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Sensitivity to face animacy and inversion in childhood: Evidence from EEG data

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ABSTRACT

Adults exhibit relative behavioral difficulties in processing inanimate, artificial faces compared to real human faces, with implications for using artificial faces in research and designing artificial social agents. However, the developmental trajectory of inanimate face perception is unknown. To address this gap, we used electroencephalography to investigate inanimate faces processing in cross-sectional groups of 5–10-year-old children and adults. A face inversion manipulation was used to test whether face animacy processing relies on expert face processing strategies. Groups of 5-7-year-olds (N = 18), 8-10-year-olds (N = 18), and adults (N = 16) watched pictures of real or doll faces presented in an upright or inverted orientation. Analyses of event-related potentials revealed larger N170 amplitudes in response to doll faces, irrespective of age group or face orientation. Thus, the N170 is sensitive to face animacy by 5–7 years of age, but such sensitivity may not reflect high-level, expert face processing. Multivariate pattern analyses of the EEG signal additionally assessed whether animacy information could be reliably extracted during face processing. Face orientation, but not face animacy, could be reliably decoded from occipitotemporal channels in children and adults. Face animacy could be decoded from whole scalp channels in adults, but not children. Together, these results suggest that 5-10-year-old children exhibit some sensitivity to face animacy over occipitotemporal regions that is comparable to adults.

1. Introduction

As social robots and computer-generated faces become commonplace, there is a growing need to understand how individuals perceive artificial human faces. Artificial appearance compromises several aspects of face processing. Compared to animate human faces, inanimate (artificial) faces are remembered more poorly (Balas and Pacella, 2015; Crookes et al., 2015) and discriminated less efficiently (Crookes et al., 2015). Artificial appearance modifies the perception of face gender (Balas, 2013) and trustworthiness (Balas and Pacella, 2017), and inhibits the attribution of psychological attributes (Looser and Wheatley, 2010). Differences in processing inanimate (artificial) versus animate (human) faces are further qualified by facial expression (Bowling and Banissy, 2017; Krumhuber et al., 2018), face inversion (Krumhuber et al., 2018), and group affiliation (Hackel et al., 2014). Even high-quality computer-generated faces can be reliably distinguished from real faces (Farid and Bravo, 2012), suggesting exquisite sensitivity to artificial appearance – even without “uncanniness” (MacDorman et al., 2009).

As face processing abilities are tuned by visual experience, a relative lack of exposure to inanimate faces may induce relative behavioral difficulty in processing inanimate faces. Reduced exposure to particular face categories (e.g. defined by race or age) leads to difficulties in discrimination, naming, or assessing other aspects of faces effectively (Lewkowicz and Ghazanfar, 2006; Pascalis and Bachevalier, 1998; Pascalis et al., 2002; Rhodes and Anastasi, 2012). A widely-studied example is the other-race effect (Kelly et al, 2007, 2009), by which relative face recognition difficulties follow from diminished exposure to minority-race faces, including difficulties with face discrimination (Walker and Tanaka, 2003), memory (Meissner and Brigham, 2001), or identification (Byatt and Rhodes, 2004). Out-group effects on face perception are typically accounted for by a common computational framework (Balas, 2012; Byatt and Rhodes, 2004; Caldara and Abdi, 2006; Furl, Phillips, & O'Toole, 2002; Hancock et al., 1996; Moghaddam et al., 2000; O'Toole et al., 1993; Valentine, 1991; Valentine and Endo, 1992; Valentine et al., 2016), stipulating that face recognition becomes

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tuned to facial appearance by experience (Sugita, 2008), leading unfamiliar types of faces to be excluded from optimal face processing. Inanimate faces typically differ from real (animate) faces not only in shape but also in texture, which may affect face processing independently of a lack of exposure. For example, animate texture cues may be necessary for faces to be processed expertly in the absence of task demands (Meinhardt-injac, Persike and Meinhardt, 2013); because textures cues are thought to contribute to face processing (Burton et al., 2015; Kaufmann and Schweinberger, 2008), a lack of animate face texture cues in inanimate faces may also lead to suboptimal processing of inanimate faces.

Experience-based tuning of face processing is ongoing during childhood, motivating an examination of how animate versus inanimate face processing may diverge during this developmental period. Though face tuning changes dramatically during infancy (Kelly et al, 2007, 2009; Pascalis et al., 2002; Pascalis and Kelly, 2009), the other-race effect is reversible in early childhood (Anzures et al., 2012; Heron-Delaney et al., 2011; Sangrigoli et al., 2005) suggesting that face processing mechanisms are not fixed at this point (but see de Heering et al., 2012). Children's use of visual features for race categorization changes between 5 and 10 years of age (Balas et al., 2015), again suggesting continued tuning of face representations during childhood as a result of experience.

