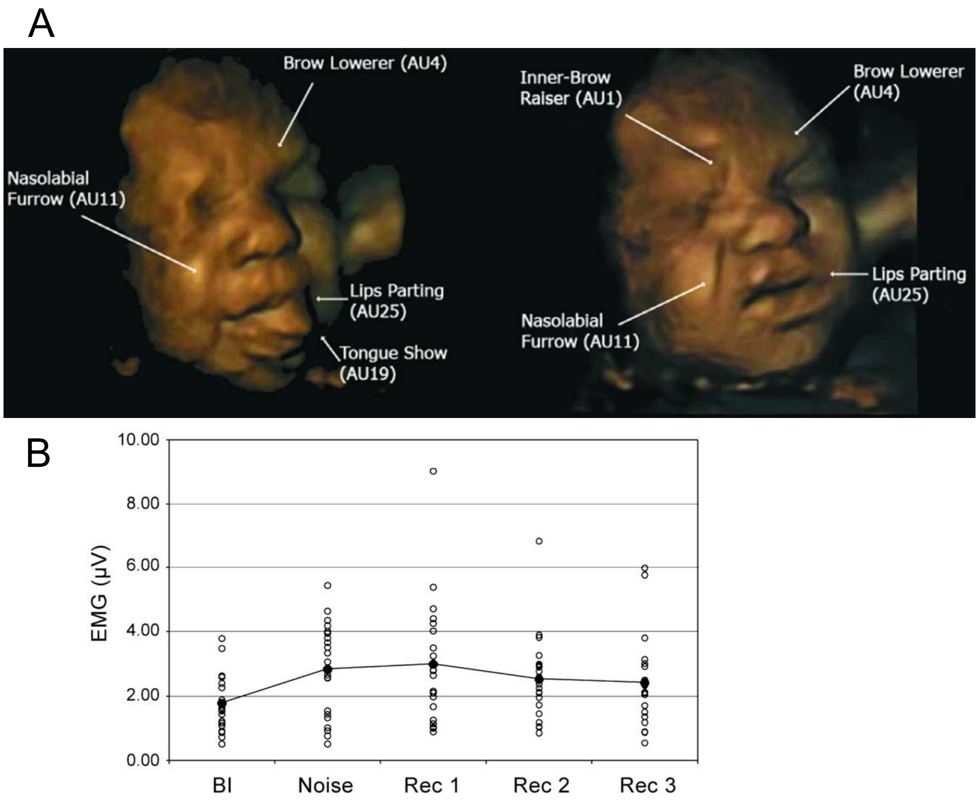

Figure 1.23: **Spontaneous and reactive production of facial expressions in fetuses and newborns.** **(A)** Complex facial expressions produced spontaneously by 32-week fetuses, involving the simultaneous contraction of several facial muscles. AU, Action Unit (Ekman & Friesen, 1976). Reprinted from Reissland et al. (2011). **(B)** Increasing contraction of the corrugator supercilii, as measured by electromyography (EMG), in response to a loud noise (85-90 dB for 1 s) by 27 healthy newborns. Bl, baseline. Rec 1, Rec 2, Rec 3, recovery phase 1, 2 and 3. Importantly, all sounds tested in this study were potentially aversive, so the effect of negative valence and sound stimulation cannot be separated. Reprinted from Trapanotto et al. (2004).

or could they reflect a subjective state (Ekman & Rosenberg, 1997)? Newborns at least produce non-random facial expressions in reactions to stimuli, for example smiling or protruding the tongue in response to the odor of vanilla or the taste of sucrose (J. E. Steiner, 1979; J. E. Steiner, Glaser, Hawilo, & Berridge, 2001), frowning in response to a loud noise (FIGURE 1.23B; Trapanotto et al., 2004), and producing a "disgust" face in response to the aversive smell of rotten eggs or to the bitter taste of quinine (J. E. Steiner, 1979; J. E. Steiner et al., 2001). Newborns also produce "neonatal smiles" during sleep without external cause (e.g. Messinger et al., 2002; Wolff, 1959), and a similar behavior has been observed in newborn chimpanzees (*Pan troglodytes*; Mizuno, Takeshita, & Matsuzawa, 2006). The motor repertoire of newborns is specific to them so that a clear mapping of expressions to discrete, adult-like emotions is difficult; however, valence could already be expressed in corrugator supercilii activity (Trapanotto et al., 2004; but note the absence of a control condition separating the effects of noise level and aversive valence). It remains an open question whether this early repertoire of facial expressions scaffolds the developing perception of facial expressions in newborns (but see SECTION 1.2.2.4; Coulon et al., 2013; Reissland, 1988).

**Perceiving and imitating changes in facial expression.** Classic studies have found evidence that newborns perceive gross changes in facial expression during live interactions. In the seminal study by Meltzoff and Moore (1977), an experimenter presented facial (lip protrusion, tongue protrusion, mouth opening) and digit movement expressions or a passive face (control condition) to 12 to 21 days old newborns. In a first experiment with 6 newborns, the experimenter repeated the movements until a response was obtained from the newborn. The newborns were videotaped, and the videos were then presented to undergraduate volunteers. The volunteers had to guess the experimental condition of a given trial by estimating which of the possible conditions (lip protrusion, etc.) was most or least likely. The experiment revealed that the volunteers were guessing better than chance, which suggested that the newborns may have imitated the face and digit movements that were presented to them. The same results were found for tongue protrusion and mouth openings in a second experiment with 12 newborns (mean age 19.3 days) in which the experimenter movements occurred independently of the response from the newborn (Meltzoff & Moore, 1977), and again in a third experiment with 40 newborns with a mean age of just 32.1 hours (Meltzoff & Moore, 1983). Despite methodological limitations, these results clearly suggest that newborns have the ability to perceive gross changes in the facial expression of an adult during an interaction, and that they may imitate at least some of the expressions which are in their own repertoire

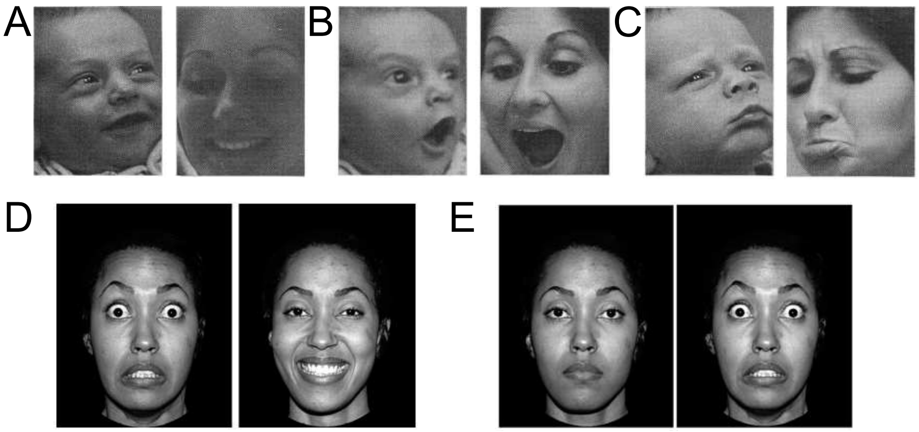

Figure 1.24: **Perception of dynamic and static emotional facial expressions by newborns. (A-C)** Newborn response to an experimenter posing the expression of **(A)** smiling, **(B)** sadness, and **(C)** surprise. Reprinted from T. M. Field et al. (1982). **(D-E)** Example stimuli from Farroni et al. (2007): **(D)** smiling versus fearful and **(E)** neutral versus fearful. Reprinted from Farroni et al. (2007).

(tongue protrusion, mouth opening). It is unclear however whether the imitation is deliberate or covert (for a discussion, see Vinter, 1985). Does it extend to the perception and imitation of *emotional* facial expressions?

**Emotional faces perception at birth: A preference for smiling?** Using an habituation paradigm, T. M. Field et al. (1982) found some evidence that newborns could discriminate the accentuated facial expressions of smiling, sadness and surprise during an interaction with a female experimenter (TABLE 1.1). The newborns produced different patterns of facial response (e.g. pouting, eye widening) to the three types of expressions (FIGURE 1.24A-C), which led the authors to hypothesize that the newborns were attempting to imitate the expressions. The hypothesis was later refuted (Kaitz, Meschulach-Sarfaty, Auerbach, & Eidelman, 1988). A more recent study by Farroni et al. (2007) further investigated the perception of the static facial expressions of fear and smiling in newborns (FIGURE 1.24D-E). Newborns were found to look longer to smiling than fearful expressions (FIGURE 1.24D), but did not discriminate between neutral and fearful expressions in both a preference task and a habituation task (FIGURE 1.24E; TABLE 1.1). The results, although somewhat mixed and hard to interpret, are important because they indicate that visual preferences for specific expressions probably cannot be explained away by differences in the local salience of any facial feature (e.g. large eyes, visible teeth), and mitigate the role of the eyes in the perception of faces by newborns (see also Dupierrix et al., 2014). Finally, they provide a useful point of comparison for studies run with older infants using static emotional faces (SECTION 1.2.2.2). A visual preference for the smiling versus neutral expression wasn't tested in this study, but it has been reported in

| Study | # | Age | Type | Faces | | | Emotions | Result |
|---|---|---|---|---|---|---|---|---|
| Farroni et al. (2007) | 1 | 46h | P | S | V | F | neutral, fear | n. s. |
| | 2 | 56h | H1 | S | V | F | neutral, fear | n. s. |
| | 3 | 54h | P | S | V | F | smile, fear | smile > fear |
| T. M. Field et al. (1982) | 1 | 36h | H1 | D | V | E | smile, sadness, surprise | dishabituation |
| Kaitz et al. (1988) | 1 | 27h | I | D | V | E | smile, sadness, surprise | n.s. |
| Rigato et al. (2011) | 1 | 45h | P | D | V | F | smile, neutral, fearful | smile > neutral |

Table 1.1: **Main studies of emotional faces perception in newborns.** D, dynamic; E, experimenter (live); F, female; H1, habituation with one model, same model at test; I, imitation; P, preference; S, static; V, visual stimuli. Adapted from Bayet et al. (2014).

a later study of the same authors (Rigato, Menon, Johnson, & Farroni, 2011). The preference could be driven by the relative familiarity of that expression. Overall, data on the perception of facial expressions by newborns is extremely lacking, but the few existing studies suggest that dynamic expressions are perceived more readily than static expressions at birth and that smiling may be among the first expressions to be perceived on static faces. More generally, the perception of emotional expressions in the visual modality appears to lag behind the perception of emotional expressions in the auditory modality (e.g. Mastropieri & Turkewitz, 1999), possibly due to the relative lack of experience of newborns with the visual world.

#### 1.2.2.2 Infants

A substantial amount of data has been obtained on the development of facial emotion perception during infancy (for reviews, see e.g. Leppänen, 2011; Leppänen & Nelson, 2009; Nelson, 1987), pointing to a change in the processing of isolated expressions between 5 and 7 months of age and to the emergence of a contextual understanding of expressions towards the end of the first year.

**Early infancy: 2 to 5 months.** During the first months of life, infants begin to produce smiles in response to social interactions ("social smiles") while the production of "neonatal smiles" diminishes (Messinger & Fogel, 2007; Wolff, 1987). Infants' expressions may also match multimodal expressions of anger, at least when produced by the mother (Haviland & Lelwica, 1987). Infants of that age also show increasing signs of expecting adults to display facial expressions during a social interaction, an expectation that is rendered evident in the "still-face paradigm": infants show a reduction in gaze and positive affect and an increase in negative affect in response to an adult keeping a "still", neutral, expressionless face while maintaining eye contact during social interaction (Bertin & Striano, 2006; Tronick,

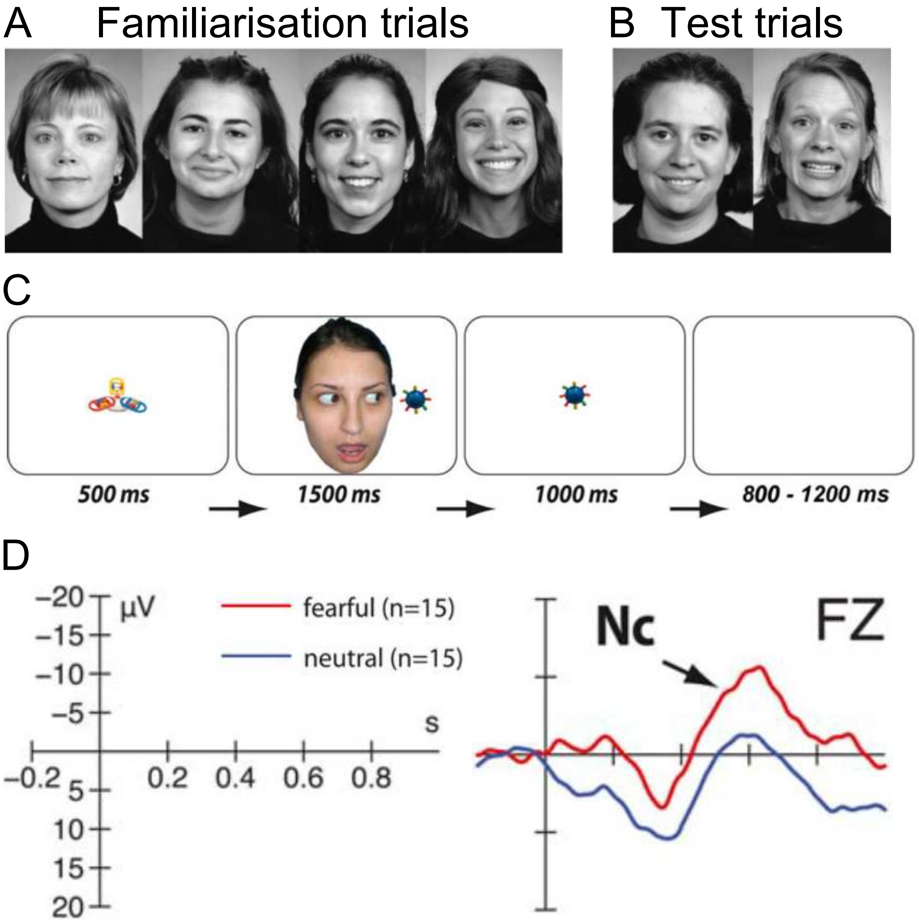

Figure 1.25: **Processing of facial expressions in 2 to 5 months old infants. (A-B)** Discrimination of fearful faces compared to smiling faces. **(A)** Habituation trials with smiles of different intensities and from different female models. **(B)** Test trials with two new female models, showing either a new intensity of smiling (left) or a fearful expression (right) in an unpaired design. 5-month-old infants looked longer to the novel expression (fear) after habituation to the smiling expressions. No preference for fearful versus smiling faces were noted in a control study without a habituation phase. Reprinted from Bornstein and Arterberry (2003). **(C-D)** Sensitivity to fearful expressions in 3.5 month-olds in an object referencing task, measured by EEG activity. **(C)** Example trial: An object is referenced by a face, then presented in isolation at test. **(D)** Larger amplitude of the negative central (Nc) component on electrode Fz during the presentation of an abstract object alone (i.e. at test) when the object was referenced by a fearful (red) versus neutral (blue) face.

Als, Adamson, Wise, & Brazelton, 1978; for reviews see Adamson & Frick, 2003; Mesman, van IJzendoorn, & Bakermans-Kranenburg, 2009). The mechanism underlying the still-face effect remains debated, but at least in older infants (4 months and above) the effect cannot be explained by the emotional valence of the neutral face, as a smiling still face will still produce the effect (Rochat, Striano, & Blatt, 2002). Rather, it seems that infants during the first months of life come to expect contingent communication, including displays of facial expression, during social interaction (Rochat et al., 2002), possibly relying on it for emotional regulation (Mesman et al., 2009). Whatever the mechanism, the still-face paradigm demonstrates that, during the first months of life, infants attend to dynamic facial expressions displayed during social interactions. During the same period of time, infants sometimes show a visual preference for smiling versus neutral faces (La Barbera, Izard, Vietze, & Parisi, 1976; TABLE 1.2; see also Rochat et al., 2002), smiling versus sad faces (Montague & Walker-Andrews, 2002), or increasing intensities of smiling versus neutral faces (Kuchuk, Vibbert, & Bornstein, 1986), but the preference isn't always reported and its origin is unclear (R. F. Caron et al., 1985; Oster, 1981). It appears to decline with age: for example, newborns show a preference for smiling versus fear (Farroni et al., 2007) but no such preference is found at 5 months (Peltola, Leppänen, Mäki, & Hietanen, 2009). In any case, converging data suggests that smiling is among the first facial expressions to be effectively perceived and categorically discriminated from other expressions such as surprise (R. F. Caron, Caron, & Myers, 1982; Young-Browne, Rosenfeld, & Horowitz, 1977), frowning (Barrera & Maurer, 1981) at 3 months, sadness at 3-5 months (A. J. Caron, Caron, Maclean, & Url, 1988), neutral (Bornstein, Arterberry, Mash, & Manian, 2011) and fear (Bornstein & Arterberry, 2003; FIGURE 1.25A-B) at 5 months. The exact age of emergence varies for specific contrasts, but a general finding is that discrimination appears earlier in paradigms involving just one or a limited number of face identities (e.g. Barrera & Maurer, 1981), and later (5 months at the earliest) in paradigms involving the extraction of expressions across multiple identities (e.g. R. F. Caron et al., 1982). This is in line with the idea that structural encoding, the view- and expression-invariant processing of facial identity, matures relatively late in infancy at around 7 months of age (e.g. M. Kobayashi et al., 2014). Some evidence of cross-modal matching have also been reported for smiling expressions in 3-4 months old infants, namely audio-visual matching of smiling versus sad and smiling versus angry expressions of the mother (Montague & Walker-Andrews, 2002) and visual-olfactory matching of smiling versus disgust expressions (Godard, Baudouin, Schaal, & Durand, 2015; the matching appears limited to the smiling expression and is not present at 5 or 7 months). Most behavioral studies find positive evidence of discrimination for contrasts involving smiling expressions only, the exception to the rule being Serrano, Iglesias, and Loeches (1992) who report a discrimination of anger, fear, and surprise expressions across several identities in 5-month-old infants.

Interactive effects of negative expressions with the direction of gaze have been reported in 3-4 month-olds using EEG, namely the interactive effect of fear with averted gaze (Hoehl, Wiese, & Striano, 2008; increased negative central Nc component, measured at 400-800 ms at fronto-central electrodes) and anger with direct gaze (Striano, Kopp, Grossmann, & Reid, 2006; increased positive slow wave PSW component). The study by Hoehl, Wiese, and Striano (2008) was particularly original in using an object referencing paradigm (SECTION 2.3.1.1) to evidence an early sensitivity to fear in 3.5-month-olds infants, whereas most studies have documented the emergence of fear sensitivity between 5 and 7 months of age (e.g. Peltola, Leppänen, Mäki, & Hietanen, 2009). In this study, Hoehl, Wiese, and Striano (2008) presented a female face with a fearful or neutral expression gazing towards an abstract object (FIGURE 1.25C). The same object was presented at test, triggering a negative central (Nc) component of higher (more negative) amplitude when the referencing face had been fearful compared to when it had been neutral (FIGURE 1.25D). The Nc component has been linked to attention allocation and its underlying sources have been localized in the anterior cingulate and prefrontal cortex in 4-7 month-old infants (Reynolds, Courage, & Richards, 2010; Reynolds & Richards, 2005, 2009). No effect of expression was found if the object presented at test was different than the object referenced or if the face was looking away from the object at test (TABLE 1.2), ruling out a general, non object-directed effect of arousal or attention. Of course, the effects of gaze and emotional expression may still be additive rather than interactive i.e. higher attention towards the fearful face and towards the referenced object (i.e. without the need for both effects to be dependent on one another), but in any case the study demonstrate a sensitivity to fear which is typically evidenced only in older infants (Leppänen & Nelson, 2012).

**A developmental shift at 6-7 months of age?** A very large number of studies on the development of emotional faces perception in infancy have targeted the group of 6-7 month-old infants. The categorical discrimination of smile and several other emotions (surprise, sadness, fear) is evident in 6-7 month-old infants (for a review, see Leppänen & Nelson, 2009; Nelson, 1987; TABLES 1.3 and 1.4), as demonstrated by identity-invariant categorization (e.g. R. F. Caron et al., 1982; Ludemann & Nelson, 1988; Nelson & Dolgin, 1985; Nelson, Morse, & Leavitt, 1979 see also A. J. Caron et al., 1988 for audiovisual stimuli) and categorical boundary

| Study | # | Age | Paradigm | Faces | | | Emotions | Result |
|---|---|---|---|---|---|---|---|---|
| Barrera and Maurer (1981) | 1 | 2.97 | H1 | S | V | Mo | smile, frown | dishabituation |
| | 2 | 2.99 | H1 | S | V | F | smile, frown | dishabituation |
| Bornstein and Arterberry (2003) | 1 | 5.10 | H1 | S | V | F | smile to fear | dishabituation |
| | 2 | 5.17 | H2 | S | V | F | smile to fear | dishabituation |
| Bornstein et al. (2011) | 1 | 5.05 | H1 | S | V | F | smile, neutral | dishabituation |
| R. F. Caron et al. (1982) | 1 | 4.11 | H3 | D | V | F | smile, surprise | n. s. |
| | 2 | 5.52 | H3 | D | V | F | smile, surprise | smile to surprise |
| A. J. Caron et al. (1988) | 1 | 3.94 | H3 | D | AV | F | smile, sadness | sadness to smile |
| | 2 | 5.27 | H3 | D | AV | F | smile, sadness | dishabituation |
| | 3 | 5.22 | H3 | D | AV | F | smile to anger | n. s. |
| | 4 | 5.22 | H3 | D | V | F | smile, sadness | dishabituation |
| Godard et al. (2015) | 1 | 3.00 | CM | D | OV | F | smile, disgust | smile: concordant > discordant/control |
| | 2 | 5.06 | CM | D | OV | F | smile, disgust | n. s. |
| Haviland and Lelwica (1987) | 1 | 2.30 | I | D | AV | Mo | smile, sadness, anger | smile, anger |
| Hoehl, Wiese, and Striano (2008) | 1 | 3.70 | OR, EEG (Nc) | S | V | F, M | fear, neutral | fear > neutral (referenced object) |
| | 2 | 3.40 | OR, EEG (Nc) | S | V | F, M | fear, neutral | n.s. (different object) |
| | 3 | 3.70 | OR, EEG (Nc) | S | V | F, M | fear, neutral | n.s. (gazes away) |
| Kuchuk et al. (1986) | 1 | 3.09 | P | S | V | F | smile (different intensities) | higher > lower intensities (vs. neutral) |
| La Barbera et al. (1976) | 1 | 3.96 | P (first look) | S | V | M | smile, anger, neutral | smile > other |
| Montague and Walker-Andrews (2002) | 1 | 3.84 | P | D | AV | Mo, F, Fa, M | smile, sadness | smile > sadness |
| | 2 | 3.84 | CM | D | AV | | smile, sadness | concordant > discordant (Mo) |
| | 3 | 3.84 | P | D | AV | Mo, F, Fa, M | smile, anger | n. s. |
| | 4 | 3.84 | CM | D | AV | | smile, anger | discordant > concordant (Mo) |
| Peltola, Leppänen, Mäki, and Hietanen (2009) | 1 | 5 | P | S | V | F | smile, fear | n. s. |
| | 2 | 5 | ERP (Nc) | S | V | F | smile, fear | n. s. |
| Serrano et al. (1992) | 1 | 5.06 | H3 | S | V | F | anger, surprise, fear | dishabituation |
| Young-Browne et al. (1977) | 1 | 2.95 | H1 | S | V | M | smile, surprise, sadness | dishabituation for smile vs. surprise |

Table 1.2: **Main studies of emotional faces perception in 2 to 5 month-old infants.** Ages are in months. *Paradigm:* CM, cross-modal matching; H1, habituation with one model, same model at test; H2, habituation with one model, different model at test; H3, habituation with different models, different model at test (i.e. generalized discrimination); I, imitation; Nc, negative central ERP component; OR, object referencing; P, visual preference. *Faces:* D, dynamic; F, female stranger; Fa, father; M, male stranger; Mo, mother; OV, olfactory and visual stimuli; S, static (picture); V, visual stimuli. Adapted from Bayet et al. (2014).

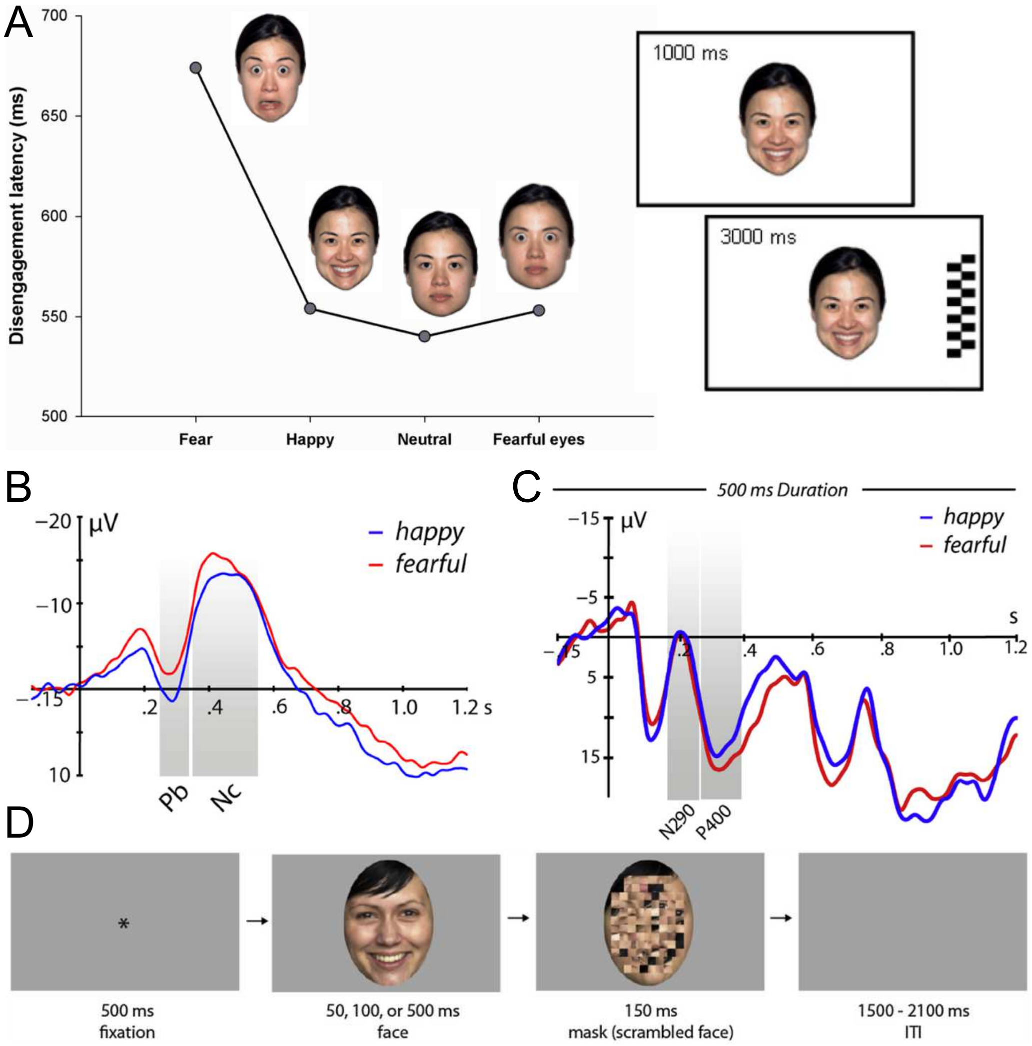

Figure 1.26: **Behavioral and electrophysiological evidence of fear-sensitivity in 7-month-old infants.** **(A)** A central fearful face increases saccadic latency to a peripheral target (checker pattern), reflecting attentional allocation. A neutral face with fearful eyes does not produce the effect. Adapted from Peltola, Leppänen, Vogel-Farley, et al. (2009). **(B-D)** Unconscious and conscious processing of fearful faces in a masking paradigm. **(B)** Measures of EEG activity over central electrodes show an increased amplitude of the Nc component when viewing fearful faces of any duration (i.e. subliminal or conscious), reflecting attention allocation. **(C)** Measures of EEG activity over occipital electrodes show a modulation of the N290 and P400 components by facial emotion at the 500 ms duration only, i.e. when faces are consciously processed. **(D)** The emotional face is presented for 50, 100 or 500 ms, followed by a mask. Face durations of 50 and 100 ms lead to subliminal perception in infants (Gelskov & Kouider, 2010; Kouider et al., 2013), while the 500 ms duration leads to conscious perception. Reprinted from Jessen and Grossmann (2015).

effects (e.g. Kotsoni, de Haan, & Johnson, 2001). EEG and fNIRS techniques further show differential processing of the expressions of anger and fear (Hoehl, Palumbo, Heinisch, & Striano, 2008; Kobiella, Grossmann, Reid, & Striano, 2008; but see Nelson & De Haan, 1996) or anger and smile (Grossmann, Striano, & Friederici, 2007; Nakato, Otsuka, Kanazawa, Yamaguchi, & Kakigi, 2011), although the specific differences observed may vary across paradigms (e.g. see Kobiella et al., 2008, and Hoehl, Palumbo, et al., 2008; TABLE 1.3 and 1.4). No evidence for a valence-based categorization of expressions was found, however (Ludemann, 1991), and a visual preference for smiling (versus neutral, angry or sad) expressions may still be observed in some cases (Soken & Pick, 1999; Striano, Brennan, & Vanman, 2002). Evidence of cross-modal matching also exists for smiling and angry expressions (Grossmann, Striano, & Friederici, 2006; Soken & Pick, 1992).

A robust effect that has been observed at that age across behavioral, physiological and electrophysiological paradigms is the holding of attention by fearful faces (Leppänen, Moulson, Vogel-Farley, & Nelson, 2007; Leppänen et al., 2010; Peltola, Leppänen, & Hietanen, 2011; Peltola, Leppänen, Mäki, & Hietanen, 2009; Peltola, Leppänen, Palokangas, & Hietanen, 2008; Peltola, Leppänen, Vogel-Farley, et al., 2009). For example, at 7 months of age fearful faces evoke stronger physiological responses of attention and arousal, such as cardiac deceleration, compared to smiling faces (Leppänen et al., 2010; Peltola et al., 2011). A central fearful face will delay disengagement to a peripheral target compared to a central neutral or smiling face, or even to a neutral face with fearful eyes (Peltola, Leppänen, Mäki, & Hietanen, 2009; Peltola et al., 2008; Peltola, Leppänen, Vogel-Farley, et al., 2009; FIGURE 1.26A). Interestingly, the latter effect does not appear to be an exaggerated holding of attention by faces in general (i.e. the fear face as a "super face"), as it shows a different developmental trajectory than the general bias to faces which is stable between 5 and 7 months (Yrttiaho, Forssman, Kaatiala, & Leppänen, 2014). The fear (versus neutral) bias in attention holding at 5-7 months is interactively modulated by individual genetic variation in serotonin synthesis pathways (tryptophan hydroxylase gene TPH2) as well as current maternal stress and depression (Forssman et al., 2014), and predicts attachment security in toddlerhood (Peltola, Forssman, Puura, Van Ijzendoorn, & Leppänen, 2015; as measured by the "strange situation" procedure). EEG studies of fearful and smiling faces processing in 7-month-old infants clearly demonstrate attention-related effects of fear in central components (such as the Nc), even when faces are presented below the threshold of consciousness (i.e. subliminally) in a backward masking paradigm (Jessen & Grossmann, 2015; Leppänen et al., 2007; Nelson & De Haan, 1996; FIGURE 1.26B,D). Conscious processing of these faces further modulates components related to face-processing in occipitotemporal regions, suggesting increased cortical resources (N290, P400; Jessen & Grossmann, 2015; Leppänen et al., 2007; Figure 1.26C-D). Subliminal processing of fearful eyes has also been demonstrated at that age (Jessen & Grossmann, 2014), again paralleling results from the adult population (Section 1.1.2.3). Is there a radical developmental shift in emotion processing at 6-7 months (Leppänen & Nelson, 2009)? Animal data suggests that there might be (Leppänen & Nelson, 2012). However, the emergence of fear sensitivity between the age of 5 and 7 months is not a discrete event: some sensitivity to fear may be evidenced by finer analyses of EEG data at 5 months (Yrttiaho et al., 2014), and in specific paradigms at 3.5 months (Hoehl, Wiese, & Striano, 2008). The developmental trajectory of (behavioral, physiological) fear sensitivity across the first year of life and its underlying mechanisms remains an open research question. For example, a recent study found a positive (although weak, Spearman's *rho* = 0.22) correlation between attentional engagement by fear faces at 5 months and N290 amplitude to fearful faces at 7 months (Yrttiaho et al., 2014): The authors tentatively suggest that an increased attention towards fearful faces (possibly from a subcortical route) may drive subsequent cortical plasticity - enhancing cortical response to fear faces. A similar attentional and arousal response has been observed in 6-7 month-olds in response to audiovisual stimuli of infants crying using pupillometric measures (Geangu, Hauf, Bhardwaj, & Bentz, 2011), this may parallel the specific engagement of threat processing pathways (amygdala) by purely auditory screams in adults (e.g. Arnal, Flinker, Kleinschmidt, Giraud, & Poeppel, 2015). Whatever the mechanism, there is now reasonable evidence for a genuine emotional processing at the age of 6-7 months - but the relative lack of data in younger groups makes it difficult to assess exactly what changes and what doesn't change between 3-5 and 6-7 months.

Finally, a number of studies have used EEG paradigms to demonstrate interactive effects of gaze and emotional expressions, most notably threat-related expressions (anger, fear), in 6-7 month-old infants. As could be expected from studies in adults, infants show increased processing (Nc) of angry faces with direct compared to averted gaze (Hoehl & Striano, 2008), direct gaze and anger being an indicator of threat. Conversely, increased processing is observed for fearful (versus neutral) faces when their gaze references a particular object but not when it is direct (Hoehl, Palumbo, et al., 2008). This is in keeping with the functional meaning of these expressions as well as with the finding that, in adults, direct gaze facilitates the recognition of "approach-related" emotional faces such as angry and smiling faces but has the reverse effect for "avoidance-related" emotional faces such as sad or fearful faces (Adams & Kleck, 2003). The interaction of positive expressions (smile, surprise) with gaze in infancy is less clear, but one study indicates that 7-month-old infants will attend more to an object referenced by a neutral face than by a smiling or sad face (Flom & Pick, 2005).

**Eight months and above.** While younger infants do demonstrate sensitivity to at least some emotional facial expressions, towards the end of the first year of life infants begin to show a more subtle understanding of social interactions in general. Such an emerging understanding of social interactions is evident in the production of anticipatory smiling expressions during social interactions (Venezia, Messinger, Thorp, & Mundy, 2004) as well as in the integration of contextual cues in the perception of facial expressions of emotions. For example, Skerry and Spelke (2014) demonstrated that 8-10 month-old infants expect agents who succeed in a goal-directed action to display positive (smile) rather than negative (sad) expressions. The reverse is true: 12-month-olds show some evidence of expecting agents who look and emote positively towards one of two objects to choose to grasp this object over the other (Phillips, Wellman, & Spelke, 2002). Infants at the end of the first year also show signs of attributing a positive (reward) emotional value to smiles that is linked with the social (attachment) value of the person smiling. While this hasn't been demonstrated behaviorally, a fNIRS study found evidence of increased activation in the orbitofrontal cortex of 9-13 month-old infants (mean age 11.7 months) when viewing their own mother smiling compared to a neutral expression (Minagawa-Kawai et al., 2009). Less activation was noted when infants were watching a stranger female smiling, pointing to a role of familiarity and attachment in attributing positive emotional value to smiles (Minagawa-Kawai et al., 2009).

At 8 months and above, infants also show rudiments of social referencing behavior (Feinman, 1982), in line with the emergence of a more complex understanding of social situations. Gaze direction cues affect object processing earlier at 4-6 months of age (Hood et al., 1998; Peña, Arias, & Dehaene-Lambertz, 2014), and even young infants may attend to their parents' facial expressions as demonstrated by the still-face paradigm (SECTION 1.2.2.2). Social referencing, as observed in infants towards the end of the first year, further implies that the infant will actively look for cues such as gaze direction and emotional expressions (e.g. fearful expression) in ambiguous situations and sometimes use those cues to guide their own locomotion or object manipulation (Walden & Ogan, 1988). For example, 12-month-olds will actively look for their mother's face in a context of uncertainty and possibly alter their behavior if the mother displays a negative expression (Sorce, Emde, Campos, & Klinnert, 1985). Further, towards the end of the first year infants may selectively attend to cues from certain people only, for example if they have proved reliable in similar (though not necessarily identical) situations

| Study | # | Age | Paradigm | Faces | | | Emotions | Result |
|---|---|---|---|---|---|---|---|---|
| R. F. Caron et al. (1982) | 1 | 6.87 | H3 | S | V | F | smile, surprise | dishabituation |
| A. J. Caron et al. (1988) | 1 | 6.69 | H3 | D | AV | F | smile to anger | dishabituation |
| | 2 | 6.78 | H3 | D | V | F | smile to anger | n.s. |
| | 3 | 6.77 | H3 | D | AV | F | anger to smile | dishabituation |
| | 4 | 6.79 | H3 | D | V | F | anger to smile | n.s. |
| Geangu et al. (2011) | 1 | 6.59 | Pu | D | AV | In | laughter, cry, babbling | cry > others |
| Grossmann et al. (2006) | 1 | 6.85 | EEG (Nc, LPC), CM | S | AV | F | smile, anger | disconcordant > concordant (Nc);<br>concordant > discordant (LPC) |
| Hoehl and Striano (2008) | 1 | 7.36 | EEG (Nc, N290, P400) | S | V | F, M | anger, fear | fear > angry (N290);<br>angry > fear (P400) |
| Jessen and Grossmann (2015) masking paradigm | 1 | 7 | EEG (N290, P400) | S | V | F | smile, fear | fear $\neq$ smile (conscious only) |
| | 2 | 7 | EEG (Pb, Nc) | S | V | F | smile, fear | smile > fear (Pb); fear > smile (Nc) |
| Kobiella et al. (2008) | 1 | 6.72 | EEG (Nc, N290, P400) | S | V | F | anger, fear | angry > fear (Nc, N290);<br>fear > angry (P400) |
| Kotsoni et al. (2001) | 1 | 7.06 | P | S | V | F | smile, fear (morphs) | fear > smile (categorical boundary vs smile) |
| | 2 | 7.13 | H1 | S | V | F | smile, fear (morphs) | dishabituation (categorical boundary) |
| La Barbera et al. (1976) | 1 | 6.07 | P (first look) | S | V | M | smile, anger, neutral | smile > others |

Table 1.3: **Main studies of emotional faces perception in 6 to 7 month-old infants.** Ages are in months. *Paradigm:* CM, cross-modal matching; H1, habituation with one model, same model at test; H2, habituation with one model, different model at test; H3, habituation with different models, different model at test (i.e. generalized discrimination); LPC, late positive complex ERP component observed at 400-800 ms over posterior central electrodes; Nc, negative central ERP component; P, visual preference; Pb, “positive before” ERP component observed at 200-400 ms over fronto-central electrodes; Pu, pupillometry. *Faces:* D, dynamic; F, female stranger; In, infant; M, male stranger; S, static (picture); V, visual stimuli. Adapted from Bayet et al. (2014).

| Study | # | Age | Paradigm | Faces | | | Emotions | Result |
|---|---|---|---|---|---|---|---|---|
| Leppänen et al. (2007) | 1 | 7.03 | EEG (Nc, N290, P400) | S | V | F | smile, fear, neutral | fear > others (P400); fear > smile (Nc) |
| Leppänen et al. (2010) | 1 | 7.08 | SL, ECG | S | V | F | smile, fear, neutral | fear > others |
| Ludemann and Nelson (1988) | 1 | 7.08 | H3 | S | V | F | smile, fear | smile to fear |
| | 2 | 7.04 | H3 | S | V | F | surprise, fear | surprise to fear |
| | 3 | 7.04 | H3 | S | V | F | surprise, smile | smile to surprise |
| Nakato et al. (2011) temporal optodes | 1 | 6.59 | fNIRS | S | V | F | smile, anger | smile > anger (left); anger > smile (right) |
| Nelson et al. (1979) | 1 | 6.95 | H1 | S | V | F | smile, fear | smile to fear |
| | 2 | 7.00 | H2 | S | V | F | smile, fear | n. s. |
| | 3 | 6.95 | H3 | S | V | F | smile, fear | smile to fear |
| Nelson and Dolgin (1985) | 1 | 7 | H3 | S | V | F, M | smile, fear | smile to fear |
| | 2 | 7 | P | S | V | F, M | smile, fear | fear > smile |
| Nelson and De Haan (1996) | 1 | 7.00 | EEG | S | V | F | smile, fear | fear ≠ smile |
| | 2 | 7.12 | EEG | S | V | F | anger, fear | n.s. |
| Peltola et al. (2008) | 1 | 6.90 | SL | S | V | F | smile, fear, funny face | fear > smile |
| Peltola, Leppänen, Mäki, and Hietanen (2009) | 1 | 7 | P, EEG (Nc) | S | V | F | smile, fear | fear > smile (P, Nc) |
| Peltola, Leppänen, Vogel-Farley, et al. (2009) | 1 | 7 | SL | S | V | F | smile, neutral, neutral with fearful eyes, fear | fear > others |
| Soken and Pick (1992) | 1 | 7.04 | P, CM | D | AV | F, PL | smile, anger | concordant > discordant |
| Soken and Pick (1999) | 1 | 7 | P, CM | D | AV | F | smile, interest, anger, sadness | concordant > discordant (except smile or interest vs. sad) |

Table 1.4: **Main studies of emotional faces perception in 6 to 7 month-old infants (continued).** Ages are in months. *Paradigm:* CM, cross-modal matching; ECG, electrocardiomyography; H1, habituation with one model, same model at test; H2, habituation with one model, different model at test; H3, habituation with different models, different model at test (i.e. generalized discrimination); Nc, negative central ERP component; P, visual preference; PL, points of light; SL, saccadic latency to peripheral target. *Faces:* D, dynamic; F, female stranger; M, male stranger; S, static (picture); V, visual stimuli. Adapted from Bayet et al. (2014).

in the past (Tummeltshammer, Wu, Sobel, & Kirkham, 2014).

#### 1.2.2.3 Children and young adolescents

**Recognition and labeling tasks.** Emotional faces processing continues to develop through childhood, but the results of studies documenting the developmental trajectory of this ability are highly inconsistent, dependent on task (e.g. discrimination, sorting, matching, labeling; Vicari, Reilly, Pasqualetti, Vizzotto, & Caltagirone, 2000) and specific expression (for a review, see e.g. Gross & Ballif, 1991; Herba & Phillips, 2004). Despite this heterogeneity of results, a robust finding is that performance increases with age in recognition tasks and that the smiling expression is recognized, matched and labeled earlier and with more accuracy, followed by sadness and anger (e.g. Durand, Gallay, Seigneuric, Robichon, & Baudouin, 2007; Gosselin, Roberge, & Lavallée, 1995; Mancini, Agnoli, Baldaro, Ricci Bitti, & Surcinelli, 2013; Montirosso, Peverelli, Frigerio, Crespi, & Borgatti, 2010; FIGURE 1.27A). Surprise, fear and especially disgust typically exhibit more protracted developmental trajectories (Camras & Allison, 1985; Gosselin et al., 1995; Rottman, 2014; but see Rodger et al., 2015; FIGURE 1.27A). For example 3-5 year-olds will readily label expressions of anger or sadness (Gross & Ballif, 1991; Widen & Russell, 2003) and spontaneously map facial expressions according to arousal and valence (Russell & Bullock, 1985), but the labeling of sad, disgust and neutral expressions continues to increase up to early adolescence (Mancini et al., 2013). Neutral faces appear particularly difficult to recognize (Gross & Ballif, 1991). It is suggested that the trajectories derive from the refinement of emotion categories during childhood, from the broad labeling of emotions as either happiness, anger or sadness to more subtle distinctions between discrete emotions (Widen, 2013; Widen & Russell, 2003, 2008). However, the refinement of semantic categories is insufficient to explain the trajectory of emotional faces perception, as recognition accuracy is modality-specific and generally higher for faces than voices in early childhood (Chronaki, Hadwin, Garner, Maurage, & Sonuga-Barke, 2015). In other words, performance on labeling tasks also reflects the children's understanding of the label's meaning (Vicari et al., 2000). The relatively low performance on labeling tasks for fear faces contrasts with the early emergence of fear sensitivity in infants (e.g. Leppänen & Nelson, 2012). It should be noted that (1) fear sensitivity is implicit while labeling is by definition an explicit task so that labeling accuracy is directly influenced by confusions between perceptually similar expressions (see Rodger et al., 2015, for an analysis of confusion matrices in emotional faces labeling across childhood and adolescence), and (2) even in adults performance is typically low for fear faces in explicit tasks presumably due to increased demands on emotional regulation

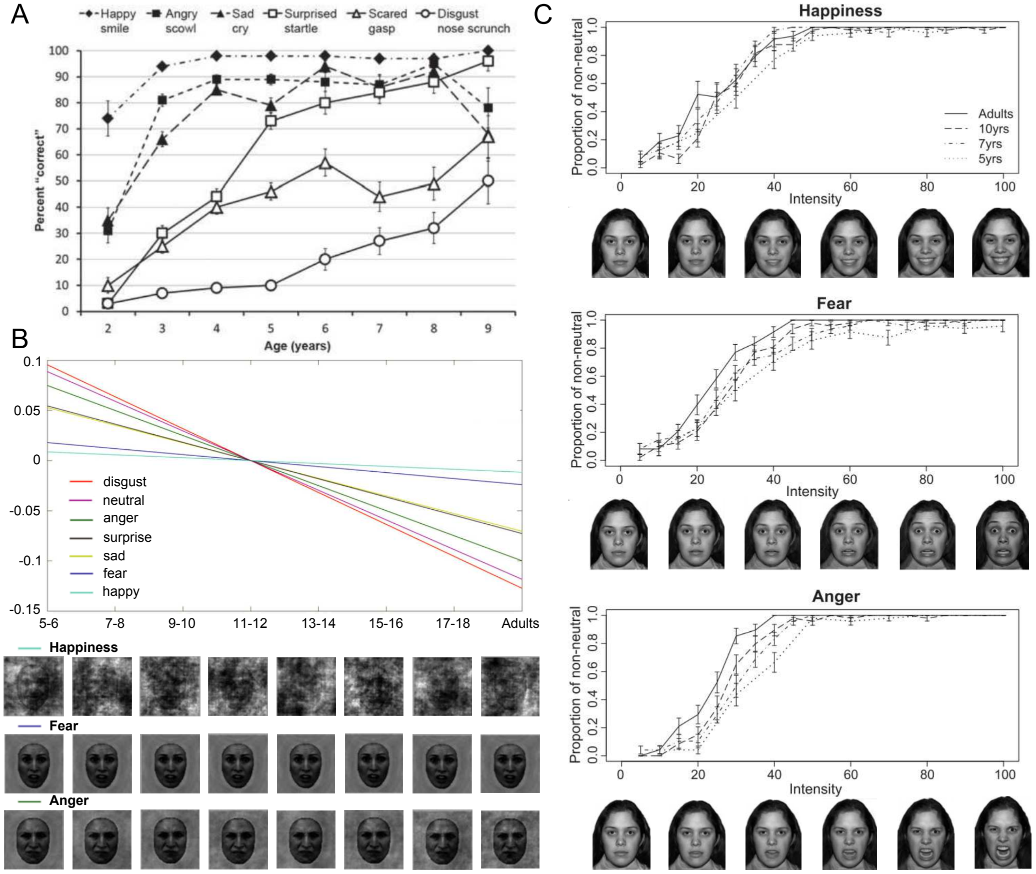

Figure 1.27: **Trajectory of emotional faces processing in childhood evidenced by behavioral tasks.** **(A)** Labeling accuracy of static pictures of emotional faces by 2-9 year old children. Smiling, angry and sad expressions are labeled earlier in development. Reprinted from (Widen, 2013). Data aggregated from several studies. **(B)** *Top:* Fitted developmental slopes of recognition thresholds in a labeling task with emotional faces mixed with noise. *Bottom:* Example stimuli demonstrating mean thresholds for each age group, with constant low threshold for the recognition of smiling, constant high threshold for the recognition of fear, and decrease in the threshold for the recognition of anger across childhood and adolescence. Thresholds were estimated using a QUEST procedure (Watson & Pelli, 1983). Adapted from Rodger et al. (2015). **(C)** Detection of smiling, fearful and angry expressions morphed with neutral faces by children and adults, with example stimuli showing emotions with an intensity of 5, 20, 40, 60, 80 and 100%. Intensity refers to the percentage of emotional expression mixed with the neutral face. A shift of the psychometric curve to the left corresponds to the detection of that particular expression at a lower intensity threshold. Reprinted from X. Gao and Maurer (2010).