Electroencephalography has the potential to shed light on the development of neural sensitivity to face animacy, as it resolves serial processing steps with millisecond resolution (e.g. Latinus and Taylor, 2006; Rossion, 2014) and is appropriate for very young participants (Csibra et al., 2008). Event-related potentials (ERPs) exhibit differential sensitivity to low-, mid-, and high-level visual processing, with low-level stimulus differences typically evident at the P100 component (Ganis et al., 2012; Rossion, 2014). Controlling for low-level stimuli differences, sensitivity to race (Stahl et al., 2008; Wiese, 2012), age (Wiese, 2012; Wiese et al., 2008), or species (Wiese et al., 2009) can be observed at the face-specific N170 and later components (Stahl et al., 2008). Contrasting responses to upright and inverted faces provides further information on which processes engage high-level, expert face processing mechanisms, as inversion selectively disrupts these mechanisms (Jacques, D'Arripe and Rossion, 2010; Maurer et al., 2002; Yovel and Kanwisher, 2005). For example, inversion effects on the N170 are larger for own-than other-race faces (Caharel et al., 2011; Foreman et al., 2010), which reflects disruption of the early stages of high-level, expert face processing (but see Wiese et al., 2009). Face inversion can more generally be considered an experimental control, as high-level face category effects are not expected from inverted faces: therefore, any differences between inverted face categories likely reflect low-level (e.g., contrast) or mid-level (e.g., texture) effects (Rossion, 2014). Thus, electroencephalography combined with an inversion manipulation provides an efficient means to uncover the time-course of animate versus inanimate face processing.

Previous investigations of neural sensitivity to face animacy in adults' visual areas, however, have yielded mixed results. N170 sensitivity to species is affected by artificial appearance (Balas and Koldewyn, 2013), and effects of face animacy are evidenced in face processing networks by fMRI (Looser et al., 2013). However, clear effects of face animacy are not always evident at the N170 (Balas et al., 2017a, 2017b; Wheatley et al., 2011), but may rather emerge at later components (Wheatley et al., 2011). For example, Balas et al., 2017a, 2017b found no difference in the amplitude or latency of the P100 and N170 components in adult participants during passive viewing of inanimate (doll) versus animate (real human) faces. Why is animacy different from other face categories, and when is information about real vs. artificial appearance available in the extended face network?

To address these questions, we examined the time-course and development of animate versus inanimate human face visual processing in 5–10-year-old children and adults. We used ERPs to test the hypothesis that face animacy would affect the N170 in interaction with face inversion. We expected to observe orientation but not animacy effects on the P100; testing for any effect of animacy on the P100 component allowed us to assess low-level stimulus confounds. We further compared animate versus inanimate human face processing between middle childhood (5-10-years of age) and adulthood, to test the hypothesis that sensitivity to face animacy remains immature by that age. In addition, we compared 5–7 and 8-10 year-olds to test the hypothesis that inanimate face processing may diverge from animate face processing during middle childhood, considering the documented developmental changes in face processing during that specific period (Balas et al., 2015). Finally, we combined traditional univariate, component-based ERP analyses with a multivariate "decoding" approach, by which we attempted to classify trials according to animacy or orientation across time points (Grootswagers et al., 2017; Holdgraf et al., 2017), agnostic to when reliable animacy or orientation information may be available during face processing (Grootswagers et al., 2017; Isik et al., 2014; Kriegeskorte and Bandettini, 2007). While univariate, component-based ERP analyses examine group and condition differences in activation over groups of channels and time-windows of interest, multivariate "decoding" analyses focus on extracting information available over distributed, multi-channel patterns (Hebart and Baker, 2018). Together, these two complementary analysis techniques comprehensively examine the time-course of the neural sensitivity to face animacy and its development across middle childhood and beyond.

2. Materials and methods

2.1. Participants

Our final sample included a total of 16 young adults (8 females, mean age 19.4 ± 1.2 years) and 36 children between the ages of 5–10-year-olds to participate in this study. Half of these children were 5-7-year-olds (N = 18, 11 female, mean age 6.2 ± 0.8 years) and the other half were 8–10-year-olds (N = 18, 10 female, mean age 8.5 ± 0.7 years). Previous ERP results from the first 15 (out of 16 total) young adult participants have been published in Balas et al., 2017a, 2017b. All participants in both the adult and child sample self-reported being of White or Caucasian race. An additional 9 children and 4 adults were recruited, but either failed to complete the task (N = 3 children), did not yield ERP data of sufficiently high-quality for further analysis (N = 6 children and N = 1 adults; e.g. excessive motion throughout recording session, unstable impedance values across the session, or fewer than 50% valid ERP trials in any condition after artifact rejection), or were excluded on the basis of left-handedness (3 adults). All participants had normal or corrected-to-normal visual acuity and right-hand dominance. Prior to the testing session, adult participants provided written informed consent, child participants' parents or guardians provided written informed consent, and child participants older than 7 years of age provided written assent to participate. All recruitment and testing procedures were approved by the NDSU IRB, in accordance with the principles laid out in the Declaration of Helsinki.

2.2. Stimuli

The stimulus set, described in Balas et al., 2017a, 2017b, was comprised of 8 grayscale images of real and artificial (doll) female faces (Fig. 1; 4 real faces, 4 dolls). Faces were cropped to remove hair, retaining the external outline of the face. Original images were 256 × 256 pixels in size. Stimuli were normalized for mean luminance, global contrast, and approximate visual angle.

2.3. Procedure

We recorded continuous EEG from all participants in this experiment using 64-Channel Hydrocel Geodesic Sensor Nets (EGI) connected to an EGI 200 NetAmps Amplifier. Prior to the recording session, each participant was fitted for a sensor net according to head circumference,

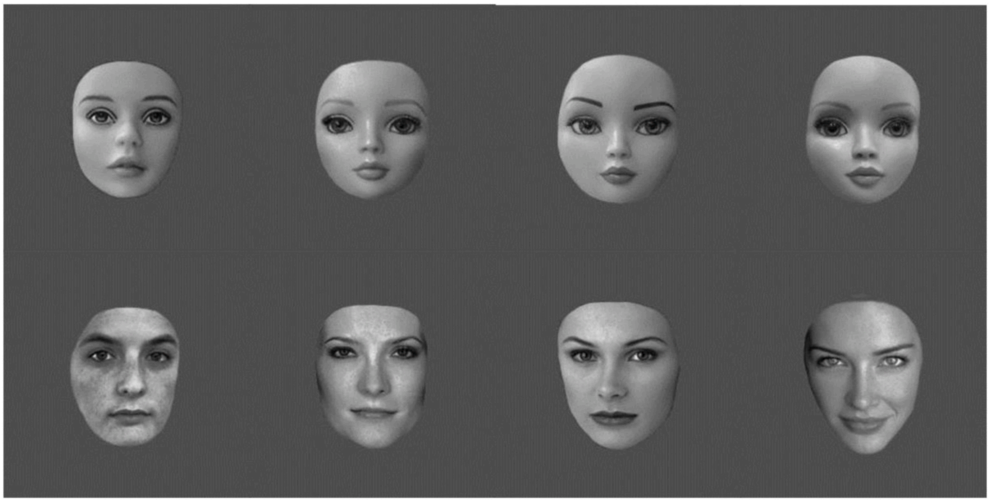

Fig. 1. Face stimuli. Top row: doll faces. Bottom row: human faces. Stimuli were normalized for mean luminance and global contrast.

at which time we also marked the location of the vertex electrode using a red grease pencil. Each net was soaked in a KCl solution for 5 min before application, at which time we established stable impedances below 25 kΩ. Continuous EEG was referenced to the vertex electrode (Cz) during recording, and the sampling rate for all participants was set at 250 Hz. Participants completed the experiment seated in an electrically isolated chamber, approximately 50 cm from the display (a 1024 × 768 LCD monitor). At this distance, stimuli subtended approximately 5–6 degrees of visual angle.

Participants were presented with a single face on each trial, presented for 500 ms, preceded by a 500 ms fixation cross, and followed by a variable inter-trial interval that was sampled from a uniform distribution defined over an interval from 500 to 1000 ms. Each of the 8 stimuli was presented 10 times upright and 10 times inverted, for a grand total of 160 experimental trials in the entire session (40 upright human faces, 40 inverted human faces, 40 upright doll faces, and 40 inverted doll faces). The stimuli presentation order was pseudo-randomized across participants in E-Prime 2.0, such that for each participant the full trial order was uniquely randomized. To ensure that participants were attending to the stimuli, participants carried out an oddball-detection task during the session such that they only provided behavioral responses to stimuli depicting a cartoon mushroom, presented on approximately 10% of the trials. Performance in this task was monitored online by an experimenter, who remained in the room during the session. All display parameters and task routines were controlled by custom software written using EPrime v2.0 and accompanying extensions for NetStation v5.0.

2.4. *EEG data preprocessing and analysis*

We carried out a fixed set of pre-processing routines for each participant's EEG data, all of which were implemented in NetStation v5.0. First, we applied a low-pass filter with a cutoff frequency of 30 Hz. Next, each participant's data was segmented and baseline corrected, with a pre-stimulus onset period of 100 ms and a post-onset period of 1000 ms. The EEG was re-referenced to the average. Finally, we applied automatic artifact-detection procedures implemented in NetStation v5.0 to remove ocular artifacts and replace bad channels. Specifically, for each segment, a channel was marked bad if the difference between its maximum and minimum voltage in that segment exceeded 200 μV. Horizontal and eye channels were used to detect ocular artifacts in each segment using an 80 ms moving window (eye blink: min-max exceeding 140 μV, eye movement: min-max exceeding 55 μV). Finally, segments were rejected if more than 10 channels were identified as bad during that segment, and channels were rejected throughout the entire recording if they were found bad in 20% of segments or more. Artifact detection was confirmed by independent examination of each subject's data to ensure that the higher signal-to-noise ratio typically obtained from child participants did not lead to overly aggressive rejection of individual trials. Mean number of included trials for each condition and age group are presented in Table 1. To examine ERP components, we continued by creating an average ERP for each participant and stimulus category. However, for our multivariate decoding analysis, we withheld calculating this per-subject average so that we could classify individual trials. We elaborate on these two approaches below.

2.5. *Channels and time-windows of interest for ERP analyses*

Channels and time-windows of interest for ERP analysis were determined by examining the grand average waveforms collapsed across all stimulus conditions, separately for each age group (adults, 5-7-year-olds, and 8-10-year-olds). Thus, the procedure was blind to any effects of inversion and animacy. Channels of interest were determined based on which channels had the largest grand averaged ERP components of interest (P100 and N170, see Results). To accurately capture peak ERP latencies in all individual participants, time-windows of interest for each ERP component were determined based on the observed range of individual peak latencies in each age group. The procedure was conducted separately in each age group to accommodate potential differences in peak latencies across age groups. Due to a technical error, ERP data from 1 8-10-year-old participant was missing in the "Doll upright" condition from both hemispheres, and from 1 adult participant in the "Doll Inverted" condition from both hemispheres.