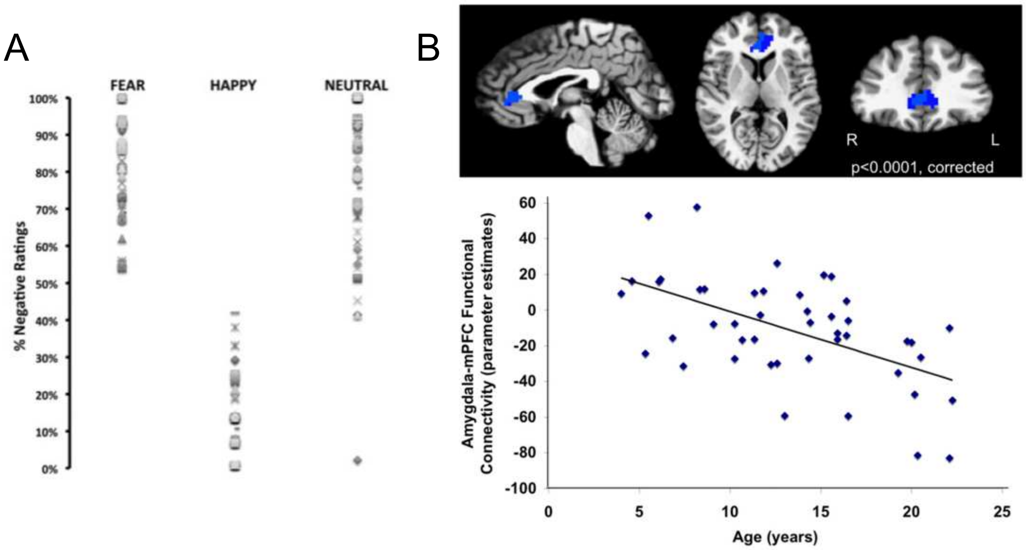

Figure 1.28: **Shifting landscapes in the processing of emotional faces during childhood. (A)** Neutral faces have negative valence in childhood, as measured by ratings and corrugator supercilii EMG activity. Each data point represents the mean for one subject. Reprinted from Tottenham et al. (2013). **(B)** A shift from positive to negative fMRI functional connectivity between amygdala and medial prefrontal cortex during childhood and adolescence. Functional connectivity between the amygdala and medial prefrontal cortex was associated with levels of separation anxiety. Reprinted from Gee et al. (2013).

and attentional control systems (e.g., Calder, Young, et al., 2000). Two more recent studies have investigated perceptual thresholds for the detection and labeling of emotional faces, using emotional faces mixed with noise (FIGURE 1.27B ; Rodger et al., 2015) or neutral faces (FIGURE 1.27C; X. Gao & Maurer, 2010) as stimuli. Those studies provide a finer understanding of emotional faces perception during childhood, both confirming the advantage of smiling faces in labeling tasks (X. Gao & Maurer, 2010; Rodger et al., 2015). Further, Rodger et al. (2015) point to the relative invariance of fearful face-in-noise recognition thresholds during childhood and adolescence. Whatever the differences in recognition thresholds and accuracy, emotional faces perception in childhood clearly relies on holistic face processing as evidenced by composite effects (Durand et al., 2007).

**Neuroimaging emotional faces processing in childhood.** Neuroimaging studies in children show the involvement of the amygdala (Gee et al., 2013; Herba & Phillips, 2004; Hung, Smith, & Taylor, 2012; Thomas et al., 2001), STS (Lobaugh, Gibson, & Taylor, 2006), and fusiform gyrus (Lobaugh et al., 2006) in processing emotional faces, paralleling although not exactly replicating the findings in adults (SECTION 1.1.2.3). A modulation of the N170 isn't evident until 14-15 years (Batty & Taylor, 2006) - possibly due to higher variability in the younger groups. The processing of attended and unattended fearful faces appears to change during childhood, with 9-13 year olds' amygdala showing more fMRI activity in response to attended neutral than to attended fearful faces possibly due to the ambiguity of neutral faces (Thomas et al., 2001). Similarly, unattended fearful faces yield greater fMRI activations in the amygdala than neutral faces in 7-10 year-olds but not 12-15 year-olds who show fear-sensitive fMRI activations in the ACC (Hung et al., 2012). In fact, the experienced valence and intensity of neutral faces or other ambiguous expressions (e.g. surprise) appear to change during development. Tottenham et al. (2013) demonstrated that children experienced ambiguous expressions (surprise) as more negative in valence than adults do: This "negativity bias" in 6-17 year olds was demonstrated by consistently negative valence ratings of neutral and surprised faces and high EMG activity of the corrugator supercilii in response to these faces (Tottenham et al., 2013; FIGURE 1.28A). A practical implication is that neutral faces may not be an appropriate control condition to study emotional faces processing in children and adolescents, since neutral faces are perceived as emotionally charged by this population. In a study comparing the processing of fearful faces to baseline, Gee et al. (2013) found fear-specific fMRI activity in the right (but not left) amygdala that decreased from 4 to 20 years of age (Gee et al., 2013). Further analyses revealed that the connectivity between the amygdala and medial prefrontal cortex (mPFC) went from positive to negative from early childhood to adulthood, in parallel with a decrease in separation anxiety as measured by parental report (Gee et al., 2013; FIGURE 1.28B).

Thus, neuroimaging studies of emotional faces processing in children and adolescents are complicated by the need to isolate perceptual from emotional factors which may both influence the response to and interpretation of emotional faces.

#### 1.2.2.4 Mechanisms of development

In this short, concluding section of the literature review we briefly outline current hypotheses regarding the mechanisms driving the development of emotional faces perception in childhood and infancy.

**Robustness and tuning: The role of experience in shaping the perception of emotional expressions.** Face perception develops largely from environmental inputs (e.g., SECTION 1.2.1.2; Pinel et al., 2014), but evidence in favor of a major role of visual experience in the development of emotional faces perception remains mixed (TABLE 1.5). Adults with a history of bilateral cataract in infancy do show subtle differences in their perception of emotional faces (X. Gao, Maurer, & Nishimura, 2013), in line with their general deficits in specific

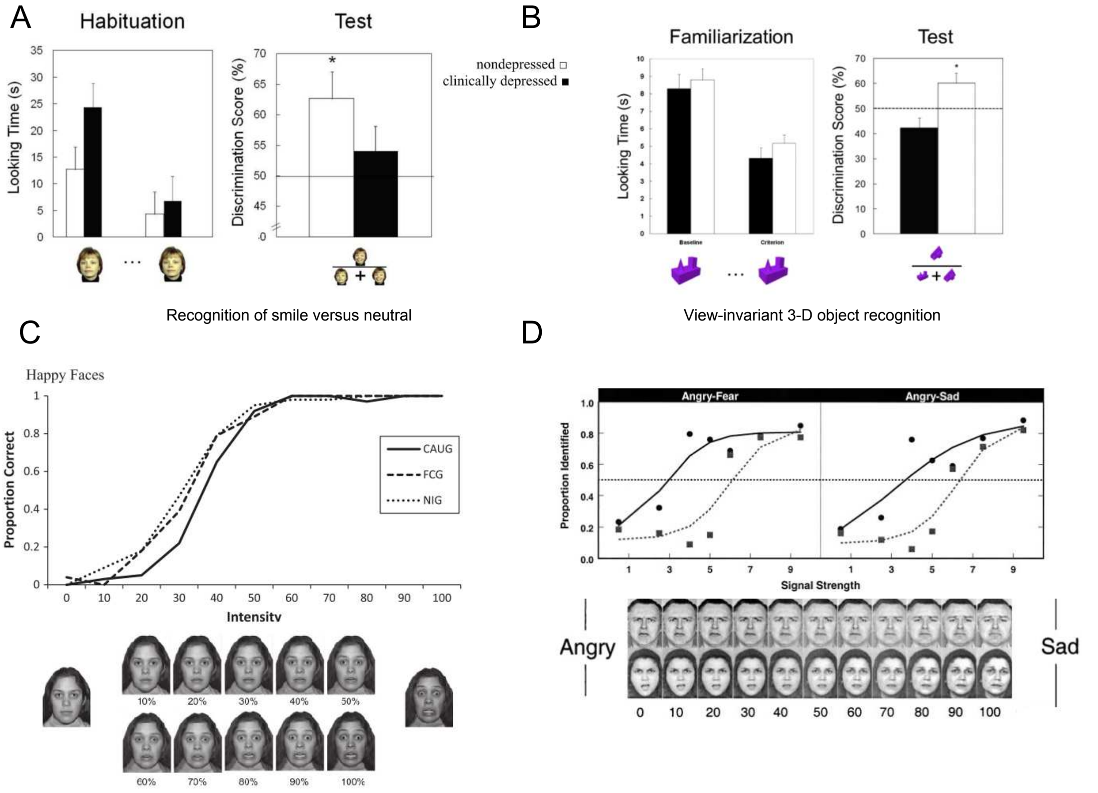

Figure 1.29: **Role of experience in shaping emotional face recognition.** **(A)** Impaired discrimination of smiling and neutral faces in 5-month-old infants with clinically depressed mothers. Reprinted from Bornstein et al. (2011). **(B)** Impaired invariant recognition of 3-D objects in 5-month-old infants with clinically depressed mothers. Reprinted from Bornstein et al. (2012). **(C)** Higher threshold for the recognition of smile (versus neutral) in children raised in neglectful institutions. CAUG, raised in an institution (care as usual); FCG, placed in foster care; NIG, never institutionalized. Example stimuli for the fear versus neutral continuum. Adapted from Moulson et al. (2014). **(D)** Higher threshold for the recognition of fear and sadness versus anger in physically abused children (dashed lines) compared to controls (solid lines), i.e. broader categorization of negative emotional faces as “angry”. Adapted from Pollak and Kistler (2002).

aspects of vision and face processing (Le Grand et al., 2003; Maurer et al., 2005), but the differences are hard to interpret (X. Gao et al., 2013). Infants from depressed mothers, who experience less smiling and expressivity from their mothers than typical infants, show delays in the perception of emotional faces (FIGURE 1.29A; Bornstein et al., 2011; Striano et al., 2002; see also de Haan, Belsky, Reid, Volein, & Johnson, 2004). These observations point to a role of experience in the development of emotional faces perception. However, further studies show that these infants also show delays in the invariant perception of 3-D objects; thus, it's unclear how specific these delays may be (FIGURE 1.29B; Bornstein et al., 2012). Studies targeting the perceptual thresholds or recognition accuracy of different emotional faces in groups of children with atypical social, emotional experience systematically report differences in emotional faces perception that relate to those atypical experiences. Such cases demonstrate the relative plasticity of emotional faces perception. For example, children living in institutions where they experience profound psychosocial deprivation tend to exhibit slightly higher perceptual thresholds for the detection of smiling (Moulson et al., 2014; FIGURE 1.29C) while children experiencing physical abuse exhibit higher perceptual threshold for the detection of fear or sadness expressions when morphed with an angry expression and lower thresholds for the detection of anger (Pollak & Kistler, 2002; Pollak, Messner, Kistler, & Cohn, 2009; Pollak & Sinha, 2002; FIGURE 1.29D). Children experiencing neglect show more complex patterns of impairment (Pollak et al., 2000). Thus, it is clear that environmental conditions may fine tune how children perceive and categorize of emotional faces. It has been suggested that links between emotional faces perception and episodic memory underlie these effects (Pollak & Kistler, 2002); alternatively, perceptual areas themselves may undergo experience-based plasticity. In any case, the differences usually appear relatively mild in contrast to the atypicality of experience and to the deficits shown by these populations in other areas; in some cases, the differences observed may actually be adaptive e.g. the superior detection anger allowing chronically abused children to predict and perhaps avoid instances of physical abuse. Emotional faces perception seems plastic but surprisingly robust to environmental insults (Moulson et al., 2014). This is in line with the relative preservation of emotion recognition performance in other-race faces despite cross-cultural differences (SECTION 1.1.3.3).

**Potential additional mechanisms.** Producing specific expressions may help infants develop the ability to perceive those same expressions (i.e. a link between perception and production; e.g. Gallese, Keysers, & Rizzolatti, 2004). Patients with Moëbius syndrome lack the ability to produce facial expressions due to facial paralysis, yet they show only subtle (Bate et

| Study | Developmental specificity | Observed difference | Age group tested |
|---|---|---|---|
| *Visual experience in general* | | | |
| X. Gao et al. (2013) | lack of visual input in infancy | differences in similarity judgments | adults |
| *Social, emotional, visual experience with faces* | | | |
| Bornstein et al. (2011) | maternal depression | delay, unspecific? | infants |
| Moulson et al. (2014) | psychosocial deprivation | higher threshold for smiling | children |
| Pollak et al. (2000) | neglect, physical abuse | lower recognition accuracy | children |
| Pollak and Kistler (2002) | physical abuse | broader "anger" category | children |
| Pollak and Sinha (2002) | physical abuse | lower threshold for anger | children |
| Pollak et al. (2009) | physical abuse | lower threshold for anger | children |
| M. Smith and Walden (1998) | low socio-economic status | higher accuracy for fear | children |
| *Perception-production* | | | |
| Bate et al. (2013) | Moëbius syndrome | lower recognition accuracy | adults |
| Bogart et al. (2010) | Moëbius syndrome | n. s. | adults |
| Calder, Keane, et al. (2000) | Moëbius syndrome | lower accuracy in some subjects | adults |

Table 1.5: **Main studies on the development of emotional faces perception following atypical perceptual, social experience or facial expression production.**

al., 2013) or no (Bogart, Matsumoto, & Bogart, 2010; Calder, Keane, Cole, Campbell, & Young, 2000) deficits in emotional faces recognition (TABLE 1.5). This suggests that producing expressions is not a necessary factor in developing the ability to recognize emotional faces, but doesn't imply that it isn't a factor in typical populations. Moëbius patients may present with a unique developmental trajectory in this regard, but due to the rarity of cases no developmental study has been conducted with these patients to date.

Animal models suggest a role for experience-expectant cerebral maturation (Leppänen & Nelson, 2009) and critical periods in the sensitivity to fear (e.g. Moriceau, Wilson, Levine, & Sullivan, 2006); such a developmental shift has been proposed to account for the emergence of threat-sensitivity during the first year of life, following a dominance of familiarity-based preferences in the first months (Leppänen & Nelson, 2012). Additionally, a recent structural imaging study found decreasing connectivity between the amygdala and parietal, occipito-temporal regions between 5 and 30 years of age, suggestive of pruning (Saygin et al., 2015). Pruning of this kind has been observed in macaques: afferences from primary visual cortices to the amygdala are present in infant macaques but disappear as afferences from mature higher visual cortices take precedence (Saygin et al., 2015). The role of experience-expectant maturation and pruning remain untested in humans to date.

## Key points

- Domain-specific face perception abilities are evident at birth, develop extensively during infancy from environmental inputs, and continue to mature until the end of adolescence. Stereotypes about race and personality traits however already influence face perception at least by early childhood.

- Sensitivity to a range of emotional expressions, fearful faces and eyes in particular, emerges in infancy at 6-7 months of age. Younger infants appear most sensitive to smiling, and older infants show a more contextual understanding of emotional expressions and social situations.

- The development of emotional faces perception appears quite robust to abnormal experience yet capable of fine tuning. The relative roles of experience, maturation, and other factors remain unclear.

## Chapter 2

# INTRODUCTION TO THE EXPERIMENTAL CONTRIBUTION

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Box 2: Résumé de l'introduction aux chapitres expérimentaux

A la suite de la revue de littérature, nous proposons d'axer la présente thèse autour de trois questions :

1. La perception des expressions faciales se développe-t-elle de manière indépendante ou intégrée à la perception des autres dimensions du visage ?
2. L'expérience des visages a-t-elle un rôle pour les nourrissons dans la manière de percevoir les expressions de visages nouveaux ?
3. Le développement de la perception des visages de peur est-il discontinu durant la première année de vie ?

Ces questions seront traitées au cours de quatre chapitres expérimentaux. Les deux premiers chapitres (CHAPITRES 3 et 4) seront consacrés à la manière dont les expressions faciales sont encodées, c'est-à-dire indépendamment ou conjointement aux autres dimensions des visages, chez l'enfant (CHAPITRE 3) et chez le nourrisson (CHAPITRE 4). Le rôle de l'expérience des visages sera également abordé. Au cours des deux chapitres suivants (CHAPITRES 5 et 6), seront mises en évidence les trajectoires développementales chez le nourrisson de deux types d'effets des expressions faciales sur l'attention et la perception, à savoir l'influence des expressions sur la perception du regard (CHAPITRE 5), et l'influence des expressions sur la détection de visages bruités (CHAPITRE 6). Le CHAPITRE 7 résume et discute l'ensemble des résultats, et propose de nouvelles perspectives de recherche.

Préalablement aux chapitres expérimentaux, le présent chapitre présente brièvement les différentes méthodes qui seront mises en oeuvre au cours des chapitres suivants, tant chez le nourrisson que chez l'enfant et l'adulte.

## 2.1 OUTSTANDING QUESTIONS

More than thirty years after the study by T. M. Field et al. (1982) of the perception of emotional faces in newborns, and more than a century after the seminal observations of Darwin (1872), experimental research has clearly demonstrated that the perception of emotional faces emerges during the first year of life but continues to be fine-tuned up to adulthood. Outstanding questions concern the interaction of emotional expressions with other facial dimensions in development, mechanisms of development, and a description of developmental trajectories during the first year of life that goes beyond categorization tasks.

### 2.1.1 Does facial emotional expression processing develop independently or integrated with the processing of other face dimensions?

Neuroimaging studies (EEG, fNIRS) show a modulation of face-related components (e.g. Jessen & Grossmann, 2015) and cortical activity (e.g. Nakato et al., 2011) by facial expressions of emotions in infants and children (SECTION 1.2.2), suggestive of an early integration of facial emotions with other dimensions of the face. While the recognition of face identity is generally thought of as an expression-independent process (SECTION 1.1.3.2) and classic models stress the functional dissociation between variant and invariant, expression-independent face processing (e.g. SECTIONS 1.1.1.2 and 1.1.1.3), numerous studies in adults suggest that facial emotions may influence, and be influenced by, other dimensions of the face (SECTION 1.1.3). Thus, a theoretical question is whether face processing development leads to an increasing integration of cues from initially independent streams, or to an increasing (though incomplete) segregation of cues as encoding gains efficiency. In other words, are interactions between face dimensions a developmental gain-of-function, or a built-in characteristic of face processing? For example, in adults and children, stereotypical beliefs cause facial emotions to directly bias the race categorization of faces (Amodio, 2014; Dunham et al., 2013). Can similar effects be described with other face dimensions (e.g. gender, gaze) in infants and children?

### 2.1.2 Does experience affect how infants perceive emotional expressions portrayed by strangers?

Tentative evidence suggests that visual, social experience shapes the perception of facial emotions from an early age (SECTION 1.2.2.4) and appears to play a bigger role than cerebral maturation in the emergence of gaze cuing (Peña et al., 2014), another aspects of variant face processing. For example, it has been observed in some studies that infants will discriminate emotional expressions portrayed by their mother more readily than expressions portrayed by their father (Kahana-Kalman & Walker-Andrews, 2001; Montague & Walker-Andrews, 2002). Would this effect of experience generalize to new faces, for example when perceiving expressions or gaze cues in female versus male faces? Surprisingly few studies of emotional face perception in infants have used male faces as stimuli, and even less have used male and female faces stimuli in the same experiment.

### 2.1.3 Is the development of fear processing continuous or discontinuous during the first year of life?

Group averages suggest an emergence of fear sensitivity between 5 and 7 months of age (Leppänen & Nelson, 2012; SECTION 1.2.2.2), an age at which a categorical perception of some expressions also becomes more evident and robust (Leppänen & Nelson, 2009). However, many studies of fear processing in infants have targeted 6-7 month-olds only, and studies using subtler analysis methods (Yrttiaho et al., 2014), individual developmental trajectories (e.g. Forssman et al., 2014), or specific paradigms (Hoehl, Wiese, & Striano, 2008) suggest a more continuous emergence of fear sensitivity during the first months of life, with some specific processing of fear existing before 6-7 months or even before 5 months. Thus, studies describing a complete developmental trajectory of fear sensitivity before, at and after the pivotal age of 6-7 months are lacking, and the existing studies typically use the same paradigm (e.g. saccadic latency to a peripheral target, visual preference for a fearful face versus smiling face; SECTION 1.2.2.2). How emotional expressions may be perceived before 5-7 months of age remains also poorly understood.

## 2.2 OBJECTIVES AND OVERVIEW OF THE THESIS

The above questions will be tackled in six studies described in four chapters.

In the first two experimental chapters, we focus on the encoding aspects of emotional faces perception. More specifically, in CHAPTER 3 we describe an effect of emotional expression on face gender categorization that is present in children as young as 5-6 years. The perceptual determinants of the effect are researched using computational models of face gender categorization. In CHAPTER 4, over the course of three short studies we concentrate on the visual preference for smiling that is sometimes reported in 3-4 month-old infants and how it is affected by experience-sensitive dimensions of the face such as gender and race.

In the following two experimental chapters, we focus on the developmental trajectory, from 3- to 12-months of age, of two different attentional or perceptual aspects of emotional faces perception. In CHAPTER 5, we ask whether gaze-cuing is influenced by positive expressions (smiling) and gender (an experience-sensitive dimension), independently or in interaction. Finally, in CHAPTER 6, we research fear sensitivity in an original face-in-noise detection task looking for an effect of emotional saliency on perceptual sensitivity.

Finally, in CHAPTER 7 we summarize the present findings, discuss their relevance and limitations, and outline possible future research directions.

## 2.3 GENERAL METHODS AND METHODOLOGICAL CONSIDERATIONS

Before moving on to the experimental contribution we now briefly describe the methods that will be used in preverbal infants, children, and adults, along with a few methodological considerations.

### 2.3.1 Studies in preverbal infants

Preverbal infants can neither follow explicit instructions nor provide verbal or fine motor responses. Thus, behavioral research in infants has developed through the innovative efforts of researchers in designing specific paradigms that draw on infants' behavioral repertoire (looking, hearing, touching, sucking, grasping) while giving access to the infants' internal, cognitive world.

#### 2.3.1.1 The preferential looking task

**General principle.** The preferential looking task was introduced by Fantz (1964) and remains one of the most used when studying infant visual perception. In this task, the infants are presented with a pair of stimuli on a display, and the amount of time spent looking at either one is measured (FIGURE 2.1). Looking time indexes the relative level of interest for each stimulus in the paired display. In the original procedure, an observer peeps through a small hole in the display, measuring looking time to either stimulus online during presentation. Each infant may be presented with a series of trials featuring different types of stimuli pairings on the display, usually with the left-right side of presentation reversed across trials for each stimuli pairing. The experiment may terminate after a fixed number of trials or when the infant becomes fussy. In the first seminal observations it was noted that infants would look longer to patterned than homogeneous surfaces (for example, a black and white grating would be preferred to a gray field), so the technique was heavily used to generate psychophysical curves and visual acuity estimates from infants and newborns (Dobson & Teller, 1978). It has been used in CHAPTERS 4, 5, and 6.

The forced-choice preferential looking task was introduced by Teller (1979; 1997) as a variant of the original preferential looking task. Interestingly, this variant does not assume which component of infants' behavior the observer should measure (first fixation, looking time, facial expression, head turns, number and durations of individual fixations...). Instead, the task of the observer is to directly infer the location of a pattern of interest (for example, a black and

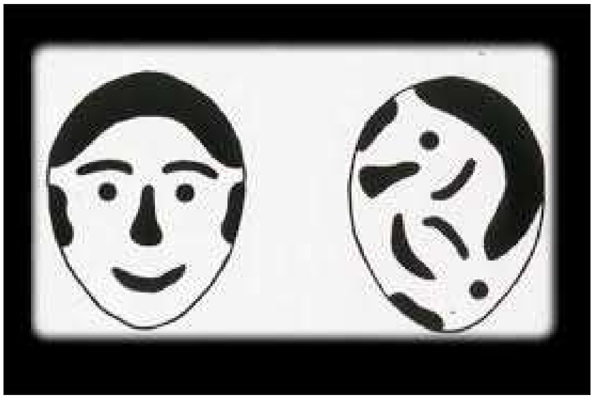


Figure 2.1: **Classical example of a preferential looking task.** A schematic face is presented paired to a schematic scrambled face during 120 s, and a looking preference for the face stimulus is observed in newborns as well as in infants aged of 1 and 2 months (Fantz, 1961, 1964).

white grating versus a gray field) based on the observation of all aspects of infants' behavior when viewing the stimuli pairing: the ability of an observer to detect whether the infants detected the pattern of interest is used as a proxy for measuring the infants' detection. The method was called *double psychophysics* because the observer is also a subject in the sense that he or she is completing a forced-choice task and his or her performance is assessed with regard to an objective standard. A twist of this method has been used in CHAPTER 6 as a way to analyze infant looking data.

**Comparison with other methods.** The reliability of preferential looking to assess visual acuity in infants has been compared to that of other behavioral and electrophysiological methods (Dobson & Teller, 1978; Teller, 1997). Preferential looking yielded estimates of visual acuity that were on par with that obtained with other behavioral methods (direction of first fixation, operant preferential looking, optokinetic nystagmus; Dobson & Teller, 1978), but lower than that obtained with electrophysiological methods (VEPs, Visually Evoked Potentials; Norcia & Tyler, 1985). Assessment of acuity by preferential looking proved to be compatible with psychophysical techniques of threshold estimation as used in adults' studies, although small adjustments were needed to reduce the number of trials per session (Lewis & Maurer, 1986). The discrepancy between the behavioral versus electrophysiological acuity estimations might reflect differences in protocol such as the use of flickering stimuli or signal averaging as well as differences in measurement, the behavioral response of the infants being an indirect consequence, or reflection, of perceptual cortical processing (Teller, 1997). Overall, preferential looking is considered as a robust, reliable method that has been successfully used to study lower- (Banks & Salapatek, 1981; Braddick & Atkinson, 2011), mid- (Kellman & Spelke, 1983, in a dis-habituation paradigm) and high-level vision (Macchi Cassia et al., 2004; Pascalis et al., 1995) in infants and newborns. It requires no training of the infant and is also appropriate for use in infant macaques, allowing cross-species studies of visual development (e.g., Paukner, Huntsberry, & Suomi, 2010).

**Difficulties and limitations.** First, the number of trials that can be obtained from a single infant in a single session of any given task is limited by difficulties in sustaining attention, general fatiguability, and rapid fluctuations in state from sleepy through calm through fussy (Teller, 1979). This limits the possibility to run fully within-subject designs, and renders the careful counterbalancing of conditions all the more important. Psychophysical studies involving the presentation of conditions in which stimuli of interest are barely visible prove especially difficult to run, as infants will quickly loose interest after a few difficult trials and become too fussy for the experiment to continue further (Teller, 1979): in such studies, the ratio of easy to hard trials should be as high as possible. Attrition rates may also be problematic.

Second, null results often cannot be interpreted. While this is often the case with null results, it is especially problematic in studies of preferential looking: a robust visual preference for stimulus A over stimulus B means that infants readily discriminate stimulus A from stimulus B, but the absence of preference doesn't imply an absence of discrimination (Teller, 1979). Comparisons with different methods, most notably the dishabituation paradigm or Visual Paired Comparison (VPC), help disambiguate the null results of visual preference studies (e.g. Di Giorgio, Leo, Pascalis, & Simion, 2012).

**Understanding visual preference.** In fact, even positive results may prove difficult to interpret unless a clear direction of preference is expected, such as the strong preference for faces versus objects or scrambled patterns (e.g. as in Macchi Cassia et al., 2004). Specific paradigms such as VPC, dishabituation or violation of expectancy provide stronger hypotheses regarding the direction of the preference that should be observed. But while in most cases infants will look longer to the novel, or unexpected, stimuli, suboptimal familiarization can lead to familiarity preferences and the direction of preference may change across age groups (Kidd, Piantadosi, & Aslin, 2012; Pascalis & de Haan, 2003). The interpretation of spontaneous visual preferences, without prior familiarization or habituation, may prove even more difficult without access to fine-grained data on infants' visual and social experience: without this data, what is familiar or novel to an individual infant remains unknown. Thus, researchers have started documenting infants' visual and social experience using infant head-mounted cameras

Figure 2.2: **Typical object referencing experiment. Familiarization phase: (A)** A central face with direct gaze and two different objects on the side is presented. **(B)** The face gazes towards one of the objects. **Test phase: (C)** The same two objects are presented without the face. A novelty preference for the uncued object is observed. Adapted from Reid and Striano (2005).

(Sugden et al., 2014) or structured parental reports (Rennels & Davis, 2008). In some cases, a correlation has been reported between infants' accumulated visual experience and spontaneous visual preferences (Liu et al., 2015) or visual categorization performance (Damon et al., manuscript in preparation). This type of paradigm will prove helpful in describing the role of visual and social experience during development.

**The particular case of object referencing.** Social referencing, the gathering of information from the expressions and behavior of other people in the environment, typically involves measuring how infants and toddlers may or may not approach unusual toys or situations depending on the emotional reactions of their caregiver (Feinman, 1982; Walden & Ogan, 1988). A simplified version of these paradigms, this time involving visual preference, has been used to study social referencing in infants as young as 3- to 4-months (Hood et al., 1998; Reid & Striano, 2005). In this version, a central face is presented and gazes towards one of two objects that are presented on the left and right side of the face. Such a situation elicits a preference for the uncued object when both objects are subsequently presented at test without the central face (FIGURE 2.2). This preference for the uncued object may be interpreted as a novelty preference similar to that that are observed in studies of visual memory using familiarization and Visual Paired Comparison (VPC). Here, the novelty preference for the uncued object reflects the encoding, or attentional, bias for the cued object that was elicited during familiarization: due to this bias the cued object is more familiar, and the uncued object more novel, at test. The method has been used in CHAPTER 5 of the present thesis.

#### 2.3.1.2 Acquisition and analysis of preferential looking data

**Experimental setup: stimuli presentation and raw video acquisition.** A representation of the experimental setup at the LPNC laboratory in Grenoble is provided below (FIGURE 2.3). The infant seats on a caregiver's lap approximately 60 cm from a 24" DELL LCD display

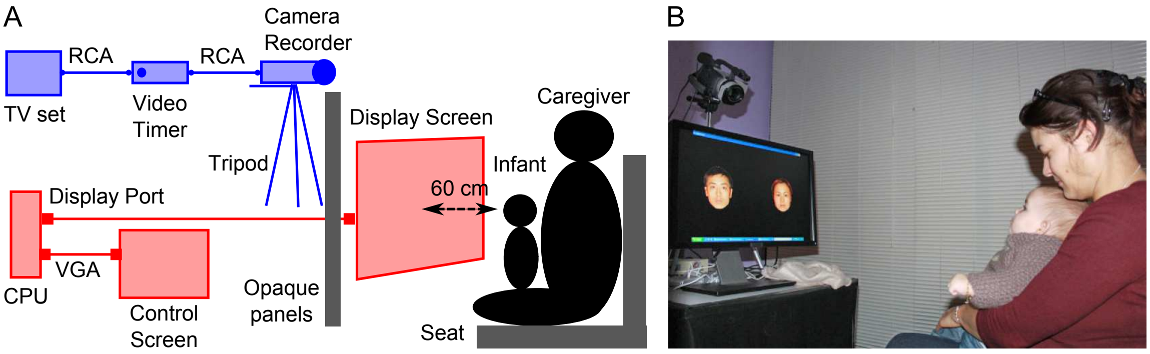


Figure 2.3: **Experimental setup**. **(A)** Materials and connections. Blue group: video acquisition and video display in real time. Red group: stimuli presentation. Electrical connections, keyboard, mouse and speakers are not shown. **(B)** Example, without panels.

screen with a resolution of 1920 by 1200 pixels and a refresh rate of approximately 60 Hz. This distance is typically employed with infants, as it is estimated that their acuity at this particular distance is optimal. Indeed, visual acuity in infants is severely limited by retinal and convergence immaturity, and only reaches adult levels at the end of the first postnatal year (Norcia & Tyler, 1985). Panels on the right, on the left, and around the display screen limit the infant's field of vision.

Stimuli presentation is controlled by the experimenter using a control screen with mouse and keyboard. The control screen and the display screen are connected to the same HP Z400 Central Processing Unit (CPU) through a Video Graphics Array (VGA) cable and a Bizlink Display Port cable, respectively.

A Canon XM2 mini-DV camera recorder with 20x optical zoom is mounted on a Hama tripod and records the infant's gaze from above the display screen. The position and zoom of the camera are controlled by a second experimenter at all times to maximize data quality. During recording, video data is transmitted through an analog RCA connector (yellow RCA) to a For-A VTG-33 video timer and displayed with a timer on a small Nikkai VW58 TV set. The experimenter may use the TV display to monitor the infant's state, and use the timer to control presentation times depending on the infant's gaze. A common way to control presentation time is to define trial duration (e.g. 5 or 10 s) from the moment of the infant's first fixation on the novel display. Such setting allows for individual variations in noticing and orienting to the novel display.

**Raw video preprocessing and analysis.** Videos are imported from the mini-DV tapes and digitalized. Individual testing sessions are parsed from the video using Windows Movie Maker.

Videos are analyzed frame by frame using the VideoLab v.3 software by Mike Coleman

(Department Of Human Communication Science, University College London, 2001). The sampling of frames from the video is done with 40 ms precision (25 frames per second) and an initial jitter to randomize sampling distribution. In a typical visual preference paradigm, the experimenter will manually code the infant's gaze as being either on the left side of the screen, right side (if two stimuli are displayed side by side), or outside of the screen, generating raw looking times data.

**Inter-coder reliability.** The reliability of manual video analysis is assessed by comparing the looking times data of a subset of the total sample (25%, typically) with the looking times data of that sample as coded by a second, independent coder. One way to estimate inter-coder reliability for numerical data is the correlation coefficient: if both coders agree most of the time, the correlation coefficient between their two data sets will be close to 1. Various correlation coefficients may be used e.g. Kendall's tau (non-parametric) or Pearson's $r$ (linear correlation). An inter-coder reliability of or above 0.90 (Pearson's $r$) is usually considered acceptable.

**The phenomenon of side bias and the question of its handling.** A problem that may arise when recording visual preference data from infants in paired stimuli designs is that some infants may fail to look at both stimuli during a trial. The behavior appears to occur more often in infants younger than 4-months, especially when tired. A least two factors support the exclusion of such trials. First, visual preference in paired stimuli designs is supposed to rest upon the comparison of two paired stimuli; obviously such comparison may not occur when one of the two stimuli has not been perceived. Thus, a minimal looking duration towards each of the two stimuli is necessary to assure that both stimuli have been perceived. Second, the cognitive processes leading to side bias are supposed to differ from task-related processes. Indeed, far from being a mere exaggeration of normal looking, at least some side biases result from obligatory looking (Stechler & Latz, 1966), the occasional failure to disengage from a visual stimulus that is thought to occur in infants prior to the maturation of inhibitory pathways from the basal ganglia to the superior colliculi (Clohessy, Posner, Rothbart, & Vecera, 1991; Colombo, 2001; Hood, 1995). Thus, in these instances at least longer looking would not actually reflect longer processing or a higher allocation of attention but a task-unrelated, physiological noise.

While the necessity to clean away such noise is clear, the criterion that should be used to define side bias may be subject to discussion. The default, a priori criterion that is used at the LPNC in Grenoble and most infant laboratories is the following. If an infant has looked less than 95% of the presentation time to either one of the two paired stimuli on a given trial, then this constitutes a side bias and the trial should be excluded. This corresponds to less than 500 ms to either side during a 10 s trial, and less than 250 ms to either side during a 5 s trial. Although the case could be made that those minimum look durations are too long given that 5-month-olds may reliably perceive visual stimuli presented for 150 ms only (preceded, followed by masks and looped 12-14 times; Gelskov & Kouider, 2010; Kouider et al., 2013), the criterion remains widespread in infant research. Note that usually trials come in pairs where the same stimuli are presented with side of presentation reversed. In such cases, then the two pairs of trials should be excluded if a side bias is detected in one or more of the two trials. This default criterion may be relaxed or tightened depending on the specific paradigm, or the specific comparison of conditions that is investigated. For example, in a paradigm where a face is presented paired with pure visual noise, infants may look less than 5% of the time to the noise side simply because there is less signal to process and a very short look is sufficient to classify such stimulus as noise to be disregarded.

### 2.3.2 Studies in children and adults

In contrast to infant studies, most studies in children and adults rely on requiring participants to perform a specific, explicit task that may range from detecting gray scale gratings (Campbell & Robson, 1968) to reporting the content of their own thoughts (Ericsson & Simon, 1980). Here we describe the two types of perceptual tasks that have been used in CHAPTERS 3 and 4 of the present thesis. Some of the analysis methods described have additionally been used in CHAPTER 6.

#### 2.3.2.1 The Two-Alternative Forced-Choice categorization task

The Two-Alternative Forced-Choice (2-AFC) task is a psychophysical method introduced by Gustav Fechner (Fechner, 1966; Link, 1994) to study perceptual decisions e.g. the comparison of two different weights to decide which one is heavier. It has been used in CHAPTER 3.

**General principle.** In a 2-AFC trial, subjects have to choose between two options, even if neither seems satisfactory, as accurately and as quickly as possible. For example, subjects may categorize stimuli along two categories (e.g. male or female), or choose which of two visual stimuli is brighter. Adults, and even children, may complete a high number of trials interspersed by short, mandatory breaks to prevent mental fatigue.

**Analysis of raw performance.** Data preprocessing typically involves four consecutive steps:

1. Removal of all data from invalid trials identified by very short reaction times (given the average time that is necessary for the motor response), or very long reaction times (e.g. outliers on the subject's own distribution) (Sternberg, 2011).
2. Removal of all reaction times from incorrect trials, since the goal of reaction time analysis is to track the difficulty of making a correct decision (Sternberg, 2011).
3. Optional transformation (e.g. log-transform, inverse transform or speed of response) of reaction times as a way to approach a normal distribution.
4. Optional removal of a small number of data points identified as outliers to improve model-fitting quality and robustness (Davies & Gather, 1993). While the first method of choice to address the problem of outliers should always be to reduce experimental noise i.e. prevent rather than attempt to cure (Sternberg, 2011), complete prevention of outliers is impossible especially in developmental populations.

Performance in the 2-AFC task is directly influenced by perceptual uncertainty.

**Analysis of accuracy using Signal Detection Theory.** Fechner's own model of the 2-AFC task, originally published in 1860, already comprised many elements found in modern Signal Detection Theory (Fechner, 1966; Green & Swets, 1966; Link, 1994). Drawing from Gauss's theory of measurement error, he postulated that Gaussian variability in estimating perceptual quantities caused perceptual errors. For the first time, the psychophysical task of discriminating between stimuli could be approached mathematically using Gaussian theory which until then hadn't been applied to subjective measurements (FIGURE 2.4). More specifically, Fechner postulated that the discrimination task could be understood as if participants, when comparing two perceived quantities, used the average of their true values as a decision criterion (FIGURE 2.4). Later developments of Signal Detection Theory (Green & Swets, 1966; Stanislaw & Todorov, 1999) proved that this criterion is optimal in the case where both quantities are estimated with random errors of equal variance. Fechner then proceeded to provide a method for estimating the measurement sensitivity $h$, as defined by Gauss, based solely on the accuracy of human participants' in a task where the true physical quantities are known from the experimenter (FIGURE 2.4). His method was very close to the modern definition of sensitivity as *d'* in Signal Detection Theory (Green & Swets, 1966; Stanislaw & Todorov, 1999).

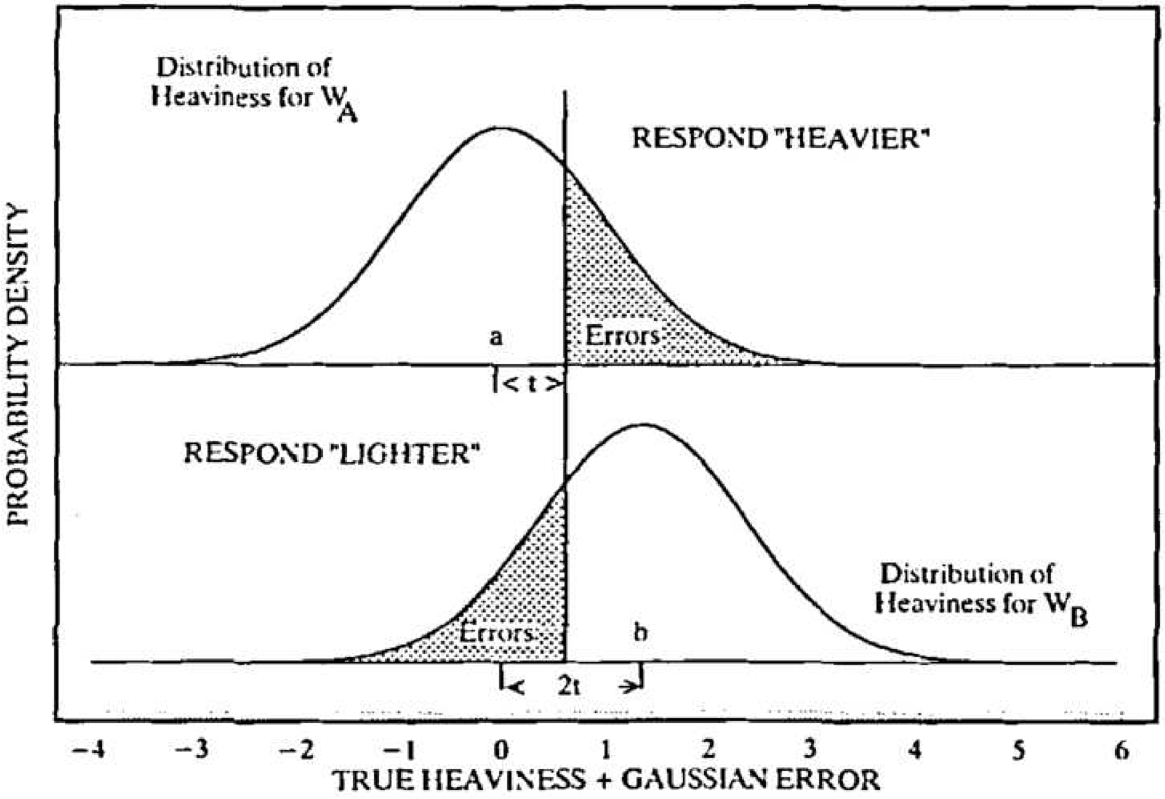


Figure 2.4: **Fechner's model of a 2-AFC task.** Participants must decide whether a stimulus $S_B$ is lighter or heavier than a stimulus $S_A$. The perceived heaviness of each ($W_A$,$W_B$) are randomly distributed around the true heaviness of each ($a$,$b$), with equal variances $\sigma^2$ for the Gaussian errors. It is hypothesized that the decision criterion (vertical line) is equal to $\frac{a+b}{2}$. Thus, if $a < b$ , errors occur when perceived heaviness crosses the criterion i.e., when $W_A < \frac{a+b}{2}$ or when $W_B > \frac{a+b}{2}$ (two gray areas, equal surface). The amount of errors thus depends only on $\sigma$ and $b - a$, two quantities of the same unknown dimension which may be combined in the dimensionless $2t = \frac{b-a}{\sqrt{2}\sigma}$ . This amounts to rescaling $b - a$ using Gauss' definition of measurement sensitivity ($h = \frac{1}{\sqrt{2}\sigma}$). If follows that $t$ may be directly estimated based on participants' accuracy, and if $b - a$ is known, the perceptual sensitivity $h$ may be deduced. Note that $d' = \frac{b-a}{\sigma} = \sqrt{2}h(b - a)$. Reprinted from Link (1994).

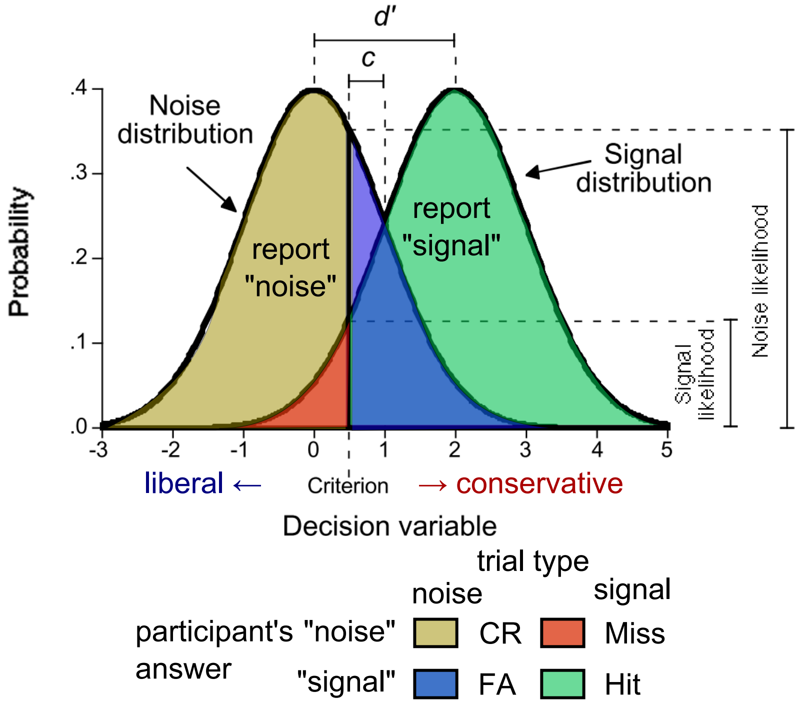


Figure 2.5: **Theoretical model of signal versus noise detection.** CR, Correct Reject, FA, False Alarm. Adapted from Stanislaw and Todorov (1999).

Today, analyses of accuracy using Signal Detection Theory are standard, and typically involve the separate derivation of sensitivity (criterion free) and response bias (criterion dependent). Signal Detection Theory stipulates that discriminating two quantities is equivalent to discriminating signal from noise based on a single measured quantity that is compared to the distribution of signal and noise. In the case were two categories are discriminated, one is arbitrarily chosen as the signal category. Different estimators for sensitivity and response-bias exist, among which *d'* and *c*, respectively, are popular choices and were used in CHAPTER 3. Both *d'* and *c* are derived experimentally by combining the Hit Rate (HR), the rate of signal trials correctly categorized as signal (“Hits” versus “Misses”), and the False Alarm Rate (FAR), the rate of noise trials falsely categorized as signal (“False Alarms” versus “Correct Rejects”) (FIGURE 2.5).

The HR and FAR are formally calculated as follows, where to the number of noise trials $n_{Noise} = n_{FA} + n_{CR}$ is the number of noise trials and $n_{Signal} = n_{Misses} + n_{Hits}$ is the number of signal trials and with $n_{Signal} > 0$, $n_{Noise} > 0$:

$$HR = \frac{n_{Hit}}{n_{Signal}} \tag{1}$$

$$FAR = \frac{n_{FalseAlarm}}{n_{Noise}} \tag{2}$$

*d'* and *c* are then derived using the standard z-score $z$ , i.e., the inverse of the cumulative distribution function (CDF) of the standard normal distribution which translates rates (probabilities) into z-scores. Because the probabilities of $0$ and $1$ are asymptotic values of the CDF, they cannot be expressed as z-scores. Thus, before computing *d'* and *c*, if $HR = 0$ it may be approached by $\frac{0.5}{n_{Signal}}$ , while if $HR = 1$ it may be approached by $HR = \frac{n_{Signal}-0.5}{n_{Signal}}$. Similarly, if $FAR = 0$ it may be approached by $\frac{0.5}{n_{Noise}}$ and if $FAR = 1$ it may be approached by $\frac{n_{Noise}-0.5}{n_{Noise}}$ (Stanislaw & Todorov, 1999). Then:

$$d' = z(HR) - z(FAR) \tag{3}$$

$$c = -\frac{z(HR) + z(FAR)}{2} \tag{4}$$

The more a subject can discriminate between signal and noise, the more his HR will be greater than his FAR (hence, a high *d'*); the more a subject is conservative (higher criterion) in reporting a signal, the more his HR and FAR will be small (hence, a high *c*).

**Modeling by the Drift-Diffusion Model.** The Drift Diffusion Model (DDM) describes how subjects may solve a 2-AFC task (P. Smith, 2000). The idea is that evidence for or against one of the possible responses is accumulated over time until a decision threshold is reached. Evidence is gathered in a stochastic manner, i.e., there is a certain amount of noise added at each step (although, on average, it will integrate to zero). Thus, noise may induce errors. If the signal is strong compared to the noise, a correct decision will be reached quickly most of the time as evidence in favor of the correct option will rapidly surpass noise. Otherwise, the error rate will increase, and correct decisions will take more time as the weak signal does not easily surpass noise. The DDM has been shown to correctly model both accuracy and reaction times, and has found some empirical support from single-electrode recordings of spiking rate (Shadlen & Newsome, 1996).

#### 2.3.2.2 The rating task

Often used in face perception research, the rating task requires participants to rate a number of faces along a subjective dimension such as attractiveness, masculinity or emotional content.

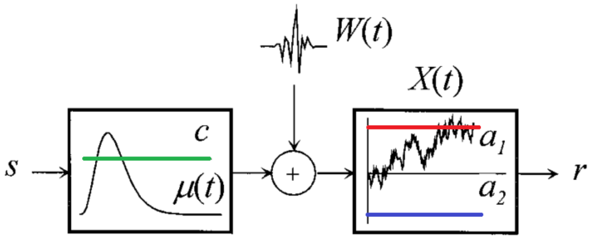


Figure 2.6: **Drift Diffusion Model.** The model is based on diffusion processes. At each time step $t$, a new piece of signed evidence $\mu(t) - c$ (positive evidence, in favor of $a_1$, when $\mu(t)$ is above $c$, green line) is drawn from the information source $s$ and perturbed by a white noise source $W(t)$. A response $r$ is made when the total evidence $X(t)$ reaches a decision threshold for either action $a_1$ (red line) or action $a_2$ (blue line). Adapted from P. Smith (2000).

The task has been used in CHAPTER 3 and 4 of the present thesis.

**General principle.** The general principle of rating tasks is extremely straightforward: participants are presented with a stimulus and a visual analog scale and are asked to rate each stimulus across a given, ordinal dimension using the scale. Most often the visual analog will be a horizontal ticked line (FIGURE 2.7), a choice warranted by the horizontal “number line” (e.g. Doricchi, Guariglia, Gasparini, & Tomaiuolo, 2005). Several non-critical parameters need to be fine-tuned for each implementation of the task:

**Stimuli presentation time.** Stimuli may stay or the screen until the participant’s response, or be displayed for a limited amount of time. Contrary to psychophysical studies, validation studies don’t usually use limited presentation times although participants’ response times may be recorded to allow the exclusion of invalid trials based on abnormal reaction times.

**Stimuli ordering.** Stimuli from different categories may be presented in blocks or random order. An important point to consider when making this choice is whether participants should compare stimuli from different categories using a similarly calibrated scale, in which case a random design may be used, or if participants should calibrate the scale for each category, in which case a blocked design might be more appropriate.

**Scale range.** Specific labels for the ordinal choices (e.g. starting from 0 or 1, centered in 0 or not) matter less than the number of available choices which will affect precision. An important point to consider is that whatever the number of available choices, participants may avoid using extreme values of the scale - reducing the actual, net range of the scale. The parity of that number does not seem to affect results significantly (Armstrong, 1987) as long

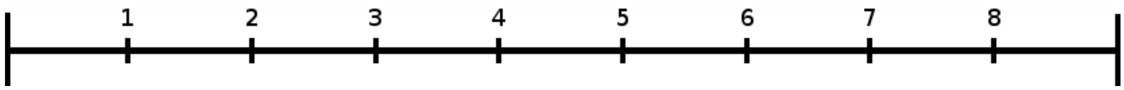


Figure 2.7: **Example rating scale.** This discrete scale ranges from 0 ("not at all") to 9 ("very") and was used in SECTION 4.3.9.1. The "neutral" position (4,5) cannot be selected by participants.

as the scale is centered (symmetric) about a "neutral" position which may or may not be an available choice to the participants. The scale may be discrete or continuous.