2.6. *Time-resolved decoding analyses*

Time-resolved decoding analyses, which do not rely on averaging over channels of interest or time-windows, examined the information content of the EEG signal at each time post-onset. Specifically, in

Table 1
Mean (±SD) number of included trials per age group and condition.

	N	Upright Doll	Upright Human	Inverted Doll	Inverted Human
5-7 year-olds	18	24.28 ± 4.34	24.06 ± 4.87	23.33 ± 4.37	24.22 ± 4.72
8-10 year-olds	18	28.17 ± 5.53	28.83 ± 4.20	27.33 ± 4.67	28.06 ± 5.67
Adults	16	33.56 ± 4.99	32.81 ± 5.86	33.25 ± 5.62	33.00 ± 6.84

decoding analyses, classification accuracy for a given stimulus property rising above chance at a given time point post-onset is considered to suggest that information corresponding to this property is available (i.e., can be reliably extracted) at the corresponding stage of processing the stimulus. To reduce the number of features used in these analyses (i.e., reduce variance), decoding analyses were restricted to posterior channels, inclusive of those used for the ERP analyses (see Fig. 2 and ERP analyses below). Similarly, to limit the number of time-points, decoding analyses focused on the period from −50 to 500 ms post-stimulus onset. We then decoded animacy (doll versus real faces) and orientation (inverted versus upright faces) separately for each participant, based on the amplitudes in these channels at each time post-onset. For each participant and for each of these binary classifications (upright versus inverted faces classification on the one hand, or doll versus real faces classification on the other hand), trials from each of the two classes (either upright versus inverted, or doll versus real) were randomly re-ordered (permuted) and separated into 4 folds. For each class, trials from each of the 4 folds were separately averaged to yield 4 pseudo-trials for each of the two classes (Grootswagers et al., 2017; Isik et al., 2014). Averaging into pseudo-trials can improve signal-to-noise ratio for time-resolved classification (Grootswagers et al., 2017; Isik et al., 2014). The first 3 of these 4 pseudo-trials were used for training the classifiers, and the remaining pseudo-trial was used for testing (i.e., 4-folds cross-validation). Thus, chance level was 50% regardless of the

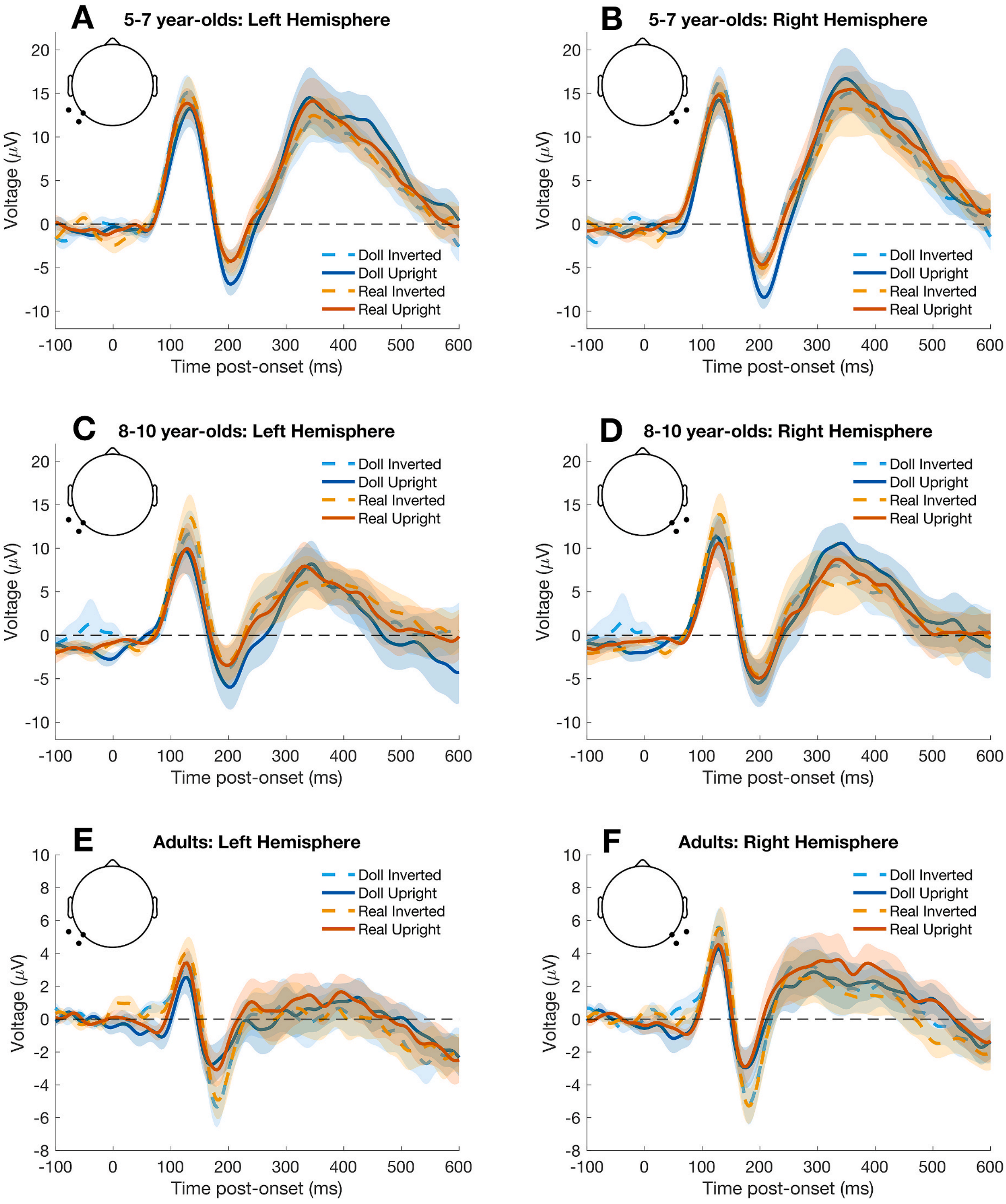

Fig. 2. Grand average ERP waveforms (±s.e.m.) from the channels of interest in the left **(A, C, E)** and right **(B, D, F)** hemispheres in each age group.

effective number of trials of each class available in each fold. Training and testing was performed for each sample (time point) post-onset independently using linear SVMs implemented in libsvm v3.11 for Matlab (Chang and Lin, 2011), leading to time-series of classification accuracies. This entire procedure of permutation, separation into folds, and classification at each time-point, was repeated 200 times for each participant and classification type (upright versus inverted, doll versus real). Classification accuracies were averaged over these 200 instances, for each participant and classification type. Statistical significance of the resulting classification accuracy time-series was established using permutation tests (right-tail test against the chance level of 50%) with cluster-wise correction over time-points (cluster-defining threshold p-value = 0.05, alpha = 0.05).

2.7. Analysis software and code

EEG data acquisition and pre-processing were conducted in Netstation v5.0 as indicated above. Decoding analyses were conducted, and figures were created, using MATLAB v 8.2.0.701. The corresponding code is freely available online at https://osf.io/ef6gw/.

3. Results

3.1. Component-based ERP analysis

We examined the P100 and the N170 to test whether they are affected by face inversion and face animacy as a function of participant age. In the left hemisphere, we identified sensors 29, 30, and 32 as channels of interest for all participant groups, and in the right hemisphere we selected channels 43, 44, and 47. These locations over occipito-temporal regions of the scalp roughly coincided with locations TP9-TP10, P7–P8 (previously T5-T6), and P9-10 on the 10–20 system (Luu and Ferree, 2005) and are largely consistent with prior studies examining N170 responses in children and adults (Balas and Stevenson, 2014; Balas et al., 2017a, 2017b). The time windows we selected to examine each component varied across age groups. In 5-7-year-olds we measured the P100's response properties within a time window between 80 and 160 ms post-stimulus onset and analyzed the N170 within a time window between 168 and 248 ms post-stimulus onset. In 8-10-year-olds, we analyzed the P100 using a time window between 96 and 160 ms post-stimulus onset and the N170 using a time window between 168 and 244 ms post-stimulus onset. In adults, we measured the P100's response properties within a time window between 100 and 160 ms post-stimulus onset and analyzed the N170 within a time window between 160 and 224 ms post-stimulus onset (Balas et al., 2017a, 2017b). For each component, we measured both the mean amplitude and the latency-to-peak within these time windows. Average N170 amplitudes were not "corrected" (re-baselined) based on the preceding P100 amplitudes.

Because adults and children may differ more from one another than the 5-7-year-olds would differ from the 8-10-year-olds, we compared the three age groups in two distinct steps, testing first for developmental changes between childhood and adulthood, and then for developmental changes evident between the two children age groups. Thus, to examine broad differences between children and adults, we first submitted these values to a 2x2x2x2 mixed-design ANOVA with face orientation (upright vs. inverted), face animacy (real vs. doll), hemisphere (left vs. right) as within-subject factors and age group (all children vs. adults) as a between-subjects factor. To further examine finer developmental effects between 5-7 and 8–10 years of age, we then submitted these values to a 2x2x2x2 mixed-design ANOVA with face orientation (upright vs. inverted), face animacy (real vs. doll), hemisphere (left vs. right) as within-subject factors and age group (5–7 vs. 8-10-year-olds) as a between-subjects factor. The grand average ERP waveforms across all experimental conditions and as a function of age and hemisphere are displayed in Fig. 2. Individual participants' average P100 and N170 amplitude and latencies are presented in Fig. 3, while individual participants' average waveforms as a function of experimental condition, age, and hemisphere are presented in Supplementary Figs. 1–4. Average effects of face orientation and face animacy on the ERP waveforms are presented as a function of age and hemisphere in Fig. 4.