**The issue of choosing an appropriate scale dimension.** Scale dimension is probably the most critical parameter. Three general questions to consider when choosing a rating dimension are:

1. Is it the relevant dimension to be rated, and is it relatively insensitive to the social desirability bias (Spector, 2004)? If not, the obtained ratings may prove to be useless.
2. Is the subjective dimension readily available for the participants to report? If not, participants may resort to confabulation or respond according to another, unknown dimension (Ericsson & Simon, 1980).
3. Is the subjective dimension truly symmetric? If not, differences in rating between stimuli cannot be compared to one another. For example, summing or averaging ratings from the negative and positive branches may be absurd.

**The case of femininity and masculinity.** Femininity and masculinity ratings are a good example of the latter problem. Folk psychology may consider masculinity and femininity as a single dimension going from "very feminine" through "androgynous" through "very masculine", but numerous studies have established that femininity and masculinity do not represent two symmetric extremes of the same dimension. Rather, femininity and masculinity reflect two independent dimensions (Heilbrun, 1976) that should be rated separately. In SECTION 3.10.1 female and male faces were rated along the dimensions of femininity and masculinity, respectively, since masculinity ratings of female faces and femininity ratings of male faces were not relevant to the experiment.

**The case of emotional dimensions.** How can we ask participants to quantify the subjective emotion that is evoked by a given stimulus? Drawing on Russell's two-dimensional model of affect (FIGURE 2.8; Russell, 1980) it is now standard practice for participants to rate along the dimensions of valence or arousal (intensity) when evaluating emotional stimuli

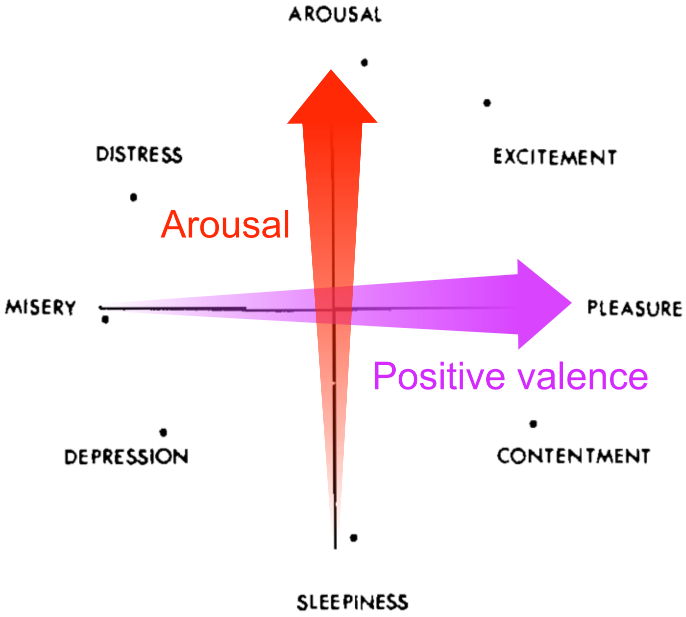


Figure 2.8: **Russell's two-dimensional model of affect.** Adapted from Russell (1980).

(Adolph & Alpers, 2010; Goeleven, De Raedt, Leyman, & Verschuere, 2008; Tottenham et al., 2009). This approach has been used in SECTION 4.3.9.1.

## Chapter 3

# ANGRY FACIAL EXPRESSIONS BIAS GENDER CATEGORIZATION IN CHILDREN AND ADULTS: BEHAVIORAL AND COMPUTATIONAL EVIDENCE

## 3.1 INTRODUCTION OF THE ARTICLE

Belief-based, stereotypical effects of emotional expressions on face race categorization are evident in adults (Amodio, 2014) and children as young as 3-4 years old (Dunham et al., 2013). Similarly, young children tend to agree with adults when inferring character from facial characteristics (Cogsdill & Banaji, 2015; Cogsdill et al., 2014). It has been suggested that stereotypes about social groups in general emerge early in ontogeny, showing a developmental invariance from childhood to adulthood (Dunham et al., 2013). The ontogeny of gender stereotypes has received relatively less attention from cognitive psychologists in recent years. Classic studies, however, point to an emergence of gender stereotype during childhood that may lead children to associate masculinity with anger and femininity with sadness, happiness or fear. For example, girls attribute less anger to themselves than boys (Brody, 1984), reflecting socialization practices (Brody, 1984); children tend to associate male protagonists with anger scenarios and female protagonists with fear scenarios (Birnbaum & Chemelski, 1984). Adults show the same kind of associations, perceiving angry faces as more masculine (Becker, Kenrick, Neuberg, Blackwell, & Smith, 2007; Hess, Adams, Kleck, & Adams Jr, 2005; Hess, Adams Jr, Grammer, & Kleck, 2009; Hess, Adams Jr, Kleck, & Adams, 2004). While children may acquire these associations through intensive experience with peers during school years, tentative evidence suggests developmental invariance (Birnbaum, Nosanchuk, & Croll, 1980).

In the present article, we explore the effect of angry expressions on face gender categorization using a two-Alternative Forced Choice paradigm with real faces of males and females

(2-AFC; FIGURE 3.1A-B; SECTION 2.3.2.1). The same task is used with 5- to 12-year-old children as well as with adults. In addition to accuracy (FIGURE 3.1A) and reaction times (FIGURE 3.1B), we use Signal Detection Theory analysis to segregate sensitivity (measured by *d'*) from response bias (measured by the *c* bias). Finally, we use other-race (Chinese) faces and computational models to explore the role of experience and stimulus-driven associations, respectively.

Box 3: Résumé de l'article : "Angry facial expressions bias gender categorization in children and adults: behavioral and computational evidence"

> Bayet L., Pascalis O., Quinn P.C., Lee K., Gentaz É., & Tanaka J. (2015) Angry facial expressions bias gender categorization in children and adults: behavioral and computational evidence. *Frontiers in Psychology* 6, 346 doi: 10.3389/fpsyg.2015.00346
>
> Les visages de colère sont perçus comme plus masculins par les adultes. Toutefois, la trajectoire développementale ainsi que le mécanisme sous-jacent à ce biais (i.e., mécanisme de bas niveau lié au stimulus ou mécanisme de haut niveau lié aux croyances) demeurent mal connus. Des analyses de détection du signal mettent en évidence l'existence de ce biais chez les enfants dès 5-6 ans, de même que la stabilité de ce biais au cours du développement jusqu'à l'âge adulte (EXPÉRIENCES 1-2, SECTIONS 3.4, 3.5). Le biais est observable pour les visages de type tant familier (visages caucasiens) que non familier (visages chinois). La stabilité et précocité développementale du biais, sa généralisation aux visages d'ethnicité non familière, suggèrent que le biais ne tire pas son origine d'une expérience sociale ou perceptive prolongée. A partir de plusieurs modèles computationnels de la catégorisation de genre (EXPERIENCE 3, SECTION 3.6), il est également montré que (1) le biais résulte, au moins partiellement, d'une stratégie d'analyse des visages accordant une attention importante à certains traits du visage ou à leurs relations de second-ordre, et que (2) mesurer la ressemblance objective de plusieurs classes de stimuli à partir d'un seul type de représentation (par exemple une Analyse en Composantes Principales) est inapproprié, car différents choix de représentations des mêmes stimuli peuvent amener à des conclusions radicalement différentes quand à l'origine du biais de perception. Ces résultats sont donc en accord avec plusieurs explications du biais liant masculinité et colère. Les effets d'interaction entre dimensions faciales façonnent les catégorisations sociales et émergent étonnament tôt dans le développement, avant même le début de la scolarisation.

## 3.2 ABSTRACT

Angry faces are perceived as more masculine by adults. However, the developmental course and underlying mechanism (bottom-up stimulus driven or top-down belief driven) associated with the angry-male bias remain unclear. Here we report that anger biases face gender categorization towards "male" responding in children as young as 5-6 years. The bias is observed for both own- and other-race faces, and is remarkably unchanged across development

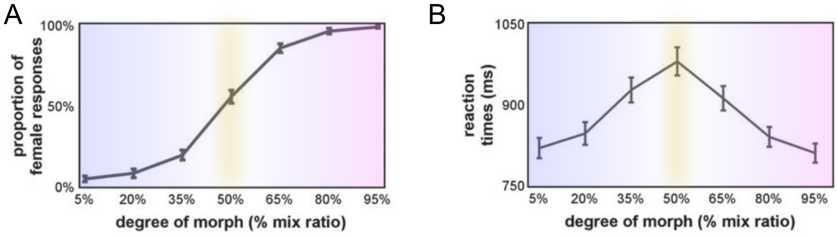


Figure 3.1: **Typical results from a 2-AFC experiment.** In this experiment, subjects categorized human voices as female or male. The voices were morphed from 0% to 100% female. **(A)** Participants' responses showed a psychophysical curve ranging from to a plateau of "male" answers (blue) to chance performance (yellow) to a plateau of "female" answers (pink). **(B)** Reaction times increased with perceptual uncertainty, with a clear peak at chance performance (yellow). Adapted from Charest et al. (2013)

(into adulthood) as revealed by signal detection analyses (Experiments 1-2, Sections 3.4, 3.5). The developmental course of the angry-male bias, along with its extension to other-race faces, combine to suggest that it is not rooted in extensive experience, e.g. observing males engaging in aggressive acts during the school years. Based on several computational simulations of gender categorization (Experiment 3, Sections 3.6), we further conclude that (1) the angry-male bias results, at least partially, from a strategy of attending to facial features or their second-order relations when categorizing face gender, and (2) any single choice of computational representation (e.g., Principal Component Analysis) is insufficient to assess resemblances between face categories, as different representations of the very same faces suggest different bases for the angry-male bias. Our findings are thus consistent with stimulus-and stereotyped-belief driven accounts of the angry-male bias. Taken together, the evidence suggests considerable stability in the interaction between some facial dimensions in social categorization that is present prior to the onset of formal schooling.

## 3.3 Introduction

Models of face perception hypothesize an early separation of variant (gaze, expression, speech) and invariant (identity, gender, and race) dimensions of faces in a stage called structural encoding (Bruce & Young, 1986; Haxby et al., 2000). Structural encoding consists of the abstraction of an expression-independent representation of faces from pictorial encodings or "snapshots". This results in the extraction of variant and invariant dimensions that are then processed in a hierarchical arrangement where invariant dimensions are of a higher order than the variant ones (Bruce & Young, 1986).

Facial dimensions, however, interact during social perception. Such interactions may have multiple origins, with some but not all requiring a certain amount of experience to develop. First, they may be entirely stimulus-driven or based on the coding of conjunctions of dimensions at the level of single neurons (Morin et al., 2014). Second, the narrowing of one dimension (Kelly et al., 2007) may affect the processing of another. For example, (O'Toole et al., 1996) found that Asian and Caucasian observers made more mistakes when categorizing the gender of other-race versus own-race faces, indicating that experience affects not only the individual recognition of faces (as in the canonical other-race effect, Malpass & Kravitz, 1969), but a larger spectrum of face processing abilities. Third, perceptual inferences based on experience may cause one dimension to cue for another as smiling does for familiarity (Baudouin, Gilibert, et al., 2000). Finally, it has been suggested that dimensions interact based on beliefs reflecting stereotypes, i.e., beliefs about the characteristics of other social groups. For example, Caucasian participants stereotypically associate anger with African ethnicity (Hehman et al., 2014). This latter, semantic kind of interaction was predicted by Bruce and Young (1986) who postulated that (1) semantic processes feedback to all stages of face perception, and (2) all invariant dimensions (such as race, gender) are extracted, i.e., "visually-derived", at this semantic level. More generally, prejudice and stereotyping may profoundly influence even basic social perception (Amodio, 2014; K. L. Johnson, Freeman, & Pauker, 2012) and form deep roots in social cognition (Contreras et al., 2012). Data on the development of these processes have reported an onset of some stereotypical beliefs during toddlerhood (Cogsdill et al., 2014; Dunham et al., 2013) and an early onset of the other-race effect in the first year of life (Kelly et al., 2009, 2007).

One observation that has been interpreted as a top-down effect of stereotyping is the perception of angry faces as more masculine (Becker et al., 2007; Hess et al., 2005, 2009, 2004), possibly reflecting gender biases that associate affiliation with femininity and dominance with masculinity (Hess, Adams Jr, & Kleck, 2007). Alternatively, cues for angry expressions and masculine gender may objectively overlap, biasing human perception at a bottom-up level. Using a forced-choice gender categorization task with signal detection analyses and emotional faces in adults (EXPERIMENT 1, SECTION 3.4) and children (EXPERIMENT 2, SECTION 3.5), and several computational models of gender categorization (EXPERIMENT 3, SECTION 3.6), we aimed to (1) replicate the effect of anger on gender categorization in adults, (2) investigate its development in children, and (3) probe possible bases for the effect by comparing human performance with that of computational models. If the bias is purely driven by top-down beliefs, then computational models would not be sensitive to it. However if the bias is driven by bottom-up stimulus-based cues, then we expect computational models to be sensitive to such objective cues. To investigate the impact of different facial dimensions on gender-categorization, both own-race and other-race faces were included as stimuli - the latter corresponding to a more difficult task condition (O'Toole et al., 1996).

## 3.4 EXPERIMENT 1: GENDER CATEGORIZATION BY ADULTS

To assess whether emotional facial expressions bias gender categorization, adults categorized the gender of 120 faces depicting unique identities that varied in race (Caucasian, Chinese), gender (male, female), and facial expression (angry, smiling, neutral). We hypothesized that the angry expression would bias gender categorization towards "male", and that this effect might be different in other-race (i.e., Chinese in the present study) faces that are more difficult to categorize by gender (O'Toole et al., 1996).

### 3.4.1 Material and methods

#### 3.4.1.1 Participants and data preprocessing

Twenty four adult participants (mean age: 20.27 years, range: 17-24 years, 4 men) from a predominantly Caucasian environment participated in the study. All gave informed consent and had normal or corrected-to-normal vision. The experiment was approved by the local ethics committee ("Comité d'éthique des centre d'investigation clinique de l'inter-région Rhône-Alpes-Auvergne", Institutional Review Board). Two participants were excluded due to extremely long reaction times (mean reaction time further than 2 standard deviations from the group mean). Trials with a reaction time below 200 ms or above 2 standard deviations from each participant's mean were excluded, resulting in the exclusion of 4.70% of the data points.

#### 3.4.1.2 Stimuli

One hundred twenty face stimuli depicting unique identities were selected from the Karolinska Directed Emotional Face database (Calvo & Lundqvist, 2008; Lundqvist, Flykt, & Öhman, 1998), the NimStim database (Tottenham, Borscheid, Ellertsen, Marcus, & Nelson, 2002; Tottenham et al., 2009), and the Chinese Affective Picture System (Lu, Hui, & Yu-Xia, 2005) database in their frontal view versions. Faces were of different races (Caucasian, Chinese), genders (female, male), and expressions (angry, neutral, smiling). Faces were gray scaled and placed against a white background; external features were cropped using GIMP. Luminance, contrast, and placement of the eyes were matched using SHINE (Willenbockel et al.,

Figure 3.2: **Example stimuli used in Experiments 1–3 (A) and in the control study (B).** The identity of the faces used in Experiments 1–3 and in the control study were identical, but in the control study all faces were in neutral expression while faces in Experiments 1–3 had either angry, smiling or neutral expressions. Sixteen of the 120 faces from Experiments 1–3 had no neutral pose in the database.

2010) and the Psychomorph software (Tiddeman, 2005, 2011). Emotion intensity and recognition accuracy were matched across races and genders and are summarized in TABLE 3.9. See FIGURE 3.2A for examples of the stimuli used. Selecting 120 emotional faces depicting unique identities for the high validity of their emotional expressions might lead to a potential selection bias, e.g., the female faces that would display anger most reliably might also be the most masculine female faces. To resolve this issue, a control study (Supplementary Material) was conducted in which gender typicality ratings were obtained for the neutral poses of the same 120 faces. See FIGURE 3.2B for examples of the stimuli used in the control study.

#### 3.4.1.3 Procedure

Participants were seated 70 cm from the screen. Stimuli were presented using E-Prime 2.0 (Schneider, Eschman, & Zuccolotto, 2002).

A trial began with a 1000 to 1500 ms fixation cross, followed by a central face subtending a visual angle of about 7 by 7 degrees. Participants completed a forced-choice gender-categorization task. They categorized each face as either male or female using different keys, and which key was associated with which gender response was counterbalanced across participants. The face remained on the screen until the participant responded. Participant response time and accuracy were recorded for each trial.

Each session began with 16 training trials with 8 female and 8 male faces randomly selected from a different set of 26 neutral frontal view faces from the Karolinska Directed Emotional Face database (Calvo & Lundqvist, 2008; Lundqvist et al., 1998). Each training trial concluded with feedback on the participant's accuracy. Participants then performed 6 blocks of 20 experimental trials, identical to training trials without feedback. Half of the blocks included Caucasian faces and half included Chinese faces. Chinese and Caucasian faces were randomly ordered across those blocks. The blocks alternated (either as Caucasian-Chinese-Caucasian... or as Chinese-Caucasian-Chinese..., counterbalanced across participants), with 5 s mandatory rest periods between blocks.

#### 3.4.1.4 Data analysis

Analyses were conducted in Matlab 7.9.0529 and R 2.15.2. Accuracy was analyzed using a binomial Generalized Linear Mixed Model (GLMM) approach (Snijders & Bosker, 1999) provided by R packages lme4 1.0.4 (Bates, Maechler, & Bolker, 2013) and afex 0.7.90 (Singmann, 2013). This approach is robust to missing (excluded) data points and is more suited to binomial data than the Analysis of Variance which assumes normality and homogeneity of the residuals. Accuracy results are presented in the Supplementary Material (FIGURE 3.6, TABLES 3.10 and 3.11). Inverted reaction times from correct trials were analyzed using a Linear Mixed Model (LMM) approach (Laird & Ware, 1982) with the R package nlme 3.1.105 (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2012). Inversion was chosen over logarithm as variance-stabilizing transformation because it led to better homogeneity of the residuals. Mean gender typicality ratings obtained in a control study (3.10 SUPPLEMENTARY MATERIAL) were included as a covariate in the analysis of both accuracy and reaction times. Finally, signal detection theory parameters (d', c-bias) were derived from the accuracies of each participant for each condition using the female faces as "signal" (Stanislaw & Todorov, 1999), and then analyzed using repeated measures ANOVAs. Because female faces were used as the "signal" category in the derivation, the conservative bias (c-bias) is equivalent to a male bias. Data and code are available online at http://dx.doi.org/10.6084/m9.figshare.1320891

### 3.4.2 Results

#### 3.4.2.1 Reaction times

A Race-by-Gender-by-Emotion three-way interaction was significant in the best LMM of adult inverse reaction times (TABLE 3.1). It stemmed from (1) a significant Race-by-Emotion effect on male ($\chi^2(2) = 6.48$, $p = 0.039$) but not female faces ($\chi^2(2) = 4.20$, $p = 0.123$), due to an effect of Emotion on Chinese male faces ($\chi^2(2) = 8.87$, $p = 0.012$) but not Caucasian male faces ($\chi^2(2) = 2.49$, $p = 0.288$); and (2) a significant Race-by-Gender effect on neutral ($\chi^2(1) = 4.24$, $p =$

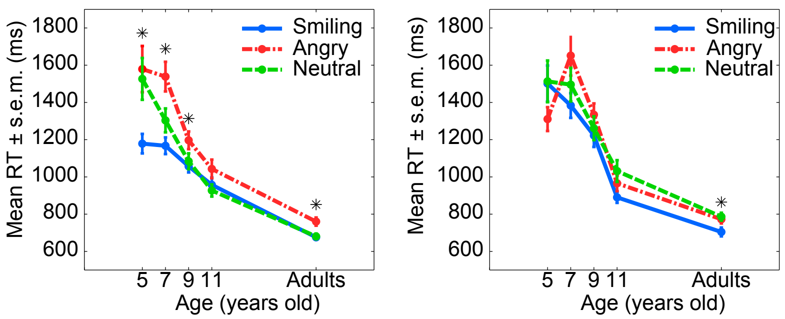
| **Fixed effects** | **d.f.** | $\chi^2$ | $p$ |
|---|---|---|---|
| (Intercept) | 1 | 334.15 | <0.001 |
| Race | 1 | 2.95 | 0.086 |
| Gender* | 1 | 6.17 | 0.013 |
| Emotion | 2 | 0.07 | 0.967 |
| Mean gender typicality rating* | 1 | 25.97 | <0.001 |
| Gender-by-Emotion* | 2 | 32.13 | <0.001 |
| Race-by-Emotion* | 2 | 6.45 | 0.040 |
| Race-by-Gender | 1 | 0.09 | 0.761 |
| Race-by-Gender-by-Emotion* | 2 | 7.56 | 0.023 |

Table 3.1: **Best LMM of adult inverse reaction time from correct trials.** The model also included a random intercept and slope for participants. Significant effects are marked by an asterisk.

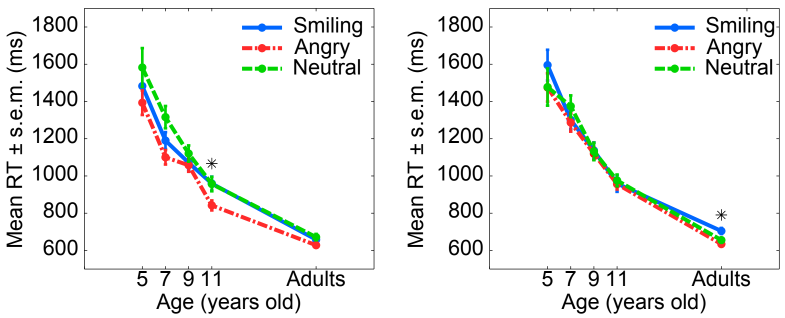
0.039) but not smiling ($\chi^2(1) = 3.31$, $p = 0.069$) or angry ($\chi^2(1) = 0.14$, $p = 0.706$) faces. The former Race-by-Emotion effect on male faces was expected and corresponds to a ceiling effect on the reaction times to Caucasian male faces. The latter Race-by-Gender effect on neutral faces was unexpected and stemmed from an effect of Race in female ($\chi^2(1) = 7.91$, $p = 0.005$) but not male neutral faces ($\chi^2(1) = 0.28$, $p = 0.600$) along with the converse effect of Gender on Chinese ($\chi^2(1) = 5.16$, $p = 0.023$) but not Caucasian neutral faces ($\chi^2(1) = 0.03$, $p = 0.872$). Indeed, reaction time for neutral female Chinese faces was relatively long, akin to that for angry female Chinese faces (FIGURE 3.3B) and unlike that for neutral female Caucasian faces (FIGURE 3.3A). Since there was no hypothesis regarding this effect, it will not be discussed further.

Importantly, the interaction of Gender and Emotion in reaction time was significant for both Caucasian ($\chi^2(2) = 18.59$, $p < 0.001$) and Chinese ($\chi^2(2) = 19.58$, $p < 0.001$) faces. However, further decomposition revealed that it had different roots in Caucasian and Chinese faces. In Caucasian faces, the interaction stemmed from an effect of Emotion on female ($\chi^2(2) = 14.14$, $p = 0.001$) but not male faces ($\chi^2(2) = 2.49$, $p = 0.288$); in Chinese faces, the opposite was true (female faces: $\chi^2(2) = 2.58$, $p = 0.276$; male faces: $\chi^2(2) = 8.87$, $p = 0.012$). Moreover, in Caucasian faces, Gender only affected reaction time to angry faces (angry: $\chi^2(1) = 11.44$, $p = 0.001$; smiling: $\chi^2(1) = 0.59$, $p = 0.442$ ; neutral: $\chi^2(1) = 0.03$, $p = 0.872$), whereas in Chinese faces, Gender affected reaction time regardless of Emotion (angry: $\chi^2(1) = 25.90$, $p < 0.001$; smiling: $\chi^2(1) = 7.46$, $p = 0.029$; neutral: $\chi^2(1) = 5.16$, $p = 0.023$).

The impairing effect of an angry expression on female face categorization was clearest on the relatively easy Caucasian faces, while a converse facilitating effect on male face cat-



(A) Female Caucasian faces (B) Female Chinese faces



(C) Male Caucasian faces (D) Male Chinese faces

Figure 3.3: **Reaction times for gender categorization in Experiments 1 (adults) and 2 (children).** Only reaction times from correct trials are included. Each star represents a significant difference between angry and smiling faces (paired Student t-tests, $p < 0.05$, uncorrected). **Top:** Caucasian (A) and Chinese (B) female faces. **Bottom:** Caucasian (C) and Chinese (D) male faces

egorization was most evident for the relatively difficult Chinese faces. The effect of Gender was largest for the difficult Chinese faces. The angry expression increased reaction times for Caucasian female faces (FIGURE 3.3A) and conversely reduced them for Chinese male faces (FIGURE 3.3D).

### 3.4.2.2 Sensitivity and male bias

A repeated measures ANOVA showed a significant Race-by-Emotion effect on both d' (TABLE 3.2) and male-bias (TABLE 3.3).

Sensitivity was greatly reduced in Chinese faces ($\eta^2 = 0.38$, i.e., a large effect), replicating the other-race effect for gender categorization (O'Toole et al., 1996). Angry expressions reduced sensitivity in Caucasian but not Chinese faces (FIGURE 3.4A-B). Male bias was high overall, also replicating the finding by (O'Toole et al., 1996). Here, in addition, we found that (1) the male bias was significantly enhanced for Chinese faces ($\eta^2 = 0.35$, another large effect), and (2) angry expressions also enhanced the male bias, as predicted, in Caucasian and Chinese faces ($\eta^2 = 0.17$, a moderate effect) - although to a lesser extent in the latter (FIGURE

| Fixed effects | SS | d.f. | MS | $F$ | $p$ | $\eta^2$ |
|---|---|---|---|---|---|---|
| Race* | 17.77 | 1 | 17.77 | 106.38 | <0.001 | 0.38 |
| Emotion* | 5.91 | 2 | 2.96 | 22.24 | <0.001 | 0.13 |
| Race-by-Emotion* | 3.56 | 2 | 1.78 | 13.84 | <0.001 | 0.08 |
| Error | 5.40 | 42 | | | | |
| Total | 47.30 | 131 | | | | |

Table 3.2: **ANOVA of d' for adult gender categorization.** The ANOVA also included a random factor for the participants, along with its interactions with both Race and Emotion. Significant effects are marked by an asterisk.

| Fixed effects | SS | d.f. | MS | $F$ | $p$ | $\eta^2$ |
|---|---|---|---|---|---|---|
| Race* | 17.16 | 1 | 17.16 | 93.03 | <0.001 | 0.35 |
| Emotion* | 8.24 | 2 | 4.12 | 40.57 | <0.001 | 0.17 |
| Race-by-Emotion* | 3.18 | 2 | 1.59 | 12.71 | <0.001 | 0.06 |
| Error | 5.26 | 42 | 0.13 | | | |
| Total | 49.55 | 131 | | | | |

Table 3.3: **ANOVA of male-bias for adult gender categorization.** The ANOVA also included a random factor for the participants, along with its interactions with both Race and Emotion. Significant effects are marked by an asterisk.

3.4C-D). Since Emotion affects the male bias but not sensitivity in Chinese faces, it follows that the effect of Emotion on the male bias is not solely mediated by its effect on sensitivity.

Further inspection of the experimental effect on the hit rate (female trials) and false alarm rate (male trials) confirmed, however, that the overall performance was at ceiling on male faces, as repeated measures ANOVAs revealed a significant interactive effect of Race and Emotion on the hit rate ($F(2,42) = 12.71$, $p < 0.001$, $\eta^2 = 0.07$) but no significant effect of Race, Emotion, or their interaction on the false alarm rate (all $p$s $> 0.05$). In other words, the effects of Race and Emotion on d' and male bias were solely driven by performance on female faces. Accuracy results are presented in the Supplementary Material (FIGURE 3.6, TABLE 3.10).

### 3.4.3 Discussion

The effect of anger on gender categorization was evident on reaction time, as participants were (1) slower when categorizing the gender of angry Caucasian female faces, (2) slower with angry Chinese female faces, and (3) quicker with angry Chinese male faces. Interestingly, the angry expression reduced sensitivity (d') of gender categorization in own-race (Caucasian), but not in other-race (Chinese) faces. In other words, angry expressions had two dissociable effects on gender categorization: (1) they increased difficulty when categorizing own-race faces, and

(2) they increased the overall bias to respond “male”.

The results are consistent with the hypothesis of a biasing effect of anger that increases the tendency to categorize faces as male. However, a ceiling effect on accuracy for male faces made it impossible to definitively support this idea. To firmly conclude in favor of a true bias, it should be observed that angry expressions both hinder female face categorization (as was observed) and enhance male face categorization (which was not observed). While a small but significant increase in accuracy for angry versus happy Chinese male faces was observed (FIGURE 3.6D), there was no significant effect on the false alarm rate (i.e., accuracy on male trials).

Different from the present results, (O'Toole et al., 1996) did not report an enhanced male bias for other-race faces (Japanese or Caucasian) faces, although they did find an effect on d' that was replicated here, along with an overall male bias. The source of the difference is uncertain, one possibility being that the greater difficulty of the task used in O'Toole et al. (a 75 ms presentation of each face followed by a mask) caused a male bias for own-race faces, or that the enhanced male bias to other-race faces found in the present study does not generalize to all types of other-race faces. Finally, (O'Toole et al., 1996) found that female participants had displayed higher accuracy on a gender categorization task than male participants. However, the sample for the current study did not include enough male participants to allow us to analyze this possible effect.

## 3.5 EXPERIMENT 2: GENDER CATEGORIZATION IN CHILDREN

One way to understand the male bias is to investigate its development. There is a general consensus that during development we are ”becoming face experts” (Carey, 1992) and the immature face processing system that is present at birth will develop with experience until early adolescence (K. Lee et al., 2013). If the angry male bias develops through extensive experience with peers observing male aggression during the school years, it follows that the angry male bias should be smaller in children than in adults and that the bias would increase during the school years, a time period when children observe classmates (mostly males) engaging in aggressive acts inclusive of fighting and bullying.

In EXPERIMENT 2, we conducted the same gender categorization task as in EXPERIMENT 1 (SECTION 3.4) with 64 children aged from 5 to 12. The inclusion of children in the age range from 5 to 6, as well the testing of 7-8, 9-10, and 11-12 year-olds, is important from a

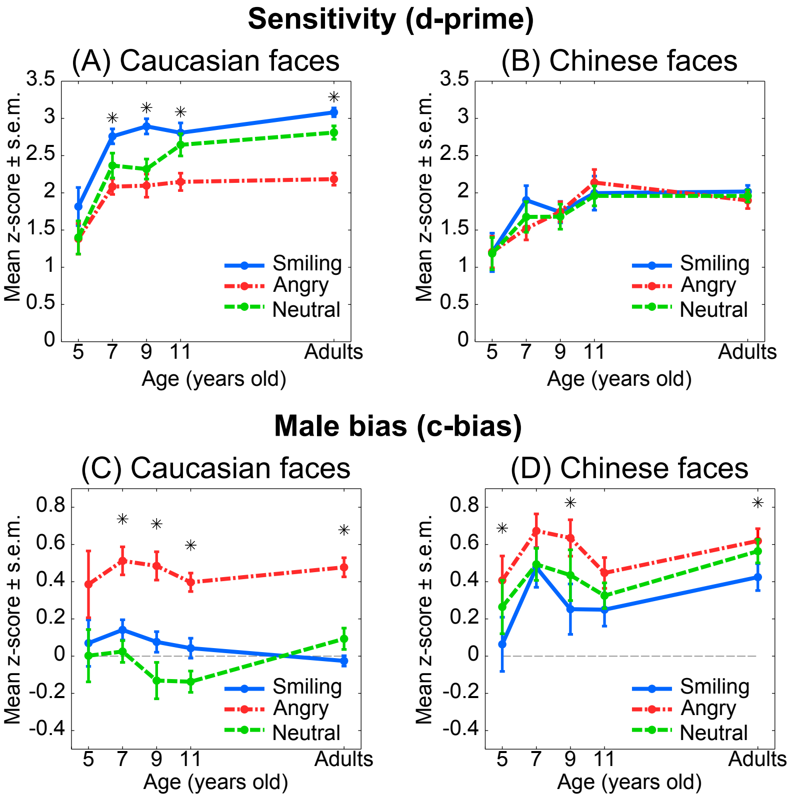


Figure 3.4: **Sensitivity and male bias for gender categorization in Experiments 1 (adults) and 2 (children).** Female faces were used as "signal" class. Each star represents a significant difference between angry and smiling faces (paired Student t-tests, $p < 0.05$, uncorrected). **Top:** Sensitivity for Caucasian (A) and Chinese (B) faces. **Bottom:** Male bias for Caucasian (C) and Chinese (D) faces.

developmental perspective. EXPERIMENT 2 should additionally allow us to (1) overcome the ceiling effect on gender categorization for male faces that was observed in EXPERIMENT 1 (SECTION 3.4) as children typically perform worse than adults in gender categorization tasks (e.g., Wild et al., 2000), and (2) determine the developmental trajectory of the biasing effect of anger in relation to increased experience with processing own-race (Caucasian) but not other-race (Chinese) faces. While facial expression perception also develops over childhood and even adolescence (Herba & Phillips, 2004), recognition performance for own-race expressions of happiness and anger have been reported to be at ceiling from 5 years of age (X. Gao & Maurer, 2010; Rodger et al., 2015).

## 3.5.1 Methods

### 3.5.1.1 Participants and preprocessing

Thirteen 5-6 year-olds (9 boys), 16 7-8 year-olds (3 boys), 15 9-10 year-olds (9 boys), and 14 11-12 year-olds (3 boys) from a predominantly Caucasian environment were included in the final sample. These age groups were chosen a priori due to the minimal need to re-design the experiment: children from 5-6 years of age may complete computer tasks and follow directions. A range of age groups was then selected from 5-6 years old onwards, covering the developmental period from middle to late childhood, and the time when children begin formal schooling. The experiment was approved by the University of Victoria Human Research Ethics Board and informed parental consent was obtained. Six additional participants were excluded due to noncompliance ($n$ = 1) or very slow reaction times for their age ($n$ = 5). Additionally, trials from participants were excluded if their reaction times were extremely short (less than 600 ms, 500 ms, 400 ms, or 300 ms for 5-6 year olds, 7-8 year olds, 9-10 year olds, or 11-12 year olds, respectively) or further than 2 standard deviations away from the participant's own distribution. Such invalid trials were handled as missing values, leading to the exclusion of 11.35% data points in the 5-6 years olds, 5.57% in the 7-8 year olds, 5.28% in the 9-10 year olds, and 4.88% in the 11-12 year olds. The cut-offs used to exclude trials with very short reaction times were selected graphically based on the distribution of reaction times within each age group.

### 3.5.1.2 Stimuli, procedure, and data analysis

Stimuli, task, procedure, and data analysis methods were identical to that of EXPERIMENT 1 (SECTION 3.4) except for the following: Participants were seated 50 centimeters from the screen so that the faces subtended a visual angle of approximately 11 by 11 degrees. Due to an imbalance in the gender ratio across age groups, the participant's gender was included as a between-subject factor in the analyses. Data and code are available online at http://dx.doi.org/10.6084/m9.figshare.1320891

## 3.5.2 Results

### 3.5.2.1 Reaction times

There was a significant Race-by-Gender-by-Emotion interaction in the best linear mixed model (LMM) of children's inverse reaction times from correct trials (TABLE 3.4), along with a three-way Age-by-Gender-by-Participant gender interaction, an Age-by-Race-by-Emotion interaction, and a Participant gender-by-Gender-by-Emotion interaction. The interaction of Age, Gender, and Participant gender was due to a significant Gender-by-Participant gender interaction in the 11-12 year olds ($\chi^2(1) = 6.19$, $p = 0.013$), with no significant sub-effects ($ps > 0.05$).

The interaction of Gender, Emotion, and Participant gender was due to the effect of Gender on angry faces reaching significance in female (female faces, inverted RT: 9.35 ± 3.67 .10-4 ms-1; male faces: 10.67 ± 3.51 .10-4 ms-1) but not male participants (female faces, inverted RT: 8.88 ± 3.24 .10-4 ms-1; male faces: 9.72 ± 3.26 .10-4 ms-1), although the effect had the same direction in both populations. Importantly, however, the overall Gender-by-Emotion interaction was significant in both male ($\chi^2(2) = 7.44$, $p = 0.024$) and female participants ($\chi^2(2) = 52.41$, $p < 0.001$). The interaction of Race and Emotion with Age reflected the shorter reaction times of 5-6 year olds when categorizing the gender of Caucasian versus Chinese smiling faces ($\chi^2(2) = 7.40$, $p = 0.007$), also evidenced by a significant Race-by-Age interaction for smiling faces only ($\chi^2(3) = 10.11$, $p = 0.018$). Faster responses to smiling Caucasian faces by the youngest participants probably reflect the familiarity, or perception of familiarity in these stimuli. Finally, the interactive effect of Gender and Emotion on reaction times was significant in Caucasian ($\chi^2(2) = 49.81$, $p < 0.001$) but not Chinese faces ($\chi^2(2) = 2.25$, $p = 0.325$) leading to a Race-by-Gender-by-Emotion interaction. Further decomposition confirmed this finding: Race significantly affected reaction times for male ($\chi^2(1) = 19.52$, $p < 0.001$) but not female angry faces ($\chi^2(1) = 1.86$, $p = 0.173$), Gender affected reaction times for Caucasian ($\chi^2(1) = 17.01$, $p < 0.001$) but not Chinese angry faces ($\chi^2(1) = 0.48$, $p = 0.489$), and Emotion significantly affected the reaction times for Caucasian female ($\chi^2(2) = 29.88$, $p < 0.001$) but not Chinese female ($\chi^2(2) = 3.82$, $p = 0.148$) or male faces ($\chi^2(2) = 5.13$, $p = 0.077$).

| **Fixed effects** | **d.f.** | $\chi^2$ | ***p*** |
|---|---|---|---|
| (Intercept) | 1 | 113.97 | <0.001 |
| Race* | 1 | 14.07 | <0.001 |
| Gender* | 1 | 4.00 | 0.046 |
| Emotion* | 2 | 7.27 | 0.026 |
| Age* | 3 | 11.18 | 0.011 |
| Participant gender | 1 | 0.16 | 0.687 |
| Mean gender typicality rating* | 1 | 75.34 | <0.001 |
| Gender-by-Emotion* | 2 | 13.32 | 0.001 |
| Race-by-Emotion* | 2 | 12.97 | 0.002 |
| Race-by-Gender | 1 | 0.38 | 0.539 |
| Age-by-Race* | 3 | 12.17 | 0.007 |
| Age-by-Gender* | 3 | 8.80 | 0.032 |
| Age-by-Emotion | 6 | 8.58 | 0.198 |
| Participant gender-by-Gender | 1 | 0.50 | 0.480 |
| Participant gender-by-Emotion | 2 | 3.45 | 0.179 |
| Participant gender-by-Age | 3 | 3.21 | 0.360 |
| Race-by-Gender-by-Emotion* | 2 | 9.89 | 0.007 |
| Age-by-Race-by-Emotion* | 6 | 18.66 | 0.005 |
| Age-by-Gender-by-Participant gender* | 3 | 9.35 | 0.025 |
| Participant gender-by-Gender-by-Emotion* | 2 | 8.16 | 0.017 |

Table 3.4: **Best LMM of children's inverted reaction times from correct trials.** The model also included a random intercept and slope for the participants. Significant effects are marked by an asterisk.

| **Fixed effects** | **SS** | **d.f.** | **MS** | ***F*** | ***p*** | $\eta^2$ |
|---|---|---|---|---|---|---|
| Race* | 28.32 | 1 | 28.32 | 80.59 | <0.001 | 0.13 |
| Emotion* | 6.14 | 2 | 3.07 | 12.65 | <0.001 | 0.03 |
| Age* | 21.04 | 3 | 7.01 | 6.40 | 0.001 | 0.09 |
| Participant gender | 4.15 | 1 | 4.15 | 3.79 | 0.057 | 0.02 |
| Race-by-Emotion* | 4.55 | 2 | 2.27 | 8.58 | <0.001 | 0.02 |
| Age-by-Race | 2.56 | 3 | 0.85 | 2.42 | 0.076 | 0.01 |
| Age-by-Emotion | 0.89 | 6 | 0.15 | 0.61 | 0.719 | <0.01 |
| Age-by-Gender-by-Emotion | 1.12 | 6 | 0.19 | 0.71 | 0.644 | 0.01 |
| Participant gender-by-Race | 0.83 | 1 | 0.83 | 2.35 | 0.131 | <0.01 |
| Participant gender-by-Emotion* | 3.99 | 2 | 1.99 | 8.21 | 0.001 | 0.02 |
| Participant gender-by-Gender-by-Emotion | 0.36 | 2 | 0.18 | 0.68 | 0.511 | <0.01 |
| Age-by-Participant gender | 3.63 | 3 | 1.21 | 1.10 | 0.356 | 0.02 |
| Error | 28.07 | 106 | 0.27 | | | |
| Total | 223.56 | 347 | | | | |

Table 3.5: **ANOVA of d' for children's gender categorization.** The ANOVA also included a random factor for the participants along with its interactions with both Race and Emotion. Significant effects are marked by an asterisk.

Children were slower when categorizing the gender of angry versus happy Caucasian female faces (FIGURE 3.3A), and slightly faster when categorizing the gender of angry versus happy Caucasian male faces (FIGURE 3.3C). The interaction of Gender and Emotion was present in all participants but most evident in female participants. It was absent in Chinese faces. In other words, an angry expression slows gender categorization in own-race (Caucasian) but not in other-race (Chinese) faces.

#### 3.5.2.2 Sensitivity and male bias

ANOVAs with participant as a random factor showed a small, but significant Race-by-Emotion interaction on sensitivity (d', TABLE 3.5, $\eta^2 = 0.02$) and male-bias (c-bias, TABLE 3.6, $\eta^2 = 0.03$). Neither for sensitivity nor for male-bias did the Race-by-Emotion interaction or its subcomponents interact with Age. Two additional effects on sensitivity (d') can be noted (TABLE 3.5). First, there was a significant effect of Age as sensitivity increased with age ($\eta^2 = 0.09$). Second, there was an interactive effect of Emotion and Participant gender that stemmed from female participants having higher sensitivity than male participants on happy ($F(1,114) = 9.14$, $p = 0.003$) and neutral ($F(1,114) = 18.39$, $p < 0.001$) but not angry faces ($F(1,114) = 0.39$, $p = 0.533$). Emotion affected the overall sensitivity of both female ($F(1,102) = 21.07$, $p < 0.001$) and male participants ($F(1,72) = 4.69$, $p = 0.014$).

| **Fixed effects** | **SS** | **d.f.** | **MS** | ***F*** | ***p*** | $\eta^2$ |
|---|---|---|---|---|---|---|
| Race* | 4.88 | 1 | 4.88 | 53.50 | <0.001 | 0.07 |
| Emotion* | 7.65 | 2 | 3.83 | 36.49 | <0.001 | 0.12 |
| Age | 0.50 | 3 | 0.17 | 0.34 | 0.797 | 0.01 |
| Participant gender | 0.49 | 1 | 0.49 | 0.99 | 0.324 | 0.01 |
| Race-by-Emotion* | 1.88 | 2 | 0.94 | 17.08 | <0.001 | 0.03 |
| Age-by-Race | 0.68 | 3 | 0.23 | 2.50 | 0.070 | 0.01 |
| Age-by-Emotion | 0.44 | 6 | 0.07 | 0.70 | 0.654 | 0.01 |
| Age-by-Gender-by-Emotion | 0.12 | 6 | 0.02 | 0.35 | 0.909 | <0.01 |
| Participant gender-by-Race | 0.03 | 1 | 0.03 | 0.31 | 0.578 | <0.01 |
| Participant gender-by-Emotion | 0.26 | 2 | 0.13 | 1.25 | 0.290 | <0.01 |
| Participant gender-by-Gender-by-Emotion | 0.27 | 2 | 0.13 | 2.42 | 0.093 | <0.01 |
| Age-by-Participant gender | 0.63 | 3 | 0.21 | 0.43 | 0.734 | 0.01 |
| Error | 5.80 | 106 | 0.06 | | | |
| Total | 66.35 | 347 | | | | |

Table 3.6: **ANOVA of male-bias for children's gender categorization.** The ANOVA also included a random factor for the participants along with its interactions with both Race and Emotion. Significant effects are marked by an asterisk.

The pattern of the interactive effect for Race and Emotion was identical to that found in adults: anger reduced children's sensitivity (d') to gender in Caucasian faces (FIGURE 3.4A), but not in the already difficult Chinese faces (FIGURE 3.4B). This pattern is remarkably similar to that found in reaction times. In contrast, anger increased the male-bias in Caucasian (FIGURE 3.4C) as well as Chinese faces (FIGURE 3.4D), although to a lesser extent in the latter category. In other words, the biasing effect of anger cannot be reduced to an effect of perceptual difficulty. Further analyses revealed that Race and Emotion affected the hit (female trials) and false alarm (male trials) rates equally, both as main and interactive effects (Race-by-Emotion effect on hit rate: $F(2,106) = 10.70$, $p < 0.001$, $\eta^2 = 0.02$; on false alarm rate: $F(2,114) = 13.48$, $p < 0.001$, $\eta^2 = 0.03$). That is, the male-biasing effect of anger is evident by its interfering effect during female trials as well as by its converse facilitating effect during male trials. Accuracy results are presented in the Supplementary Material (FIGURE 3.6, TABLE 3.11).

These last observations are compatible with the idea that angry expressions bias gender categorization. The effect can be observed across all ages and even with unfamiliar Chinese faces, although in a diminished form. The biasing effect of anger towards "male" does not seem to depend solely on experience with a particular type of face and is already present at 5 to 6 years of age.

### 3.5.3 Discussion

The results are consistent with a male-biasing effect of anger that is in evidence as early as 5-6 years of age and that is present, but less pronounced in other-race (Chinese) than in own-race (Caucasian) faces. The ceiling effect observed in EXPERIMENT 1 (SECTION 3.4) on the gender categorization of male faces (i.e. the false alarm rate) was sufficiently overcome so that the male-biasing effect of anger could be observed in male as well as female trials.

Participant gender interacted with Emotion on sensitivity and with Emotion and Gender on the reaction times of children. This finding partly replicates the finding by (O'Toole et al., 1996) that female participants present higher face gender categorization sensitivity (d') than male participants, particularly with female faces. Here, we further showed that in children, this effect is limited to neutral and happy faces, and does not generalize to angry faces.

It is perhaps surprising that anger was found to affect the male-bias on Chinese as well as Caucasian faces, but only affected sensitivity (d') and reaction times on Caucasian faces. Two dissociable and non-exclusive effects of angry expressions may explain this result. First, angry expressions may be less frequent (e.g., Malatesta & Haviland, 1982), which would generally slow down and complicate gender categorization decisions for familiar (Caucasian) but not for the already unfamiliar (Chinese) faces. This effect is not a bias and should only affect sensitivity and reaction time. Second, angry expressions may bias gender categorization towards the male response by either lowering the decision criterion for this response (e.g., as proposed by Miller, Maner, & Becker, 2010) or adding evidence for it. It naturally follows that such an effect should be evident on the male-bias (c-bias), but not on sensitivity. Should it be evident in reaction time, as we initially predicted? Even if a bias does not affect the overall rate of evidence accumulation, it should provide a small advantage on reaction time for "male" decisions, and conversely result in a small delay on reaction time for "female" decisions. While this effect would theoretically not depend on whether the face is relatively easy (own-race) or difficult (other-race) to categorize, it is possible that it would be smaller in other-race faces for two reasons: (1) the extraction of the angry expression itself might be less efficient in other-race faces, leading to a smaller male-bias; and (2) the small delaying or quickening effect of anger could be masked in the noisy and sluggish process of evidence accumulation for other-race faces.

Three possible mechanisms could explain the male-biasing effect of angry expressions: Angry faces could be categorized as "male" from the resemblance of cues for angry expressions and masculine gender, from experience-based (Bayesian-like) perceptual inferences, or from belief-based inferences (i.e., stereotype). Of interest is that the male-biasing effect of anger was fairly constant from 5 to 12 years of age. There are at least two reasons why the male-biasing effect of anger would already be present in adult form in 5 to 6 years olds: (1) the effect could develop even earlier than 5 to 6 years of age, or (2) be relatively independent of experience (age, race) and maturation (age). Unfortunately, our developmental findings neither refute nor confirm any of the potential mechanisms for a male-bias. Indeed, any kind of learning - whether belief-based or experience-based - may happen before the age of 5 years without further learning afterwards. For example, Dunham et al. (2013) evidenced racial stereotyping in children as young as 3 years of age using a race categorization task with ambiguous stimuli. Similar findings were reported on social judgments of character based on facial features (Cogsdill et al., 2014). Conversely, the resemblance of cues between male and angry faces would not necessarily predict a constant male-biasing effect of anger across all age groups: for example, the strategy used for categorizing faces based on gender may well vary with age so that the linking of cues happens at one age more than another because children use one type of cue more than another at some ages. For example, it has been established that compared to adults, children rely less on second-order relations between features for various face processing tasks, and more on individual features, external features, or irrelevant paraphernalia, with processing of external contour developing more quickly than processing of feature information (Mondloch et al., 2003, 2002). Holistic processing, however, appears adult-like from 6 years of age onwards (Carey & Diamond, 1994; Maurer et al., 2002; J. W. Tanaka et al., 1998). Therefore, each age group presents a unique set, or profile, of face processing strategies that may be more or less affected by the potential intersection of cues between male and angry faces. Whichever mechanism or mechanisms come to be embraced on the basis of subsequent investigations, what our developmental findings do indicate is that the angry-male bias is not dependent on peers observing an association between males and aggression during the school age years.

## 3.6 EXPERIMENT 3: COMPUTATIONAL MODELS OF GENDER CATEGORIZATION

To determine if the effect of anger on gender categorization could be stimulus driven, i.e., due to the resemblance of cues for angry expressions and masculine gender, machine learning algorithms were trained to categorize the gender of the faces used as stimuli in EXPERIMENTS 1-2 (SECTIONS 3.4, 3.5). If algorithms tend to categorize angry faces as being male, as humans do, then cues for anger and masculinity are conjoined in the faces themselves and

| **Representation** | **Classifier** | | **Training & test faces** | | | **Sets size ($n$)** | |
|---|---|---|---|---|---|---|---|
| | | | **Partition** | **Training set** | **Test set** | **Training** | **Test** |
| Principal component analysis | Logistic regression | A | "Familiar" | Neutral, happy Caucasian | Angry, Chinese | 40 | 80 |
| | | B | "Full set" | All faces | - | 120 | 0 |
| | | C | "Test angry" | Neutral & happy | Angry | 80 | 40 |
| Independent component analysis | Support vector machine | D | "Familiar" | Neutral, happy Caucasian | Angry, Chinese | 40 | 80 |
| | | E | "Full set" | All faces | - | 120 | 0 |
| | | F | "Test angry" | Neutral & happy | Angry | 80 | 40 |
| Sparse auto-encoder | Logistic regression | G | "Familiar" | Neutral, happy Caucasian | Angry, Chinese | 40 | 80 |
| | | H | "Full set" | All faces | - | 120 | 0 |
| | | I | "Test angry" | Neutral and happy | Angry | 80 | 40 |
| Hand-engineered features | Logistic regression | J | "Familiar" | Neutral, happy Caucasian | Angry, Chinese | 40 | 80 |
| | | K | "Full set" | All faces | - | 120 | 0 |
| | | L | "Test angry" | Neutral & happy | Angry | 80 | 40 |

Table 3.7: **Representations, classifiers, and face sets used in the computational models of gender categorization.**

there should be no need to invoke experience- or belief-based inferences to explain the human pattern of errors.

## 3.6.1 Methods

### 3.6.1.1 Stimuli

Stimuli were identical to those used in Experiments 1-2 (Sections 3.4, 3.5) .

### 3.6.1.2 Different computational models

Analyses were run in Matlab 7.9.0529. The raw stimuli were used to train different classifiers (Figure 3.5A). The stimuli were divided into a training set and a test set that were used separately to obtain different measures of gender categorization accuracy (Figure 3.5B). Several models and set partitions were implemented to explore different types of training and representations (Table 3.7; Figure 3.5A).

Different types of representations (Principal Component Analysis, Independent Components Analysis, Sparse Auto-encoder, and Hand-Engineered features; Table 3.7; Figure 3.5A) were used because each of them might make different kinds of information more accessible to the classifier; i.e., the cue-dimension relationship that drives human errors may be more easily accessible in one representation than another. Sparse auto-encoded representations are considered the most "objective" of these representations in contrast to other unsupervised representations (Principal Component Analysis, Independent Components Analysis) that use a specific, deterministic method for information compression. Conversely, hand en-

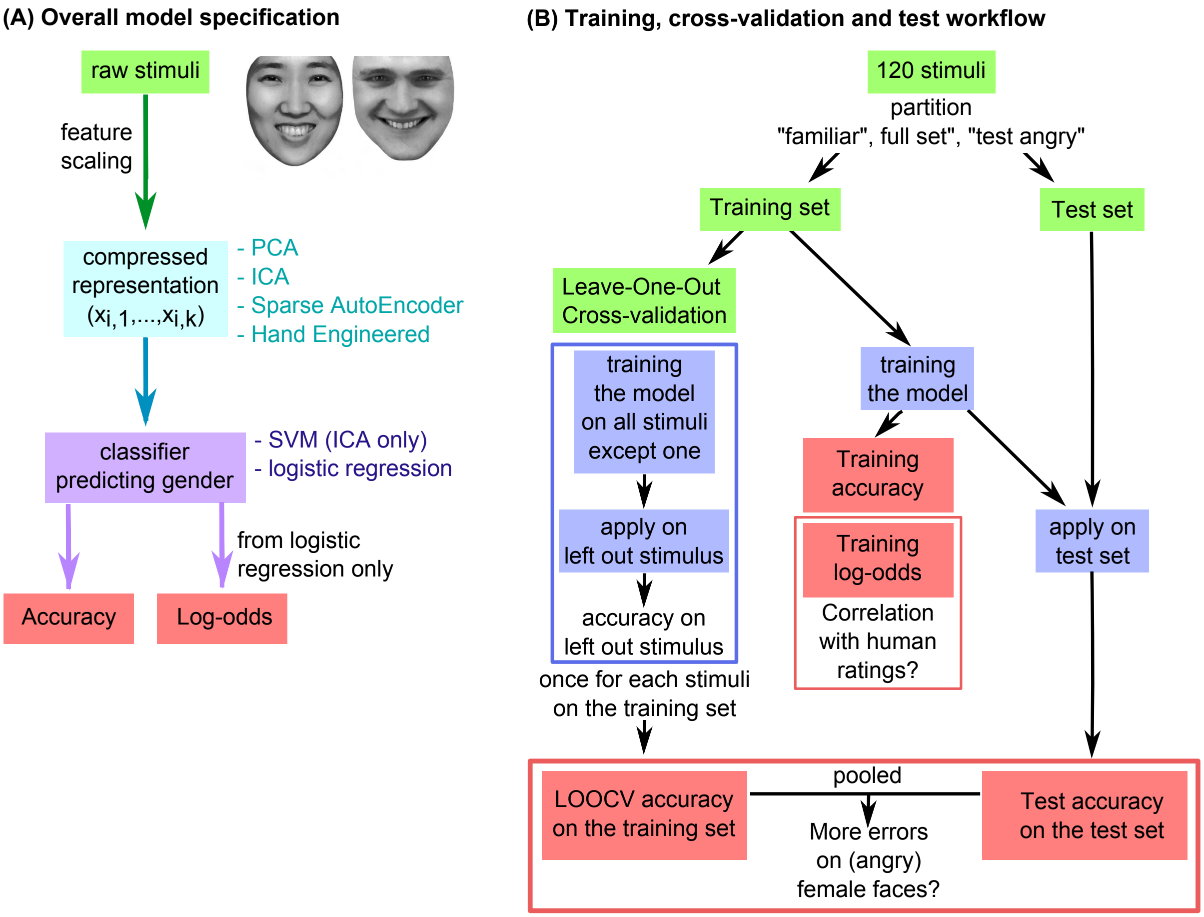


Figure 3.5: **Computational models.** **(A)** Overall model specification. Each model had an unsupervised learning step (either PCA, ICA) followed by a supervised learning step (logistic regression or SVM). **(B)** Training, cross validation and test workflow. Stimuli were partitioned into a training set and a test set. Variables used in further analysis were the Leave-One-Out Cross-validation (LOOCV) accuracy, the test accuracy, and the log-odds at training. Human ratings were obtained in the control study (Supplementary Material).

gineered features are the most "human informed" representation, since they were defined in Burton et al. (1993) using human knowledge about what facial features are (eyes, brows, mouth) and about the assumed importance of these features for gender categorization and face recognition. The choice of Principal Component Analysis as an unsupervised representation method (PCA, used in models A-C, and as a preprocessing step in models D-F) was motivated by the knowledge that PCA relates reliably to human ratings and performance (O'Toole, Deffenbacher, Valentin, & Abdi, 1994; O'Toole et al., 1998) and has been proposed as a statistical analog of the human representation of faces (Calder & Young, 2005).

All models included feature scaling of raw pixels as a first preprocessing step. Models based on Principal Component Analysis (PCA, models A-C) used the first 16 principal components for prediction (75% of variance retained). Models based on Independent Components Analysis (ICA, models D-F) used the Fast-ICA implementation for Matlab (Gävert, Hurri, Särelä, & Hyvärinen, 2005) that includes PCA and whitening as a preprocessing step. Sparse representations (models G-I) were obtained using the sparse auto-encoder neural network implemented in the NNSAE Matlab toolbox (Lemme, Reinhart, & Steil, 2012). A sparse auto-encoder (SAE) is a particular kind of neural network that aims to obtain a compressed representation of its input by trial and error. The hand-engineered (HE) features used in models J-L were the 11 full-face 2D-features and second-order relations identified in Burton et al. (1993) as conveying gender information (for example, eyebrow thickness, eyebrow to eye distance, etc.).

Most models used a logistic regression classifier because this method provides log-odds that were useful for human validation. Models D-F used the Support Vector Machine Classifier (SVM) implementation from the SVM-KM toolbox for Matlab (Gaussian kernel, h = 1000, quadratic penalization; Canu, Grandvalet, Guigue, & Rakotomamonjy, 2005) because in those models the problem was linearly separable (meaning that using logistic regression was inappropriate and would lead to poor performance). Each model was trained on a set of faces (the training set, leading to the computation of training set accuracy), and then tested on a different set of faces (the test set, resulting in computation of test accuracy). Accuracy on the training sets was further evaluated using Leave-One-Out cross-validation (LOOCV), which is thought to reflect generalization performance more accurately than training accuracy. Accuracies at test and cross-validation (LOOCV) were pooled together for comparing the performance on (angry) female versus male faces. See FIGURE 3.5B for a schematic representation of this set up.

The partitioning of faces as training and test sets differed across the models (FIGURE

3.5B). The partitioning of models A, D, G, and J ("familiar") was designed to emulate the actual visual experience of human participants in EXPERIMENTS 1-2 (SECTIONS 3.4, 3.5). The partitioning for models B, E, H, and K ("full set") was designed to emphasize all resemblances and differences between faces equally without preconception. The partitioning for models C, F, I, and L ("test angry") was designed to maximize the classification difficulty of angry faces, enhancing the chance to observe an effect.

#### 3.6.1.3 Human validation

Gender typicality ratings from a control experiment (3.10 SUPPLEMENTARY MATERIAL) were used to determine how each model accurately captured the human perception of gender: the classifier should find the most gender-typical faces easiest to classify, and vice-versa. Ratings from male and female faces from the training sets were z-scored separately, and the Pearson's correlation between those z-scored ratings and the linear log-odds output from each model at training were computed. The log-odds represent the amount of evidence that the model linearly accumulated in favor of the female response (positive log-odds) or in favor of the male response (negative log-odds). The absolute value of the log-odds was used instead of raw log-odds so that the sign of the expected correlation with gender typicality was positive for both male and female faces and one single correlation coefficient could be computed for male and female faces together. Indeed, the faces with larger absolute log-odds are those that the model could classify with more certainty as male or female: if the model adequately emulated human perception, such faces should also be found more gender typical by humans.

Data and code are available online at http://dx.doi.org/10.6084/m9.figshare.1320891

### 3.6.2 Results

Results are summarized in TABLE 3.8 below.

#### 3.6.2.1 Overall classification performance

Sparse-based models (TABLE 3.8, SAE, G-I) performed poorly (around 50% at test and cross-validation) and showed no correlation with human ratings, probably due to the difficulty of training this kind of network on relatively small training sets. Those models were therefore discarded from further discussion. PCA-based models (TABLE 3.8, PCA, A-C) on the other hand had satisfactory test (68.75-77.50%) and cross-validation (66.25-76.67%) accuracies, comparable to that of 5-6 year old children (FIGURE 3.6). ICA- and SVM- based models

| | | **Accuracy(%)** | | | **Correlation with ratings** | | **Female vs male: Angry faces** | | | **Female vs male: All faces** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **Training** | **CV** | **Test** | ***r*** | ***p*** | **$\Delta$%** | ***p*** | **$\chi^2(1)$** | **$\Delta$%** | ***p*** | **$\chi^2(1)$** |
| PCA | A | 82.50 | 72.50 | 68.75 | 0.46 | 0.003 | 45.00 | 0.001 | 10.16 | 30.00 | <0.001 | 12.9 |
| | B | 92.50 | 76.67 | - | 0.23 | 0.019 | 35.00 | 0.013 | 6.14 | 6.67 | 0.388 | 0.75 |
| | C | 81.25 | 66.25 | 77.50 | 0.11 | 0.357 | 15.00 | 0.256 | 1.29 | 6.67 | 0.426 | 0.64 |
| ICA | D | 100.00 | 85.00 | 68.75 | - | - | 50.00 | <0.001 | 10.99 | 35.00 | <0.001 | 19.18 |
| | E | 100.00 | 85.00 | - | - | - | 15.00 | 0.256 | 1.29 | 3.33 | 0.609 | 0.26 |
| | F | 100.00 | 85.00 | 72.50 | - | - | 25.00 | 0.077 | 3.14 | 5.00 | 0.487 | 0.48 |
| SAE | G | 72.50 | 50.00 | 48.75 | 0.14 | 0.379 | 10.00 | 0.519 | 0.42 | -18.33 | 0.045 | 4.03 |
| | H | 62.50 | 50.00 | - | -0.05 | 0.587 | -10.00 | 0.527 | 0.40 | -6.67 | 0.465 | 0.53 |
| | I | 61.25 | 53.75 | 50.00 | 0.06 | 0.643 | 0.00 | 1.000 | 0.00 | -1.67 | 0.855 | 0.03 |
| HE | J | 85.00 | 72.50 | 62.50 | 0.11 | 0.494 | -45.00 | 0.004 | 8.29 | -1.67 | 0.847 | 0.04 |
| | K | 81.67 | 76.67 | - | 0.25 | 0.012 | -40.00 | 0.006 | 7.62 | -3.33 | 0.666 | 0.19 |
| | L | 83.75 | 76.25 | 62.50 | 0.24 | 0.043 | -75.00 | <0.001 | 24.00 | -30.00 | <0.001 | 13.30 |

Table 3.8: **Accuracy, correlation with human ratings, and replication of experimental effects by different computational models of gender categorization.** Models used either Principal Component Analysis (PCA, models A-C), Independent Component Analysis (ICA, models D-F), features generated by a sparse auto-encoder (SAE, models G-I), or hand-engineered features (HE, models J-L). Correlations with ratings are Pearson correlation coefficients between absolute log-odds at training and z-scored gender typicality ratings from humans. Results from the sparse auto-encoder vary at each implementation as the procedure is not entirely deterministic; a single implementation is reported here.

(TABLE 3.8, ICA, D-F) performed, as expected, slightly better than models A-C at training (100%) and cross-validation (85%). However, performance at test (68.75-72.50%) was not better. Models based on hand-engineered features (TABLE 3.8, HE, J-L) had test and cross-validation performance in comparable ranges (62.50-76.67%), and their training accuracy (81.00-85.00%) was comparable to that of 85.5% reported by Burton et al. (1993) on a larger set of neutral Caucasian faces ($n$ = 179). Most notably, the latter models all included eyebrow width and eye-to-eyebrow distance as significant predictors of gender.

#### 3.6.2.2 Human validation

Classification evidence (absolute log-odds) correlated with z-scored human ratings in 2 of the 3 models from the PCA based model family (TABLE 3.8, A-B) as well as in 2 of the 3 models based on hand-engineered features (TABLE 3.8, K-L). The highest correlation (Pearson $r$ = 0.46, $p$ = 0.003) was achieved in model A that used PCA and a training set designed to emulate the content of the participants' visual experience ("familiar"). PCA-based representations might dominate when rating the gender typicality of familiar faces, while a mixture of "implicit" PCA-based and "explicit" feature-based representations might be used when rating the gender typicality of unfamiliar faces. 2.3. Replication of human errors Only one of the models

(TABLE 3.8, D) exhibited an other-race effect, and this effect was only marginal ($\Delta$ = -15.00 %, $p$ = 0.061, $\chi^2(1) = 3.52$). Two models actually exhibited a reverse other-race effect, with better classification accuracy on Chinese than Caucasian faces (model C: $\Delta$ = 16.67 %, $p$ = 0.046, $\chi^2(1) = 3.97$; model K: $\Delta$ = 16.67 %, $p$ = 0.031, $\chi^2(1) = 4.66$). Overall, the computational models failed to replicate the other-race effect for human gender categorization that was reported in EXPERIMENTS 1-2 (SECTIONS 3.4, 3.5) and in O'Toole et al. (1996).

The pattern of errors from PCA- or ICA-based models (TABLE 3.8, A-F) and feature-based models (TABLE 3.8, J-L) on female versus male faces were in opposite directions. Four out of 6 PCA- and ICA- based models made significantly (TABLE 3.8, A, B, D) or marginally more mistakes (F) on male versus female angry faces. Conversely, all 3 feature-based models (TABLE 3.8, J-L) made more mistakes on female versus male angry faces, as did humans in Experiments 1-2. Similar patterns were found when comparing classification performance on all female versus male faces, although the effect only reached significance in 2 out of 6 PCA- or ICA-based models (TABLE 3.8, A, D) and in 1 out of 3 feature-based models (TABLE 3.8, L). Hence, two different types of representations led to completely different predictions of human performance, only one of which replicated the actual data. Thus, the features of angry faces resemble that of male faces, potentially biasing gender categorization. However, this information is absent in PCA and ICA representations that actually convey the reverse bias.

Absolute log-odds obtained by the feature-based model J on familiar (neutral and happy Caucasian) faces significantly correlated with mean human (children and adults) accuracy on these faces in Experiments 1-2 (Spearman $r$ = 0.39, $p$ = 0.013), while the absolute log-odds obtained by the PCA-based model A on those same faces correlated only marginally with human accuracy (Spearman's $r$ = 0.28, $p$ = 0.077). In other words, feature-based models also better replicated the human pattern of errors in categorizing the gender of familiar faces. See TABLE 3.12 for a complete report of correlations with human accuracies for models A-C and J-L.

### 3.6.3 Discussion

Overall, the results support the idea that humans categorize the gender of faces based on facial features (and second-order relations) more than on a holistic, template-based representation captured by Principal Component Analysis (PCA). In contrast, human ratings of gender typicality tracked feature-based as well as PCA-based representations. This feature-based strategy for gender categorization leads to a confusion between the dimensions of gender and facial expression, at least when the faces are presented statically and in the absence of cues such as hairstyle, clothing, etc. In particular, angry faces tend to be mistaken for male faces (a male-biasing effect).

Several limitations should be noted, however. First, training sets were of relatively small size (40-120 faces), limiting the leeway for training more accurate models. Second, the ratings used for human validation were obtained from neutral poses (control study, 3.10 SUPPLEMENTARY MATERIAL) and not from the actual faces used in EXPERIMENT 3 (SECTION 3.6), and there were several missing values. Thus, they do not capture all the variations between stimuli used in Experiment 3. While a larger set of faces could have been manufactured for use in Experiment 3, along with obtaining their gender typicality ratings, it was considered preferable to use the very same set of faces in EXPERIMENTS 1-2 (SECTIONS 3.4, 3.5) . Indeed, it allowed a direct comparison between human and machine categorization accuracy. Finally, our analysis relied on correlations that certainly do not imply causation: for example, one could imagine that machine classification log-odds from feature-based models correlated with mean human classification accuracy not because humans actually relied on these features, but because those features are precisely tracking another component of interest in human perception – for example, perceived anger intensity. A more definitive conclusion would require a manipulation of featural cues (and second-order relations) as is usually done in studies with artificial faces (e.g., Oosterhof & Todorov, 2009). Here, we chose to use real faces: although they permit a more hypothesis-free investigation of facial representations, they do not allow for fine manipulations.

That a feature-based model successfully replicated the human pattern of errors does not imply that such errors were entirely stimulus driven. Indeed, a feature-based strategy may or may not be hypothesis-free: for example, it may directly reflect stereotypical or experiential beliefs about gender differences in facial features (e.g., that males have thicker eyebrows) so that participants would use their beliefs about what males and females look like to do the task – beliefs that are reinforced by cultural practices (e.g., eyebrow plucking in females). In fact, a feature-based strategy could be entirely explicit (Frith & Frith, 2008); anecdotally, one of the youngest child participants explicitly stated to his appointed research assistant that “the task was easy, because you just had to look at the eyebrows”. On a similar note, it would be inappropriate to conclude that angry faces “objectively” resemble male faces as representations from Principal Component Analysis may be considered more objective than feature-based representations. Rather, it is the case that a specific, feature-based representation of angry faces resembles that of male faces. This point applies to other experiments in which a conjoinment of variant or invariant facial dimensions was explored computationally using human-defined features (e.g., Zebrowitz & Fellous, 2003; Zebrowitz, Kikuchi, & Fellous, 2010, 2007). It appears then that the choice of a particular representation has profound consequences when assessing the conjoinment of facial dimensions. Restricting oneself to one particular representation of faces or facial dimensions with the goal of emulating an "objective" perception may not be realizable. Evaluating multiple potential representational models may thus be the more advisable strategy.

## 3.7 GENERAL DISCUSSION

Overall, the results established the biasing effect of anger towards male gender categorization using signal detection analyses. The effect was present in adults as well as in children as young as 5 to 6 years of age, and was also evident with other-race faces for which anger had no effect on perceptual sensitivity.

The present results (1) are in accord with those of Becker et al. (2007) who reported that adults categorized the gender of artificial male versus female faces more rapidly if they were angry, and female versus male faces if they were smiling, and (2) replicate those of Hess et al. (2009) who reported that adults took longer to categorize the gender of real angry versus smiling Caucasian female faces, but observed no such effect in Caucasian male faces. Similarly, Becker et al. (2007) found that adults were faster in detecting angry expressions on male versus female faces, and in detecting smiling expressions on female versus male faces. Conversely, Hess et al. (2004) found that expressions of anger in androgynous faces were rated as more intense when the face had a female rather than male hairline, a counter-intuitive finding that was explained as manifesting a violation of expectancy. Here, we complement the prior findings taken together by providing evidence for a male-biasing effect of anger using signal detection analyses, real faces, and a relatively high number of different stimuli.

We did not observe an opposing facilitation of gender categorization of female smiling faces, as could be expected from the results of Becker et al. (2007) and Hess et al. (2009), probably because in the present study, facial contours were partially affected by cropping. Furthermore, our results differ from those of Le Gal and Bruce (2002) who reported no effect of expression (anger, surprise) on gender categorization in 24 young adults, a null finding that was replicated by Karnadewi and Lipp (2011). The difference may originate from differences in experimental procedure or data analysis; both prior studies used a Gardner paradigm with a relatively low number of individual Caucasian models (10 and 8, respectively) and analyzed reaction times only, while reporting very high levels of accuracy suggestive of a ceiling effect (in fact, 22 participants from Le Gal and Bruce (2002) that had less than 50% accuracy in some conditions were excluded; not doing so would have violated assumptions for the ANOVAs on correct reaction times).

The findings yield important new information regarding the development of the angry-male bias. In particular, the male-biasing effect of anger was fairly constant from 5-6 years of age to young adulthood; the extensive social observation gained during schooling does not seem to impact the bias. This result is in accord with recent reports by Banaji and colleagues (Cogsdill et al., 2014; Dunham et al., 2013) showing that even belief-based interactions in the categorization of faces appear in their adult form much earlier than expected and do not appear to require extensive social experience. For example, Caucasian children as young as 3 years of age (the youngest age studied) were as biased as adults in categorizing racially ambiguous angry faces as Black rather than Caucasian (Dunham et al., 2013), an implicit association usually understood to reflect stereotyping (Hehman et al., 2014). Similarly, children aged from 3 to 5 stereotypically associated maleness with anger in cartoon faces (Birnbaum et al., 1980). Such biases may begin to develop in early infancy, a developmental period characterized by the emergence of gendered face representations rooted in visual experience (Quinn et al., 2002). Indeed, studies of racial prejudice have demonstrated a link between the other-race effect, a perceptual effect developing in infancy, and belief-based racial biases that are apparent from early childhood through adulthood such as associating other-race African faces with the angry expression (W. S. Xiao et al., 2015). It is possible that similar trajectories from perceptual to social representations may be found for gender. For example, a recent, unpublished study found that 3.5-month-old infants preferred a smiling to a neutral female expression, but preferred a neutral to a smiling male expression (Bayet et al., manuscript under review), suggesting an early association between female faces and positive emotions that results from differential perceptual or social experience with female caregivers. Such an early association could be a precursor to the increased performance of 5-6 year old children on smiling female faces that was observed in EXPERIMENT 2 (SECTION 3.5). Future studies on the developmental origins of stereotypes should focus on (1) finding precursors of stereotypes in infancy, and (2) bridging the gap between infancy and early childhood, thus providing a basis for early intervention that could curtail formation of socially harmful stereotypes.

Here, the male-biasing effect of anger appeared to be at least partially mediated by featural (e.g., brow thickness) and second-order (e.g., brow to eye distance) cues. While children have been reported to be less sensitive than adults to second-order relationships in some studies (e.g., Mondloch et al., 2002) and are less accurate in identifying facial emotional expressions (Chronaki et al., 2015), their encoding of featural information appears already mature at 6 years of age (Maurer et al., 2002) and they can recognize angry and smiling expressions most easily (Chronaki et al., 2015). Thus, the stability of the male-biasing effect of anger does not contradict current knowledge about children's face processing skills.

As discussed above, neither our behavioral nor our computational findings allowed us to embrace a particular mechanism for the male-biasing effect of anger, i.e., whether it was stimulus driven (an inherent conjoinment of dimensions) or stemmed from belief-based inferences. The findings are, however, relevant to the ongoing debate about the nature of face representations in the human brain. As stated by Marr (1982), any type of representation makes some kind of information evident while obscuring other kinds of information, so that studying the nature and origin of representational processes is at the heart of explaining low, middle, and high level vision. Various types of face representations have been proposed. For example, an important study in rhesus macaques found face-specific middle temporal neurons to be tuned to particular features or their combination while being affected by inversion (Freiwald et al., 2009). Other studies in humans have (1) emphasized the role of 2-D and 3-D second order relations in addition to features (Burton et al., 1993), and (2) argued for a double dissociation of featural and configural encoding (Renzi et al., 2013). An opposing line of argument has been advanced for a role of unsupervised representation analogs to Principal Component Analysis (Calder & Young, 2005) or Principal Component Analysis combined with multi-dimensional scaling (X. Gao & Wilson, 2013) or Gabor filters (Kaminski et al., 2011). All of those potential representations are fully compatible with the general idea of a face space (Valentine, 2001) since the face space may, in theory, present with any particular set of dimensions. Here, we provide additional evidence supporting the importance of features and second-order relations in the human processing of faces, and argue for the need to systematically consider various representational models of face processing when determining whether performance is stimulus driven, and to evaluate their respective contributions in perception depending on task, species, and developmental stage.

In conclusion, the present results indicate that the angry-male bias, whether stimulus- or belief- driven, does not require extensive social interaction with school-age peers to develop. It is in evidence as early as 5 years of age, and appears remarkably unaffected by experience during the primary grade levels, a developmental period that presumably includes observation of males engaging in aggressive acts.

## 3.8 AUTHOR CONTRIBUTIONS

Study design was performed by LB, KL, OP, PCQ and JT. Data acquisition was conducted by LB, OP and JT. Data analysis was performed by LB. All authors contributed to data interpretation, approved the final version of the article, revised it critically for intellectual content, and agree to be accountable for all aspects of the work.

## 3.9 ACKNOWLEDGMENTS

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## 3.10 SUPPLEMENTARY MATERIAL

### 3.10.1 Control study

#### 3.10.1.1 Material and methods

**Participants and data preprocessing.** Twenty four adult participants (mean age: 19.65 years, range: 16-24 years, 3 men) from a predominantly Caucasian environment participated in the control study. None had participated in EXPERIMENT 1 (SECTION 3.4). All gave informed consent and had normal or corrected to normal vision. The experiment was approved by the local ethics committee ("Comité d'éthique des centre d'investigation clinique de l'inter-région Rhône-Alpes-Auvergne", Institutional Review Board). One participant was excluded due to extremely long reaction times. Trials with a reaction time below 200 ms or above 2 standard deviations from each participant's mean were excluded, resulting in the exclusion of 4.68% data points.

**Stimuli.** One hundred four face stimuli of unique identities were selected from the Karolinska Directed Emotional Face database (Calvo & Lundqvist, 2008; Lundqvist et al., 1998), the NimStim database (Tottenham et al., 2002, 2009) and the Chinese Affective Picture System (Lu et al., 2005) database under their neutral frontal view versions. Faces were of different races (Caucasian, Chinese) and genders (female, male). The 104 faces (60 Caucasian, 44 Chinese) had the same identities as the faces used in EXPERIMENTS 1-3 (SECTIONS 3.4, 3.5, 3.6), but were in neutral expression. A remaining 16 of the 120 faces used in EXPERIMENTS 1-3 (SECTIONS 3.4, 3.5, 3.6) had no neutral expression available in the databases. Luminance, contrast, and eye position were matched as in EXPERIMENTS 1-3 (SECTIONS 3.4, 3.5, 3.6). See FIGURE 3.2B for examples of the stimuli used.

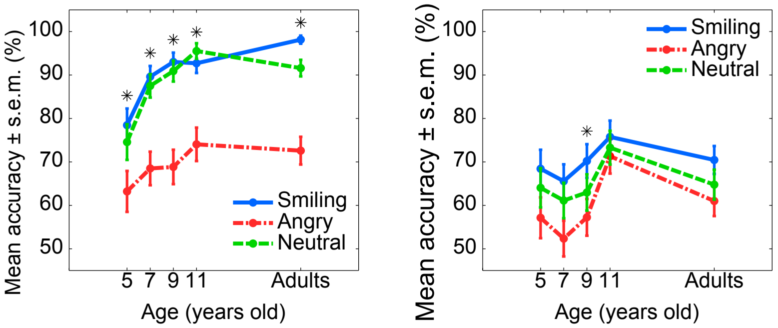
**Procedure.** The general procedure was similar to that of EXPERIMENT 1 (SECTION 3.4), but the participants had to use the mouse to rate the gender typicality of each face on a scale underneath the face going from 0 (not very masculine or feminine) to 10 (very masculine or feminine). The face and scale remained on the screen until the participant responded. Each participant's rating and response time were recorded. Each session began with 4 training trials that were identical to the experimental trials except that the faces were 2 females and 2 males randomly selected from the same set of 26 training faces used in EXPERIMENTS 1-2 (SECTIONS 3.4, 3.5). Each trial terminated with feedback to the participant showing which rating had been selected. Participants then performed 8 blocks of experimental trials. Half of the blocks included Caucasian faces (15 trials per block) and the other half included Chinese faces (11 trials per block). Blocks and trials were ordered as in EXPERIMENTS 1-2 (SECTIONS 3.4, 3.5).

**Data analysis.** Analyses were conducted in Matlab 7.9.0529. Data and code are available online at http://dx.doi.org/10.6084/m9.figshare.1320891

#### 3.10.1.2 Results and discussion

Mean ratings for each stimulus category are presented in TABLE 3.9 along with the emotional properties of the stimuli used in EXPERIMENTS 1-3 (SECTIONS 3.4, 3.5, 3.6). Overall, female faces were judged to be less gender typical than male faces. The mean ratings of each face were used as a control covariate in EXPERIMENTS 1-2 (SECTIONS 3.4, 3.5), and provided a human validation for the models in EXPERIMENT 3 (SECTION 3.6).

The gender typicality ratings of neutral poses obtained in this experiment effectively control for differences in perceived gender typicality for the stimuli used in EXPERIMENT 1-3 (SECTIONS 3.4, 3.5, 3.6). The effects of each stimulus category (Race, Gender, Emotion) in EXPERIMENTS 1-2 (SECTIONS 3.4, 3.5) cannot be attributed to the perceived gender typicality of the models. It should be noted, still, that since the ratings were obtained predominantly from young female adults they may not accurately capture the gender typicality of the faces as perceived by children or by the general population.


(A) Female Caucasian faces (B) Female Chinese faces

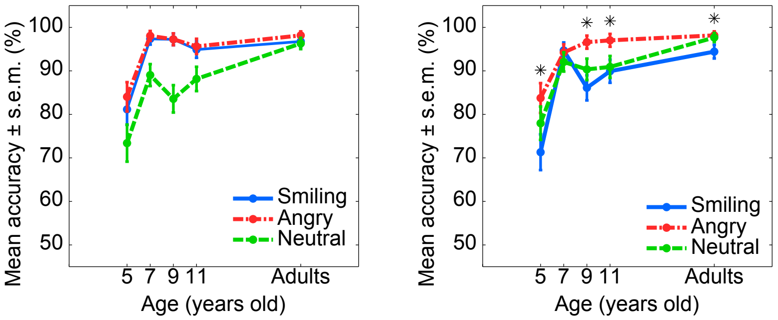

(C) Male Caucasian faces (D) Male Chinese faces

Figure 3.6: **Gender categorization accuracy in Experiments 1 (adults) and 2 (children).** Each star represents a significant difference between angry and smiling faces (paired Student t-tests, $p < 0.05$, uncorrected).

### 3.10.2 Supplementary Tables and Figures

## 3.11 SUMMARY

Here we reported the developmental invariance, from 5-6 years of age onwards, of an "angry male bias" where angry faces tended to be categorized as male. The effect was found for own-race (Caucasian) as well as other-race (Chinese) faces, and computational models suggest that it may at least partially be mediated by a strategy of attending to specific features (e.g. brow) or second-order relations (e.g., eye-to-brow distance). Because some but not all computational models replicated the human pattern of error, the findings neither refute nor confirm stimulus-driven and belief-based accounts of the effect. It is clear, however, that the angry male bias presents an early ontogeny and developmental invariance highly reminiscent of other implicit racial or social biases (Cogsdill et al., 2014; Dunham et al., 2013); social biases in face perception may emerge as early as infancy.

| | | **Chinese faces** | | | | **Caucasian faces** | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | ***n*** | **Hit rate (%)** | **Intensity (1-9)** | **Rating (0-10)** | ***n*** | **Hit rate (%)** | **Intensity (1-9)** | **Rating (0-10)** |
| Angry | Male | 10 | 88.4 ± 5.4 | 6.6 ± 0.5 | 5.8 ± 1.4 | 10 | 93.1 ± 9.5 | 6.6 ± 0.8 | 6.3 ± 1.4 |
| | Female | 10 | 87.4 ± 7.8 | 6.5 ± 0.6 | 4.0 ± 1.3 | 10 | 92.3 ± 8.4 | 6.2 ± 0.6 | 4.8 ± 1.5 |
| Smiling | Male | 10 | 99.4 ± 0.9 | 6.8 ± 0.4 | 6.9 ± 0.7 | 10 | 99.4 ± 0.8 | 6.8 ± 0.4 | 6.2 ± 1.4 |
| | Female | 10 | 99.1 ± 0.6 | 6.8 ± 0.4 | 5.0 ± 1.7 | 10 | 98.8 ± 1.6 | 6.8 ± 0.3 | 5.4 ± 1.6 |
| Neutral | Male | 10 | 88.7 ± 5.1 | 5.5 ± 0.2 | 6.3 ± 1.2 | 10 | 88.0 ± 3.8 | 5.3 ± 0.6 | 5.9 ± 1.0 |
| | Female | 10 | 89.2 ± 6.9 | 5.6 ± 0.1 | 3.2 ± 1.5 | 10 | 88.9 ± 4.6 | 5.3 ± 0.2 | 5.2 ± 1.3 |
| Overall | | 60 | 92.0 ± 7.2 | 6.3 ± 0.7 | 5.1 ± 1.9 | 60 | 93.4 ± 7.1 | 6.2 ± 0.8 | 5.6 ± 1.4 |

Table 3.9: **Mean emotional expression's hit rate, emotional expression's intensity, and gender typicality ratings of neutral poses for the stimuli used in Experiments 1-3.** Hit rates and intensity ratings were obtained from the CFAPS documentation (unpublished data), the NimStim documentation (Tottenham et al., 2009) and a KDEF validation study (**?**). Emotion hit rates and intensities were used to match the stimuli across races and genders. Gender typicality ratings were obtained in a control study (3.10 Supplementary Material) and used a control covariate in Experiments 1-2 (3.4, 3.5) and as a validation tool in Experiment 3 (3.6).

| **Fixed effects** | **d.f.** | $\chi^2$ | ***p*** |
|---|---|---|---|
| (Intercept) | 1 | 33.56 | <0.001 |
| Race* | 1 | 11.85 | 0.001 |
| Gender* | 1 | 3.95 | 0.020 |
| Emotion | 2 | 0.41 | 0.390 |
| Mean gender typicality rating* | 1 | 94.63 | <0.001 |
| Gender-by-Emotion* | 2 | 30.55 | <0.001 |
| Race-by-Emotion* | 2 | 29.86 | <0.001 |

Table 3.10: **Best binomial GLMM of adult gender categorization accuracy.** The model also included a random intercept and slope for participants. Significant effects are marked by an asterisk.

| **Fixed effects** | **d.f.** | $\chi^2$ | $p$ |
|---|---|---|---|
| (Intercept) | 1 | 37.9 | <0.001 |
| Race* | 1 | 21.05 | <0.001 |
| Gender* | 1 | 6.34 | 0.010 |
| Emotion | 2 | 2.81 | 0.250 |
| Age* | 3 | 14.87 | 0.002 |
| Mean gender typicality rating* | 1 | 160.35 | <0.001 |
| Gender-by-Emotion* | 2 | 88.14 | <0.001 |
| Race-by-Emotion* | 2 | 44.17 | <0.001 |
| Race-by-Gender | 1 | 0.72 | 0.390 |
| Age-by-Race* | 3 | 8.60 | 0.040 |
| Age-by-Gender* | 3 | 8.85 | 0.030 |
| Age-by-Emotion | 6 | 8.45 | 0.210 |
| Race-by-Gender-by-Emotion* | 2 | 10.22 | 0.006 |
| Age-by-Gender-by-Emotion* | 6 | 14.26 | 0.030 |

Table 3.11: **Best binomial GLMM of children's gender categorization accuracy.** The model also included a random intercept and slope for the participants. Significant effects are marked by an asterisk.

| **Representation** | **Partition** | **Model** | **Correlation with human accuracy** | |
|---|---|---|---|---|
| | | | $r$ | $p$ |
| Principal component analysis | "Familiar" | A | 0.28 | 0.077 |
| | "Full set" | B | 0.11 | 0.256 |
| | "Test angry" | C | 0.04 | 0.704 |
| Hand-engineered features | "Familiar" | J | 0.39 | 0.013 |
| | "Full set" | K | 0.25 | 0.007 |
| | "Test angry" | L | 0.16 | 0.158 |

Table 3.12: **Correlation of human (adults and children) gender categorization accuracy and the absolute log-odds obtained at training by selected computational models of gender categorization.** Correlations are Spearman correlation coefficients between absolute log-odds obtained by the model at training and mean human (children and adults) accuracy on the same faces. Log-odds from models that used principal components (PCA, models A-C) correlated less with human accuracy than those from models that used hand-engineered features (HE, models J-L).

## Chapter 4

# SMILE PERCEPTION IN EARLY INFANCY

## 4.1 FACE GENDER INFLUENCES THE LOOKING PREFERENCE FOR SMILING EXPRESSIONS IN 3.5-MONTH-OLD HUMAN INFANTS

### 4.1.1 Introduction of the article

In the previous set of studies we reported evidence of an early ontogeny of the association between angry facial expressions and the male gender, as measured by an increased bias for the "male" response for angry faces in a face gender categorization task. While neither belief-based nor perceptual-based accounts of the effect could be ruled out, studies of racial biases point to a possible developmental trajectory going from perceptual biases in infant's face perception to implicit, social biases in early childhood (W. S. Xiao et al., 2015). May similar mechanisms apply to gender categorization, that is, do infants perceive gender differently depending on facial expressions and vice-versa? Most infants routinely experience more female than male faces as females tend to take on caregiver roles (e.g. Sugden et al., 2014); face gender is salient dimension of their experience that may potentially affect how they perceive emotional expressions.

In this article, we apply these questions to the phenomenon of smiling preference that is sometimes reported in 3-4 month-old infants (La Barbera et al., 1976). The phenomenon remains poorly understood, with some authors suggesting a mere attraction to the salience of the teeth (Oster, 1981). We demonstrate that face gender modulates 3.5-month-old infant's visual preference for a smiling (versus neutral) expression, an effect that cannot be explained by differences in teeth salience. These results (1) demonstrate that the visual preference for smile in young infants is less rigid or universal than previously thought; (2) point to a role of experience in the perception of facial expressions of emotions in infancy, even before the onset of robust facial emotion categorization at 6-7 months (Leppänen & Nelson, 2009); and (3) tentatively suggest a perceptual-to-social trajectory for gender stereotypes that parallels that of racial stereotypes (W. S. Xiao et al., 2015). The reciprocal experiment (i.e. testing for an effect of facial expression on the female versus male preference in young infants) wasn't carried out as it was hypothesized that the female face preference might be too strong to overcome; the original study reporting a preference for female faces used both neutral and smiling faces and found no such effect (Quinn et al., 2002).

Box 4: Résumé de l'article : "Face gender influences the looking preference for smiling expressions in 3.5-month-old human infants"

> Bayet L., Quinn P. C., Tanaka J. W., Lee K., Gentaz É., & Pascalis O. (2015) Face gender influences the looking preference for smiling expressions in 3.5-month-old human infants. *PLoS ONE* 10(6): e0129812 doi: 10.1371/journal.pone.0129812
>
> Il est souvent supposé, et parfois rapporté, que les nourrissons de moins de 5-7 mois préfèrent regarder les visages souriants. Le mécanisme sous-jacent demeure pourtant mal connu. Plusieurs auteurs suggèrent le rôle causal d'un mécanisme automatique et universel, reposant sur l'imitation, ou la simple saillance physique des dents rendues visibles dans le sourire. Nous faisons en revanche l'hypothèse que cette préférence des jeunes nourrissons pour le sourire n'est pas rigide et pourrait varier selon les autres dimensions du visage, notamment son genre. En effet, les nourrissons montrent très jeune une sensibilité au genre des visages. Par exemple, les nourrissons de 3 mois élevés principalement par des femmes montrent typiquement une préférence visuelle pour les visages féminins plutôt que masculins. Nous avons présenté à des nourrissons de 3.5 mois ($n$ = 25) des paires de visages féminins ou masculins montrant le même individu souriant ou neutre, en contrôlant plusieurs indices de bas niveau (luminance globale, contraste global, fréquences spatiales). Les nourrissons ont regardé plus longtemps le visage souriant lorsque les visages appariés étaient féminins, et plus longtemps le visage neutre lorsque les visages appariés étaient masculins. En d'autres termes, le genre du visage influence la préférence pour le sourire à 3.5 mois. Ce résultat indique que la préférence pour le sourire à 3.5 mois est limitée aux visages féminins, reflétant probablement les différences d'expérience sociale et perceptive des nourrissons avec les visages féminins ou masculins.

### 4.1.2 Abstract

Young infants are typically thought to prefer looking at smiling expressions. Although some accounts suggest that the preference is automatic and universal, we hypothesized that it is not rigid and may be influenced by other face dimensions, most notably the face's gender. Infants are sensitive to the gender of faces; for example, 3-month-olds raised by female caregivers typically prefer female over male faces. We presented neutral versus smiling pairs of faces from the same female or male individuals to 3.5-month-old infants ($n$ = 25), controlling for low-level cues. Infants looked longer to the smiling face when faces were female but longer to the neutral face when faces were male, i.e., there was an effect of face gender on the looking preference for smiling. The results indicate that a preference for smiling in 3.5-month-olds is limited to female faces, possibly reflective of differential experience with male and female

faces.

### 4.1.3 Introduction

Faces are complex hierarchical stimuli displaying much information at once. The original Bruce and Young model (Bruce & Young, 1986) postulates that variant (expression, gaze, speech movements) and invariant (identity, race, gender) dimensions are separated during the structural encoding stage of face perception; an early-stage pictorial code (or snapshot) converts into a set of expression-independent representations for each view, simultaneously resulting in the extraction of variant features that are independently streamlined to process speech movements and facial expressions. Invariant dimensions then arise at the semantic level from an integration of expression-independent representations, view-centered representations of particular features, and other inputs. A recent adaptation of this model proposed by Haxby, Hoffman, and Gobbini (2000) suggests a more symmetrical division between variant and invariant aspects of faces, with possible interactions between both streams at the perceptual level. Indeed, in human adults there is evidence that variant and invariant face dimensions interact relatively early, even in subcortical structures (Dumas et al., 2013). For example, facial expressions can influence face recognition in adults, with a smile acting like a cue to familiarity (Baudouin, Gilibert, et al., 2000).

One example of variant facial dimension perception in infancy is the preference for smiling faces that is sometimes reported in infants younger than 5 months; newborns look longer at smiling over fearful faces (Farroni et al., 2007) and 4-month-olds prefer smiles to other facial expressions (La Barbera et al., 1976). This early preference for smiling faces is not stable during development (older infants look longer to fearful faces instead, Ludemann & Nelson, 1988), and its cause remains unclear as sensitivity to other types of emotional expressions (e.g., fear) doesn't emerge until later around 5-7 months of age (Leppänen & Nelson, 2009). Young infants may prefer the salience of teeth (Oster, 1981), perceive smiles as positive because they mirror them via affect matching (Gallese et al., 2004; Meltzoff & Moore, 1977, 1983), or are equipped with a basic universal module for emotion recognition (Ekman & Oster, 1979; Ekman et al., 1969). It is also possible that infants prefer the expression most familiar to them, given that caregivers tend to display faces depicting positive affect (Malatesta & Haviland, 1982). Similarly, infants may come to prefer smiling faces because they tend to signal the onset of positive interactions with caregivers which are inherently rewarding (i.e., classical conditioning). Strikingly, it has been reported that 3-month-old infants recognize a face better when the face is smiling dynamically during familiarization (Brenna et al., 2012;

Turati et al., 2011), suggesting a possible influence of expression on identity perception.

We posited that the perception of smiling by young infants is integrated into the face perception system, so that it may be influenced by other facial dimensions, and particularly by the dimension of gender. Face gender is a salient dimension in infancy, as gender differences in nonverbal communication and caretaking (Halberstadt, Hayes, & Pike, 1988; Quinn et al., 2002) cause systematic differences in the relative familiarity of infants with male and female faces. Most infants are indeed primarily raised by a female caregiver and experience fewer male than female faces during their first year (Rennels & Davis, 2008; Sugden et al., 2014). Infants may thus react differently to male and female smiles. For example, if infants prefer smiling faces because caregivers tend to display faces depicting positive affect (Malatesta & Haviland, 1982), and if most infants are raised by female caregivers (Rennels & Davis, 2008; Sugden et al., 2014), it follows that infants may prefer female smiles more than male smiles.

Our study aimed to test the effect of face gender on the looking preference of infants for smiling expressions. We presented male and female smiling faces paired with neutral faces of the same individual to 3.5-month-old infants (FIGURE 4.1, $n$ = 25), an age at which a preference for smiling has been reported (La Barbera et al., 1976). Low-level properties of the faces were equated, two different stimulus sets were used (TABLE 4.1), and looking preferences were measured. Some accounts of the preference for smiling faces in young infants based on salience (Oster, 1981), mimicking (Gallese et al., 2004; Meltzoff & Moore, 1977, 1983), or a module for emotion recognition (Ekman & Oster, 1979; Ekman et al., 1969) would predict that face gender is irrelevant to eliciting preferential responding to smiling faces, and that infants should prefer both male and female smiles. However, given that the parental distribution of caregiving has been found to modulate the reaction of 14-month-olds to emotional expressions displayed by their mother and father (Gredebäck, Eriksson, Schmitow, Laeng, & Stenberg, 2012), and given the increased familiarity of infants with female faces, it is also possible that the preference for smiling facial expressions would be greater, or at least more robust, in female faces than in male faces.

### 4.1.4 Methods

#### 4.1.4.1 Partitipants

Twenty-five 3.5-month-old infants (13 girls, mean age 115.4 ± 5.6 days, range 101-122 days) were included in the study. All caregivers gave informed written consent before testing, and all infants were born full term (39.1 ± 1.2 weeks of amenorrhea). Ten infants were excluded

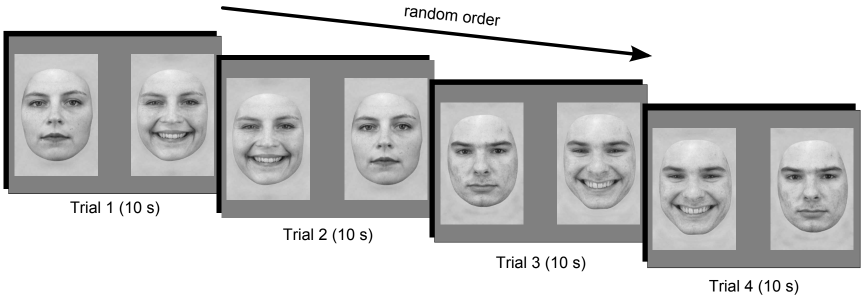


Figure 4.1: **Example session.** Each infant saw all four trials, featuring stimuli from one of two stimulus sets.

due to fussiness (*n* = 3), technical failure (*n* = 2), or experimental error (*n* = 5). Thirty-seven infants were excluded due to side-bias, i.e. they looked in one direction more than 95% of the time in one or more of the four trials. Although the attrition rate was high, the definition and handling of side biases was decided a priori, in accordance with common methods in infant research (Hillairet de Boisferon, Uttley, Quinn, Lee, & Pascalis, 2014), and motivated by the need to run within-participant comparisons between male and female pairings. Means for each condition were substantially unchanged if data points from those excluded participants that had no side bias for the male (*n* = 10) or female pairing (*n* = 8) were included. All caregiver(s) reported a percent of female caretaking of at least 50% (mean 69 ± 2%), meaning that no infant in our sample was primarily raised by a male caregiver, and providing results that are consistent with those previously reported (Rennels & Davis, 2008; Sugden et al., 2014).

#### 4.1.4.2 Stimuli

Two sets of stimuli were used that had different face identities (sets A and B, TABLE 4.1). Stimulus set was counterbalanced across infants (12 of the 25 3.5-month olds viewed set A). Face stimuli were selected from the Karolinska Directed Emotional Face database (Goeleven et al., 2008; Lundqvist et al., 1998) under their smiling and neutral frontal view versions. They were gray scaled; external features were cropped. Luminance, contrast, spatial frequencies, and placement of the eyes were matched using SHINE (Willenbockel et al., 2010) and Psychomorph (Tiddeman, 2005) for each set. Faces subtended a visual angle of about 9 degrees (vertically) by 7 degrees (horizontally). Physical and emotional properties of the stimuli are summarized in TABLE 4.1.

#### 4.1.4.3 Procedure

We presented male or female smiling faces paired with neutral faces of the same individual to 25 3.5-month-old infants (FIGURE 4.1) using E-Prime 2.0 (Schneider et al., 2002). The infants sat on their caregiver's lap about 60 cm from a screen. Each infant saw 4 trials showing 1 female and 1 male pair of faces. There were 2 trials for each pair, with left-right side of presentation reversed. The 4 trials were randomly ordered and lasted 10 s from first look. The infant's gaze was redirected to the center of the screen between each trial. The experiment was approved by the local ethics committee ("Comité d'éthique des centre d'investigation clinique de l'inter-région Rhône-Alpes-Auvergne", Institutional Review Board).