3.2. P100 amplitude

Analysis of the P100 amplitude comparing children and adults (Fig. 3) revealed significant main effects of orientation ($F(1,48) = 6.31$, $p = 0.015$, partial $\eta^2 = 0.12$) and age group ($F(1,48) = 16.65$, $p < 0.001$, partial $\eta^2 = 0.26$). P100 amplitudes were larger (more positive) for inverted faces (M = 5.72 μv) relative to upright faces (M = 4.86 μv; 95% CI of the difference [0.17 μv, 1.55 μ]), and in children (M = 7.28 μv) compared to adults (M = 3.30 μv; 95% CI of the difference [2.02 μv, 5.95 μv]). No other main effects or interactions reached significance. Our analysis of the P100 amplitude comparing 5–7 and 8-10 year-olds revealed only a significant main effect of orientation ($F(1,33) = 6.72$, $p = 0.014$, partial $\eta^2 = 0.17$). Again, this effect was the result of systematically larger (more positive) amplitudes for inverted faces (M = 7.044 μv) relative to upright faces (M = 5.90 μv; 95% CI of the difference [0.25 μv, 2.06 μv]). No other main effects or interactions reached significance. Similar results were found when estimating the overall effect of age as a 3-level factor (5-7-year-olds, 8-10-year-olds, and adults), showing a significant main effects of orientation ($F(2,47) = 9.06$, $p = 0.004$, partial $\eta^2 = 0.16$) and age ($F(2,47) = 8.77$, $p < 0.001$, partial $\eta^2 = 0.27$).

3.3. P100 latency

Analysis of the P100 latency-to-peak comparing children and adults (Fig. 3) revealed a significant main effect of orientation ($F(1,48) = 9.03$, $p = 0.004$, partial $\eta^2 = 0.16$). P100 latencies were slower for inverted (M = 130.70 ms) than upright faces (M = 126.36 ms; 95% CI of the difference [1.44 ms, 7.25 ms]). No other main effects or interactions reached significance. Our analysis of the latency-to-peak of the P100 comparing 5–7 and 8-10 year-olds similarly revealed significant main effects of face orientation ($F(1,33) = 6.45$, $p = 0.016$, partial $\eta^2 = 0.176$) and hemisphere ($F(1,33) = 5.14$, $p = 0.030$, partial $\eta^2 = 0.14$). The former effect was the result of significantly slower latencies in response to inverted faces (M = 131.19 ms) relative to upright faces (M = 126.96 ms; 95% CI of the difference [0.84 ms–7.61 ms]). The latter effect was the result of slower latencies in the left hemisphere (M = 130.69 ms) relative to the right hemisphere (M = 127.46 ms; 95% CI of the difference = [0.84 ms, 7.61 ms]). These main effects were qualified by a 3-way interaction between face orientation, hemisphere, and age group ($F(1,33) = 6.34$, $p = 0.017$, partial $\eta^2 = 0.16$). Similar results were found when estimating the overall effect of age as a 3-level factor (5-7-year-olds, 8-10-year-olds, and adults), with a significant main effect of orientation ($F(1,47) = 10.27$, $p = 0.002$, partial $\eta^2 = 0.18$) and a significant interaction between age, orientation, and hemisphere ($F(2,47) = 4.29$, $p = 0.019$, partial $\eta^2 = 0.15$). To examine the nature of the latter 3-way interaction, we carried out post-hoc paired-samples t-tests to compare inverted vs. upright latencies in each hemisphere for each age group. Briefly, 5-7-year-old children exhibited a numerically stronger inversion effect over the right hemisphere (mean latency difference for inverted vs. upright faces: M = 8.33 ms) than over the left hemisphere (M = 0.30 ms), while older children exhibited a numerically stronger inversion effect over the left (M = 5.53 ms), than over the right hemisphere (M = 2.75 ms), and adults exhibited numerically similar inversion effects over the left (M = 4.28 ms) and right hemisphere (M = 4.63 ms). No post-hoc pairwise comparison reached significance after correction for multiple comparisons ($ps > 0.05$).