#### 4.1.4.4 Data acquisition, pre-processing, and analysis

Infant looking was recorded by a camera and coded off line with 40 ms precision (25 frames per second). A sub-sample of the videos was coded by a second observer with 0.98 agreement (Pearson's $r$, 24% of the videos). Analyses were run in Matlab R2009b using the Statistics toolbox. Looking preferences towards each stimulus were derived from looking times (Percentage of Total Looking Time, PTLT). For example, the looking preference (PTLT) for the smiling female face for each infant was created by averaging the percentage of looking time to the smiling female face (versus the neutral female face) in the two trials featuring female stimuli. PTLTs to male (3 infants) or female faces (1 infant) that were further than 2 standard deviations away from the corresponding group mean were considered outliers and excluded (8% of trials). The handling of outliers was decided a priori and in accordance with common methods in infant research (Beier & Spelke, 2012; Surian, Caldi, & Sperber, 2007). There was no significant difference in the mean total looking times during male and female trials (paired Student's $t$-tests, t(20) = 1.16, $p$ = 0.261). Data and code are available online at http://dx.doi.org/10.6084/m9.figshare.1363637.

### 4.1.5 Results

#### 4.1.5.1 An effect of face gender on the looking preference for smiling

A preliminary ANOVA revealed no effect of the two between-participant factors of stimulus set ($F$(1,17) = 0.06, $p$ = 0.809) or participant gender ($F$(1,17) = 0.79, $p$ = 0.386) or their interaction ($F$(1,17) = 1.37, $p$ = 0.258) on the looking preference (PTLT) for the smiling expression. Three similar, preliminary ANOVAs on the looking preferences (PTLT) for female and male smiles and on the difference between them also revealed no effect of the between-subject factors of stimulus set, participant gender, or their interaction (all $p$s $> 0.05$). Consequently, data from all participants were pooled together.

Infants did not look longer at the smiling than at the neutral faces ($t(20) = -0.33$, $p = 0.746$, paired Student's $t$-test). A repeated-measure ANOVA on the looking preference for the smiling expression further revealed a significant effect of face gender ($F(1,20) = 16.68$, $p < 0.001$). Infants looked longer to the smiling female face versus neutral female face ($t(23) = 2.16$, $p = 0.041$, Cohen's $d = 0.44$, Fig. 2, Student's $t$-test against chance level, uncorrected), but longer to the neutral male face versus smiling male face ($t(21) = -2.27$, $p = 0.034$, Cohen's $d = -0.48$, FIGURE 4.2, Student's $t$-test against chance level, uncorrected). They also looked longer at the smiling expression when the faces were female than when they were male, and conversely longer at the neutral expression when the faces were male than when the faces were female (both comparisons: $t(20) = 4.08$, $p < 0.001$, Cohen's $d = 0.89$, FIGURE 4.2, paired Student's t-test, uncorrected). Looking behavior was consistent across individuals; 17 out of 21 infants showed a stronger preference for the smiling face on female face trials (i.e., smiling vs. neutral female face) than on male face trials (i.e., smiling vs. neutral male face; FIGURE 4.3, 17 out of 21 data points are below the identity line). Seventeen out of 24 infants looked longer to the smiling versus neutral female faces, while 7 out of 22 infants looked longer to the smiling versus neutral male faces.

#### 4.1.5.2 A correlation of individual looking preferences for male and female smiles

The pattern of opposite preference for smiling in male and female faces suggests that 3.5-month-old infants process male and female smiles independently. However, individual looking preferences to male and female smiles correlated significantly (Pearson's $r = 0.53$, $p = 0.015$, FIGURE 4.3). Regression analyses (one per factor) revealed no effect of stimulus set or participant gender in this relationship, either as a main effect or in interaction with looking preferences (all $p$s $> 0.05$). Infants at 3.5 months of age process male and female smiles using partly common mechanisms, but seem to consistently prefer the female smile more than the male smile.

### 4.1.6 Discussion

Contrary to predictions from saliency (Oster, 1981), mimicking via affect matching (Gallese et al., 2004; Meltzoff & Moore, 1977, 1983), and universal emotion recognition accounts (Ekman & Oster, 1979; Ekman et al., 1969), face gender modulated the response of 3.5-month-olds to the smiling facial expression. The correlation of individual preferences for male and female

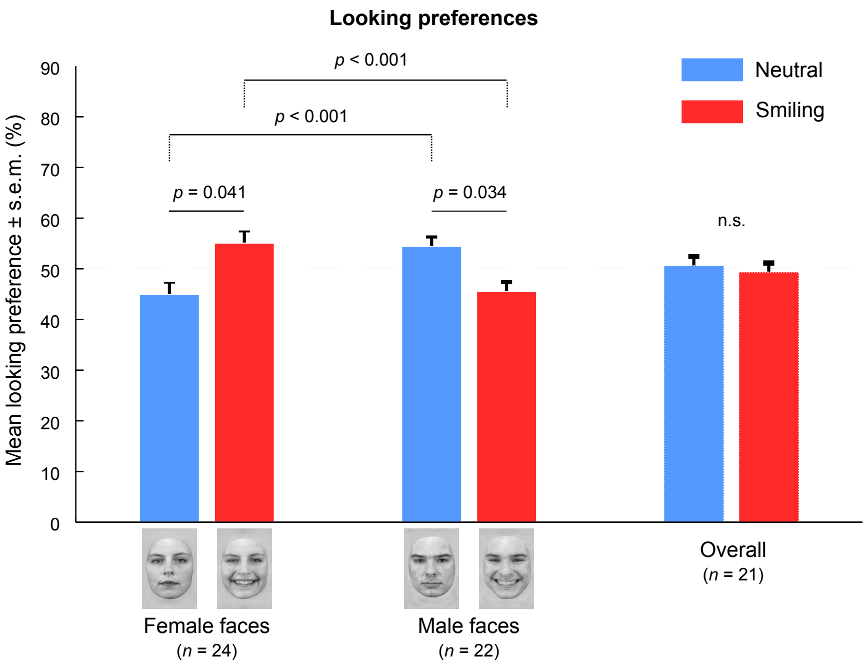


Figure 4.2: **Face gender influences the looking preference for smile.** A looking preference of 50% represents chance level. Overall, infants preferred looking to the smiling face in female pairings, and to the neutral face in male pairings (as measured by Percentages of Total Looking Time, PTLT). There was no overall preference when pooling female and male trials together. Paired Student $t$-tests, $\alpha = 0.05$, uncorrected.

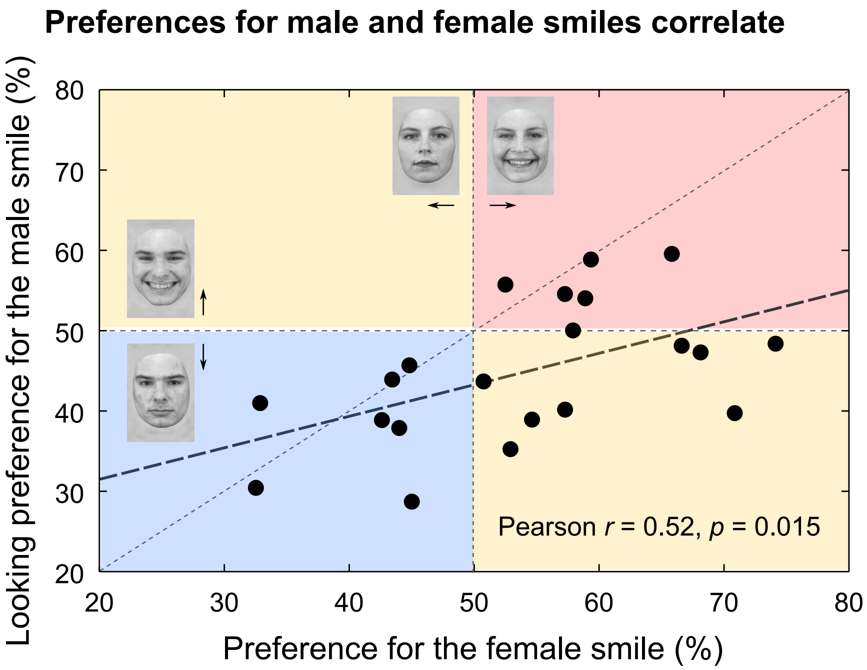


Figure 4.3: **Individual looking preferences for male and female smiles correlate.** Most infants showed a stronger preference for the smiling face on female face trials (i.e., smiling vs. neutral female face) than on male face trials (i.e., smiling vs. neutral male face), as is indicated by the position of the regression line below the identity line.

smiles suggests partially common mechanisms in the processing of male and female smiles, which is in keeping with saliency, mimicking, or universal facial expression processing accounts; however, the female smile was systematically more preferred than the male smile, sharply contrasting with the predictions from those accounts. Moreover, at the group level, a preference for smiling was only found for female faces, evidencing the dependence of expression perception on broader face processing. While several studies have reported interactive effects of eye gaze and expression (Hoehl, Wiese, & Striano, 2008; Striano et al., 2006) or eye gaze and facial identity (Hoehl, Wahl, Michel, & Striano, 2012) in 3- to 4-month-olds at the electrophysiological level, this is the first study reporting an effect of face gender on behavioral responses to facial expression in this population.

#### 4.1.6.1 Experience shapes the response of infants to smiling faces

Younger infants have limited perceptual and social experience with male faces (Rennels & Davis, 2008; Sugden et al., 2014), which could lead to differential processing of male and female facial expressions in at least two ways. First, adult females may smile more than males when interacting with infants (Halberstadt et al., 1988); the looking preferences of infants for female smiles and male neutral expressions would thus represent a primitive form of stereotyping based on familiarity. Second, young infants primarily raised by a female could tend to see females, but not males, as potential caregivers; this could lead them to respond more to a female than to a male smile. In adults, a smile's positive value depends on the relationship shared between the observer and the person smiling (Minagawa-Kawai et al., 2009) and might stem from it being an affiliative cue (Baudouin, Gilibert, et al., 2000). Finally, Quinn et al. have argued that the social character of stimuli influences infant responding to particular characteristics of those stimuli (Quinn et al., 2011); infants may perceive male faces as less social than female faces.

#### 4.1.6.2 Conclusions

Infants at 3.5 months of age show different, but not independent, preferences for male and female smiles. They prefer looking to smiling (versus neutral) female faces and to neutral (versus smiling) male faces, although individual preferences for male and female smiles correlate. Thus, the preference for smiling by 3.5-month-old infants is neither universal nor automatic, but is already shaped by experience. Indeed, the data present an effect of face gender on smiling preference that possibly stems from the association of female faces with positive expressions and from the lack of perceptual and social experience infants have with male faces. The modulation of this effect by static versus dynamic smiles, its evolution during development, and its presentation in infants primarily raised by male caregivers as well as in newborns (in which a smiling preference may well be independent of experience) all remain to be tested in future research. We predict that infants raised primarily by a male caregiver would show a reverse pattern of preference, i.e., a preference for smiling versus neutral male faces and for neutral versus smiling female faces.

### 4.1.7 Acknowledgments

This work was funded by the NIH Grant R01 HD-46526 to KL, OP, PQ, and JT, the FNS Grant 100019-156073 to EG, and a PhD scholarship from the French Department of Research and Higher Education to LB. The authors are grateful to the families that took part in the study, and thank Marie Sarremejeanne for technical support.

### 4.1.8 Supporting information

| | | | **A. Physical properties** | | | | | **B. Emotional properties** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Face (px) | Eyes (px) | (% face) | Teeth (px) | (% face) | Brightness (0-255) | Hit rate (%) | Intensity (1-9) | Arousal (1-9) |
| **Set A** | Female | Smiling | 89834 | 1421 | 1.58 | 2086 | 2.32 | 196 ± 41 | 100 | 6.8 ± 1.5 | 3.9 ± 2.2 |
| | | Neutral | 87041 | 2047 | 2.35 | 0 | 0 | 196 ± 41 | 96.88 | 5.6 ± 2.0 | 2.2 ± 1.4 |
| | | Difference | 2793 | - 626 | - 0.77 | 2086 | 2.32 | | | | |
| | Male | Smiling | 98579 | 1150 | 1.17 | 2375 | 2.41 | 196 ± 42 | 98.44 | 6.9 ± 1.5 | 4.2 ± 2.1 |
| | | Neutral | 84948 | 1609 | 1.89 | 0 | 0 | 196 ± 41 | 85.94 | 5.1 ± 1.9 | 2.6 ± 1.3 |
| | | Difference | 13631 | - 459 | - 0.73 | 2375 | 2.41 | | | | |
| **Set B** | Female | Smiling | 159636 | 1680 | 1.05 | 3530 | 2.21 | 186 ± 29 | 100 | 6.9 ± 1.6 | 3.7 ± 1.9 |
| | | Neutral | 160646 | 2606 | 1.62 | 0 | 0 | 186 ± 29 | 68.75 | 4.6 ± 2.4 | 2.7 ± 1.7 |
| | | Difference | -1010 | - 926 | - 0.57 | 3530 | 2.21 | | | | |
| | Male | Smiling | 168884 | 1286 | 0.76 | 4828 | 2.86 | 186 ± 29 | 100 | 7.4 ± 1.6 | 4.7 ± 2.1 |
| | | Neutral | 158846 | 2056 | 1.29 | 0 | 0 | 186 ± 29 | 64.06 | 4.1 ± 2.3 | 2.3 ± 1.1 |
| | | Difference | 10038 | - 770 | - 0.53 | 4828 | 2.86 | | | | |

Table 4.1: **Stimulus properties. A.** Physical properties. Pixel values are approximate. Differences between male and female faces used here can be noted. Male faces enlarge more with smiling, and have smaller eyes but bigger teeth. Both male and female faces get wider with smaller eyes when smiling. **B.** Emotional properties from a validation study in adults (Goeleven et al., 2008). All stimuli adequately conveyed the desired emotion. Differences between sets were greater than differences between male and female faces within each set. Hit rates, intensity, and arousal ratings are typical of neutral and smiling faces (Goeleven et al., 2008).

## 4.2 DEVELOPMENTAL TRAJECTORY

Box 5: Résumé des données concernant la trajectoire développementale de l'effet du genre du visage sur la préférence pour le sourire chez le nourrisson

> Les données présentées au cours de la section précédente ont mis en évidence un effet du genre du visage sur la préférence visuelle pour les visages souriants à 3.5 mois. Dans cette section sont présentées des analyses supplémentaires ainsi qu'une réplication de la même expérience dans un groupe de nourrissons de 9 mois. Aucun effet du genre du visage sur la préférence visuelle pour le sourire n'a pu être mis en évidence à l'âge de 9 mois (SECTION 4.2.1), et une nouvelle analyse des données concernant les nourrissons de 3.5 mois montrent que, même dans cette population, l'effet du genre du visage décroit avec l'âge (gestationnel ou de naissance ; SECTION 4.2.2.3). Enfin, une relation entre la préférence visuelle pour le sourire et la production de sourire par les nourrissons est recherchée, mais reste marginale ou absente lorsque l'âge est pris en compte et contrôlé dans l'analyse (SECTION 4.2.3).

### 4.2.1 Experimental data at 9 months of age

#### 4.2.1.1 Introduction

In the previous experiment (SECTION 4.1) we observed that the preference for smiling faces in 3.5-month-old infants is modulated by the face gender. In particular, infants showed a group preference for the smiling female face (versus neutral) and a group preference for the neutral male face (versus smiling). The effect presumably stems from the differential experience of infants with male and female faces (Rennels & Davis, 2008; Sugden et al., 2014). Recent studies have demonstrated that 9-month-olds, contrary to 3- or 6-month-olds, cease to show a visual preference for own-race female over own-race male faces as their experience with male faces accumulates (Liu et al., 2015; FIGURE 4.4). Thus, it is possible that the effect of face gender on the preference for smiling changes at 9-months of age. While a general visual preference for smiling versus neutral faces hasn't been reported in 9-month-old infants (SECTION 1.2.2.2), it has been reported in 6-month-old infants in one study (La Barbera et al., 1976).

#### 4.2.1.2 Methods

Thirty 9-month-old infants (13 girls, mean age 284.8 ± 7.2 days, range 270-306 days) were included in the study. All caregivers gave informed written consent before testing, and all infants were born full term (39.0 ± 1.0 weeks of amenorrhea). Ten infants were excluded due to fussiness ($n$ = 3), experimental error ($n$ = 1), or side-bias ($n$ = 6). All caregiver(s) reported a percent of female caretaking of at least 50% (mean 67 ± 2%).

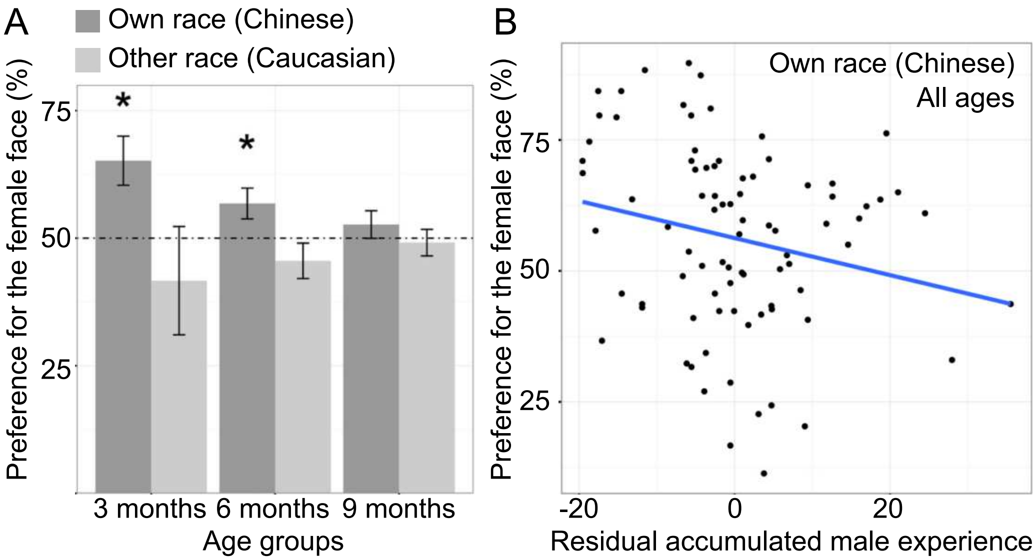


Figure 4.4: **Preference for female faces in infancy as a function of experience. (A)** A visual preference for female versus male own-race faces in 3-, 6- but not 9-month-old infants. **(B)** Female face preference decreases with accumulated male face experience across age groups, controlling for the ratio of female versus male face experience. Adapted from Liu et al. (2015).

All other methods are identical to that of the previous experiment (SECTION 4.1).

A sub-sample of the videos was coded by a second observer with 0.93 agreement (Pearson's $r$, 27% of the videos). PTLTs to male ($n$ = 2) or female faces ($n$ = 2) that were further than 2 standard deviations away from the corresponding group mean were considered outliers and excluded (7% of trials). There was no significant difference in the mean total looking time during male and female trials (paired Student's $t$-test; $t(25) = 0.93$, $p = 0.363$).

#### 4.2.1.3 Results

Preliminary ANOVAs similar to those run in the previous experiment (SECTION 4.1.5.1) revealed no effect of stimulus set ($F(1,22) = 0.35$, $p = 0.562$), participant gender ($F(1,22) = 0.07$, $p = 0.796$) or their interaction ($F(1,22) = 0.02$, $p = 0.901$) on the PTLT for the smiling expression as well as on the PTLT for male smiles, female smiles, and the difference between them (all $p$s > 0.05). Consequently, data from all participants were pooled together.

The 9-month-old infants looked marginally longer to the neutral versus smiling face of both gender, but the difference did not reach statistical significance ($t(25) = -1.99$, $p = 0.058$, Cohen's $d = -0.39$, FIGURE 4.5). Face gender did not modulate the looking preference for the smiling expression (repeated-measure ANOVA, $F(1,25) = 0.26$, $p = 0.616$); individual looking preferences to male and female smiles did not significantly correlate (Pearson's $r = 0.22$, $p = 0.289$; FIGURE 4.6).

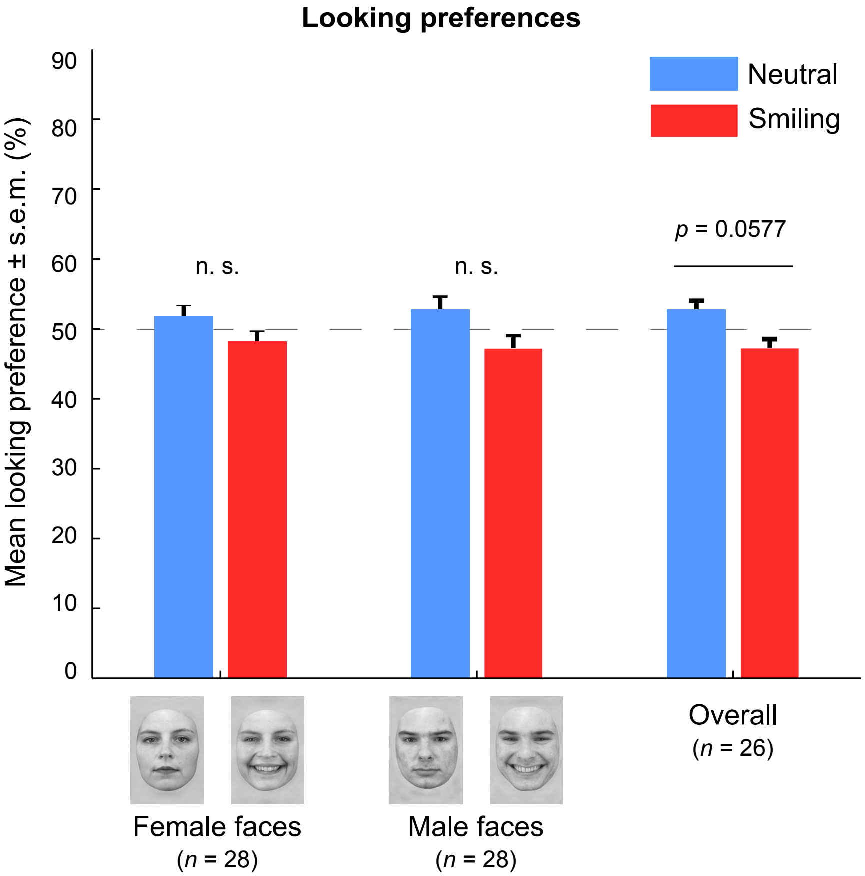


Figure 4.5: **No effect of face gender on the preference for smiling at 9-months of age.** A looking preference of 50% represents chance level. Overall, infants only marginally preferred looking to the neutral face rather than to the smiling face (as measured by Percentages of Total Looking Time, PTLTs). There was no difference between male and female face pairings. Paired Student *t*-tests, $\alpha = 0.05$, uncorrected.

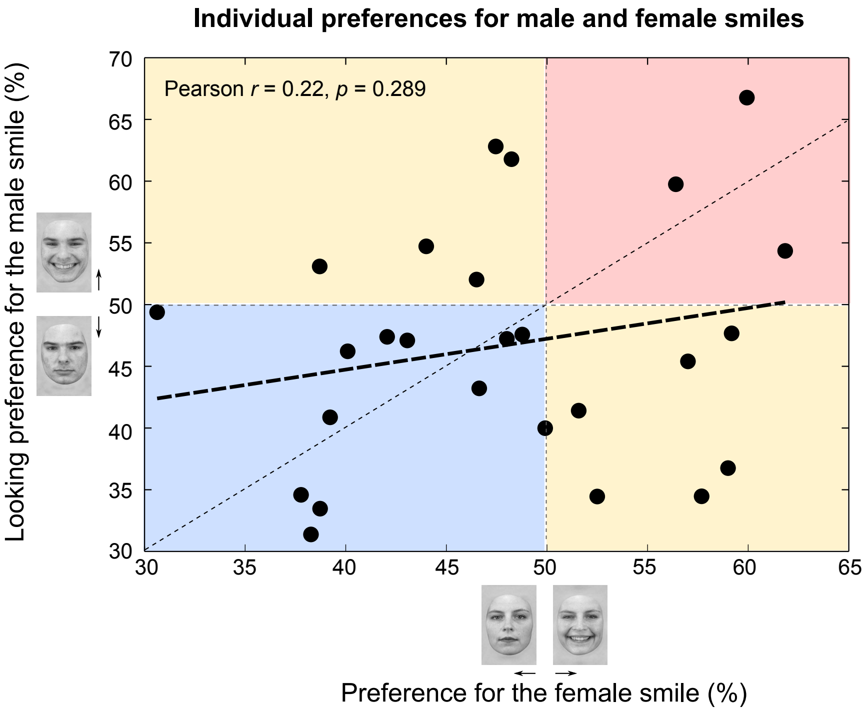


Figure 4.6: **Individual preferences for smiling versus neutral male and female faces at 9 months of age.** The correlation between individual preferences for male and female smiles at 9 months was not significant. Twelve out of 26 infants had a visual preference for the neutral (versus smiling) male face as well as for the neutral (versus smiling) female face.

#### 4.2.1.4 Discussion

A marginal preference for neutral versus smiling faces was observed in 9-month-old infants. While a within-subject relationship between the female versus male visual preference and the modulation of smiling versus neutral preference by face gender was neither researched nor demonstrated here, the results are consistent with the hypothesis that the effect observed at 3.5 months disappears during development at the same period of time that infants acquire more experience with male faces and stop exhibiting a female versus male face preference.

The lack of correlation between individual preferences for male and female smiles was more surprising, and hard to interpret. It is possible that by 9 months of age infants begin to exhibit idiosyncratic patterns of experience with male and female faces and smiles. Obtaining measures of the day-to-day visual experience of infants with male and female faces and smiles (Sugden et al., 2014) and relating those measures with individual visual preferences may allow a better understanding of these patterns.

### 4.2.2 Revisiting the 3.5-month-olds' data in a developmental light

#### 4.2.2.1 Introduction

In the last section, we observed that face gender did not modulate the visual preference for smiling versus neutral faces at 9 months of age. Next, we reanalyze the data from 3.5-month-old infants (SECTION 4.1) to determine whether the downward developmental trend of the face gender effect was in fact already evident in this group.

#### 4.2.2.2 Methods

All methods were identical to that of SECTION 4.1.

#### 4.2.2.3 Results

To investigate the developmental trajectory of the effect of face gender on the preference for smiling versus neutral, we compute rank (Spearman) correlations between measures of age and maturation (birth age, gestational age at birth, age from term) and measures of visual preference for smiling faces (female, male, difference). For example, gaze following at 3.5-months relates with age from birth but not age from term in healthy infants (Peña et al., 2014); this result highlights the need to explore different measures of age when researching the developmental trajectory of visual processing abilities. This analysis is exploratory in nature, but given the marginal preference for neutral male and female faces that was found in 9 month-olds, an expected developmental trend in 3.5-month-olds would either be a decrease of the preference for female smiling (versus neutral) or a reduction of the difference in preference for female and male smiling. Using several measures of age and maturation (birth age, gestational age at birth, age from term) will allow obtaining a finer picture of the contribution of experience and maturation. If a developmental trend is driven solely by visual experience, then it should correlate tightly with age from birth independently of gestational age at birth. Conversely, if a developmental trend is driven solely by maturation, then it should correlate tightly with age from term but not with age from birth.

Spearman rank correlations (TABLE 4.2) revealed two significant developmental trends. Older infants (age from term) and infants born at an older gestational age tended to exhibit less difference in their visual preferences for female smiles (versus neutral) and male smiles (versus neutral), i.e. a decreased effect of face gender on the preference for smiling (FIGURE 4.7). The visual preference for the female smile (versus neutral) also tended to decrease with age, but the trend was not statistically significant.

| | Distribution | Female smiles | Male smiles | Difference |
|---|---|---|---|---|
| | | $n$ = 24 | $n$ = 22 | $n$ = 21 |
| Age from birth | 115 ± 6 | - 0.10 (n. s.) | - 0.25 (n. s.) | - 0.14 (n. s.) |
| Birth - term | - 7 ± 8 | - 0.16 (n. s.) | 0.24 (n. s.) | - 0.50 * |
| Age from term | 109 ± 10 | - 0.25 (n. s.) | 0.02 (n. s.) | - 0.53 * |

Table 4.2: **Developmental trends in visual preferences for male and female smiles.** 3.5 month-olds tended to visually prefer male and female smiles (versus neutral) more equally with increasing age, especially age as measured from term. Spearman correlations between measures of age and visual preference for smiling versus neutral in female and male faces by 3.5-month-old infants. * $p < 0.05$; (n.s.) $p > 0.20$

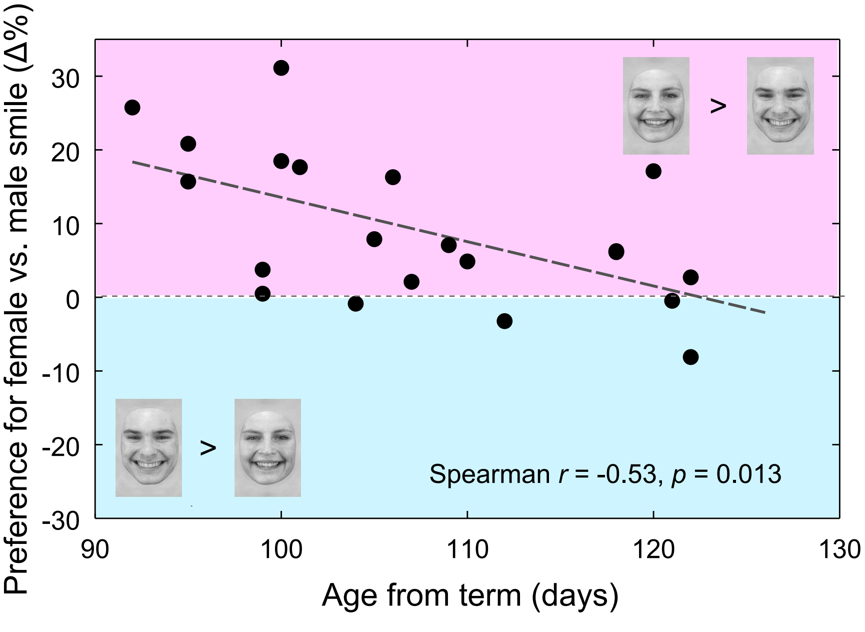


Figure 4.7: **Decreasing effect of face gender on smiling versus neutral visual preferences in 3.5-month-old infants.** Younger infants (age from term) tended to exhibit stronger preferences for female smiles (versus neutral) than for male smiles (versus neutral). Older infants (age from term) tended to show equal preferences for male and female smiles (versus neutral). Dotted line: Linear trend.

#### 4.2.2.4 Discussion

Visual preferences for smiling versus neutral in infants from the 3.5-month-old group exhibited developmental trends consistent with the idea that the effect of face gender on the preference for smiling decreases with age even in early infancy. The effect of face gender on the visual preference for smiling versus neutral faces is present at group level in 3.5-month-old infants (SECTION 4.1), declines with age in this group, and is absent in 9-month-old infants (SECTION 4.2.1).

The developmental trend suggests a maturational process, as variations in the effect of face gender correlated more strongly with variations in age from term or gestational age at birth than with variations in age from birth. This is surprising, and hard to interpret, given than effects of face gender in infant face perception are generally found to be driven by their differential visual experience with female and male faces (Liu et al., 2015; Quinn et al., 2002; Ramsey-Rennels & Langlois, 2006). It is possible that the null correlation between the effect of face gender and age from birth originated from the limited variations of this variable in our sample (TABLE 4.2). However, gestational age at birth had only slightly more variations than age from birth and still correlated significantly with variations in the effect of face gender (TABLE 4.2). Further, although our sample consisted of typically developing, healthy infants born within 3 weeks of term date (i.e. born “full term”), it should be noted that gestational age at birth is associated not only with maturational age, but also with a range of confounding factors affecting infant and mother (e.g., maternal prenatal stress; Wadhwa, Sandman, Porto, Dunkel-Schetter, & Garite, 1993). Thus, it is possible that, in our sample, gestational age at birth was tracking another relevant factor. Whatever the mechanism, the effect of face gender on the preference for smiling which was observed in 3.5 month-old infants appears to be short lived, possibly relating to a developmental window closing at around 110 days from term (FIGURE 4.7). Interestingly, it has been suggested based on animal models that the first months of life correspond to a critical period for familiarity-based preferences formation (Leppänen & Nelson, 2012). Such a critical period would account for the developmental trend observed here for the visual preferences for smiling versus neutral faces. Future studies of this phenomenon should attempt to relate the effect of face gender on the preference for smiling with individual variations in female versus male preference and finer measures of accumulated experience with male and female faces, in addition to the usual measures of birth and gestational age.

### 4.2.3 Relation with developmental trends in smiling behavior

#### 4.2.3.1 Introduction

Facial expression production in the first months of life is characterized by an increase in social smiles, smiles in response to someone else's smiling during social interaction (SECTION 1.2.2.2). Differences in infant smiling behavior between male and female trials could signal differences in the social value attributed to static male and female faces. Further, smiling behavior from the infant may scaffold the perception of smiling in faces - unfamiliar faces in particular (SECTION 1.2.2.4).

Here, we re-analyze the data obtained from 3.5-month-old (SECTION 4.1) and 9-month-old (SECTION 4.2.1) infants, focusing not on visual preferences but on the infant's smiling behavior. The analysis was exploratory, but we tentatively hypothesized that (1) 3.5-month-old but not 9-month-old infants may smile less during male than female trials; and (2) that increased smiling during male trials may be associated with higher visual preference for smiling male faces or that increased smiling in general may be associated with a reduced effect of face gender on the preference for smiling in 3.5-month-old infants.

#### 4.2.3.2 Methods

Infants' smiling was operationalized as the visible rising of the lip corners, coded offline with 40 ms precision for the duration of the trials i.e. 10 s from first look. A sub-sample of the videos was coded by a second observer with 0.87 agreement (84 % of the videos) for the 3.5-month-old group and a 0.83 agreement (27 % of the videos) for the 9-month-old group. Trials where the mouth was not visible (pacifier use, fingers in mouth) were handled as missing values (1 3.5-month-old and 4 9-month-old infants on some or all trials). Because trials had a fixed duration, raw smiling times per trial could be analyzed directly and not as a percentage of time.

All other methods were identical to that of SECTIONS 4.1 and 4.2.1.

#### 4.2.3.3 Results

**Preliminary analyses.** A preliminary ANOVA revealed no effect of the two between-participant factors of stimulus set ($F(1,20) = 2.58$, $p = 0.124$), participant gender ($F(1,20) = 1.57$, $p = 0.225$) or their interaction ($F(1,20) = 0.08$, $p = 0.780$) on the mean smiling time of 3.5-month-olds. Three similar, preliminary ANOVAs on the smiling time of 3.5-month-old infants during female and male trials and on the difference between them also revealed no effect of the

Figure 4.8: **Smiling behavior as a function of age and trial type.** Nine-month-old infants smiled for longer durations than 3.5-month-old infants, regardless of trial type (i.e. male or female faces). Student *t*-tests for independent samples, $\alpha = 0.05$, uncorrected.

between-subject factors of stimulus set, participant gender, or their interaction (all *p*s > 0.05). Four similar ANOVAs on the smiling times of 9-month-old infants with the same dependent variables also revealed no effect of stimulus set, participant gender, or their interaction (all *p*s > 0.05). Consequently, data from all participants in each age group were pooled together.

**No difference in infants' smiling behavior between male and female trials.** A repeated-measure ANOVA on smiling times further revealed a significant effect of age ($F(1,48) = 12.16$, $p = 0.001$) but no effect of face gender either alone ($F(1,48) = 0.07$, $p = 0.792$) or in interaction with age ($F(1,48) = 0.68$, $p = 0.413$). Further Student *t*-tests for independent samples confirmed that 9-month-olds smiled more than 3.5-month-olds in female trials ($t(48) = -3.12$, $p = 0.003$), male trials ($t(49) = -3.07$, $p = 0.004$), and overall ($t(48) = -3.32$, $p = 0.002$). Thus, the hypothesis that 3.5-month-old infants would smile more during female trials than during male trials was not supported, but the expected developmental trend was observed i.e. more smiling in older infants.

**Relation with visual preferences.** Because important differences were observed in smiling behavior between 3.5- and 9-month-old infants, and in order to allow for the finer estimation of the effect of age as a continuous variable, linear models were fitted separately for the 3.5- and 9- month-old groups.

A linear model of the visual preference for smiling versus neutral male faces in 3.5 month-old infants revealed no significant effects of smiling time during male trials, gestational age at

| Predictor | β | *t*(17) | *p* |
|---|---|---|---|
| (Intercept) | 0.46 | 21.69 | < 0.001 |
| Smiling time in male trials | - 0.02 | - 0.85 | 0.406 |
| Birth - term | 0.02 | 1.10 | 0.288 |
| Age from birth | - 0.03 | - 1.27 | 0.220 |

Table 4.3: **Linear model of the visual preference for smiling versus neutral male faces in 3.5-month-old infants.** All predictors were continuous, centered and scaled. There were no significant effects. $R^2 = 0.15$

| Predictor | β | *t*(18) | *p* |
|---|---|---|---|
| (Intercept) | 0.47 | 21.99 | < 0.001 |
| Smiling time in male trials | 0.01 | 0.56 | 0.584 |
| Birth - term | < 0.01 | 0.05 | 0.963 |
| Age from birth | < 0.01 | 0.02 | 0.982 |

Table 4.4: **Linear model of the visual preference for smiling versus neutral male faces in 9-month-old infants.** Three data points were excluded based on Cook's distance ($4/n$ cutoff, 12% data points). There were no significant effects. All predictors were continuous, centered and scaled. $R^2 = 0.02$

birth, or age from birth in either age group (TABLE 4.3). The hypothesis that smiling during male faces trials would be associated with a greater preference for male smiling faces in 3.5-month-old infants was not supported. Similar results were obtained for the 9-month-old group (TABLE 4.4).

A linear model of the effect of face gender on smiling versus neutral preference in 3.5-month-old infants revealed that mean smiling time was weakly associated with a lesser effect of face gender on smiling versus neutral preferences, controlling for the effect of age from birth and gestational age at birth (TABLE 4.5). The association was only marginally significant, however. Thus, the hypothesis that increased smiling would reduce the effect of gender on smiling versus neutral in 3.5-month-olds was not supported. The additive effects of age from birth and gestational age at birth, as observed in SECTION 4.2.2.3, were replicated in this new analysis of the same data. A similar model applied to the 9-month-old group showed no significant effect (TABLE 4.6).

#### 4.2.3.4 Discussion

Analysis of smiling behavior revealed that 9-month-olds smiled for longer periods of time than 3.5-month-olds. There was no difference in smiling time during male and female trials in either group, and hypotheses regarding a relationship between smiling behavior and visual preferences, controlling for the effects of birth and gestational age, were not or only weakly

| Predictor | β | *t*(15) | *p* |
|---|---|---|---|
| (Intercept) | 0.09 | 4.84 | < 0.001 |
| Mean smiling time (.) | - 0.03 | - 1.85 | 0.085 |
| Birth - term * | - 0.06 | - 3.21 | 0.006 |
| Age from birth * | - 0.04 | - 2.29 | 0.037 |

Table 4.5: **Linear model of the effect of face gender on the visual preference for smiling versus neutral faces in 3.5-month-old infants.** The effect of face gender was the difference between the visual preference for smiling versus neutral female faces and the visual preference for smiling versus neutral male faces. One data point was excluded based on Cook's distance (4/*n* cutoff, 5% data points). Significant effects are marked with an asterisk, marginal effects are marked with a dot (.). All predictors were continuous, centered and scaled. $R^2$ = 0.58. The effect of Age from birth is not statistically significant and $R^2$ drops to 0.42 if Mean smiling time is removed from the model.

| Predictor | β | *t*(17) | *p* |
|---|---|---|---|
| (Intercept) | < 0.01 | 0.15 | 0.882 |
| Mean smiling time | - 0.036 | - 1.51 | 0.149 |
| Birth - term | 0.033 | 1.28 | 0.216 |
| Age from birth | - 0.01 | - 0.61 | 0.550 |

Table 4.6: **Linear model of the effect of face gender on the visual preference for smiling versus neutral faces in 9-month-old infants.** The effect of face gender was the difference between the visual preference for smiling versus neutral female faces and the visual preference for smiling versus neutral male faces. One data point was excluded based on Cook's distance (4/*n* cutoff, 4.55% data points). There were no significant effects. All predictors were continuous, centered and scaled. $R^2$ = 0.24

supported. In conclusion, no definite evidence could be found for an effect of smile production on smile perception in our data.

Existing variations in smiling behavior between male and female trials may have been missed by our coding system which did not differentiate between Duchenne and non-Duchenne smiles (see Methods, SECTION 4.2.3.2) - such variations could be captured by finer methods of coding such as "Baby FACS" (Oster, 2006). More generally, it should be emphasized that the present analyses were merely exploratory as the experiment was not initially designed to test for the effect of smiling behavior. Here, smiling time might have been tracking another relevant variable such as temperament, state, or emotional development - even if birth and gestational age were controlled in the analysis. There was no non-social control condition and smiling, visual behavior unfolded during the course of the same experiment; because of this design the smiling data is hard to interpret. It would have been preferable to run two different experiments in order to separately test (1) whether infants would smile as much in response to male than female smiling or neutral faces, in an unpaired design including a non-social control condition (e.g. picture of object), and (2) whether the physical act of smiling would modulate visual preference for smiling, directly manipulating infant's facial expression to a neutral or smiling expression using specifically shaped pacifiers (Yeung & Werker, 2013).

### 4.2.4 Conclusions

In SECTION 4.1 an effect of face gender on the visual preference for smiling versus neutral expressions was found in a sample of 3.5-month-old infants. Over the course of SECTION 4.2, it was further observed that: (1) the effect is absent in 9-month-old infants, who instead show a general, marginal preference for neutral over smiling expressions; (2) the effect significantly declines with age in 3.5-month-old infants, and infants born earlier from term show a significantly stronger effect; (3) the effect is only marginally reduced in 3.5-month-old infants who smiled more, controlling for birth and gestational age. The effect of gestational age at birth may be attributed either to maturational status or to confounding factors such as maternal stress. Whatever the mechanism, the effect was clearly found to disappear between 3.5 and 9 months of age, already declining by 3.5-months. However, while the developmental trajectory of the effect was consistent with the hypothesis that it would decline as visual experience with male faces accumulate, the causal role of visual experience was not indisputably supported by the data.

## 4.3 EXPERIENCE-DEPENDENT AND EXPERIENCE-INDEPENDENT CONTRIBUTIONS TO THE VISUAL PREFERENCE FOR SMILING AT 3.5 MONTHS

### 4.3.1 Introduction of the article

In SECTIONS 4.1 and 4.2 we described that the visual preference of 3.5-month-old infants for smiling versus neutral expressions was modulated by the face gender, in interaction with gestational age. An effect of face gender is evocative of an experience-dependent effect, as infants typically experience more female than male caretaking (Ramsey-Rennels & Langlois, 2006; Rennels & Davis, 2008; Sugden et al., 2014). In order to confirm the role of experience, we next conducted a follow-up experiment with 3.5-month-old infants. In this experiment, faces are male or female of own- or other-race. Infants appear sensitive to face gender in own- but not other-race faces (Quinn, Uttley, et al., 2008), and even adults categorize the gender of other-race faces with difficulty compared to own-race faces (O'Toole et al., 1996). Faces were either neutral or smiling, and all smiles were closed-mouth - meaning that teeth salience couldn't bias visual preferences. Because an effect of gestational age from birth was found in SECTION 4.2, individual variations in visual preferences that follow gestational age from birth and birth age were researched.

### 4.3.2 Abstract

Infants are sensitive to face gender; three-month-olds raised by female caregivers look longer at female over male faces when the faces are of familiar ("own-race") but not unfamiliar race ("other-race"), and the preference is reversed in infants raised by male caregivers. As the visual preference for female depends on face race and rearing conditions, it is interpreted as resulting from visual, social experience with faces. Moreover, 3.5-month-old infants prefer looking at smiling faces but the preference appears limited to female faces. We investigated the role of experience on the preference for smiling faces by presenting neutral versus smiling pairs of faces from the same female or male, own- or other-race individuals to 3.5-month-old infants (n = 54), controlling for low-level cues. All smiling expressions were closed-mouth in order to avoid any effect of teeth salience. Age from birth and gestational age were used in conjunction with face race and face gender to research experience-dependent developmental trajectories of the visual preference for smiling. There was an experience-independent effect of infant gender and an experience-dependent of gestational age at birth but not age from

Box 6: Résumé de l'article : "Experience-dependent and experience-independent contributions to the visual preference for smiling at 3.5 months"

> Bayet L., Quinn P. C., Lee K., Gentaz É., & Pascalis O. (en préparation) Experience-dependent and experience-independent contributions to the visual preference for smiling at 3.5 months.
>
> Les nourrissons sont sensibles au genre des visages. Les nourrissons de 3.5 mois élevés principalement par des femmes montrent une préférence visuelle pour les visages de femmes comparés aux visages d'hommes lorsque ces visages sont d'un type familier (*"own-race*"), mais pas lorsque ces visages sont d'un autre type (*"other-race*"). De plus, cette préférence visuelle est inversée chez les nourrissons élevés par des hommes. Comme la préférence visuelle pour les visages de femmes dépend du type de visage et de l'environnement du nourrisson, elle est interprétée comme résultant de l'expérience visuelle et sociale des nourrissons avec les visages. Au même âge de 3.5 mois, les nourrissons montrent également une préférence visuelle pour les visages souriants comparativement aux visages neutres, mais cette préférence est limitée aux visages de femmes. Nous avons cherché à mettre en évidence le rôle de l'expérience dans cette préférence en présentant à des nourrissons de 3.5 mois (n = 54) des visages souriants appariés à des visages neutres de la même personne. Les visages étaient féminins ou masculins, d'un type familier ou bien d'un autre type. Les propriétés bas niveaux des visages ont été contrôlées, et aucun des sourires ne découvrait les dents afin d'éviter tout effet de saillance physique des dents. L'âge de naissance ainsi que l'âge gestationel des nourrissons ont été utilisés conjointement au type et au genre des visages pour mettre en évidence le rôle de l'expérience dans la trajectoire développementale de la préférence pour le sourire. Les résultats montrent (1) un effet du genre des nourrissons, indépendemment de leur expérience, et (2) un effet de l'expérience modéré par l'âge gestationel à la naissance. Les nourrissons féminins, mais pas masculins, ont montré une préférence visuelle pour les visages souriants. La préférence visuelle pour le sourire croissait avec l'âge gestationnel des nourrissons à la naissance pour les visages de femmes d'un type familier, mais pas pour les autres visages. A 3.5 mois, la préférence visuelle des nourrissons pour les visages souriants est influencée par des facteurs individuels, indépendamment et en interaction avec leur expérience des visages.

birth. Girls, but not boys, showed an overall visual preference for smiling faces. The visual preference for smiling depended on gestational age at birth for own-race female face only, in line with the prevalence of own-race female faces in infants' everyday experience with faces. The visual preference for smiling at 3.5-months reflected experience-dependent and experience-independent individual differences.

### 4.3.3 Introduction

Facial expressions of emotion contribute to daily human interactions (Dezecache, Mercier, & Scott-Phillips, 2013). The ability to process several of these expressions appears to emerge in infancy around the age of 5-7 months of life (Leppänen & Nelson, 2009), but younger infants and newborns already show sensitivity to exagerated dynamic expressions (e.g. T. M. Field et al., 1982) as well as a visual preference for smiling expressions in static faces (Farroni et al., 2007; La Barbera et al., 1976; Rigato et al., 2011). This early visual preference for smiling faces decreases during infancy (e.g. Ludemann & Nelson, 1988) and its cause remains unclear, with some authors attributing it to the physical salience of teeth (Oster, 1981). Alternatively, it could be driven by experience with smiling faces, caregivers in particular (Malatesta & Haviland, 1982), and the association of smiling with positive interactions. In line with this hypothesis, 3.5-month-old infants experiencing predominantly female caregiving have been shown to visually prefer smiling (versus neutral) own-race female but not male faces (Bayet, Quinn, et al., 2015). Three-month-old infants experiencing mostly female caregiving also tend to visually prefer own-race female over male faces, but the effect is absent when faces are other-race and reversed in infants with male primary caregivers (Quinn, Uttley, et al., 2008; Quinn et al., 2002) . The interaction of face race with face gender in the visual preferences of infants at this age parallels the "other-race effect" for gender caregorization found in adults (O'Toole et al., 1996). In a similar line of reasoning, it could be predicted that face race would interact with face gender in the visual preference for smiling in 3.5-month-old infants, so that face gender would affect the visual preference for smiling in own- but not other-race faces.

The Bruce and Young model (1986) of face perception postulates a separation of variant (emotion, gaze) and invariant (identity, gender, race) face processing streams during structural encoding, the generation of a view-invariant, expression-invariant representation. Current models acknowledge a relative, but incomplete division of variant and invariant face processing streams in adults (Calder & Young, 2005; Haxby et al., 2000; Tiberghien et al., 2003). It remains an open question whether infants experience a more complete, or less complete, segregation of variant and invariant face processing streams, whether face processing develops through an increasing integration between the streams or whether variant and invariant streams interact from infancy and possibly become more independent with expertise; current evidence suggests that variant and invariant face processing streams interact in infants at least as much and possibly more than in adults (Hoehl & Striano, 2008). For example, 3-month-old infants recognize a face better when it is smiling dynamically during familiarization (Brenna et al., 2012; Turati et al., 2011), paralleling similar associations in adults (Baudouin, Gilibert, et al., 2000). The effect of face gender on the visual preference for smiling at 3.5-months is another example of interaction between variant and invariant face processing in infants (Bayet, Quinn, et al., 2015). Thus, smiling perception in infants could be affected by face race.