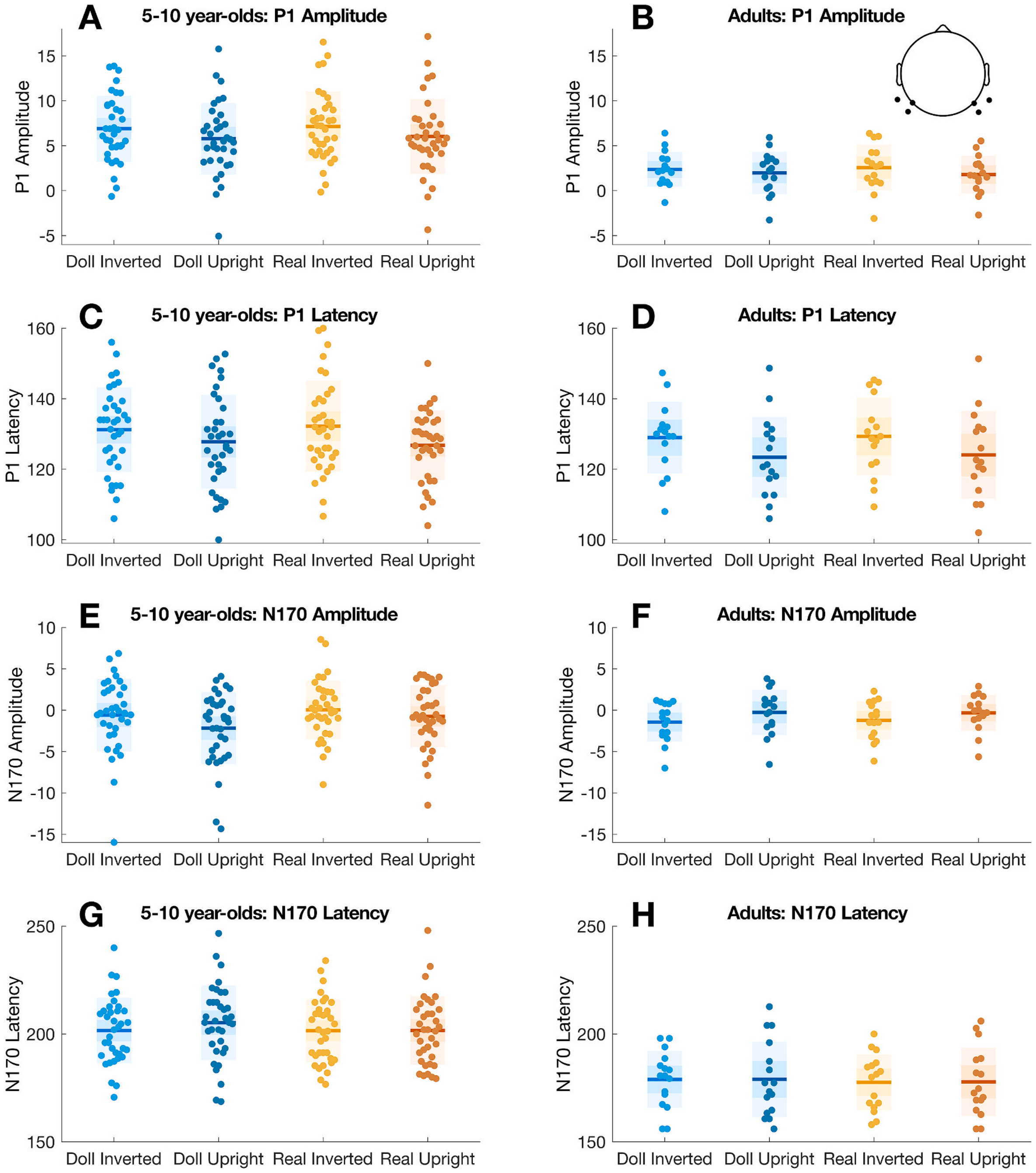

Fig. 3. Individual and average P100 amplitude **(A–B)**, P100 latency **(C–D)**, N170 amplitude **(E–F)**, and N170 latency **(G–H)** by condition in children **(A, C, E, G)** and adults **(B, D, F, H)**, averaged over hemispheres.

3.4. N170 amplitude

Analysis of the N170 amplitude comparing children and adults (Fig. 3) revealed a large significant interactive effect of orientation and age group ($F(1,48) = 14.19, p < 0.001$, partial $\eta^2 = 0.23$) and a medium-sized, significant main effect of animacy ($F(1,48) = 4.72$, $p = 0.035$, partial $\eta^2 = 0.09$) as N170 amplitudes were larger (more negative) in response to doll (M = −1.10 µv) than real faces (M = −0.55 µv, 95% CI of the difference [-1.06 µv, −0.04 µv]). In addition, N170 amplitudes were larger (more negative) for inverted than upright faces (mean difference: M = −1.12 µv, 95% CI [-2.56 µv, 0.32 µv]) in adults, and larger for upright than inverted faces (mean difference: M = −1.24 µv; 95% CI [-2.18 µv, −0.29 µv]) in children. No other main effects or interactions reached significance, though we did also observe a marginally significant interaction between animacy and age group (F(1,48) = 3.21, p = 0.080, $\eta^2 = 0.063$). This trend appeared to be driven by larger animacy effects in children compared to adults; as the effect did not reach traditional thresholds of significance, we do not examine it further. A peak-to-through analysis of the N170 peak amplitude comparing children and adults and correcting for the P100 peak amplitude yielded similar findings, with a large, significant interactive effect of orientation and age group ($F(1,48) = 13.16, p < 0.001$, partial $\eta^2 = 0.22$) as well as a medium-sized, marginal main effect of animacy ($F(1,48) = 3.30, p = 0.075$, partial $\eta^2 = 0.06$), as the P100-corrected peak N170 amplitudes were marginally larger (more negative) in response to doll than real faces. A peak-to-through analysis of the N170 peak amplitude comparing children and adults and correcting for the P100 peak amplitude yielded similar findings, with a large, significant