The present study aimed to test whether the effect of face gender on the looking preference of infants for smiling expressions depends on face race, as predicted by an experience-based account. We presented male and female own- (Caucasian) and other- (Chinese) race smiling faces paired with neutral faces of the same individual to 3.5-month-old infants (FIGURE 4.9, $n = 54$), an age at which an effect of face gender on the visual preference for smiling has been reported (Bayet, Quinn, et al., 2015). Low-level properties of the faces were equated, two different stimulus sets with closed-mouth smiles were used in order to avoid a "teeth saliency effect" (TABLE 4.1), and looking preferences were measured. It was predicted that face gender would modulate the visual preference for smiling in own- but not other-race faces, and more specifically, that infants may show a stronger visual preference for smiling in own-race female faces than in other face categories due to predominanly female caregiving (Rennels & Davis, 2008; Sugden et al., 2014). Birth and gestational age at birth were used to model the developmental trajectories of the visual preference for smiling versus neutral faces as it develops through experience and maturation. Age from birth reflects both maturation and experience, gestational age at birth reflects maturation but not experience, and face race and face gender reflect experience but not maturation. For example, if smiling versus neutral preferences stem mostly from experience, then it is to be expected that the visual preferences for smiling versus neutral Caucasian (own-race) but not Chinese (other-race) faces will be predicted by age from birth but not by gestational age, and modulated by the face gender (Bayet, Quinn, et al., 2015). If smiling versus neutral preferences are independent of visual experience, then it is expected that they will be independent of face race, but possibly vary according to birth and gestational age. Alternatively, the preferences may stem from the combined effects of developmental readiness (maturation) and environmental input (experience).

### 4.3.4 Methods

#### 4.3.4.1 Participants

Fifty-four 3.5-month-old infants (22 girls, mean age 116.0 ± 0.8 days) were included in the study. All caregivers gave informed written consent before testing, and all infants were born full term (39.0 ± 0.9 weeks of amenorrhea). Four additional infants were excluded due to fussiness ($n = 1$), technical failure ($n = 1$), or experimental error ($n = 2$). Twenty of the included infants exhibited side-bias (i.e., they looked in one direction more than 95% of the time) in either the male or female pairing, but not both. For those infants, the invalid pairing was excluded but the other pairing was included. Fourteen additional infants exhibited a side-bias in both female and male stimuli pairings and were excluded. All caregiver(s) reported a percent of female caretaking of at least 50% (mean 73 ± 1%), meaning that no infant was primarily raised by a male caregiver, and providing results that are consistent with previously reported estimates (Rennels & Davis, 2008; Sugden et al., 2014).

#### 4.3.4.2 Stimuli

Two sets of stimuli were used that had different face identities (sets A and B, TABLE 4.9). Face stimuli were selected from the same unpublished cross-race database of Chinese and Caucasian emotional faces (see SECTION 4.3.9.1 for the validation study). Emotional properties of the stimuli are summarized in TABLE 4.9. None of the faces had visible teeth (the mouth was closed). Stimuli were gray scaled; external features were cropped. Luminance, contrast, spatial frequencies, and placement of the eyes were matched using SHINE (Willenbockel et al., 2010) and Psychomorph (Tiddeman, 2005). Faces subtended a visual angle of about 18 degrees (vertically) by 14 degrees (horizontally).

#### 4.3.4.3 Procedure

The infants sat on their caregiver's lap about 60 cm from the screen. Stimuli were presented using E-Prime 2.0 (Schneider et al., 2002). Each infant saw trials arranged in two pairings of two consecutive trials. In the female pairing, infants saw a neutral female face paired with a smiling face from the same individual (FIGURE 4.9). Left-right side of presentation was reversed across the two trials of each pairing. The order of the pairings, the order of the trials within each pairing, stimulus set, and face race were counterbalanced across infants. Each trial lasted 10 s from first look. Each infant saw 4 trials showing 1 female and 1 male pair of faces. There were 2 trials for each pair, with left-right side of presentation reversed. The infant's gaze was redirected to the center of the screen between each trial. The experiment was approved by the local ethics committee (Institutional Review Board).

#### 4.3.4.4 Data acquisition, pre-processing, and analysis

Infant looking was recorded by a camera and coded off line with 40 ms precision (25 frames per second). A sub-sample of the videos was coded by a second observer with 0.97 agreement (Pearson's $r$, 26% of the videos). Analyses were run in Matlab 7.9.0529 using the Statistics toolbox and in R 3.0.2 using the nlme 3.1 package (Pinheiro et al., 2012). Looking preferences towards each stimulus were derived from looking times (Percentage of Total Looking Time, PTLT). For example, the looking preference (PTLT) for the smiling female face for each infant was the average of the percentages of looking time to the smiling female face (versus the neutral female face) in the two trials featuring female stimuli. PTLTs from male or female

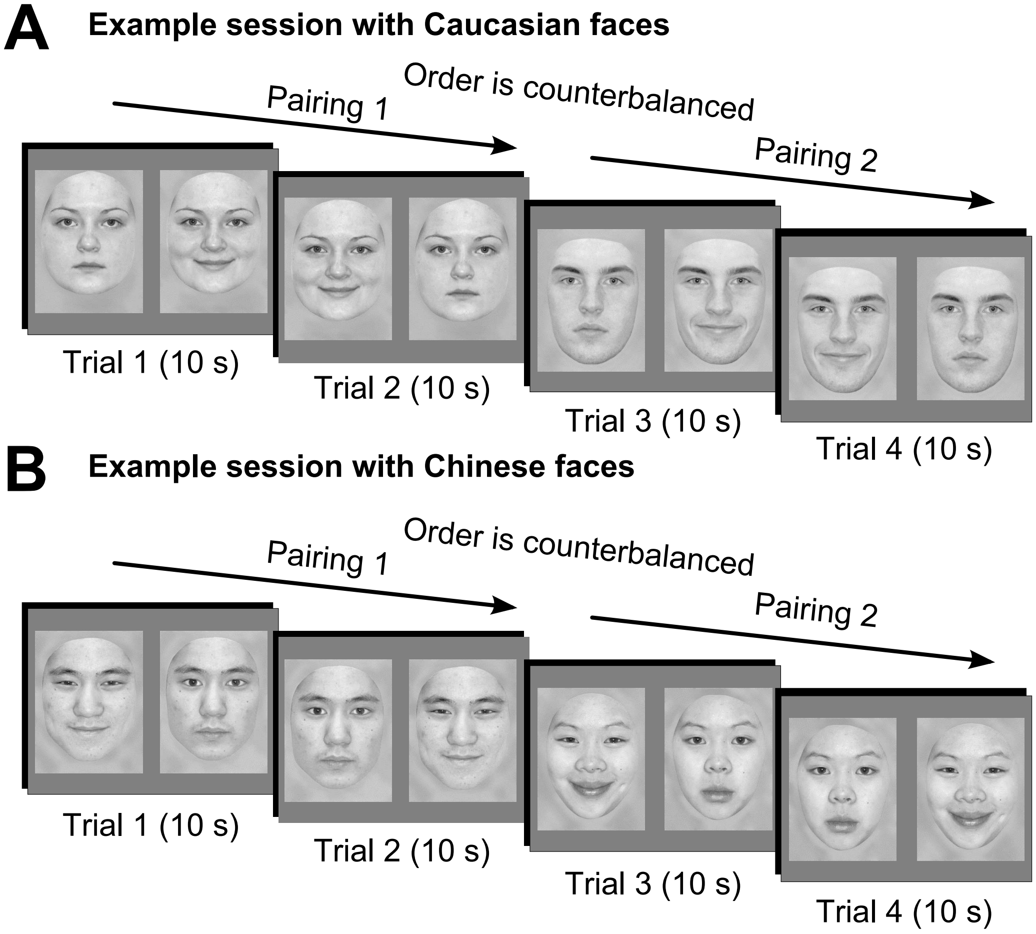


Figure 4.9: **Example sessions.** Each infant saw four trials, featuring faces that were either (A) own-race or (B) other-race. Infants were drawn from a predominantly Caucasian environment.

pairings in the Caucasian or Chinese face condition further than 2 standard deviations away from the corresponding group mean were considered outliers and excluded (3 data points, 4.5%). The handling of outliers was decided a priori and in accordance with common methods in infant research (e.g. Beier & Spelke, 2012; Surian et al., 2007).

## 4.3.5 Results

### 4.3.5.1 Preliminary analyses and an effect of infant gender

A preliminary ANOVA on the visual preference for smiling versus neutral faces revealed no significant effect of stimulus set, either alone ($F(1,50) = 0.61$, $p = 0.438$), or in interaction with participant's gender ($F(1,50) = 0.28$, $p = 0.599$). There was, however, a significant effect of the participant's gender on this variable ($F(1,50) = 6.31$, $p = 0.015$). Preliminary ANOVAs found no further effect of these factors on the visual preference for smiling female faces, smiling male faces, or the difference between both variables (all $p$s > 0.05). Thus, data was pooled across stimulus sets but participant's gender was retained as a factor in subsequent analyses.

There was no overall visual preference for either smiling or neutral faces in boys (paired Student $t$-test, $t(31) = -0.80$, $p = 0.430$), but there was a general visual preference for smiling versus neutral faces in girls (paired Student $t$-test, $t(21) = 2.53$, $p = 0.020$; mean preference for smiling: 56.45 ± 11.98 %). Student $t$-tests for independent samples revealed no significant differences between boys and girls in terms of age from birth, gestational age at birth, age from term, or reported female versus male caretaking ratio (all $p$s > 0.05).

### 4.3.5.2 Effect of face gender and face race on group-level preferences

We next analyze the effect of face gender and face race on the group-level visual preference for smiling versus neutral faces. Because the analysis involves both within- (face gender) and between- (face race, participant gender) subjects effects with several missing data points (from the participants who had a side-bias on one of the pairings), a linear mixed model approach is used.

A linear model of the visual preference for smiling versus neutral faces revealed no significant group effects of Face gender or Face race, either alone or in interaction (TABLE 4.7). Similar null effects for face race and face gender were found when analyzing the visual preferences of boys and girls separately (all $p$s > 0.05).

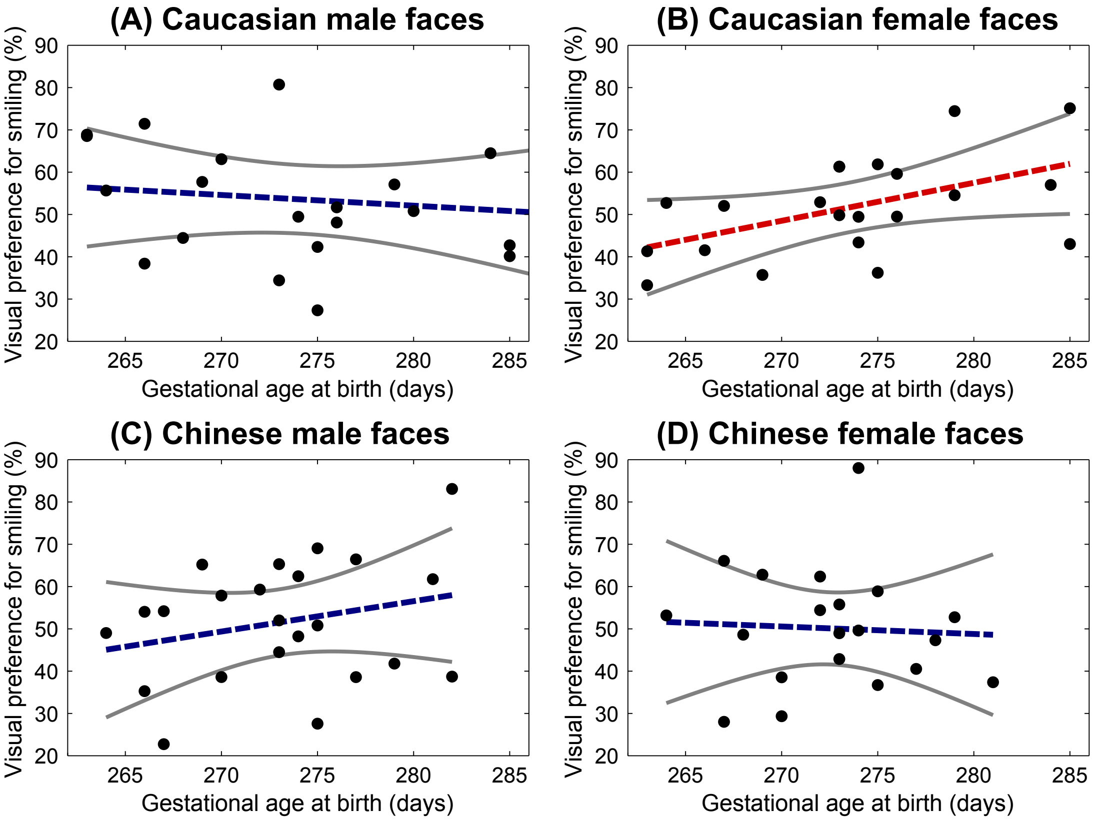


Figure 4.10: **Combined effect of gestational age and visual experience in the the visual preference for smiling versus neutral faces.** Percentages of Total Looking Time (PTLT) to the smiling versus neutral face. Faces were either Caucasian own-race (A-B) or Chinese other-race (C-D), male (A, C) or female (B, D). A linear model of visual preferences revealed a triple interaction of face gender, face race, and the infant's gestational age at birth. Further analysis revealed a significant effect of gestational age at birth on the visual preference for smiling versus neutral Caucasian female faces (B). No effect could be found on the visual preference for smiling versus neutral Chinese or male faces (A, C-D). Similar trends were found for birth age, but were not statistically significant. One observation is not visible on the plot (gestational age at birth > 290 days) but included in the analysis. Dashed lines represent linear tendencies (red, statistically significant; blue, non statistically significant), with 95% confidence intervals represented by gray lines.

| Fixed effect | β | *t*(74) | *p* |
|---|---|---|---|
| (Intercept) | 0.53 | 14.23 | < 0.001 |
| Face gender (male) | 0.04 | 0.76 | 0.449 |
| Face race (Chinese) | - 0.04 | - 0.53 | 0.600 |
| Participant gender (male) | - 0.02 | - 0.32 | 0.747 |
| Face gender by Face race | - 0.01 | - 0.12 | 0.903 |
| Face gender by Participant gender | - 0.06 | - 0.73 | 0.466 |
| Face race by Participant gender | 0.01 | 0.10 | 0.918 |
| Face race by Face gender by Participant gender | 0.07 | 0.53 | 0.597 |

Table 4.7: **Linear model of the group-level visual preference for smiling versus neutral faces.** Visual preference was measured by PTLT, percentage of total looking time. Random effects for the participant factor were dropped based on Akaike information criterion (AIC). Estimated slopes for categorical factors are based on the levels indicated between parentheses. Three observations were excluded based on the distribution of residuals. Note that the effect of Participant gender was not statistically significant in this analysis. $R^2 = 0.06$.

#### 4.3.5.3 Experience-dependent developmental trajectories

It is possible that the null results found at group level result from infants in our group having different response profiles depending on developmental factors such as age. We next estimate the developmental trajectories of the visual preference for smiling versus neutral faces of both races and genders, combining continuous developmental factors (age from birth, gestational age at birth) with experience-sensitive face dimensions (face race, face gender) and controling for participant gender.

A linear model of the visual preference for smiling versus neutral revealed a three-way interaction between face race, face gender and gestational age at birth, controling for infant gender (TABLE 4.8). Further analyses revealed that the triple interaction stemmed from an interaction of face gender and gestational age at birth for Caucasian ($t(33) = -2.39$, $p = 0.023$) but not Chinese ($t(35) = 1.26$, $p = 0.218$) faces, and from an additional marginal interaction of face race and gestational age at birth for female ($t(33) = -1.78$, $p = 0.084$) but not male ($t(35) = 1.59$, $p = 0.122$) faces. A significant main effect of gestational age at birth was evident overall and in the visual preferences for smiling in Caucasian ($t(33) = 2.33$, $p = 0.032$) and female ($t(33) = 2.41$, $p = 0.022$) faces, but not Chinese ($t(35) = -0.47$, $p = 0.639$) or male ($t(35) = -0.95$, $p = 0.351$), and in Caucasian female ($t(17) = 2.54$, $p = 0.021$) but not Caucasian male ($t(15) = -0.99$, $p = 0.343$) faces (FIGURE 4.10). No additional significant effects were found. In particular, no significant effect was found for age from birth, either alone or in interaction with stimulus properties (all *p*s >0.05).

| Fixed effect | β | *t*(69) | *p* |
|---|---|---|---|
| (Intercept) | 0.59 | 14.54 | < 0.001 |
| Face gender (male) | - 0.05 | - 0.96 | 0.341 |
| Face race (Chinese) | - 0.11 | - 1.52 | 0.134 |
| Birth - term * | 0.06 | 2.10 | 0.040 |
| Age from birth | 0.03 | 0.91 | 0.369 |
| Participant gender (male) | - 0.04 | - 1.08 | 0.285 |
| Face gender by Face race (.) | 0.18 | 1.87 | 0.066 |
| Face gender by Birth - term * | - 0.08 | - 2.24 | 0.028 |
| Face race by Birth - term | - 0.08 | - 1.54 | 0.129 |
| Face gender by Age from birth | 0.02 | 0.36 | 0.717 |
| Face race by Age from birth | - 0.02 | - 0.49 | 0.623 |
| Face race by Face gender by Birth - term * | 0.15 | 2.34 | 0.022 |
| Face race by Face gender by Age from birth | - 0.05 | - 0.73 | 0.466 |

Table 4.8: **Linear model of the visual preference for smiling versus neutral faces, accounting for developmental factors.** Three observations were excluded from the model, one based on missing gestational age information and two based on the distribution of residuals. Visual preference was measured by PTLT, percentage of total looking time. Birth - term represents gestational age at birth. Random effects for the participant factor were dropped based on Akaike information criterion (AIC). Estimated slopes for categorical factors are based on the levels indicated between parentheses. Continuous predictors were centered and scaled. Significant effects are marked with an asterisk, marginal effects are marked with a dot (.). Note that the effect of Participant gender was not statistically significant in this analysis. $R^2 = 0.17$.

### 4.3.6 Discussion

This study investigated the role of visual experience on the looking preferences for neutral versus smiling faces in 3.5-month-old infants. An overall preference for smiling versus neutral faces was found in female but not male infants, and both face race and face gender were found to interact with gestational age. Specifically, increasing gestational age at birth was associated with a higher preference for smiling versus neutral female own-race (Caucasian) faces only, a restriction that is consistent with the increased visual and social experience of young infants with these types of faces. The results confirms earlier reports of a female advantage in facial emotion perception during early development, support the hypothesis that experience with types of faces affects the visual preference for smiling emotional faces of 3.5-month-old infants, and reveal an additional moderating role of gestational age at birth on the effect of visual experience.

An effect of infant gender was found in some but not all analyses, where female infants had a higher visual preference for smiling versus neutral faces than male infants. Gender differences favoring girls in facial emotion perception task performance have been reported in developmental studies (for a meta-analysis, see McClure, 2000). Some authors have suggested that these differences could, at least partially, be explained by a slower development of temporal lobe structures in male than female infants that is mediated by androgen levels (McClure, 2000). There is also some evidence that mothers typically display more positive affect towards their female than towards their male infants (Malatesta, Rich, & An, 1989), which could underly the present effect. Finally, it is possible that the present gender differences were mediated by temperamental dimensions such as perceptual sensitivity (Else-Quest, Hyde, Goldsmith, & Van Hulle, 2006), especially since the smiles presented were closed-mouth and relatively subtle.

The results clearly demonstrate that visual preferences for smiling versus neutral facial expressions are neither rigid nor universal in 3.5-month-old infants, replicating earlier findings (Bayet, Quinn, et al., 2015). While the present pattern of preferences for male and female smiles and neutral faces differed from these earlier findings, possibly due to differences in smile intensity, it supports the hypothesis that these preferences are experience-dependent, affected by face gender as well as face race. Face gender and face race interacted so that the gender of own-race but not other-race faces had an effect on visual preferences. A similar pattern has been described for female versus male face preferences (Quinn, Uttley, et al., 2008). It is possible that experience-based biases in infants act as a stepping stone to later interactive effects of face gender and facial emotion in the perception of children and adults (e.g. Bayet, Pascalis, et al., 2015; Hess et al., 2009). Such perceptual-to-social trajectories are beginning to emerge in the study of racial prejudice (Quinn et al., 2015; W. S. Xiao et al., 2015). More generally, future investigations of early facial emotion processing should favor cross-cultural studies with own- and other-race faces (e.g. as in Kelly et al., 2009) and include enough male and female faces stimuli to estimate the effect of face gender. Although face gender (Ramsey-Rennels & Langlois, 2006) and face race (Kelly et al., 2007) on face perception abilities in infants, as many studies of facial emotion processing in infancy use only own-race female faces as stimuli. It remains an open question whether the visual preference for smiling expressions in newborns (Farroni et al., 2007; Rigato et al., 2011) also depends on visual, social experience with faces. It also remains unknown whether the visual preference for female versus male faces would correlate with the visual preference for smiling in female faces in a within-subject fashion, controlling for general development.

A modulatory effect of gestational age at birth (birth minus term), but not age from birth, was reported. The effect of gestational age interacted with experience-sensitive dimensions of the faces, meaning that gestational age at birth modulated experience-dependent facial emotion processing in our sample. It was initially predicted that the developmental trajectory of visual preferences would be reflected by either age from birth alone or by the additive effect of gestational age at birth and age from birth. Here, only gestational age at birth was found to affect the infants' visual preferences, even though all included infants were healthy and considered to be born full term. More specifically, increased gestational age at birth was associated with higher visual preferences for smiling versus neutral female own-race faces. It is likely that gestational age at birth captured individual variations in general developmental readiness, visual acuity, maternal stress (Wadhwa et al., 1993), infant temperament (e.g. attention, perceptual sensitivity, negative emotionality), or emotion socialization (Malatesta, Grigoryev, Lamb, Albin, & Culver, 1986) that were not captured by the variations in age from birth in our sample. For example, there is neurophysiological evidence that infant temperament affects the processing of emotional faces in 7-month-old infants (Ravicz, Perdue, Westerlund, Vanderwert, & Nelson, 2015; see also Jessen & Grossmann, 2015).

It is in any case intriguing that even normal variations in gestational age at birth influence experience-dependent visual preferences more than 3 months after birth. It is also demonstrated that the accumulation of experience around the age of 3.5-months doesn't reliably modulate infants' visual preference for smiling versus neutral faces. Further studies are needed to determine whether this is a false negative (e.g. the effect is small and necessitates larger samples and increased variations in age to be detected) and what critical parameter (e.g. general development, visual acuity, temperament, or maternal stress) mediated the effect of gestational age at birth. More generally, future studies of individual differences in emotion processing in infancy could include gestational age at birth as a predictor along with measures of infant temperament or environmental stress.

Cognitive as well as neurophysiological models of face perception in adults emphasize the relative separation of variant (e.g. gaze, emotion) and invariant (e.g. identity, gender) streams (Bruce & Young, 1986; Calder & Young, 2005). The separation is not complete, however. For example, adults are slower to identify the expression portrayed by unfamiliar than familiar faces when the task is rendered difficult by experimental manipulation (Baudouin, Sansone, & Tiberghien, 2000). More specifically, it has been suggested that the relative independence of emotion and identity processing derives from the relative speed of both streams, with emotion information being typically extracted faster than identity information (Baudouin, Sansone, & Tiberghien, 2000). Increased perception of emotional expression in familiar rather than unfamiliar faces has also been described in infants (Kahana-Kalman & Walker-Andrews, 2001; Montague & Walker-Andrews, 2002), and the parental distribution of caregiving has been found to modulate the reaction of 14-month-olds to emotional expressions displayed by their mother and father (Gredebäck et al., 2012). Here, we extend these findings by showing that emotional expression processing in unfamiliar faces (at least in terms of visual preferences) is partly affected by the familiarity of the face category (race, gender), an invariant dimension. This is not typically the case in adults; emotion recognition is one of the few face processing abilities that is spared by the "other-race effect" (Ekman, 1980).

It has been suggested that variant and invariant streams of face processing are more interdependent in infants than in adults (Hoehl & Striano, 2008; see also M. H. Johnson, 2000), in line with the less robust structural encoding in young infants (Gliga & Dehaene-Lambertz, 2007; M. H. Johnson et al., 2005). For example, the infant N290 is modulated by gaze in static pictures, but the adult N170 is not (Farroni et al., 2002), and infants younger than 5 or 7 months typically fail to show evidence of an identity-invariant representation of emotional expression (e.g. R. F. Caron et al., 1985) as well as of an expression-independent representation of face identity (e.g. M. Kobayashi et al., 2014). The present results, together with earlier studies (e.g. Bayet, Quinn, et al., 2015), partly support this hypothesis. It appears that the relative and incomplete independence of variant and invariant face processing streams may be acquired during development in infancy, possibly through increased speed of emotion information processing (Baudouin, Sansone, & Tiberghien, 2000) and increased experience with different types of faces in different viewing conditions (i.e. an exemplar-based generalization process). Models of face perception in adults (Bruce & Young, 1986; Tiberghien et al., 2003) further suggest that the invariant recognition of different faces (structural encoding), and the extraction of variant information in different faces would scaffold each other in development so that individual differences in one ability may predict individual variations in the other at a given age.

### 4.3.7 Conclusion

In conclusion, here we show that the visual preferences of 3.5-month-old infants to smiling versus neutral faces are interactively shaped by visual, social experience with faces (face race, face gender) and individual factors (gestational age at birth). No relation with age from birth was found in our sample. The results are partly consistent with the hypothesis that facial emotion processing develops through experience in infancy, and that variant and invariant face processing are more interdependent in infants that in adults. Future studies of emotional faces perception in infants and newborns should research individual differences including differences in temperament, gestational age and male-female caregiving arrangements, cross-cultural differences, and a developmental link between invariant recognition and expression processing abilities.

### 4.3.8 Acknowledgments

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### 4.3.9 Supplementary materials and methods

#### 4.3.9.1 Stimuli validation

**Participants and data pre-processing.** Twenty-two young adults from a predominantly Caucasian environment were included in the validation study (mean age 20.64 years, range 17-29, 5 men). All gave informed consent and had normal or corrected-to-normal vision. The experiment was approved by the local ethics committee (Institutional Review Board). Two additional participants were excluded, one because of antidepressant use and one because of abnormally low accuracy during the training phase (less than 75% accuracy). Labelling and rating trials with a reaction time below 200 ms or above 2 standard deviations from each participant's own mean were considered invalid, resulting in the exclusion of 9.09% of the data points.

**Stimuli.** A set of 240 color photographs of faces from 80 young adults displaying angry, neutral or smiling expressions was selected from an unpublished cross-race database of emotional faces. Models wore hair caps and were either male or female, Chinese or Caucasian. The rationale for including angry faces in the procedure was that neutral expressions are often confused with angry or sad expressionss (e.g. Goeleven et al., 2008). No sad faces were available in the cross-race database.

**Procedure.** Participants were seated 70 cm from the screen. Stimuli were presented using E-Prime 2.0 (Schneider et al., 2002).

A trial began with a 1000 to 1500 ms fixation cross, followed by a central face subtending a visual angle of about 6 by 8 degrees. Participants responded using the mouse. First, participants labeled the expression of the face as either "joy", "anger", "neutral", or "other" by clicking on the appropriate label beneath the face. Then, participants rated the intensity of the expression on a horizontal rating scale beneath the face ranging from 0 (not intense at all) to 9 (very intense).

Each session began with 8 training trials. In the training phase, participants labeled and rated the intensity of the expression of 8 highly valid, male and female face stimuli from the Karolinska Directed Emotional Face database displaying neutral, smiling, angry, and sad expressions (Calvo & Lundqvist, 2008; Lundqvist et al., 1998), and received feedback. The 8 faces were presented in random order.

During the experimental phase, participants labeled and rated the intensity of each of the 240 emotional faces. No feedback was provided. The 240 faces were presented in random order, with 5 s mandatory breaks every 40 trials.

**Data analysis.** Analyses were conducted in Matlab 7.9.0529 and R 2.15.2. Mean hit rates and intensity ratings were computed for each of the emotional faces, and two sets of models displaying smiling and neutral expressions were selected on the basis of (1) high validity and (2) comparable values across stimuli categories (Chinese, Caucasian; male, female).

| Stimuli category | | Set | Age | Smiling faces | | | Neutral faces | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Hit rate (%) | Intensity (0-9) | Most frequent misidentification | Hit rate (%) | Intensity (0-9) | Most frequent misidentification |
| Caucasian | Female | A | 19 | 100 ± 0 | 5.05 ± 2.31 | - | 100 ± 0 | 5.86 ± 2.97 | - |
| | | B | 19 | 100 ± 0 | 4.25 ± 1.77 | - | 100 ± 0 | 5.00 ± 2.79 | - |
| | Male | A | 22 | 100 ± 0 | 4.56 ± 1.62 | - | 100 ± 0 | 4.11 ± 2.38 | - |
| | | B | 19 | 100 ± 0 | 4.50 ± 1.50 | - | 100 ± 0 | 4.59 ± 2.84 | - |
| Chinese | Female | A | 19 | 100 ± 0 | 6.06 ± 1.61 | - | 96 ± 21 | 4.48 ± 2.94 | Other |
| | | B | 25 | 100 ± 0 | 5.68 ± 2.10 | - | 100 ± 0 | 4.89 ± 2.96 | - |
| | Male | A | 22 | 100 ± 0 | 4.29 ± 2.03 | - | 96 ± 21 | 4.87 ± 2.83 | Other |
| | | B | 30 | 95 ± 22 | 4.55 ± 2.01 | Other | 97 ± 22 | 4.85 ± 2.91 | Other |

Table 4.9: **Stimuli properties.** Mean (± standard deviation) hit rates and ratings obtained from a group of young adults from a predominantly Caucasian environment (SECTION 4.3.9.1).

#### 4.3.9.2 Supplementary tables and figures

## 4.4 SUMMARY

In this chapter we reported that the visual preference of 3.5-month-olds for full-blown, open-mouth smiling (versus neutral) expressions is limited to female faces and reversed in male faces (SECTION 4.1). No effect could be detected in 9-month-olds (SECTION 4.2.1), and in 3.5-month-olds the effect of face gender in the visual preference for smiling decreased with age from birth as well as with gestational age (SECTION 4.2.2.3). The relationship between smiling preference and smiling behavior was marginal or absent in both age groups when controlling for age and gestational age at birth (SECTION 4.2.3). A follow-up study on the visual preference for closed-mouth smiling (versus neutral) expressions in 3.5-month-olds revealed a slightly different, though converging, picture (SECTION 4.3). There was no reliable visual preferences at group level, presumably due to increased task difficulty of closed-mouth ("subtle") smiles. However, the visual preference for smiling expressions was found to be mediated by gestational age at birth in an experience-dependent fashion, as the relationship was limited to own-race female faces. The reversed direction of the effect of gestational age compared to the earlier study could be attributed to the increased task difficulty compared to the earlier study using open-mouth smiles. The effect of age from birth was also not replicated.

In summary, the visual preference of young infants for smiling expressions appears mediated by the interaction of (1) smile intensity or teeth visibility, (2) experience with faces, and (3) developmental factors including gestational age at birth. It is possible that such early links between face race, face gender, and facial expressions may pave the way to the early ontogeny of similar associations in children and adults (e.g. SECTION 3). Because experience with faces and developmental factors are mostly dependent on the individual infant, future studies of early facial emotion processing should better account for individual variations. A direct follow-up would be to repeat the experiment in SECTION 4.3 with open-mouth smiles. Ideally, the effect of smile intensity versus teeth visibility could be systematically researched as well in order to resolve long standing controversies on the role of irrelevant stimuli parameter (e.g. Oster, 1981). Smile intensity and teeth visibility (local contrast) were conflated in our studies. Of course, within-subject studies with numerous categorical and continuously varying predictors are challenging in young infants, but the case can be made that they should be favored when methodological difficulties can be overcome (e.g. Aslin & Fiser, 2005).

## Chapter 5

# WHO TO FOLLOW, WHAT TO LEARN: FACE GENDER AND POSITIVE EMOTION EFFECTS ON GAZE REFERENCING IN INFANCY

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## 5.1 INTRODUCTION OF THE ARTICLE

The last two chapters (CHAPTERS 3 and 4) were dedicated to encoding aspects of emotional facial expression perception by infant and children, i.e. how expressions are processed in integration, or independently from, other types of face processing. At the beginning of the thesis, we asked whether interactions between face dimensions (gender, emotion) were a developmental gain-of-function or a built-in characteristic of face processing. The results of the last two chapters are in favor of the later; interactions between face gender and facial emotion processing could be found not only in children (CHAPTER 3), but also in 3.5-month-old infants (CHAPTER 4). Studies in newborns with very limited visual and social experience are necessary to draw definite conclusions, but overall there is ground to support the idea that variant and invariant streams of face perception interact at least as much and possibly more in infancy than in adulthood and that experience with faces affects how infants perceive the smiling expressions portrayed by strangers even before the pivotal age of 5-7 months. More specifically, we found that the visual preference for smiling expressions was restricted to own-race female faces in 3.5-month-olds, and that experience with faces interacted with individual characteristics (gestational age).

The next two chapters (CHAPTERS 5 and 6) are dedicated to attentional and perceptual aspects of emotional expression perception in infants, i.e. how emotional faces may guide infants' social attention either by interacting with gaze direction (CHAPTER 5) or because of their salience (CHAPTER 6). Both chapters will consider developmental trajectories in infancy ranging from 3.5 to 12 months. In particular, the following chapter will examine whether positive emotional expressions (e.g. smile), like their negative counterparts (e.g. fear), are processed as referring to objects in a behavioral object referencing paradigm, and whether infants follow and use male gaze as much as female gaze.

Box 7: Résumé de l'article "Who to follow, what to learn: Face gender and positive emotion effects on gaze referencing in infancy"

> Bayet L., Quinn P. C., Lee K., Gentaz É., & Pascalis O. (en préparation) Who to follow, what to learn: Face gender and positive emotion effects on gaze referencing in infancy
>
> Le comportement de référencement du regard chez le nourrisson se caractérise par (1) le suivi du regard référentiel et (2) la mémorisation accrue des objets référencés mise en évidence par un test de reconnaissance. Nous avons examiné la trajectoire développementale de l'influence du genre du visage et de l'expression du sourire sur le référencement du regard à 3.5, 9 et 12 mois en utilisant un paradigme classique de référencement du regard. Le suivi du regard était affecté par le genre du visage ainsi que par le sourire à 12 mois, le suivi du regard étant alors maximal pour les visages féminins souriants. Cependant, seul le genre du visage a modulé la mémorisation des objets référencés : les nourrissons de 9 mois ont montré une meilleure mémorisation des objets référencés par les visages féminins. Les résultats n'ont montré aucun effet de l'expression du sourire sur la mémorisation des objets référencés, et ni les nourrissons de 3.5 mois ni les nourrissons de 12 mois n'ont montré de préférence visuelle pour l'objet référencé en phase de test. Les résultats confirment l'hypothèse d'une dissociation fonctionnelle entre le suivi du regard et la mémorisation des objets référencés, d'une part, et l'hypothèse d'un développement précoce du biais de négativité, d'autre part.

## 5.2 ABSTRACT

Gaze referencing behavior in infants is evidenced by (1) gaze following and (2) referential object learning, i.e. superior recognition of a cued object in subsequent presentation. Here, we document the developmental trajectory of face gender and positive emotion influences on gaze referencing in 3.5-, 9- and 12-month-olds using a gaze referencing paradigm. Gaze following was affected by face gender and positive emotion in the oldest age group as 12-month-olds displayed maximal gaze following in the smiling female face condition. Only face gender influenced 9-month-olds referential object learning as a superior recognition of the cued object was found only in the female condition. No evidence for a modulation of referential object learning by positive emotion was found, and neither 3.5- nor 12-month-olds showed a preference for the cued (or uncued) object in subsequent presentation. The results are consistent with the functional dissociation of gaze following versus referential object learning in gaze referencing tasks and with the hypothesis of an early negativity bias in infants.

## 5.3 INTRODUCTION

Gaze following develops early in infancy, becoming more sophisticated towards the end of the first year (Gredebäck, Theuring, Hauf, & Kenward, 2008; Hoehl, Reid, & Parise, 2009; Shepherd, 2010). The behavior is shared with other species and is thought to rest upon both a retinotectal pathway and a cortical pathway implicating the superior temporal sulcus as well as other areas of the extended face processing network in humans (Haxby et al., 2000; Shepherd, 2010). Gaze following in human infancy has been linked to the later development of language and theory of mind abilities (Shepherd, 2010), is thought to scaffold learning about objects (Becchio, Bertone, & Castiello, 2008; Pauen, Birgit, Hoehl, & Bechtel, 2015; Reid & Striano, 2005), and appears to emerge from visual experience and learning (Paulus, 2011; Peña et al., 2014; Triesch, Teuscher, Deak, & Carlson, 2006). The relationship between gaze following and referential object learning is not linear; referential object learning involves more social understanding than gaze following (Becchio et al., 2008). For example, 4-month-old infants follow a stranger's gaze more than their mother's gaze (Gredebäck, Fikke, & Melinder, 2010), but show increased recognition only for objects cued by their caregiver's gaze (Hoehl et al., 2012). Similarly , 12-month-olds follow a robot's gaze as much as a human gaze, but show increased recognition only for objects cued by human gaze (Okumura, Kanakogi, Kanda, Ishiguro, & Itakura, 2013).

Infants younger than 5-7 months of age spontaneously attend more to smiling than neutral expressions (Farroni et al., 2007; La Barbera et al., 1976; Rigato et al., 2011), and more to female than male faces (Quinn et al., 2002). The preference for smiling is more robust in female than male faces (Bayet, Quinn, et al., 2015). We hypothesized that these spontaneous visual preferences could translate to biases in gaze following and referential object learning depending on the face gender and smiling expression. Indeed, gaze and facial emotions - two variant aspects of face processing - are processed interactively in infants (Hoehl, Palumbo, et al., 2008; Hoehl & Striano, 2008, 2010; Hoehl, Wiese, & Striano, 2008; Striano et al., 2006). Interactions between variant and invariant aspects of face processing have also been reported (Hoehl & Striano, 2008), such as between gaze and identity (Hoehl et al., 2012), gaze and gender (Pickron, Fava, & Scott, 2014), or expression and gender (Bayet, Quinn, et al., 2015). However, the impact of smiling expressions on gaze cueing in infants remains unknown. Some authors suggest that the negativity bias, the tendency for negative but not positive emotional information to guide attention, could be present in infancy (Vaish, Grossmann, & Woodward, 2008) - but conflicting results have been obtained in 3-month-olds (Hoehl & Striano, 2010), 18-month-olds (Egyed, Király, & Gergely, 2013), and 24-month-olds (Vaish, Grossmann, & Woodward, 2015). Thus, whether infants use object-directed smiling expressions from male and female faces to attend to and learn about objects remains an open question.

In the present study, we used a typical gaze cuing paradigm (Reid & Striano, 2005) in which pictures of male or female faces displaying smiling or neutral expressions gazed towards unfamiliar objects after a period of direct gaze. The same objects were subsequently presented without the face as a test of visual recognition (Okumura et al., 2013; Pascalis & de Haan, 2003; Reid & Striano, 2005). We compared 3.5- ($n$ = 84), 9- ($n$ = 64), and 12-month-old infants ($n$ = 60) infants. The visual preference for the cued (versus uncued) side at test was also briefly examined, as the gaze shift may direct the infants' attention towards the cued side rather than towards the cued object. The experiment aimed (1) to document the developmental trajectory of interactive effects of face gender and smiling expression on gaze processing between 3.5 and 12 months of age and (2) to test for an effect of positive emotions on gaze following and referential object learning in infancy.

## 5.4 METHODS

### 5.4.1 Participants

A total of 84 3.5-month-ols (39 girls, mean age. 116.3 ± 0.6 days s. e. m), 64 9-month-olds (31 girls, mean age 284.8 ± 0.6 days) and 60 12-month-olds (30 girls, mean age 375.4 ± 0.7 days) from a predominantly Caucasian environment were included in the study. All caregivers gave informed written consent before testing, and all infants were born full term (39.1 ± 0.1 weeks of amenorrhea). All caregiver(s) reported a percent of female caretaking of at least 50% (mean 72.7 ± 0.8 %), meaning that no infant was primarily raised by a male caregiver, and providing results that are consistent with previous reports (Rennels & Davis, 2008; Sugden et al., 2014). Test trials with side bias (more than 95% of looking time to the same side of the screen) were excluded.

Fifteen additional infants (8 3.5-month-olds, 3 9-month-olds, 4 12-month-olds) were excluded due to fussiness (1 3.5-month-old, 3 9-month-olds, 1 12-month-old), technical failure (3 3.5-month-olds, 2 12-month-olds), side-bias on all trials at test (3 3.5-month-olds), or insufficient looking time during familiarization (< 2 s; 4 3.5-month-olds, 1 9-month-old; 1 12-month-old).

### 5.4.2 Stimuli

Two sets of Caucasian faces were selected from the RAFD Radboud Faces Database (Langner et al., 2010). Within each set, faces varied in gender (male, female), emotional expression (neutral, smiling) and gaze direction (direct, averted). Stimuli were gray scaled; external features were cropped. Luminance, contrast, spatial frequencies, and placement of the eyes were matched using SHINE (Willenbockel et al., 2010) and Psychomorph (Tiddeman, 2005). Faces subtended a visual angle of about 22 degrees (vertically) by 16 degrees (horizontally). Displacement of the pupils between the direct and averted gaze pictures was equivalent across conditions. Emotional and physical properties of the face stimuli are summarized in SUPPLEMENTARY TABLE 5.3.

Two pairs of objects were selected for each age group from the BOSS bank of standardized stimuli (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010) on the basis that no significant spontaneous visual preference for either object of the pairs could be found in this age group (all $ps > 0.500$; SUPPLEMENTARY TABLE 5.4; see SUPPLEMENTARY MATERIALS AND METHODS). Objects subtended a visual angle of about 13 degrees (vertically) by 13 degrees (horizontally).

### 5.4.3 Procedure

The infants sat on their caregiver's lap about 60 cm from the screen. Stimuli were presented using E-Prime 2.0 (Schneider et al., 2002). The experiment was approved by the local ethics committee (Institutional Review Board). Each infant saw two trials consisting of one familiarization and one test (FIGURE 5.1). Familiarization consisted in one central face flanked with two objects. After 1000 ms of direct gaze, the central face gazed towards one of the two objects and stayed in this position for 3000 ms. Previous studies have demonstrated that an initial period of direct gaze is critical in triggering gaze following in infants (Senju & Csibra, 2008; Senju, Csibra, & Johnson, 2008). Familiarization was followed by a paired preference test of the same two objects, without the central face, and with side of presentation reversed in half of the trials. Test lasted 5 s from first look. Similar paradigms in infants have been found to elicit gaze following effects during familiarization (e.g. Senju & Csibra, 2008) as well as visual preferences towards the cued or uncued object at test (e.g. Reid & Striano, 2005). Faces in the familiarization phase were either male or female (within-subjects) and displayed smiling or neutral expressions (between-subjects). Trial order, direction of gaze, object referenced, and side of presentation at test were counterbalanced across subjects. Face and object stimulus sets were counterbalanced independently (i.e. random selection without replacement). The

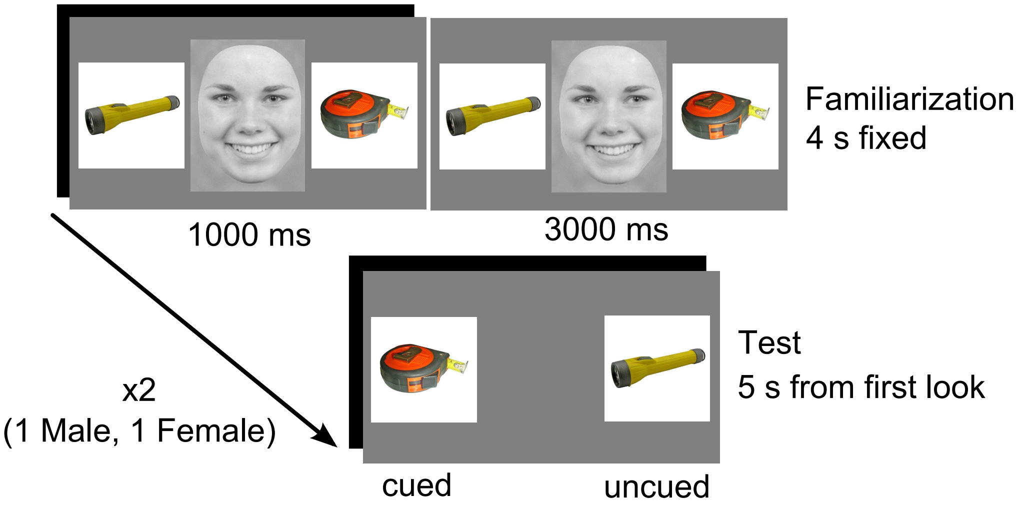

Figure 5.1: **Example session.** Each infant saw two trials consisting of a familiarization phase and a test phase; one of the trials featured a female face while the other featured a male face. Faces were either smiling or neutral. Infants were drawn from a predominantly Caucasian environment.

infant's gaze was redirected to the center of the screen before both familiarization and test.

### 5.4.4 Data acquisition, pre-processing, and analysis

Infant looking was recorded by a camera and coded off line with 40 ms precision (25 frames per second). A sub-sample of the videos was coded by a second observer with 0.96, 0.94 and 0.95 agreement in the 3.5-, 9- and 12-month-old group, respectively (Pearson's $r$, 25% of the videos). Analyses were run in Matlab 7.9.0529 using the Statistics toolbox and in R 3.0.2 using the nlme 3.1 package (Pinheiro et al., 2012). A (generalized) linear mixed model approach was used to account for the mix of within-subject (face gender) and between-subject (emotional expression) effects as well as for missing data points (from the participants who had a side-bias on one of the trials).

Gaze following was assessed during the familiarization phase, and the peak latency of the overall gaze following was measured as the latency where the maximal proportion of infants was looking towards the cued object (FIGURE 5.2). The proportion of infants looking towards each object at this latency was used for further analysis of looking behavior during familiarization.

Looking preferences towards each object at test were derived from looking times (Percentage of Total Looking Time, PTLT). In each condition and age group, PTLTs to the cued or uncued object at test further than 2 standard deviations away from the corresponding group mean were considered outliers and excluded (3.5-month-olds: 4 outliers, 2.7 % data points; 9-month-olds: 5 outliers, 3.9 % data points; 12-month-olds: 6 outliers, 5.1 % data points). The handling of outliers was decided a priori and in accordance with common methods in infant research (e.g. Beier & Spelke, 2012; Surian et al., 2007).

## 5.5 RESULTS

Gaze cuing is evidenced by (1) overt gaze following during familiarization, and (2) increased recognition of the cued object at test. The visual preference for the cued side at test is also examined.

### 5.5.1 Gaze following during familiarization

Looking behavior during familiarization was consistent with an overall cuing effect, as significantly more infants looked towards the cued than uncued object during a period of about 1000 to 2500 ms following the gaze shift by the central face (FIGURE 5.2). The overall proportion of infants looking towards the cued object peaked at the 2680 ms latency, i.e. 1680 ms after the gaze shift. This latency was similar across age groups (SUPPLEMENTARY FIGURE 5.5A-C).

The proportion of infants looking towards each of the two objects at the overall peak latency of gaze cuing (1680 ms post-shift) was used as a dependent variable to assess the effect of age group, face gender and emotional expression on gaze following during familiarization. Preliminary analyses revealed no significant effect of participant gender ($\chi^2(1) = 0.61$, $p = 0.435$), face stimulus set ($\chi^2(1) = 0.02$, $p = 0.896$), or their interaction ($\chi^2(1) = 0.34$, $p = 0.562$), alone or in interaction with Cuing (all $p$s $> 0.4$). A binomial generalized linear mixed model revealed significant main effects of Cuing ($\chi^2(1) = 18.09$, $p < 0.001$) and Age group ($\chi^2(2) = 16.04$, $p < 0.001$) as more infants looked towards the cued object at this latency and 3.5-month-olds were looking more towards both objects than older infants generally (TABLE 5.1, FIGURE 5.3A-D). There was also a significant four-way interaction between Cueing, Age group, Face gender and Emotional expression ($\chi^2(2) = 8.06$, $p < 0.018$). Further decomposition revealed a significant effect of Age group on the proportion of infants looking towards the cued object at peak gaze following latency ($\chi^2(2) = 11.69$, $p = 0.003$), as a greater proportion of 3.5-month-olds looked towards the cued object than 9- or 12-month-olds at this latency (FIGURE 5.3A-D). A triple interaction between Face gender, Emotional Expression and Age group on the proportion of infants looking towards the uncued object at peak gaze following latency ($\chi^2(2) = 9.76$, $p = 0.008$) also emerged, reflecting the fact than in the smiling, but not neutral face

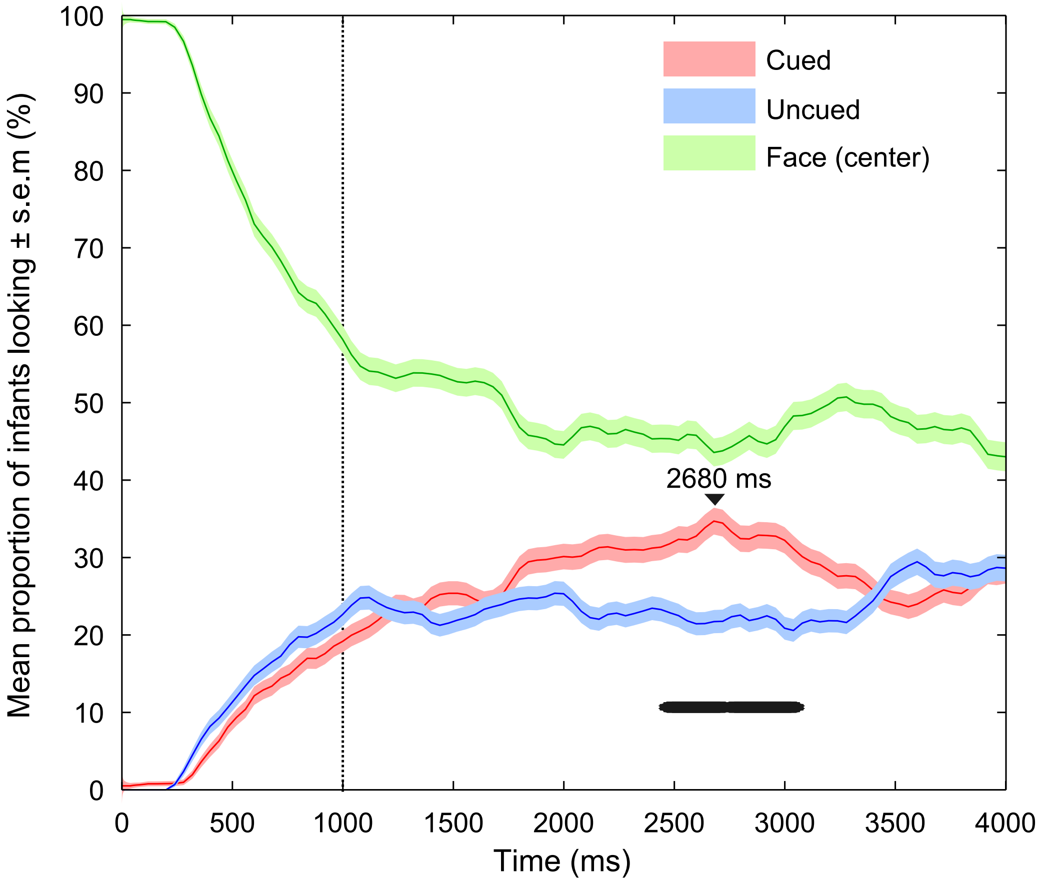

Figure 5.2: **Overall gaze cueing during familiarization.** The central face shifted gaze towards the cued object after 1000 ms of direct gaze (vertical dotted line). The shift elicited an increase in the proportion of infants looking towards the cued (versus uncued) object between 2500 ms and 3000 ms post-shift (black bars, $\alpha < 0.01$). Means have been temporally smoothed for display using a sliding moving average with 80 ms lag. The temporally-smoothed proportion of infants looking towards the cued object is maximal at 2680 ms, 1680 ms post-shift (triangle). The infant's gaze was directed to the center of the screen before familiarization.

| Fixed effect | $\chi^2$ | d.f. | $p$ |
|---|---|---|---|
| Cuing (Cued, Uncued) | 18.09 | 1 | < 0.001 * |
| Face gender (Male, Female) | 0.36 | 1 | 0.546 |
| Emotional expression (Smiling, Neutral) | 0.49 | 1 | 0.484 |
| Age group (3.5, 9, 12) | 16.04 | 2 | < 0.001 * |
| Cueing by Face gender | 2.51 | 1 | 0.113 |
| Cueing by Emotional expression | 0.26 | 1 | 0.610 |
| Face gender by Emotional expression | 1.56 | 1 | 0.211 |
| Cueing by Age group | 0.71 | 2 | 0.703 |
| Face gender by Age group | 1.27 | 2 | 0.530 |
| Emotional expression by Age group | 1.20 | 2 | 0.549 |
| Cueing by Face gender by Emotional expression | 0.36 | 1 | 0.548 |
| Cueing by Face gender by Age group | 2.49 | 2 | 0.288 |
| Cueing by Emotional expression by Age group | 0.84 | 2 | 0.658 |
| Face gender by Emotional expression by Age group | 4.17 | 2 | 0.125 |
| Cueing by Face gender by Emotional expression by Age group | 8.06 | 2 | 0.018 * |

Table 5.1: **Binomial Generalized Linear Mixed Model of the proportion of infants looking towards the cued and uncued objects at the overall peak latency of gaze cueing during familiarization.** The model included a random intercept for the participant factor. The random slope was dropped based on AIC. Significant fixed effects are marked by an asterisk.

condition, 12-month-olds (but not 3- or 9-month-olds) looked much less towards the uncued object when faces were female than when they were male, i.e. they showed a stronger effect of gaze cuing for female faces at the peak gaze following latency ($\chi^2(1) = 8.65$, $p = 0.003$, FIGURE 5.3A,C). The effect of cuing (i.e. a significant difference in the proportion of infants looking towards the cued versus uncued object) was limited to the neutral female face condition in the 3.5-month-old group ($\chi^2(1) = 11.44$, $p < 0.001$, FIGURE 5.3B) and to the smiling female condition in the 12-month-old group ($\chi^2(1) = 8.65$, $p = 0.003$, FIGURE 5.3B), but the overall Cuing by Face gender by Emotional expression interaction was only significant in the older group (3.5-month-olds, $\chi^2(1) = 1.92$, $p = 0.166$; 9-month-olds, $\chi^2(1) = 0.38$, $p = 0.536$; 12-month-olds, $\chi^2(1) = 5.77$, $p = 0.016$). There was no difference between experimental conditions in the 9-month-old group (FIGURE 5.3A-D).

### 5.5.2 Object recognition at test

A preliminary ANOVA revealed no significant effect of participant gender ($F(1,203) = 0.23$, $p = 0.634$), face stimulus set ($F(1,203) = 0.68$, $p = 0.410$), or their interaction ($F(1,203) = 0.76$, $p = 0.384$) on the visual preference for the cued (versus uncued) object at test. Similar null

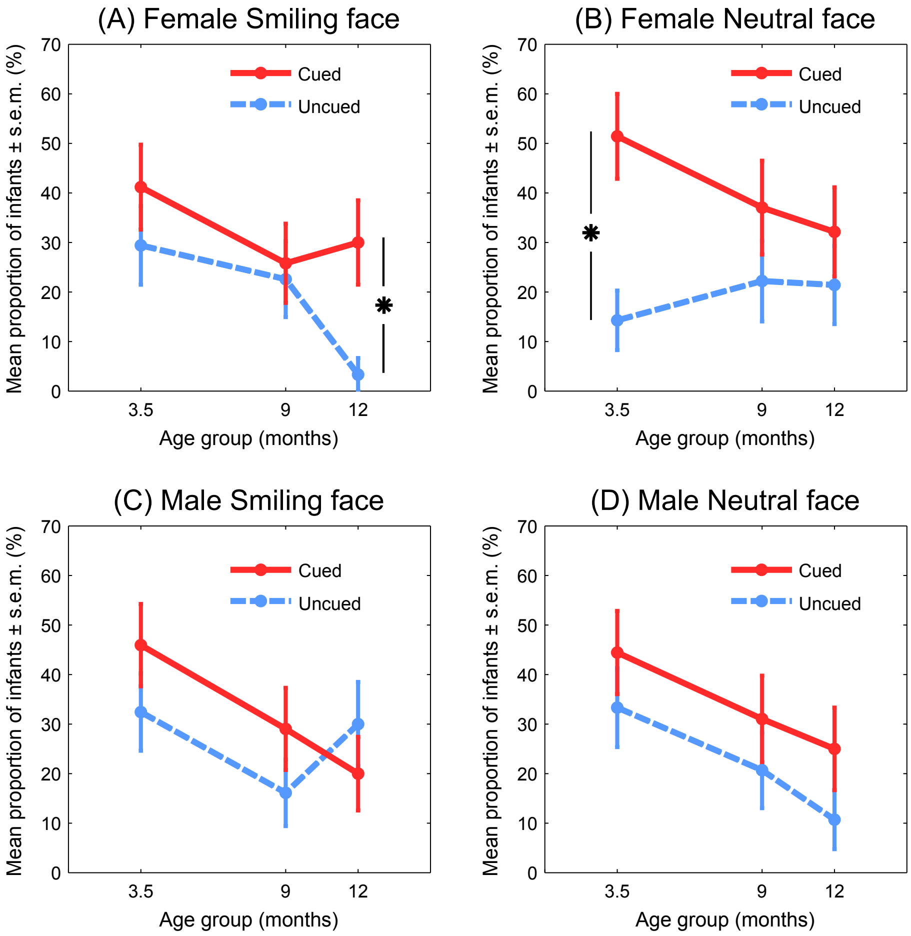

Figure 5.3: **Gaze cueing at the peak latency.** The proportion of infants looking to the cued and uncued object at the peak latency of gaze cueing (1680 ms post-shift) during familiarization is used as a dependent variable. **(A)** Smiling female face condition; **(B)** Neutral female face condition; **(C)** Smiling male face condition; **(D)**, Neutral male face condition. Significant differences between cued and uncued objects are marked by an asterisk (GLMMs, α = 0.05).

| Fixed effect | $\chi^2$ | d.f. | $p$ |
|---|---|---|---|
| Face gender (Male, Female) | 0.27 | 1 | 0.605 |
| Emotional expression (Smiling, Neutral) | 1.04 | 1 | 0.307 |
| Age group (3.5, 9, 12) | 1.00 | 2 | 0.606 |
| Face gender by Emotional expression | 1.14 | 1 | 0.285 |
| Face gender by Age group | 7.72 | 2 | 0.021 * |
| Emotional expression by Age group | 2.68 | 2 | 0.262 |

Table 5.2: **Linear model of the visual preference for cued versus uncued objects at test.** Visual preference was measured by PTLT, percentage of total looking time. The model included a random intercept and slope for the participant factor. Two observations were dropped based on the distribution of residuals. Significant fixed effects are marked by an asterisk. The model was selected back from a full Face gender by Emotional expression by Age group model.

effects were found on the visual preference for the cued (versus uncued) side at test (all *p*s > 0.05). Thus, visual preferences at test were pooled across these variables.

There was no significant overall visual preference at test for either the cued (or uncued) object (Student *t*-test, $t(206) = 1.144$, $p = 0.254$) or for the cued (or uncued) side (Student *t*-test, $t(206) = -0.07$, $p = 0.945$). Next, we estimated whether the visual preferences at test differed between age groups and experimental conditions.

The analysis revealed a significant interaction between Face gender and Age group in the visual preference for the cued (versus uncued) object at test, without any effect of Emotional expression (TABLE 5.2, FIGURE 5.4A). Further decomposition revealed that the interaction stemmed from a significant effect of age group in the female face ($\chi^2(2) = 6.82$, $p = 0.033$) but not male face ($\chi^2(2) = 2.65$, $p = 0.266$) condition. The effect of face gender was restricted to the 9-month-old group ($\chi^2(1) = 3.93$, $p = 0.047$, FIGURE 5.4B). In this age group, a visual preference for the cued object was present in the female face (one-sample Student *t*-test against chance, $t(61) = 2.32$, $p = 0.024$) but not male face ($t(59) = -0.76$, $p = 0.451$) condition. There was, however, no effect of Emotional expression in this age group, either across both genders ($\chi^2(1) = 1.38$, $p = 0.240$) or for female faces only ($\chi^2(1) = 0.02$, $p = 0.901$).

A linear mixed model of the visual preference for the cued side at test revealed a significant effect of Age group ($\chi^2(2) = 7.00$, $p = 0.030$) driven by a larger preference for the cued side at test in 9- than in 3.5-month-olds ($\chi^2(1) = 4.65$, $p = 0.031$; SUPPLEMENTARY FIGURE 5.6A), and a statistically marginal effect of Emotional expression ($\chi^2(1) = 3.29$, $p = 0.070$) reflecting the slightly higher preference for the cued side in the smiling (versus neutral) face condition in all three age groups of the sample (SUPPLEMENTARY FIGURE 5.6B). There were no further significant or marginal effects or interactions (SUPPLEMENTARY TABLE 5.5).

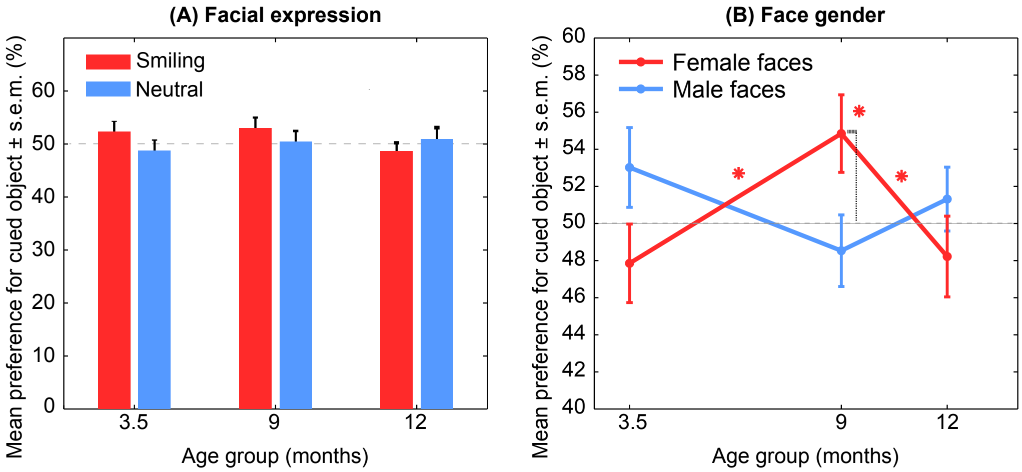

Figure 5.4: **Visual preference for the cued object at test.** **(A)** Gaze referencing by female but not male faces led to a visual preference for the cued object at test in 9-month-olds. Significant differences between the visual preferences of 3.5-, 9- and 12-month-olds (Student *t*-tests for independent samples) and significant visual preferences compared to chance (Student *t*-tests, versus 50%) are marked by an asterisk ($\alpha = 0.05$). **(B)** Emotional expression had no effect on the gaze cuing of objects.

## 5.6 DISCUSSION

The results supported the general hypothesis that the facial dimensions of gender and positive (versus neutral) emotion influence gaze cuing in infancy, but this influence differed across age groups and tasks. In particular, an effect of face gender and emotional expression was found in gaze following during familiarization but not in object recognition at test in 3.5- and 12-month-olds, while an effect of face gender but not facial emotion was found in object recognition at test but not gaze following during familiarization in 9-month-olds.

### 5.6.1 Face gender and positive emotional expression influence gaze following across the first year of life

Gaze following at peak latency was interactively affected by age, face gender, and emotional expression. More specifically, gaze following at this latency was stronger in the female neutral face condition in 3.5-month-olds and in the smiling female face condition in 12-month-olds, and the overall interaction of face gender and emotional expression reached significance in the 12-month-old group only. Most effects were confined to the proportion of gaze towards the uncued object, suggesting that face-processing dependent gaze following implicates the successful inhibition of gazing towards unreferenced but physically salient objects. Results in 3.5-month-olds align with earlier results in 7-month-olds (Flom & Pick, 2005; note that the adult posers were primarily female) and possibly reflect the increased visibility of the eyes in the neutral expression as well as the increased familiarity of infants with female faces (Sugden et al., 2014). The mechanism underlying the increased gaze following of 12-month-olds in the smiling female face condition is less clear, but since 12-month-olds show emerging evidence of understanding the intentional nature of gaze (S. C. Johnson, Slaughter, & Carey, 1998; but see A. J. Caron, Butler, & Brooks, 2002) and emotional expressions (Phillips et al., 2002) directed towards objects, it is reasonable to suspect that the increased gaze following reflects genuine interest motivated by the positive valence of the female smile in this population or expectations regarding this object and its relationship with the face (Phillips et al., 2002). In any case, the results are unlikely to reflect familiarity alone as it is doubtful that smiling female faces would be more familiar than neutral female faces to 12-month-olds and less familiar than neutral female faces to 3.5-month-olds. Whatever the mechanism, the results show a limited interaction of face gender and positive emotion on gaze following at 3.5-months, no interaction at group-level at 9-months, and a clear interaction at 12-months i.e. a relatively U-shaped trajectory with a strengthening at 12-months.

### 5.6.2 An effect of face gender on referential object learning in 9-month-olds

In line with earlier research, patterns of effect in the object recognition task differed strikingly from that of the gaze following task (Okumura et al., 2013). Here, no reliable preference for the cued or uncued object was found at test either in the 3.5- or in the 12-month-old group. This null result is difficult to interpret; it is possible that the objects were too complex and new, and that the faces and gaze shifts were not naturalistic enough. In any case, this floor effect precludes from drawing any conclusions on the modulation of referential object learning by face gender and expression in these groups. There was, however, evidence of referential object learning in 9-month-olds, and the effect was restricted to female faces. This result replicates previous findings in a similar paradigm with 5-month-olds (Pickron et al., 2014), and is in line with previous research showing limited male face processing ability in infants predominantly raised by a female caregiver (Quinn, Uttley, et al., 2008; Quinn et al., 2002; Ramsey-Rennels & Langlois, 2006; Righi, Westerlund, Congdon, Troller-Renfree, & Nelson, 2014). That referential learning about objects would be limited to female faces at this age probably stems from familiarity as well as the fact that infants consider female faces as more “social” than male faces due to their extended social experience with these types of faces (Ramsey-Rennels & Langlois, 2006; Rennels & Davis, 2008; Sugden et al., 2014). Indeed, previous research has revealed superior referential learning of objects in infants from caregivers compared to strangers (Hoehl et al., 2012), from social agents compared to non-social agents (Okumura et al., 2013; Pauen et al., 2015), and increased reliance on gaze cues from reliable versus non reliable informants (Tummeltshammer et al., 2014).

### 5.6.3 No evidence for an impact of positive emotions on referential object learning in infancy

The effect of positive emotion at test was marginal and not object-centered, as it was only manifest in a marginally significant preference for the cued side but not for the cued (or uncued) object across all age groups. More importantly, there was no effect of emotion on the visual preference for the cued (versus uncued) object in 9-month-olds who did however show reliable recognition of the cued object (as evidenced by a familiarity preference). Overall, there was no evidence for an effect of positive emotion on referential object learning, although positive emotion did influence gaze following in interaction with face gender. This dissociation is in line with previous electrophysiological findings in infants; positive emotions, compared to the neutral face, elicited a greater attentional component (negative central Nc) during the familiarization part of an object referencing paradigm but had no effect during the subsequent presentation of the cued (versus uncued) object (Hoehl & Striano, 2010). This null effect of positive facial emotion on referential object learning despite (1) effects of positive emotion on gaze following (although not at 9-month-olds in the present task and sample); (2) previously reported effects of negative emotions on referential object learning (Hoehl, Palumbo, et al., 2008; Hoehl, Wiese, & Striano, 2008) is consistent with the hypothesis of an early emergence of the negativity bias in infancy (Vaish et al., 2008, 2015). According to this hypothesis, infants, as adults (Ohman & Mineka, 2001), learn more about objects from the negative than from the positive emotions of others, perceiving positive emotions as person-centered and negative emotions as object-centered (Vaish et al., 2008). The hypothesis has received indirect support from social referencing experiments in 10- to 18- and 24-month-olds (Vaish et al., 2008, 2015). If infants perceive positive emotions as person- and not object-centered, then this would explain the null effect of smiling (versus neutral) on referential object learning despite some differences in gaze following and a marginal difference in side cuing. Further studies directly comparing the effect of positive and negative emotional expressions on gaze following versus object referencing in infants controlling for emotional intensity are needed to confirm this interpretation.

In summary, face gender and positive (versus neutral) facial emotions were found to affect gaze following in 3.5- and 12-month-old infants. The pattern of results suggests considerable reshaping and possible strengthening of interactive effects of face gender and emotions on gaze following across the first year of life, with 12-month-olds showing stronger interactive effects consistent with an understanding of the intentionality of referential emotion. Referential object learning was evidenced in the 9-month-old group only and was restricted to the female face condition. No evidence was found in favor of a modulation of referential object learning by positive emotions. The results are consistent with previous research pointing to a dissociation of gaze following and referential object learning in gaze referencing tasks and with the hypothesis of an early emergence of the negativity bias.

## 5.7 ACKNOWLEDGMENTS

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## 5.8 SUPPLEMENTARY MATERIALS AND METHODS

### 5.8.1 Object stimuli validation study

All methods were identical to that of the main experiment, except for the following.

#### 5.8.1.1 Participants

Forty-seven 3.5-month-olds (25 girls, mean age 116.2 ± 0.7 days), 38 9-month-olds (15 girls, mean age 284.9 ± 0.8 days) and 17 12-month-olds (8 girls, mean age 373.5 ± 1.5 days) were included in the study. All infants were born full term (39.1 ± 0.1 weeks of amenorrhea). Nineteen of the included 3.5-month-olds, 6 of the included 9-month-olds had side bias in one of the two pairs; 4 of the included 12-month-olds had side-bias (3) or missing data (1) in only one of the two pairs; those pairs were excluded. Twelve additional 3.5-month-olds, 4 additional 9-month-olds and 1 additional 12-month-olds were excluded on the basis of fussiness (1 3.5-month-old, 3 9-month-olds, 1 12-month-old), side bias on both pairs of trials (10 3.5-month-olds, 1 9-month-old), or experimental error (1 3.5-month-old).

#### 5.8.1.2 Stimuli

Eighteen pairs of pictures of non-living objects were selected from the BOSS bank of standardized stimuli on the basis of (1) presumed unfamiliarity to the infants and (2) close or approximate match in the visual complexity and manipulability dimensions as reported in the BOSS documentation (Brodeur et al., 2010). New pairs of pictures were tested and new participants were tested until two valid pairs of stimuli per age group were identified.

#### 5.8.1.3 Procedure

Each infant saw two pairs of trials. Each pair of trials consisted in two successive trials featuring pairs of the same two objects, with side of presentation reversed between trials. Trial order was counterbalanced across participants. Objects subtended a visual angle of about 13 degrees (vertically) by 13 degrees (horizontally). Trials lasted 5 s from first look.

#### 5.8.1.4 Data acquisition, pre-processing, and analysis

Inter-coder agreement was of 0.96, 0.98, and 0.99 in the 3.5-, 9- and 12-month-old group, respectively (Pearson's r, 23%, 24%, and 24% of the videos, respectively). In each age group, PTLTs to each object of each pair further than 2 standard deviations away from the corresponding group mean were considered outliers and excluded (1 data point in the 9-month-old group).

Results for the selected stimuli are presented in SUPPLEMENTARY TABLE 5.4.

### 5.8.2 Supplementary figures and tables

| Set | Gender (#ID) | Expression | Gaze | Hit rate (%) | Intensity | Valence | Distance direct vs. averted (10^5) |
|---|---|---|---|---|---|---|---|
| A | Female (#19) | Neutral | direct | 88 | 3.62 | 2.92 | - |
|  |  |  | left | 81 | 3.11 | 2.93 | 3.43 |
|  |  |  | right | 85 | 2.96 | 3.07 | 2.67 |
|  |  | Smiling | direct | 100 | 4.08 | 4.58 | - |
|  |  |  | left | 100 | 4.04 | 4.35 | 3.09 |
|  |  |  | right | 100 | 3.96 | 4.48 | 2.99 |
|  | Male (#30) | Neutral | direct | 92 | 3.54 | 3.33 | - |
|  |  |  | left | 78 | 3.13 | 3.04 | 3.11 |
|  |  |  | right | 78 | 3.26 | 3.04 | 3.19 |
|  |  | Smiling | direct | 100 | 4.22 | 4.17 | - |
|  |  |  | left | 96 | 4.21 | 4.29 | 3.52 |
|  |  |  | right | 100 | 4.22 | 4.13 | 2.88 |
| B | Female (#32) | Neutral | direct | 100 | 3.58 | 3.08 | - |
|  |  |  | left | 76 | 3.32 | 2.80 | 2.97 |
|  |  |  | right | 92 | 3.42 | 3.08 | 2.85 |
|  |  | Smiling | direct | 96 | 3.92 | 4.50 | - |
|  |  |  | left | 100 | 3.96 | 4.42 | 4.91 (*) |
|  |  |  | right | 96 | 3.92 | 4.19 | 2.84 |
|  | Male (#23) | Neutral | direct | 100 | 4.09 | 3.43 | - |
|  |  |  | left | 86 | 3.41 | 3.05 | 3.43 |
|  |  |  | right | 91 | 3.52 | 3.22 | 3.21 |
|  |  | Smiling | direct | 100 | 4.14 | 4.50 | - |
|  |  |  | left | 100 | 4.17 | 4.42 | 3.30 |
|  |  |  | right | 100 | 4.43 | 4.65 | 2.91 |

Table 5.3: **Face stimuli properties.** Mean hit rate, intensity rating, and valence rating are from the Radboud Face Database (RAFD) documentation. Distance between stimuli with direct and averted gaze is measured by the Manhattan norm on elementwise pixel values. (*) Excess distance is due to the model slightly closing the eyes in the averted image.

| Age group | Set | Object | Visual complexity | Manipulability | PTLT (%) | $t$ | d.f. | $p$ | Cohen's $d$ |
|---|---|---|---|---|---|---|---|---|---|
| 3.5- months | 1 | Flash light | 2.6 | 3.0 | 48.7 ± 2.4 | - 0.46 | 10 | 0.653 | - 0.14 |
| | | Measuring tape | 2.6 | 3.4 | 51.3 ± 2.4 | | | | |
| | 2 | Hand fan | 3.2 | 4.0 | 47.8 ± 3.9 | - 0.55 | 13 | 0.591 | - 0.15 |
| | | Violin | 3.2 | 4.4 | 52.2 ± 3.9 | | | | |
| 9- months | 1 | Box cutter | 2.9 | 2.8 | 49.8 ± 5.3 | - 0.03 | 8 | 0.978 | - 0.01 |
| | | Walkman | 2.9 | 2.8 | 50.2 ± 5.3 | | | | |
| | 2 | Hand fan | 3.2 | 4.0 | 48.1 ± 4.6 | - 0.38 | 7 | 0.719 | - 0.13 |
| | | Violin | 3.2 | 4.4 | 51.9 ± 4.6 | | | | |
| 12- months | 1 | Box cutter | 2.9 | 2.8 | 50.9 ± 4.6 | 0.19 | 6 | 0.857 | 0.07 |
| | | Walkman | 2.9 | 2.8 | 49.1 ± 4.6 | | | | |
| | 2 | Hand fan | 3.2 | 4.0 | 48.4 ± 3.0 | - 0.54 | 9 | 0.606 | - 0.17 |
| | | Violin | 3.2 | 4.4 | 51.6 ± 3.0 | | | | |

Table 5.4: **Object stimuli properties.** Values for visual complexity and manipulability are from the BOSS validation study (Brodeur et al., 2010). Visual preference refers to the Percentage of Total Looking Time (PTLT), mean ± s.e.m. Paired Student $t$-tests on PTLTs, $\alpha = 0.05$, uncorrected.

| Fixed effect | $\chi^2$ | d.f. | $p$ |
|---|---|---|---|
| Face gender (Male, Female) | 1.60 | 1 | 0.206 |
| Emotional expression (Smiling, Neutral) | 3.29 | 1 | 0.070 (.) |
| Age group (3.5, 9, 12) | 7.00 | 2 | 0.030 * |
| Face gender by Emotional expression | 0.40 | 1 | 0.527 |
| Face gender by Age group | 0.91 | 2 | 0.634 |
| Emotional expression by Age group | < 0.01 | 2 | 1.000 |

Table 5.5: **Linear model of the visual preference for the cued versus uncued side at test.** Visual preference was measured by PTLT, percentage of total looking time. The model included a random intercept and slope for the participant factor. Two observations were dropped based on the distribution of residuals. Significant fixed effects are marked by an asterisk.

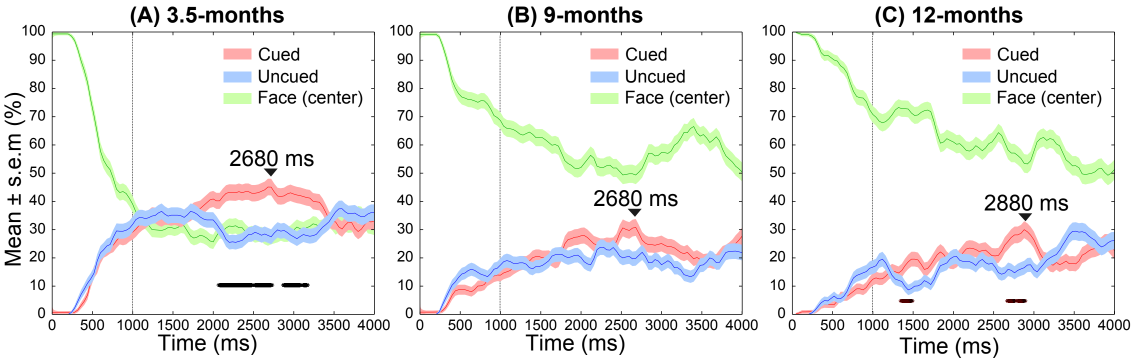

Figure 5.5: **Proportion of infants looking towards the central face, cued object, and uncued object during familiarization in (A) 3.5, (B) 9, and (C) 12-month-olds.** The central face shifted gaze towards the cued object after 1000 ms of direct gaze (vertical dotted line). The proportion of infants looking towards the cued (versus uncued) object increased post-shift (black bars, $\alpha < 0.05$) and peaked around 2680 ms, 2680 ms, and 2880 ms in the 3.5-, 9-, and 12-month-old group, respectively (black triangles). Means have been temporally smoothed for display using a moving average with 80 ms lag.

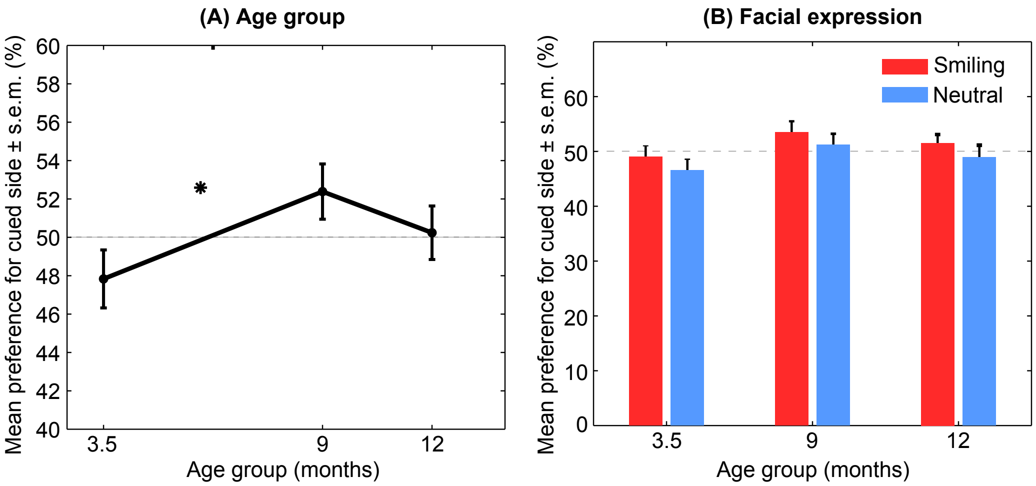

Figure 5.6: **Visual preference for the cued side at test.** **(A)** The visual preference for the cued side increased between 3.5 and 9 months of age (Student t-test for independent samples, $\alpha = 0.05$). **(B)** Emotional expression had a marginal effect on spatial gaze cuing (overall $\chi^2(1) = 3.29$, $p = 0.070$), with smiling faces leading to a slightly higher visual preference for the cued side.

## Chapter 6

# FACILITATED DETECTION OF FEAR FACES FROM EARLY INFANCY

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## 6.1 INTRODUCTION OF THE ARTICLE

In this last experimental chapter, we examined the developmental trajectory of the perceptual salience of fearful faces. In adults, fearful faces, and fearful eyes in particular, hold attention and are processed preferentially (Adolphs, 2008; Phelps, Ling, & Carrasco, 2006; Vuilleumier, 2005). A holding of attention by fearful faces (but not fearful eyes embedded in neutral faces) has been documented in infants from the age of 7, but not 5, months (Leppänen & Nelson, 2009, 2012; Leppänen et al., 2010; Peltola et al., 2011; Peltola, Leppänen, Mäki, & Hietanen, 2009; Peltola et al., 2008; Peltola, Leppänen, Vogel-Farley, et al., 2009). However, there is currently no behavioral evidence that fear faces are processed preferentially, i.e. perceptually salient, in infants. There is, however, electrophysiological evidence that they might be at least at 7-months of age, as the N290 (a component associated with cortical face perception in infants, de Haan et al., 2002; M. H. Johnson et al., 2005) is enhanced for fearful faces compared to smiling faces when those faces are consciously perceived (Jessen & Grossmann, 2015; Leppänen & Nelson, 2009).

## 6.2 ABSTRACT

Human adults detect fearful faces more quickly and show an attentional bias to fearful eyes, an adaptive behavior that tracks amygdala function. Behavioral and electrophysiological studies of facial emotion perception in infants point to the emergence of increased attention to fear faces and fearful eyes between the ages of 5 and 7 months, with possible precursors at 3.5 and 5 months. We tested whether infants from 3.5-months to 12-months of age show facilitated detection of fear faces and eyes, using a novel face-in-noise psychophysical task with two univariate (face versus noise visual preference) and multivariate (face versus noise

Box 8: Résumé de l'article "Facilitated detection of fear faces from early infancy"

Bayet L., Quinn P.C., Laboissière R., Caldara R., Lee K., & Pascalis O. (en préparation) "Facilitated detection of fear faces from early infancy"

Les adultes humains détectent les visages de peur plus rapidement et accordent automatiquement plus d'attention aux yeux de peur. Ce comportement adaptatif reflète le fonctionnement de l'amygdale. Les études comportementales et electrophysiologiques de la perception des expressions faciales émotionnelles chez le nourrisson suggèrent que le biais attentional en faveur des visages de peur émerge entre 5 et 7 mois, avec de possibles précurseurs à 3.5 et 5 mois. Nous avons testé l'hypothèse selon laquelle les nourrissons de 3.5 à 12 mois détectent plus facilement les visages et yeux de peur. A cette fin, nous avons développé une tâche psychophysique originale de détection de visage dans le bruit, combinant deux mesures de détection du visage : une mesure univariée classique de préférence visuelle pour le visage, et une mesure multivariée issue de la classification automatique du visage par rapport au bruit. Enfin, les seuils de détection ont été estimés sur la base de la modélisation des courbes psychométriques (modèles mixtes non-linéaires). La détection des visages de peur ayant le plus de signal dans la région de yeux (plutôt que la bouche) était systématiquement meilleure que pour les visages souriants ayant plus de signal dans la région de la bouche (plutôt que les yeux). La détection était intermédiaire pour les visages de peur ayant plus de signal dans la région de la bouche ou pour les visages souriants ayant plus de signal dans la région des yeux. Les données confirment l'hypothèse selon laquelle une détection facilitée des visages de peur est présente avant l'émergence du biais attentional en faveur des visages de peur chez les nourrissons entre 5 et 7 mois.

decoding) measures of detection, and non-linear mixed-modeling of the infants' psychometric curves. Detection thresholds were consistently lower, and higher evidence of detection could be found around the threshold, for fearful faces with more signal in the eye region. Detection was intermediate for fearful faces with more signal in the mouth region and smiling faces with more signal in the eye region, and lowest for smiling faces with more signal in the mouth region. Overall, the data supports the hypothesis of a superior detection of fearful faces that is present before the onset of attention holding by fear faces between 5- and 7-months.

## 6.3 RESEARCH HIGHLIGHTS

- We used previously validated face stimuli in a detection task to research the detection of fearful and smiling faces in noise by infants.
- Face detection was measured by the preference for the face in face versus noise pairs, and by the overall evidence for face versus noise discrimination in the infants' looking behavior.
- Psychometric curve modelling with non-linear mixed models revealed lower thresholds for fear faces and faces with most visible eyes than for smiling faces and faces with less

visible eyes.

- The advantage of fearful faces in signal levels close to the detection threshold, possibly indicative of emotional salience, was equal or greater in 3.5-month-olds than in 6- and 12-month-olds.

## 6.4 INTRODUCTION

Humans from all cultures display facial expressions of emotions (Ekman & Oster, 1979), a behavior that engages complex facial musculature and that humans share with all mammals - and with other primates most particularly (Burrows, 2008; Darwin, 1872; Waller & Micheletta, 2013). Indeed, producing facial expressions of emotions doesn't seem to require much learning or maturation apart from some facial motor control, as newborns (Reissland et al., 2011; J. E. Steiner, 1979; Trapanotto et al., 2004) and blind persons (Galati et al., 2003; Peleg et al., 2006; Tracy & Matsumoto, 2008) produce at least some facial expressions without the opportunity of learning by imitation. The perception of these expressions follows a distinct path. While remarkably robust to even dramatic social deprivations (Moulson et al., 2014; Pollak & Kistler, 2002), suggesting deep evolutionary roots, the ability to categorize some facial emotions (Nelson, 1987) appears to emerge in infants between the ages of 5 and 7 months (Leppänen & Nelson, 2009) along with a sensitivity to consciously or unconsciously perceived fearful faces (Jessen & Grossmann, 2015). Behavioral (Peltola, Leppänen, Mäki, & Hietanen, 2009; Peltola et al., 2008; Peltola, Leppänen, Vogel-Farley, et al., 2009), physiological (Leppänen et al., 2010; Peltola et al., 2011) and electrophysiological (Hoehl, Wiese, & Striano, 2008; Jessen & Grossmann, 2014, 2015; Kobiella et al., 2008) measures, as well as comparative work in rats (Moriceau, Roth, Okotoghaide, & Sullivan, 2004; Moriceau & Sullivan, 2006; Moriceau et al., 2006; Sullivan & Holman, 2010) and macaques (Bauman, Toscano, Mason, Lavenex, & Amaral, 2006; Leppänen & Nelson, 2012; Payne, Machado, Bliwise, & Bachevalier, 2010) concur to suggest that this developmental tipping point reflects the maturational onset of functional connectivity between limbic regions (e.g., the amygdala nuclei), extra-striate visual regions (e.g., the fusiform gyrus) and attentional control regions (e.g., the anterior cingulate cortex) between the ages of 5 and 7 months (Leppänen & Nelson, 2009, 2012) and may correspond to the closing of a sensitive period for preference and attachment formation (Leppänen & Nelson, 2012).

In infants, fear sensitivity has mainly been examined from the angle of increased attentional engagement by fear faces compared to neutral or smiling faces. Indeed, in adults, fear faces engage increased attentional resources in a Stroop-like manner, leading to increased reaction times to fear faces in labeling or perceptual judgment tasks (e.g., Calder, Young, et al., 2000). Six to seven month-old infants, but not younger infants, also show converging evidence of increased attentional engagement by fear faces i.e. an increased negative central electrophysiological component, increased cardiac deceleration, and increased saccadic latency to a peripheral target when presented with fearful compared to non-fearful faces (Jessen & Grossmann, 2014, 2015; Leppänen & Nelson, 2009, 2012; Leppänen et al., 2010; Peltola et al., 2011, 2008; Peltola, Leppänen, Vogel-Farley, et al., 2009). By contrast, younger infants show a visual preference for smiling but not fearful faces (Bayet, Quinn, et al., 2015; Farroni et al., 2007; La Barbera et al., 1976; Rigato et al., 2011). However, some sensitivity to fear has been found by finer analyses of electrophysiological data at 5 months (Yrttiaho et al., 2014) and in an object-referencing paradigm at 3.5 months (Hoehl, Wiese, & Striano, 2008). Yrttiaho et al. (2014) reported that the holding of attention by faces at 5-months positively correlated with the increased amplitude of the N290 component in response to fear faces at 7-months. The N290 is an electrophysiological component associated with face processing in infants (de Haan et al., 2002; M. H. Johnson et al., 2005); Yrttiaho et al. (2014) interpreted the result as the plastic enhancement of cortical responses to fear faces that is driven by increased attention, possibly under subcortical control. Yrttiaho et al. (2014) also found that, contrary to the attentional bias for fear faces, the attentional bias for faces over phase-scrambled controls (as measured by the saccadic latency to a peripheral target) was stable between 5- and 7-months, suggesting that the attentional bias to fear faces can't be an exaggeration of the general bias to faces.

In addition to attentional engagement, the processing of fear faces and fearful eyes in particular by adults is characterized by superior detection in visual search (Lobue, 2009), early amygdala activity leading to enhanced processing (Adolphs, 2008; Krolak-Salmon et al., 2004; Schyns, Petro, & Smith, 2007) and increased contrast sensitivity irrespective of attention (Phelps et al., 2006). This is interpreted as "emotional salience" and caused, directly and indirectly, by the up-regulation of ventral visual pathways by amygdala nucleuses receiving inputs from the visual cortices and possibly from the pulvinar and superior colliculi (Garvert et al., 2014; M. H. Johnson, 2005; Morris et al., 2002, 1998, 1999; Pessoa & Adolphs, 2010; Vuilleumier et al., 2003). While such pathways could be present from birth (M. H. Johnson, 2005) and the conscious cortical processing of faces (as measured by the N290 electrophysiological component) appears increased for fearful faces in 7-month-olds (Jessen & Grossmann, 2015; Leppänen & Nelson, 2009), it is unknown whether fearful faces are better detected in infancy. There is, however, evidence that the eyes engage infants' attention from 3-4 months onwards (e.g. Damon et al., 2015; Dupierrix et al., 2014; Gallay et al., 2006; Gliga & Csibra, 2007; Senju & Johnson, 2009). Because the eyes are critical to the emotional salience of fearful faces (Morris et al., 2002), it is possible that infants would better detect fearful faces from 3.5-months.

We presented pairs of fearful or smiling faces mixed with random noise (Dakin, Hess, Ledgeway, & Achtman, 2002) and matched pure noise to 192 infants at 3.5, 6 and 12 months of age in a face-versus-noise detection task. We hypothesized that fear faces would be more easily detected at the same level of signal by 6- and 12-month-old infants. Furthermore, we hypothesized that a perceptual paradigm could uncover early fear sensitivity in 3.5-month-olds as a face versus noise detection task does not require attentional engagement. Theoretically, fear faces could be better detected at that age even though they do not cause a holding of attention. Alternatively, 3.5-month-old may show a lower detection threshold for smiling rather than fear faces.

## 6.5 METHODS

### 6.5.1 Participants

A total of 64 3.5-month-ols (31 girls, mean age. 116.9 ± 0.6 days s.e.m), 64 6-month-olds (31 girls, mean age 191.0 ± 0.8 days) and 64 12-month-olds (32 girls, mean age 375.6 ± 0.7 days) from a predominantly Caucasian environment were included in the study. All caregivers gave informed written consent before testing, and all infants were born full term (38.8 ± 0.1 weeks of amenorrhea). All caregiver(s) reported a percent of female caretaking of at least 50% (mean 71.5 ± 0.8 %), meaning that no infant was primarily raised by a male caregiver, and providing results that are consistent with previous reports (Rennels & Davis, 2008; Sugden et al., 2014). Thirty additional infants (16 3.5-month-olds, 6 6-month-olds, 8 12-month-olds) participated but were excluded due to fussiness (9 3.5-month-old, 2 6-month-olds, 8 12-month-old), technical failure (1 3.5-month-olds, 1 6-month-old), experimenter error (3 3.5-month-olds, 3 6-month-olds) or side-bias on half or more of the trials (3 3.5-month-olds). Side-bias in a trial was defined as looking to the same side more than 95% of the time.

### 6.5.2 Stimuli

Smiling and fearful frontal view faces from the same 12 models (6 males, 6 females) were selected from the Karolinska Directed Emotional Faces database (Calvo & Lundqvist, 2008;

Goeleven et al., 2008; Lundqvist et al., 1998). Stimuli were gray scaled; external features were cropped. Luminance, contrast, spatial frequencies, and placement of the eyes were matched using SHINE (Willenbockel et al., 2010) and Psychomorph (Tiddeman, 2005). Faces subtended a visual angle of about 18 degrees (vertically) by 12 degrees (horizontally). Noise was generated in MATLAB 7.9.0.529 using a weighted mean phase noise algorithm preserving global contrast and frequency spectrum (Dakin et al., 2002), and stimuli were gamma-corrected ($\gamma$ = 1.7286). Similar stimuli have been used with children in an emotion labeling task (Rodger et al., 2015).

### 6.5.3 Procedure

The infants sat on their caregiver's lap about 60 cm from the screen. Stimuli were presented using Matlab's Psychtoolbox. The experiment was approved by the local ethics committee (Institutional Review Board). Each infant saw 6 trials consisting of a face paired with matched pure visual noise (FIGURE 6.1A). Faces were mixed with 0-70% noise, i.e. had 30-100% signal (FIGURE 6.1B). Models and signal levels differed between trials and were randomly ordered. Faces were smiling or fearful, male or female, counterbalanced across participants. The stimuli presentation lasted 10 s from the first look. At each signal level except 100%, half of the infants saw a face with eyes noisier than the mouth, and vice versa (as measured by Peak Signal to Noise Ratio, PSNR; FIGURE 6.1B). To ensure maximal variation of noise spatial distribution, a face and pure noise pair was randomly sampled from 3 pre-generated pairs for each model, facial emotion condition, feature visibility condition (more signal in the eyes or mouth region), and signal level. Control analyses revealed no significant effect of facial emotion (either alone or in interaction with feature visibility) on the quantity of signal (measured by the Peak Signal to Noise Ratio, PSNR, or by Structural Similarity, SSIM) in the global image or in the eye region (all $p$s > 0.500).

### 6.5.4 Data pre-processing and analysis

Infants' looking was recorded and coded offline with 40 ms precision. A subsample of the videos was coded by a second observer with 0.98, 0.96 and 0.96 agreement in the 3.5- 6- and 12 month-olds group, respectively (Pearson's $r$, 25% of the videos). Percentages of total looking time (PTLTs) were derived. At each condition, age group and signal level, trials with PTLT further from 2 standard deviations from the mean were considered outliers and excluded (4.17 %, 2.60%, and 4.43 % of trials in 3.5-, 6- and 12-month-olds, respectively).

A second measure of face detection was derived from attempting to classify trials as "face

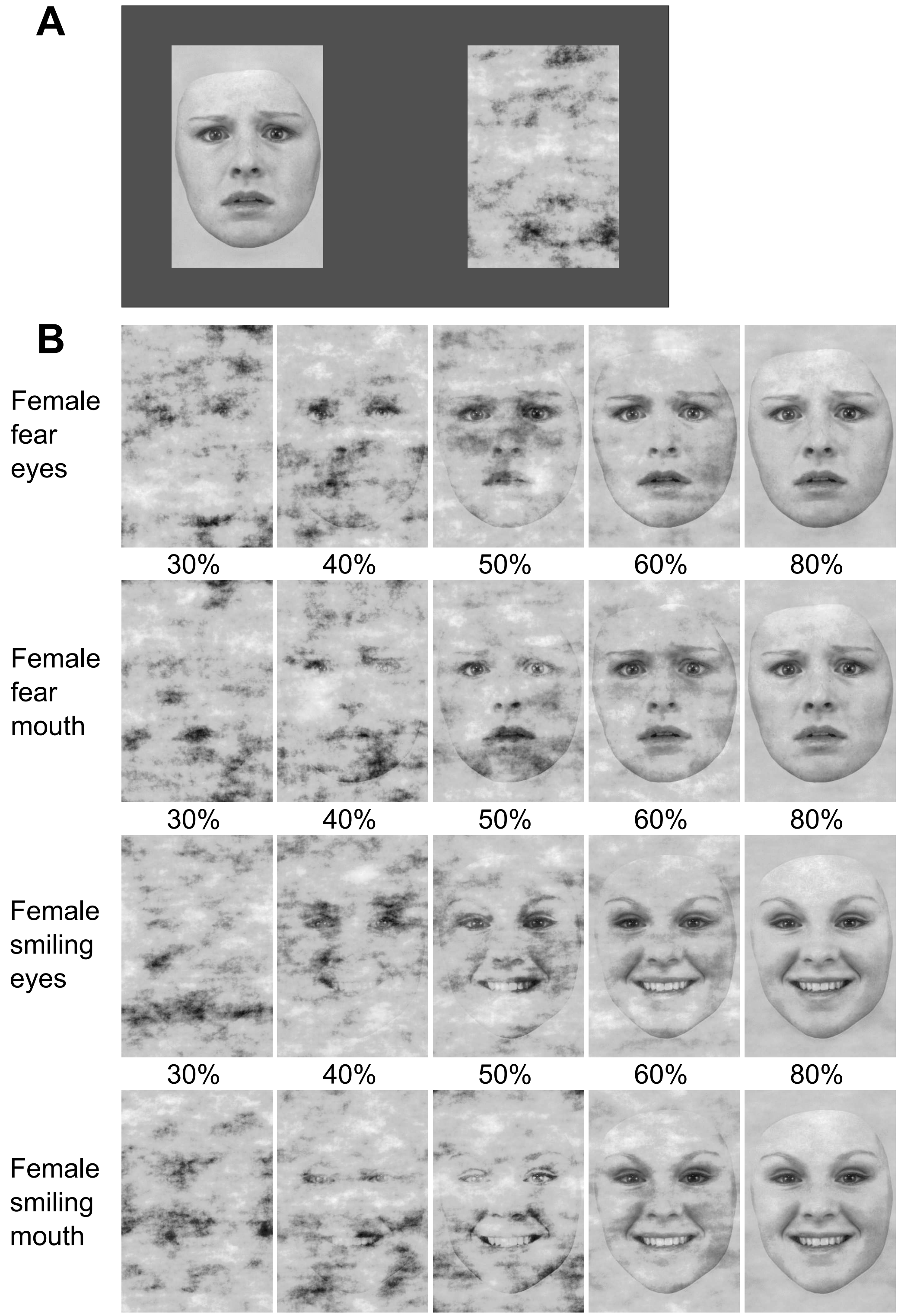

Figure 6.1: **Example stimuli.** **(A)** Example trial featuring a female face with a fear expression at 100% signal (left) paired with matched pure weighted-mean phase noise (right; Dakin et al., 2002). **(B)** Example stimuli featuring the same female model with 30-80% signal level, in different experimental conditions: fear or smiling, more signal in the eye region or more signal in the mouth region (Peak Signal-to-Noise Ration, PSNR). Stimuli were gamma-corrected before display (not shown).

is on the left” or “face is on the right”. The rationale for this metric is similar to the idea of “double psychophysics” (Teller, 1979, 1997): if an ideal observer can reliably guess on which side of the screen the face was presented by looking at the infant’s behavior, then the infant is discriminating between the face and the noise sides. For example, if on a given trial an infant makes frequent looks towards the left side of the screen or show an overall visual preference for that side, then an outside observer could guess that the face is on this side – but this guess could be incorrect. How correct overall the observer is in making predictions would reflect how consistently the infant’s looking behavior differentiates the face and noise sides. If the observer is generally good, but guesses at random in a particular experimental condition, then it may be inferred that the infant’s did not reliably discriminate between face and noise in that condition. Here, the idea was implemented with supervised machine learning using a multivariate description of the infant’s looking behavior comprised of eight a priori defined trial-level features: (1) visual preference for the left side, (2) number of looks to the left side, (3) number of looks to the right side, (4) duration of first look to the left side, (5) duration of first look to the right side, (6) median duration of looks to the left side, (7) median duration of looks to the right side, and (8) direction of the first look (left or right). Durations were log-transformed to approach a Gaussian distribution, and all continuous features were standardized within-subject. Note that the visual preference for the right side is equal to 100% minus the visual preference for the left side and as such does not need to be included as a feature. The features were chosen a priori for their likelihood to reflect the actual position of the face in the display given the documented visual preference of infants for faces in general (e.g., Fantz, 1961). A logistic regression was repeatedly trained on all trials except one and tested on the trial that was left-out (Leave One Out Cross-Validation, LOO-CV), leading to predictions for each trial that reflect genuine generalization. Logistic regression was chosen as a classifier because it outputs log-odds, a continuous measure of evidence in favor of each response. Log-odds in favor of the correct face side were used as the most direct multivariate measure of trial-level classification performance.

Infants’ psychometric curves presented with a positive asymptote well below the level of maximal response. For example, the visual preference for the face side approached 75% at the maximal level of signal, even though on a given trial infants could look more than 90% of the time to the face side. This violates the assumption of usual models of psychometric curves such as the logistic regression. Thus, a Non-Linear Mixed Model approach was used that did not necessitate this assumption, with the following formula:

$$f(x,z) = Y_0 + \frac{(Y_F + \delta_S(z).dY_S) - Y_0}{1 + e^{-a*(x-(x_{0FE} + \delta_F(z).\delta_M(z).dx_{0FM} + \delta_S(z).\delta_E(z).dx_{0SE} + \delta_S(z).\delta_M(z).dx_{0SM}))}}$$

Where $f(x)$ is the fitted response (logit-transformed visual preference, or correct decoding log-odds), $x$ the level of signal, $z$ the experimental condition, $Y_0$ the asymptote at 0% signal, $Y_F$ the asymptote at 100% signal in the fear face condition, $dY_S$ the difference in asymptote for the smiling face condition, $a$ the slope, $x_{0FE}$ the perceptual threshold in the fear face with more signal in eyes condition, and $dx_{0FM}$, $dx_{0SE}$, and $dx_{0SM}$ the differences in threshold for the fear faces with more signal in mouth, smiling faces with more signal in eyes, and smiling faces with more signal in mouth conditions, respectively. $\delta_S(z)$, $\delta_F(z)$, $\delta_M(z)$, $\delta_E(z)$ are binomial variables equal to 1 in the smiling face, fearful face, more signal in mouth region and more signal in eyes region conditions, respectively, and equal to 0 otherwise. In order to estimate the effect of eye versus mouth visibility, the fit was restricted to trials with 30-80% signal (as eye and mouth are equally visible at 100% signal). The selection of random effects was based on Akaike (AIC) and Bayesian (BIC) information criterion.

Analyses were conducted in Matlab 7.9.0529 and R 3.2.0. Linear and non-linear mixed model analyses (Laird & Ware, 1982) were run in R using *nlme* 3.1.120 (Pinheiro et al., 2012), *car* 2.0.25 (J. Fox, 2009), and *lme4* 1.1.7 (Bates et al., 2013).

## 6.6 RESULTS

### 6.6.1 Two measures of face versus noise detection

A visual preference for the face side has been used in earlier studies as a proxy for face detection because the visual preference for faces over noise in infants is expected to be very strong (Gelskov & Kouider, 2010). As expected, infants in all age groups showed a visual preference for the face side (PTLT) that increased with face visibility (overall PTLT to the face side: 66.18 ± 0.68; FIGURE 6.2A). In addition, a multivariate measure of face detection was introduced by decoding the face side (i.e., discriminating face from noise) based on looking behavior in single-trials. The rationale is equivalent to Teller's "double psychophysics" (Teller, 1979): if on a given trial the infant's looking behavior (for example, looking longer to the face side) is sufficient for an outside observer to guess on which side of the screen the face was, then the infant's behavior discriminates between face and noise and it may be inferred that the infant detected the face. Overall, the side of the face could be accurately decoded from the infants' looking behavior at the level of single trials with 80.92% ± 1.22 cross-validation accuracy (TABLE 6.1); accuracy and classification evidence (log-odds) increased with face visibility as expected (FIGURE 6.2B-C).

Preliminary Linear Mixed Models (LMMs) revealed no effect of infant gender on the visual

| Predictor | β | s.e. | $t$ | $p$ |
|---|---|---|---|---|
| Intercept | 0.04 | 0.09 | 0.48 | 0.629 |
| PTLT to the left side * | - 1.09 | 0.16 | - 6.70 | < 0.001 |
| Duration of first look to the left side * | - 0.28 | 0.14 | - 2.01 | 0.044 |
| Duration of first look to the right side * | 0.59 | 0.13 | 4.68 | < 0.001 |
| Median duration of looks to the left side * | - 0.63 | 0.15 | - 4.10 | < 0.001 |
| Median duration of looks to the right side * | 0.47 | 0.14 | 3.34 | 0.001 |

Table 6.1: **Multivariate decoding of the face side based on infant looking behavior.** The side of the face, a binary variable, was coded as 0 (left) or 1 (right) and predicted by the infant's looking behavior using logistic regression. The number of looks to each side and the direction of the first look were rejected during forward feature selection. Look durations were log scaled. Non-binary variables were Z-scored (within-subject). Degrees of freedom in the error: 1037.

preference to the face side (logit-transformed, $\chi^2(1) = 0.34$, $p = 0.559$) or on the face versus noise decoding evidence (correct log-odds, $\chi^2(1) = 0.16$, $p = 0.687$). Data was pooled across this variable in further analyses.

Next, we used Non-Linear Mixed Models to model the psychometric curves and estimate differences in the threshold of face detection between age groups and experimental conditions, as measured by (1) the visual preference for the face side (logit-transformed) and (2) the face versus noise decoding evidence (log-odds).

### 6.6.2 Variations in face detection as measured by visual preference

A model based on the visual preference for the face side revealed that, across all age groups, the threshold for face detection was higher for smiling faces with more signal in the mouth region (increase in threshold: 5.20 ± 2.62 % face signal, 95% C.I [0.001 0.103]) compared to fearful faces with more signal in the eye region (44.41 ± 1.98 % face signal; TABLE 6.2; FIGURE 6.3A). Detection thresholds for smiling faces with more signal in the eye region or fear faces with more signal in the mouth region were not significantly different from the latter condition (TABLE 6.2; FIGURE 6.3A).

A reduced model (comprising only the terms that were significant in the former model) was then used to estimate whether this difference in detection threshold between the fearful face with more signal in the eye region condition and the smiling face with more signal in the mouth region condition differed across the three age groups, and revealed no significant differences between age groups (Wald confidence intervals, $\alpha = 5\%$). Restricting the analyses to (logit-transformed) visual preferences at the visibility threshold (40-50% face signal; FIGURE 6.3B-C) however revealed a significant main effect of age ($\chi^2(2) = 9.62$, $p = 0.008$) as well as

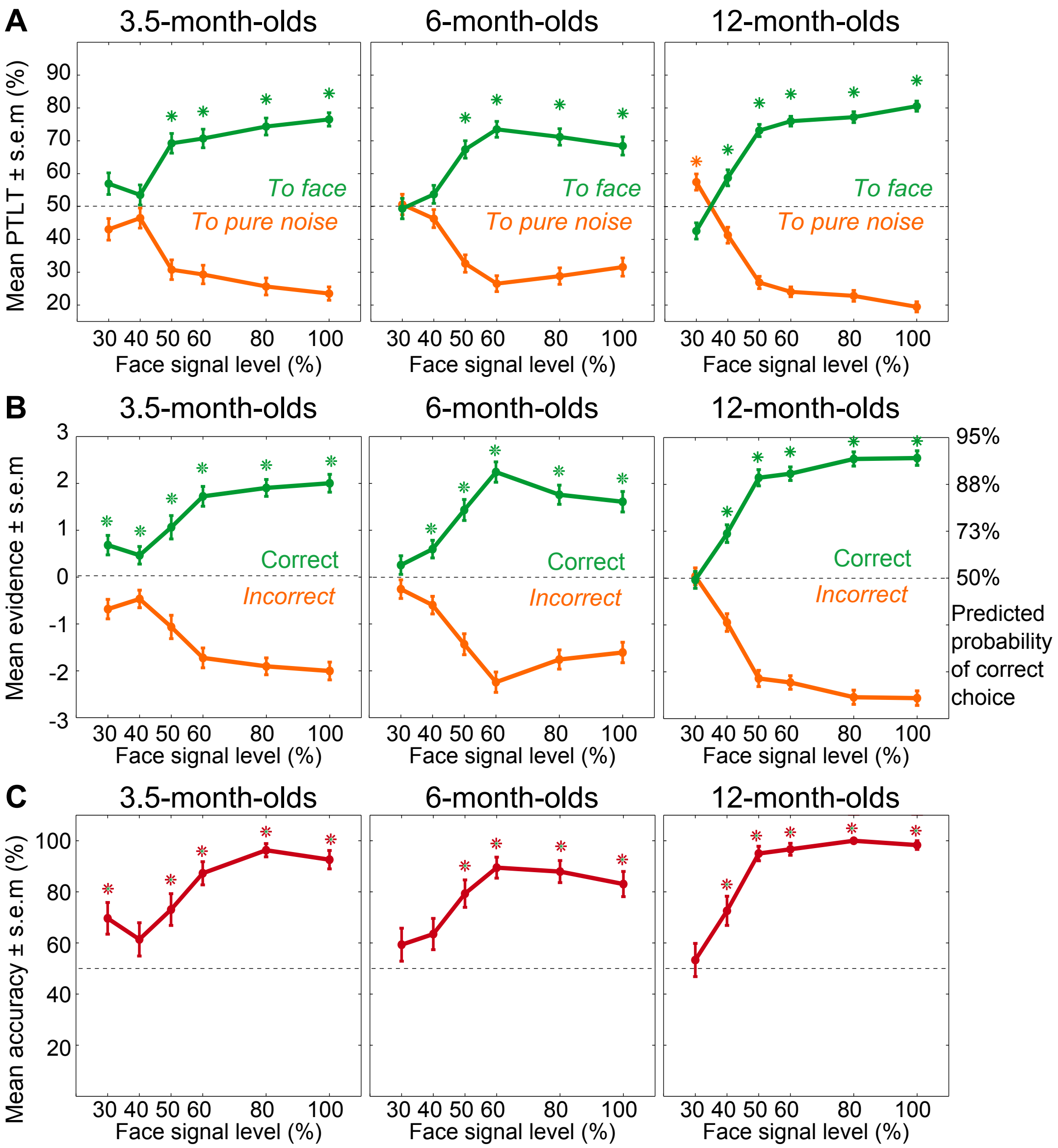

Figure 6.2: **Face detection across signal levels and age groups.** **(A)** Visual preference for the face side versus the noise side. **(B-C)** Decoding the face side from looking behavior. **(B)** Decoding evidence (log-odds) **(C)** Decoding accuracy. Student *t*-tests against chance, $\alpha = 0.05$, Holm-Bonferroni corrected.

| Parameter | β | s. e. | $t$ | 2.5% | 97.5% |
|---|---|---|---|---|---|
| Asymptote at 0% signal | 0.01 | 0.09 | 0.07 | - 0.165 | 0.178 |
| Asymptote at 100% signal: Fear * | 1.25 | 0.08 | 15.76 | 1.091 | 1.401 |
| Asymptote at 100% signal: Smiling vs. Fear | - 0.13 | 0.10 | - 1.25 | - 0.332 | 0.073 |
| Slope * | 26.53 | 8.41 | 3.15 | 10.039 | 43.014 |
| Threshold: Fear x Eyes * | 0.44 | 0.02 | 22.49 | 0.405 | 0.483 |
| Threshold: Smiling x Mouth vs. Fear x Eyes * | 0.05 | 0.03 | 1.99 | 0.001 | 0.103 |
| Threshold: Fear x Mouth vs. Fear x Eyes | 0.01 | 0.03 | 0.48 | - 0.039 | 0.064 |
| Threshold: Smiling x Eyes vs. Fear x Eyes | 0.00 | 0.03 | 0.08 | - 0.055 | 0.060 |

Table 6.2: **Psychometric curve modeling of face versus noise visual preference.** The logit-transformed visual preference for the face side was used as the dependent variable of a Non-linear Mixed Model with a standard psychometric curve formula. Parameters significantly different from 0 (Wald confidence intervals, $\alpha = 5\%$) are marked by an asterisk.

an interaction of age with facial emotion and eye visibility ($\chi^2(2) = 6.62$, $p = 0.037$) driven by a significant effect of facial emotion ($\chi^2(1) = 6.33$, $p = 0.012$) and a marginal interaction of facial emotion and eye visibility ($\chi^2(1) = 3.1046$, $p = 0.078$) at 3.5 months, and a marginal effect of eye visibility at 12 months ($\chi^2(1) = 3.05$, $p = 0.081$). Thus, when face detection was measured by the infants' visual preference for the face side overall there was evidence of a higher detection threshold for smiling (but not fearful) faces with more signal in the mouth than the eye region compared to fearful faces with more signal in the eye region (TABLE 6.2; FIGURE 6.3A,C), and the effect appeared to be at least partially driven by the 3.5-month-old group (FIGURE 6.3B).

### 6.6.3 Variations in face detection as measured by face versus noise decoding

A similar approach was used to analyze the face versus noise classification evidence decoded from the infants' multivariate looking behavior (visual preference, duration of individual looks, duration of first look, etc.). Again, the detection threshold for fear faces with more signal in the eye region (44.07 ± 2.14 % face signal; TABLE 6.3; FIGURE 6.3D) was significantly lower than the detection threshold for smiling faces with more signal in the mouth region (increase in threshold: 7.90 ± 2.52 % face signal, 95% C.I [0.030 0.128]) but equivalent to the threshold in the other conditions (fear faces with more signal in the mouth region, smiling faces with more signal in the eye region, Wald confidence intervals, $\alpha = 5\%$; TABLE 6.3; FIGURE 6.3D).

A reduced model was again used to estimate differences between age groups, and no sig-

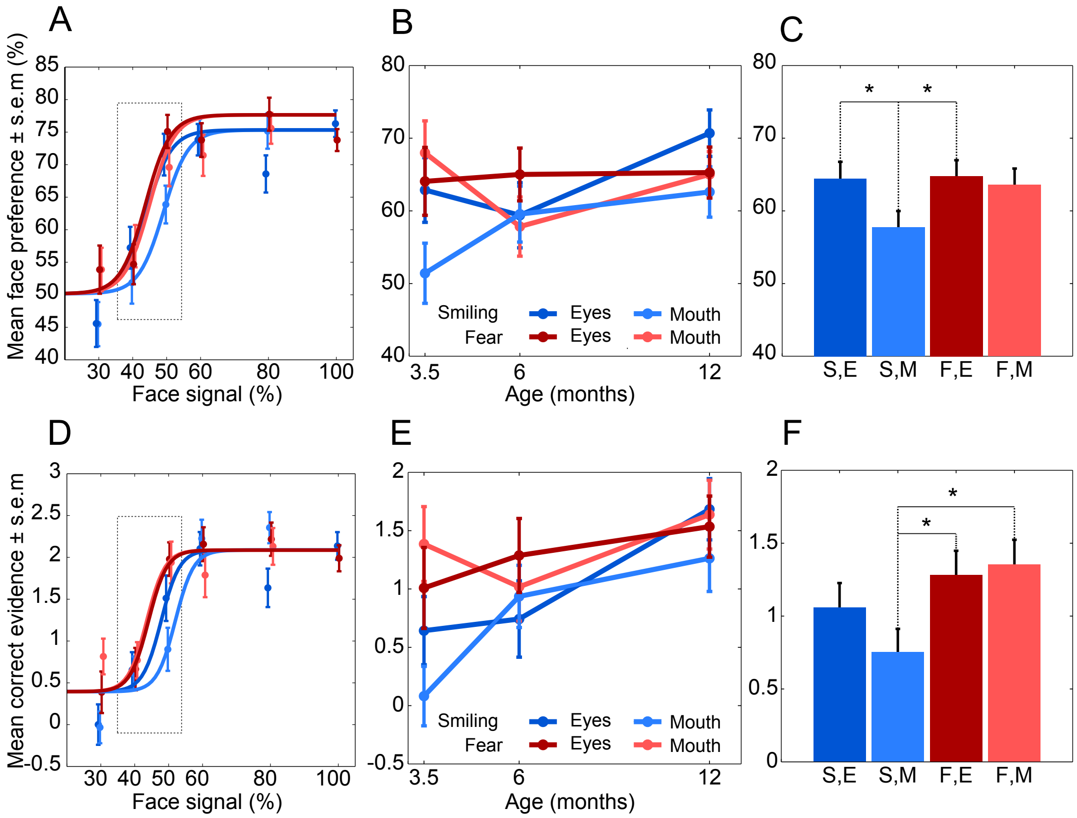

Figure 6.3: **Influence of facial emotion and facial feature visibility on face detection.** Face detection was measured by **(A-C)** visual preference for the face side and by **(D-F)** face versus noise classification evidence (log-odds). **(A, D)** Psychometric curve modeling estimates the overall threshold to be between 40% and 50% face signal (gray dotted boxes), with a significantly higher threshold for the smiling faces with more signal in mouth region (light blue) than for the fear faces with more signal in the eye region (dark red). **(B-C, E-F)** Analyses restricted to data at the threshold of visibility, **(B, E)** at each age group and **(C, F)** across the three age groups (**C**, **F**: Student t-tests for independent samples or Linear Mixed Model, as appropriate, $\alpha = 0.05$). E, Eyes, more signal (PSNR) in the Eye region; F, Fear; M, Mouth, more signal (PSNR) in the Mouth region; S, Smiling.

| Parameter | $\beta$ | s. e. | $t$ | 2.5% | 97.5% |
|---|---|---|---|---|---|
| Asymptote at 0% signal | 0.39 | 0.11 | 3.49 | 0.173 | 0.617 |
| Asymptote at 100% signal: Fear * | 2.09 | 0.11 | 19.12 | 1.873 | 2.301 |
| Asymptote at 100% signal: Smiling vs. Fear | 0.00 | 0.15 | 0.01 | - 0.301 | 0.303 |
| Slope * | 36.70 | 15.31 | 2.40 | 6.690 | 66.714 |
| Threshold: Fear x Eyes * | 0.44 | 0.02 | 20.56 | 0.399 | 0.483 |
| Threshold: Smiling x Mouth vs. Fear x Eyes * | 0.08 | 0.03 | 3.14 | 0.030 | 0.128 |
| Threshold: Fear x Mouth vs. Fear x Eyes | - 0.01 | 0.03 | - 0.20 | - 0.058 | 0.048 |
| Threshold: Smiling x Eyes vs. Fear x Eyes | 0.04 | 0.03 | 1.16 | - 0.026 | 0.100 |

Table 6.3: **Psychometric curve modeling of face versus noise decoding evidence.** Correct decoding evidence in favor of the face side (log-odds) was used as the dependent variable of a Non-linear Mixed model with a standard psychometric curve formula. Parameters significantly different from 0 (Wald confidence intervals, $\alpha = 5\%$) are marked by an asterisk.

nificant differences in threshold were found between age groups (Wald confidence intervals, $\alpha = 5\%$). Analyses restricted to face versus noise decoding evidence around the detection threshold (40-50% face signal; Linear Mixed Model; FIGURE 6.3E-F) revealed a general increase in decoding evidence with age (main effect of age, $\chi^2(2) = 14.35$, $p < 0.001$; FIGURE 6.3E), and a significant main effect of facial emotion reflecting higher face versus noise discrimination evidence for fear than smiling faces ($\chi^2(1) = 6.03$, $p = 0.014$; FIGURE 6.3F), with no interaction between the two factors and no other significant effect (all $p$s > 0.05).

Overall, analyses of face detection based on the multivariate evidence of face versus noise discrimination in the infants' looking behavior confirmed the earlier finding of a higher detection threshold for smiling (but not fearful) faces with more signal in the mouth than the eye region compared to fearful faces with more signal in the eye region (TABLE 6.3; FIGURE 6.3D). Additionally, there was more face versus noise discrimination evidence for fear than smiling faces around the detection threshold, and the effect did not interact with age although discrimination evidence increased with age generally (FIGURE 6.3E-F).

## 6.7 DISCUSSION

. We used univariate and multivariate measures of face versus noise discrimination with 3.5-, 6- and 12-month-old infants to test the hypothesis that fearful faces are better detected than smiling faces in noise by infants. The data supported the hypothesis, and revealed a possible additional interaction with eye visibility. Perceptual thresholds were lowest for fear faces with more signal in the eye region, intermediate for fear faces with more signal in the mouth region and for smiling faces with more signal in the eye region, and highest for smiling faces with more signal in the mouth region. The effect was equivalent or stronger in the 3.5-month-old group than in the two older groups.

### 6.7.1 Facilitated detection of fear faces by infants

The present study revealed that fearful faces are detected more easily than smiling faces by infants, in particular when less signal is available in the eye region – as if the fearful eyes acted as an additional signal. While the amount of signal in the face or eye region, global contrast and spatial frequency power spectrum were constant across conditions, the current data does not distinguish between physical and emotional causes of the salience of fearful faces and eyes (Vuilleumier, 2005). Thus, the large sclera and local contrast of fearful eyes, but not an enhanced response of the amygdala to these biologically relevant stimuli, may underlie the lower detection threshold of fear faces. However, local contrast in different regions (for example, teeth visibility in the smiling face) did not yield the same effect. Thus, the salience of fearful faces and eyes cannot be reduced to local contrast. Rather, it is possible that the eyes already are crucial to the face template from 3.5-month-old onwards (Dupierrix et al., 2014), so that the enlarged eyes of fear faces facilitate face detection, or that fearful eyes themselves are perceived as biologically (threat) relevant, leading to facilitated detection. The later hypothesis is preferred as there was a main effect of facial emotion on face versus noise detection around the threshold (as measured by face versus noise decoding), but no main effect of the visibility of eyes on either measure of detection. Comparing infant's detection thresholds with that of machine-based face and eye detection algorithms , or using fearful or surprised eyes embedded in neutral faces (Morris et al., 2002; Peltola, Leppänen, Vogel-Farley, et al., 2009), could be used in future studies to evidence possible signal amplification by fearful eyes and distinguish between featural and configural contributions to the facilitated detection of fear faces in infancy.

### 6.7.2 Precursors to threat sensitivity in infancy

An attentional bias to fear faces emerges in infancy between the ages of 5- and 7-months but not younger (Leppänen & Nelson, 2009, 2012), although some electrophysiological fear sensitivity has been reported in younger infants (Hoehl, Wiese, & Striano, 2008; Yrttiaho et al., 2014) that partially predicts fear sensitivity at 7-months (Yrttiaho et al., 2014). The readiness to detect fear faces could represent a precursor of or act as a scaffold to the later emergence of attentional capture by fear faces around the age of 7-months. Further research will reveal whether the facilitated detection of fear faces at 3.5-months and later is related to behavioral and physiological fear sensitivity at 5- and 7-months.

### 6.7.3 Methodological challenges in infant psychophysics

The use of within-subject "stimulus-response" paradigms (Aslin & Fiser, 2005) in infancy is limited by the number of valid trials that may be obtained per infant and, in the case of stimulus detection study, by the number of trials with undetectable stimuli that infants can tolerate (Teller, 1979). Here, we were able to sample 6 different signal levels, only 2 of which (40%, 50%) were ultimately relevant to the precise estimation of face visibility threshold. Future infant studies using weighted-mean phase noise (Dakin et al., 2002) may use the thresholds found here as starting points. Further, detection or discrimination studies usually do not present with a specific hypothesis regarding which behavioral variable (overall visual preference, number of looks, direction of first look, or number of looks...) should distinguish between stimuli categories – the hypothesis is on the discrimination itself. Thus, we introduced a multivariate measure of face versus noise discrimination that used visual preference as well as the duration of individual looks to both sides of the screen and other variables, without selecting any of these variables a priori but combining them according to how well they discriminated between face and noise. This method may be generalized to the discrimination of any kinds of stimuli. For example, a limitation of the current study is that all the patterned stimuli presented were faces. Thus, face detection cannot be distinguished from the general detection of organized patterns: did infant orient preferentially to the faces because they detected them as faces, or because they detected a pattern? Using a face paired with an object or pattern of similar complexity, with the same level of noise in both stimuli and varying levels of noise across trials, would allow testing not only the detection of a face, but the detection that a pattern is, indeed, a face and not any other kind of pattern.

### 6.7.4 Conclusion

In conclusion, in the present study we used face versus noise visual preference (an univariate measure) and face versus noise decoding of looking behavior (a multivariate measure) to estimate the detection thresholds of fearful and smiling faces in 3.5, 6 and 12-month-old infants. The data supported the hypothesis of a superior detection of fearful faces in infancy, as evidenced by fitted detection thresholds and measures of detection around the threshold. The effect was equivalent or stronger in the 3.5-month-old group than in the two older groups, supporting the idea that at least some aspects of fear sensitivity are developmentally constant during infancy and emerge as early as 3.5-months.

## 6.8 ACKNOWLEDGMENTS

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# Chapter 7

# GENERAL DISCUSSION

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Box 9: Résumé de la discussion générale

Les résultats des différents chapitres expérimentaux sont discutés au regard de trois questions : (1) La perception des expressions faciales se développe-t-elle de manière indépendente ou intégrée à la perception des autres dimensions du visage ? ; (2) L'expérience des visages a-t-elle un rôle dans la manière dont les nourrissons perçoivent les expressions de visages nouveaux ? ; et (3) Le développement de la perception des visages de peur est-il discontinu durant la première année de vie ? Au regard du point (1), les résultats des CHAPITRES 3, 4,et 5 montrent que le traitement des expressions faciales dépend du et module le traitement des autres dimensions du visage, que ce soit chez l'enfant ou chez le nourrisson. Cependant, dans l'ensemble, les interactions entre dimensions variantes et invariantes des visages ne semblent pas se produire plus chez le nourrisson que chez l'enfant ou l'adulte. Au regard du point (2), les données présentées au cours du CHAPITRE 4 concernant la préférence visuelle pour le sourire à 3.5 mois confirment le rôle de l'expérience mais soulignent l'importance d'autres facteurs tels que les propriétés des stimuli (intensité de l'expression, dents visibles ou non) ou les différences inter-individuelles. Enfin, au regard du point (3), le CHAPITRE 6 présente des données confortant l'idée que certains aspects au moins du traitement préférentiel des visages et yeux de peur sont présents avant l'âge de 6-7 mois, c'est-à-dire avant l'émergence d'un biais attentional pour ces visages. Sont également discutées les implications de ces résultats à propos de (1) la manière dont les nourrissons de moins de 6-7 mois perçoivent les expressions faciales émotionnelles, et (2) l'émergence au cours du développement de biais dans la perception sociale mettant en jeu le genre et l'expression faciale.

Enfin, une dernière section présente une série de limites et perspectives générales, sans prétendre à l'exhaustivité. Y-est notamment développé l'apport potentiel de techniques telles que l'imagerie ou la modélisation à l'étude de la perception du sourire et des visages de peur chez le nourrisson, ainsi que l'intérêt d'étudier la perception des expressions faciales émotionnelles en intégrant les avancées de la recherche sur la perception des visages et son développement - que ce soit par l'emploi de tâches spécifiques ou par la prise en compte du rôle de l'expérience visuelle. Les difficultés rencontrées dans l'étude des émotions chez le nourrisson sont enfin abordées, ainsi que quelques pistes de progrès possibles en ce qui concerne la prise en compte des différences inter-individuelles et de trajectoires développementales, la mise en contexte des expressions émotionnelles et notamment leur mise en contexte social, et la question de leur valence émotionnelle.

## 7.1 MAIN RESULTS

The present thesis attempted to further the current scientific understanding of the development of facial expression perception in infants and children, with three separate questions in mind: (1) Does facial emotional expression processing develop independently from the processing of other facial dimensions?; (2) Does experience affect how infants perceive emotional expressions portrayed by strangers?; and (3) Is the development of fear processing continuous or discontinuous during the first year of life? The precise results obtained in each chapter of the current thesis will not be repeated here, but will instead be summarized according to each of those three questions.

### 7.1.1 Does facial emotional expression processing develop independently from the processing of other facial dimensions?

Models of face perception in adults have emphasized the relative separation of variant (e.g. expression) and invariant (e.g. identity, gender) streams in face processing, in a hierarchical fashion where the invariant stream has precedence over the variant stream (Bruce & Young, 1986; Calder & Young, 2005). The separation is, however, incomplete, and interactions occur between both streams (Tiberghien et al., 2003). In CHAPTER 3, we found that an angry facial expression biases face gender categorization towards the "male" category from early childhood (5-6 years of age) and up to adulthood. The effect was constant across development. In CHAPTER 4, a series of studies investigated the effect of face gender and face race on the visual preference for smiling faces at 3.5-months of age. Results were mixed, as face gender significantly affected the visual preference for open-mouth (SECTION 4.1) but not closed-mouth smiles (SECTION 4.3, although there was a significant interaction between face race, face gender, and infant gestational age at birth). The effect decreased with age from birth and with gestational age at birth, and was absent at 9 months (SECTION 4.2). Finally, in CHAPTER 5, the effect of face gender and positive expression on gaze referencing was evaluated at 3.5, 9 and 12 months of age. Again, results were mixed as gaze following was maximal for neutral female faces at 3.5 months but for smiling female faces at 12 months, with no differences between conditions at 9-months despite a significant effect of face gender on the subsequent recognition of gaze cued objects. Overall, there was substantial evidence that the processing of emotional facial expressions depends on and modulates the processing of other facial dimensions, such as gender or gaze, from the age of 3.5-months to later infancy and childhood. However, the hypothesis that less complete structural encoding in younger infants leads to higher levels of interaction between variant and invariant dimensions in early infancy than after the age of 7-8 months was not entirely supported.

### 7.1.2 Does experience affect how infants perceive emotional expressions portrayed by strangers?

Infants are more familiar to own-race female faces (Rennels & Davis, 2008; Sugden et al., 2014); this translates to spontaneous preferences for familiar types of faces in 3- to 4-month-olds (Kelly et al., 2005; Quinn, Uttley, et al., 2008; Quinn et al., 2002). The series of experiments in CHAPTER 4 was meant as a test of the hypothesis that infants' experience with faces would modulate the visual preference of 3.5-month-olds for smiles portrayed by strangers. Indeed, an effect of experience has been demonstrated in the processing of emotional expressions from caregivers (Kahana-Kalman & Walker-Andrews, 2001). We found that, at 3.5-months of age, the visual preference for smiling (La Barbera et al., 1976) did not apply rigidly to all types of faces and was modulated by face gender (SECTION 4.1), in line with a role of experience in this behavior. The effect was not replicated with closed-mouth smiles (SECTION 4.3). The preference for own-race, female, closed-mouth smiling faces (SECTION 4.3), and the effect of face gender on the preference for own-race, open-mouth smiling faces (SECTION 4.2), linearly followed individual variations in age from birth or gestational age at birth. The results confirmed a role of experience with faces but highlighted the role of stimuli properties (closed- or open-mouth smile) and individual factors (including gestational age at birth) in the visual preference for smiling faces at 3.5-months of age. It is possible that closed-mouth smiles were too subtle for young infants to be perceived as smiles - the same limitation may apply to other kinds of subtle expressions.

### 7.1.3 Is the development of fear processing continuous or discontinuous during the first year of life?

M. H. Johnson (2005) has argued that the amygdala may be functional at birth, enhancing the cortical processing of biologically relevant stimuli - such as faces, eyes or threat-related emotional expressions. However, fear faces hold visual attention in infants from about 7 months of age only, raising the possibility that the amygdala doesn't assume the function of threat detector before that age (Leppänen & Nelson, 2009, 2012). In CHAPTER 6 we observed a superior detection of fearful faces in noise by infants from 3.5-months of age. Depending on the measure used to infer detection, the effect was equivalent or greater to that of additional signal in the eye region. The results are consistent with the involvement of the amygdala in the processing of eyes, fear and other biologically relevant stimuli by adults (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Sato, Yoshikawa, Kochiyama, & Matsumura, 2004), as well as with two earlier electrophysiological studies reporting some fear sensitivity at 5 (Yrttiaho et al., 2014) or even 3.5 months of age (Hoehl, Wiese, & Striano, 2008). They support the hypothesis that some aspects of fear processing are developmentally stable in infancy, at least from 3.5-months of age onwards.

## 7.2 IMPLICATIONS

Two transversal axes emerge from the results of the present studies.

### 7.2.1 The perception of emotional facial expressions before the age of 5 months

Relatively few studies have investigated the perception of emotion in infants younger than 5 months (SECTION 1.2.2.2) as the categorical discrimination of several emotional expressions emerges at 6-7 months of age (Leppänen & Nelson, 2009; SECTION 1.2.2.2). This population has been specifically studied in CHAPTER 4, and was included in CHAPTERS 5 and 6. While the results of CHAPTER 4 were difficult to interpret, overall the results outlined in CHAPTER 4 imply that, at 3.5-months of age, experience with faces influences the processing of expressions portrayed by strangers - at least when those expressions are intense and clearly visible. Thus, a question is whether the processing of emotion at a later age builds on this early experience, or whether it emerges as a replacement of earlier modes of processing. The results described in CHAPTER 6 also imply that at least some aspects of facial emotion processing exist in early infancy. These results are a motivation to direct more research efforts to studying the processing of facial emotion in early infancy and in newborns: even though their abilities are limited, studying these populations provides insights regarding the possible precursors of later abilities found in older infants, children, and adults.

### 7.2.2 The early ontogeny of social perception biases involving gender and emotional facial expressions

Social perception biases involving race or character traits have recently been described from early childhood (Cogsdill & Banaji, 2015; Cogsdill et al., 2014; Dunham et al., 2013). In CHAPTER 3, we described the developmental invariance of a social perception bias involving gender and emotional expression from 5-6 year-old to adulthood. In CHAPTER 4, we reported differences in the processing of smiling expressions by 3.5-month-olds that depended on face gender and race. These results directly imply that social perception biases involving gender and emotional facial expressions emerge surprisingly early, possibly from infancy. A remaining question is whether these perceptual biases present in infancy directly translate to social biases in the same way that perceptual biases involving face race may do (Quinn et al., 2015; W. S. Xiao et al., 2015). It is indeed difficult to relate those early behaviors to the ones observed later during infancy and childhood.

## 7.3 General limitations and perspectives

The specific limitations of each study have been discussed earlier, and each study calls for direct and conceptual replications. Additional, general limitations and perspectives will now be briefly outlined.

### 7.3.1 Integrating behavioral, computational and neuroimaging approaches

The infant studies included in the present thesis were solely (Chapters 4 and 5) or mostly (Chapter 6) behavioral. Thus, an obvious avenue of research would be to integrate this approach with computational and neuroimaging methods. Combining behavioral, computational and neuroimaging approaches has been fruitful in adult studies (e.g. in the domain of sequence learning; Dehaene, Meyniel, & Wacongne, 2015) as well as infant studies (Aslin & Fiser, 2005).

#### 7.3.1.1 Reward processing and the neural basis of the smiling versus neutral preference in 3.5-month-old infants

Spatially-resolved neuroimaging (e.g., NIRS) could be used to investigate the neural basis of the visual preference for smiling versus neutral faces in 3.5-month-old infants studied in Chapter 4. Studies of smile processing in older infants have revealed frontal responses consistent with orbitofrontal sources of activations, as could be expected from the processing of rewarding stimuli in adults (Minagawa-Kawai et al., 2009). Are the same areas involved in the visual preference for smiling at 3.5-months? For example, would infants who consistently show stronger visual preference for smiling (versus neutral) faces in a paired visual preference paradigm also show consistently stronger frontal responses to these faces in a NIRS study? Would frontal responses to smiling faces be modulated by face gender and race, and possibly stronger for own-race female faces than other types of faces - in older infants, they are affected by the model's familiarity and stronger for the infant's own mother than for a female stranger (Minagawa-Kawai et al., 2009)? While there was no positive effect of smiling on gaze following or referential object learning in 3.5-month-olds (Chapter 5), this may be because of the referential nature of the task (i.e. a negativity bias in learning about objects; Vaish et al., 2008) rather than because the smiling faces are not inherently rewarding or positively valenced at that age. Similarly, the conflicting results of Chapter 4 were difficult to interpret on their own as the behavioral and neuroimaging literature on smile processing in young infants is limited.

While neuroimaging wouldn't give access to the actual emotional valence, it could provide converging evidence when understood in association with behavioral data on visual preference or choice-based behavioral paradigms. Gaze-contingent paradigms are increasingly used in infant research (e.g. Bonn & Aslin, 2014; Q. Wang et al., 2012), potentially opening the way to using eye-tracking to study action learning and decision making including the effect of different types of rewards, context, and contingency parameters. For example, would infants gaze more towards a gaze-contingent "button" displaying smiling faces than towards a gaze-contingent "button" displaying neutral faces? Would this effect be sensitive to outcome devaluation (a hallmark of instrumental, action-outcome learning as opposed to Pavlovian, stimulus-outcome learning; Balleine & O'Doherty, 2010; Dickinson & Balleine, 1993; Ostlund & Balleine, 2007) i.e. be weaker or even reversed if the infant was habituated to smiling faces before testing? More generally, and providing that existing methodological difficulties (e.g. learning speed versus number of valid trials per session) can be overcome, these types of paradigms could open the way to the study of action learning and decision making in infancy and how it relates to social interactions and attentional control. For example: it has already demonstrated that infants use social cues from faces to guide their looking behavior (Tummeltshammer et al., 2014). Could such cues be used to jump start learning in gaze-contingent paradigms? Would faces be more rewarding than objects, and familiar faces more rewarding than stranger faces? Would these effects depend on attachment or developmental (e.g. autism risk) status? Would infants respond adaptively to continence reversal? What if the contingency is predicted by contextual cues? Does the rewarding quality of stimuli depend mostly on their familiarity or novelty (Kidd et al., 2012), or does it also reflect emotional valence?

#### 7.3.1.2 Face, eyes, and fear detection in infancy

Similarly, combining the behavioral approach with computational and neuroimaging methods could be applied to the study of face and fear detection in infants, as well as to the study of face perception in infants in general. A direct perspective would be to adapt the paradigm from CHAPTER 6 to EEG or NIRS, using unpaired presentations and taking components related to face processing (N290 and P400 for EEG, de Haan et al., 2002; temporal responses for NIRS, Nakato et al., 2011) as a measure of face detection. Ideally, neuroimaging and behavioral measures of detection could be linked at the level of single trials, and their determinants researched. For example, is there any difference in the baseline activity or in the early response to the stimuli (0-250ms) that relates to later face detection? Models of emotional salience suggest a possible role for fast sub-cortical inputs, and very little is known about the function of sub-cortical structures in infancy because of methodological limitations (Minagawa-Kawai et al., 2008). Conversely, later components such as the attentional component Nc (Jessen & Grossmann, 2015) or Late Positive Potentials (Flykt & Caldara, 2010) may differ depending on (1) condition and (2) trial-level detection, suggestive of more elaborate processing following face or fear detection.

Further, computational models of face detection could be used as a comparison to behavioral and neuroimaging measures, as was done in CHAPTER 3 when comparing behavioral accuracy to different computational models of the same task. For example, would face detection at birth co-vary with models based on broad patterns (PCA, ICA), and later align more closely to models based on feature detection - most notably, the eyes (Dupierrix et al., 2014)? Can classic paradigms used in adults to evidence the face space (SECTION 1.1.1.2) be adapted for infant research?

### 7.3.2 Facial emotion perception as a face processing skill

In the current thesis, facial expressions of emotions were studied in the context of broader face perception phenomenon such as the processing of gaze (CHAPTER 5), gender (CHAPTERS 3, 4, and 5), or race (CHAPTERS 3 and 4). Overall, the results suggest that emotion perception is integrated with face perception from early on, validating this approach. An avenue of progress would be to build on the rich body of knowledge accumulated on the development of face perception (SECTION 1.2.1) to get better insights on the development of facial emotion perception.

#### 7.3.2.1 Encoding aspects: Beyond visual preference and categorization

Infant studies of emotional faces perception, including this thesis (CHAPTERS 4, 5, and 6), typically limit themselves to visual preference or categorization paradigms. An accomplishment of face perception research has been the development of tasks tailored to uncover face encoding strategies - for example, the composite effect task (Maurer et al., 2002). While the composite task has been used in infants (Turati et al., 2010), it has never been applied on the perception of facial emotions in this age group. Adapting this paradigm would allow understanding whether infants use featural or configural information when processing emotional faces such as smiling or fear faces. This is important as many studies of emotional faces processing in infancy, including the studies included in the present thesis, do not distinguish between featural and configural processing: for example, is the processing of smiling reducible to the processing of the smiling mouth? Is the response to fear faces reducible to the processing of fearful eyes? A notable exception is Peltola, Leppänen, Vogel-Farley, et al. (2009), where neutral faces with embedded fear eyes were used as control stimuli and it could be demonstrated that, at 7-months of age, fearful faces but not fearful eyes in neutral faces elicit an attentional bias.

More generally, the questions relevant to face processing - such as the role of facial movement (N. G. Xiao et al., 2014), viewpoint invariance, or underlying representations (Valentine, 2001) - all apply to the study of facial expressions processing. For example, how and when do emotional expressions and articulation movements begin to be processed in partly divergent ways, and can perception-production links account for this divergence?

#### 7.3.2.2 Comparative developmental studies and the role of experience with faces

Some results have already been obtained on the perception of emotional expressions in other-race faces by infants (SECTION 4.3), and studies in children suggest a relative robustness to environmental conditions (Moulson et al., 2014). Cross-cultural (e.g. Kelly et al., 2009), and cross-species studies (e.g. Fernandez-Carriba, Loeches, Morcillo, & Hopkins, 2002) of emotion perception in infancy and childhood from birth would provide a much deeper understanding of the sensitivity of this ability to experience with faces and of its phylogeny. For example, do younger infants differentiate other-species facial expressions more readily, or better associate them cross-modally with emotional vocalizations, than older infants? Are the developmental timelines of emotional facial expression processing comparable across primate (or even mammal) species? Do infants readily categorize emotions from other-race faces as they do with own-race faces?

### 7.3.3 A finer approach to emotions in infancy

General areas of progress apply to the study of emotions in infancy, including the use of finer-grained paradigms rather than “yes/no” paradigms (Aslin & Fiser, 2005), the integrated understanding of behavioral and neuroimaging responses (Aslin & Fiser, 2005), and the sharing of negative results within the scientific community. A few more specific avenues of research may be outlined as follows.

#### 7.3.3.1 Individual differences and developmental trajectories

In CHAPTER 4, non-trivial individual differences related to gestational age at birth were found in the response of 3.5-month-olds to smiling faces. Individual differences related to temperament have been reported earlier in the processing of smiling faces in infants (Ravicz et al., 2015). Similarly, group differences have been reported in the perception of emotional faces that depend on maternal depression (T. Field, Pickens, Fox, Gonzalez, & Nawrocki, 1998). It appears that the study of individual differences such as temperament, genotype or rearing conditions - relevant to emotional, social and perceptual development - may provide a finer picture to the development of emotional faces processing in childhood and infancy, as would the inclusion of infants younger and older than 5-7 months.

Another area of progress would be the study of developmental trajectories including a wider range of emotions. For example, the developmental trajectory of the processing of threat-related expressions (anger, fear) in infancy may prove to be fundamentally different than the developmental trajectory of the processing of smile or other kinds of expressions. The negativity bias (Vaish et al., 2008) suggests this kind of dissociation, but studies in children reveal a relative robustness of facial emotion processing with subtle alterations that directly reflect differences in rearing conditions and do not appear to depend on valence (e.g. increased threshold for the detection of smiling versus neutral in institutionalized children; Moulson et al., 2014; and increased threshold for the detection of fear or sadness versus anger in physically abused children; Pollak & Kistler, 2002)

#### 7.3.3.2 Context and appraisal

Studies in adults have demonstrated the role of contextual information (including “social affordances”) in the processing and appraisal of emotional facial expressions (e.g. Dezecache et al., 2015; Grèzes & Dezecache, 2014). In the current thesis, emotional faces were processed without context (CHAPTERS 3, 4, and 6) or as referring to cued objects (CHAPTER 5). Little is known about how context, including social context, may modulate the processing of emotional expression in infants, although current data suggest that such contextual influences may start to emerge from about 8 months of age (Phillips et al., 2002; Skerry & Spelke, 2014). For example, would infant use physical or social context to disambiguate ambiguous expressions such as neutral expressions, surprised expressions, or morphed expressions? A methodological issue here would be the design of paradigms that are naturalistic enough to trigger contextual inferences. This may involve using puppets or live models.

Conversely, there is still progress to be made on understanding how infants use emotional expressions from others to understand the world. In particular, it is unknown how infants interpret emotional expressions directed towards people rather than objects. For example, would infants assume that people who smile towards each other, or share specific emotions, will associate together later?

#### 7.3.3.3 Emotional valence

Finally, a very intriguing yet common observation is the lack of apparent distress of infants exposed to fearful faces in the laboratory, despite behavioral and electrophysiological markers of fear sensitivity including increased attention and arousal (Leppänen & Nelson, 2009, 2012; CHAPTER 6). This suggests dissociation between emotional valence and fear sensitivity at this age, in line with the hypothesis of an automatic fear detection mechanism irrespective of appraisal. Alternatively, negative valence could be dissociated from distress in the same way that pain can be felt without distress (Rainville, Duncan, Price, Carrier, & Bushnell, 1997). Similarly, it is unknown whether the visual preference for smiling in 3.5-month-olds reflects the positive valence of these stimuli at this age (CHAPTER 4). The validation of electromyographic recordings of corrugator activity as an implicit measure of emotional valence (Larsen et al., 2003; Magnée et al., 2007; Neta et al., 2009; Tottenham et al., 2013) in infants would provide a tool in this respect as it is currently unclear whether infants experience emotional faces as "positive" or "negative" (e.g. see Ludemann, 1991). Hemispheric asymmetry of frontal EEG activity has been used as a marker of approach-avoidance in infants (N. A. Fox, 1991), but valence appears more elusive. More generally, the characterization of emotional experience in preverbal infants is an area of current and active research.

# CONCLUSION

In the course of this thesis, we have tried to replace the development of the perception of emotional faces into the theoretical framework of the development of face perception - encoding and representational aspects, the role of experience, and social attention. This approach led to several insights regarding the ontogeny and underlying cause of gender-emotion relationships in face perception (CHAPTERS 3 and 4) and the sensitivity to fear in infancy (CHAPTER 6).

We hope that this modest contribution will inform future research on the matter, as we thrive to understand the minds of the smallest among us.

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# RÉSUMÉ

Cette thèse se propose d'examiner le développement de la perception des expressions faciales émotionnelles en le replaçant dans le cadre théorique de la perception des visages : séparation entre aspects variants (expression, regard) et invariants (genre, type), rôle de l'expérience, attention sociale. Plus spécifiquement, nous avons cherché à mettre en évidence l'existence, tant chez l'enfant que chez le nourrisson, d'interactions réciproques entre la perception d'expressions faciales de colère, de sourire ou de peur et la perception du genre (Études 1-2), la perception du regard (Étude 3), et la détection des visages (Étude 4).

Dans un premier temps, nous avons montré que les adultes et les enfants de 5 à 12 ans tendent à catégoriser les visages en colère comme masculins (Étude 1). Comparer les performances humaines avec celles de classifieurs automatique suggère que ce biais reflète l'utilisation de certains traits et relations de second-ordre des visages pour en déterminer le genre. Le biais est identique à tous les âges étudiés ainsi que pour les visages de types non-familiers. Dans un second temps, nous avons testé si, chez le nourrisson, la perception du sourire dépend de dimensions invariantes du visage sensibles à l'expérience - le genre et le type (Étude 2). Les nourrissons ont généralement plus d'expérience avec les visages féminins d'un seul type. Les nourrissons de 3.5 mois montrent une préférence visuelle pour les visages souriants (dents visibles, versus neutre, de type familier) lorsque ceux-ci sont féminins ; l'inverse est observé lorsqu'ils sont masculins. L'effet n'est pas répliqué lorsque les dents des visages souriants (d'un type familier ou non) ne sont pas visibles. Nous avons cherché à généraliser ces résultats à une tâche de référencement d'objet chez des nourrissons de 3.5, 9 et 12 mois (Étude 3). Les objets préalablement référencés par des visages souriants étaient autant regardés que les objets préalablement référencés par des visages neutres, quel que soit le groupe d'âge ou le genre du visage, et ce malgré des différences en terme de suivi du regard. Enfin, en employant une mesure univariée (préférence visuelle pour le visage) et une mesure multivariée (évidence globale distinguant le visage du bruit) de la détection du visage à chaque essai, associées à une modélisation des courbes psychométriques par modèles non-linéaire mixtes, nous mettons en évidence une meilleure détection des visages de peur (comparés aux visages souriants) dans le bruit phasique chez les nourrissons à 3.5, 6 et 12 mois (Étude 4).

Ces résultats éclairent le développement précoce et le mécanisme des relations entre genre et émotion dans la perception des visages ainsi que de la sensibilité à la peur.

# ABSTRACT

This thesis addressed the question of how the perception of emotional facial expressions develops, reframing it in the theoretical framework of face perception: the separation of variant (expression, gaze) and invariant (gender, race) streams, the role of experience, and social attention. More specifically, we investigated how in infants and children the perception of angry, smiling, or fearful facial expressions interacts with gender perception (Studies 1-2), gaze perception (Study 3), and face detection (Study 4).

In a first study, we found that adults and 5-12 year-old children tend to categorize angry faces as male (Study 1). Comparing human performance with that of several automatic classifiers suggested that this reflects a strategy of using specific features and second-order relationships in the face to categorize gender. The bias was constant over all ages studied and extended to other-race faces, further suggesting that it doesn't require extensive experience. A second set of studies examined whether, in infants, the perception of smiling depends on experience-sensitive, invariant dimensions of the face such as gender and race (Study 2). Indeed, infants are typically most familiar with own-race female faces. The visual preference of 3.5 month-old infants for open-mouth, own-race smiling (versus neutral) faces was restricted to female faces and reversed in male faces. The effect did not replicate with own- or other-race closed-mouth smiles. We attempted to extend these results to an object-referencing task in 3.5-, 9- and 12-month-olds (Study 3). Objects previously referenced by smiling faces attracted similar attention as objects previously cued by neutral faces, regardless of age group and face gender, and despite differences in gaze following. Finally, we used univariate (face side preference) and multivariate (face versus noise side decoding evidence) trial-level measures of face detection, coupled with non-linear mixed modeling of psychometric curves, to reveal the detection advantage of fearful faces (compared to smiling faces) embedded in phase-scrambled noise in 3.5-, 6-, and 12-month-old infants (Study 4). The advantage was as or more evident in the youngest group than in the two older age groups.

Taken together, these results provide insights into the early ontogeny and underlying cause of gender-emotion relationships in face perception and the sensitivity to fear.