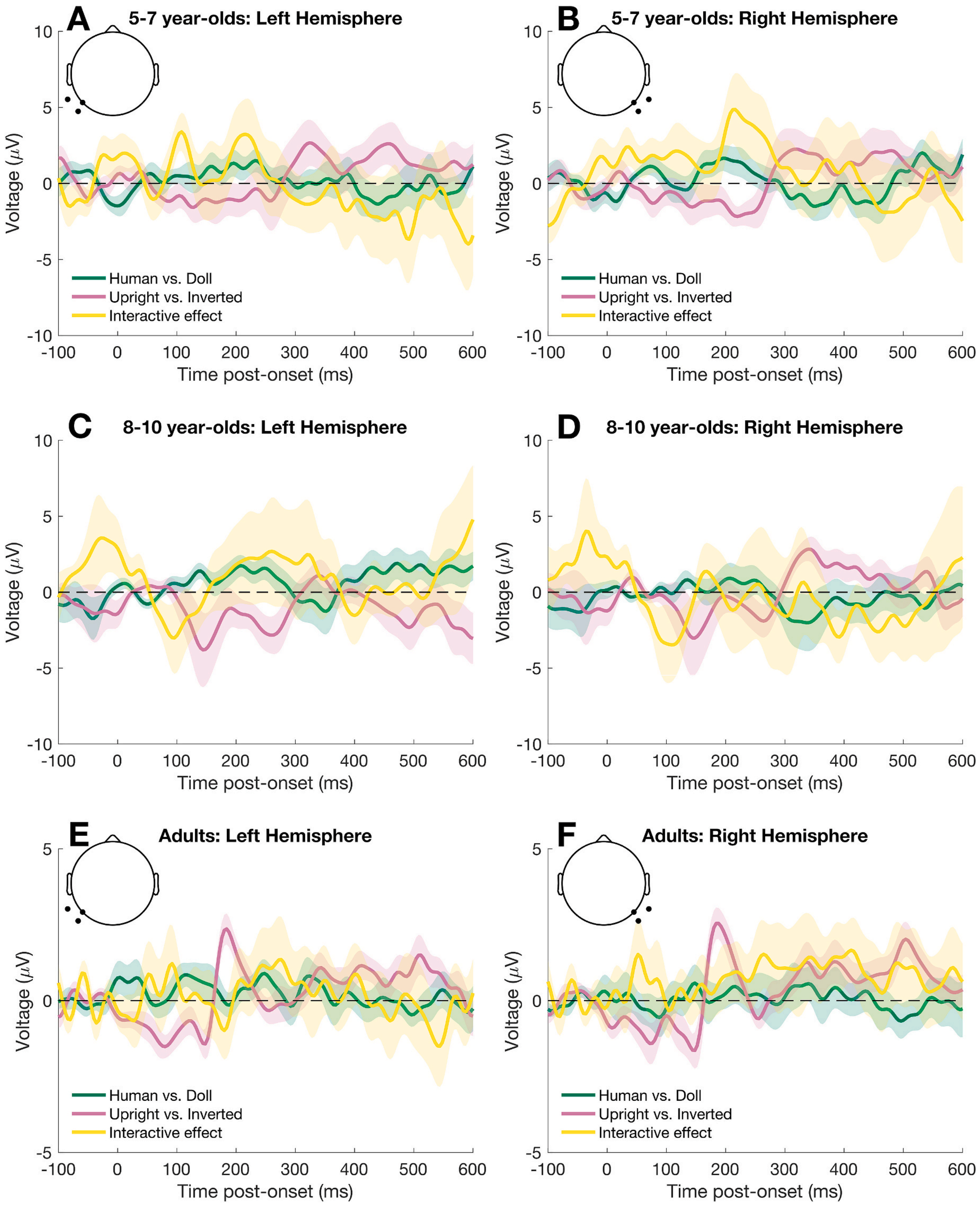

Fig. 4. Grand average ERP effects (±s.e.m.) in channels of interest in the left and right hemispheres in all age groups.

interactive effect of orientation and age group ($F(1,48) = 13.16$, $p < 0.001$, partial $\eta^2 = 0.22$) as well as a medium-sized, marginal main effect of animacy ($F(1,48) = 3.30$, $p = 0.075$, partial $\eta^2 = 0.06$), as the P100-corrected peak N170 amplitudes were marginally larger (more negative) in response to doll than real faces. Similar results were found when estimating the overall effect of age as a 3-level factor (5-7-year-olds, 8-10-year-olds, and adults), showing a large, significant interactive effect of orientation and age group (peak-to-through: $F(2,47) = 6.49$, $p = 0.003$, partial $\eta^2 = 0.22$) as well as a medium-sized, significant main effect of animacy (peak-to-through: $F(1,47) = 6.38$, $p = 0.015$, partial $\eta^2 = 0.12$).

We next focused on comparing the two children age groups separately, to test for any effect of age between the two children age groups. Our analysis of the N170 mean amplitude comparing 5–7 and 8-10 year-olds revealed significant main effects of face orientation ($F(1,33) = 9.18$, $p = 0.005$, partial $\eta^2 = 0.22$) and face animacy ($F(1,33) = 10.04$, $p = 0.003$, partial $\eta^2 = 0.23$). The former effect was driven by larger (more negative) amplitudes in response to upright faces (M = −1.45 μv) relative to inverted faces (M = −0.22 μv; 95% CI of the difference [-2.06 μv, −0.41 μv]). Again, the latter effect was the result of larger (more negative) amplitudes in response to doll faces (M = −1.34 μv) relative to real faces (M = −0.33 μv; 95% CI of the difference [-1.66 μv, −0.36 μv]).

No other main effects or interactions reached significance. A peak-to-through analysis of the N170 peak amplitude comparing the two children groups and correcting for the P100 peak amplitude also yielded a significant main effect of animacy ($F(1,34) = 7.02$, $p = 0.012$, $\eta^2 = 0.18$), with larger (more negative) P100-corrected peak N170 amplitudes in response to doll faces ($M = -7.69$ μv) relative to real faces ($M = -6.94$ μv; mean difference: 95% CI of the difference [-1.32 μv, −0.17 μv]). However, the effect of orientation on the P100-corrected peak N170 amplitudes was not significant, either alone or in interaction with age ($ps > 0.1$).

3.5. N170 latency

Finally, analysis of the N170 peak latency comparing children and adults (Fig. 3) revealed a significant main effect of age group ($F(1,48) = 31.28$, $p < 0.001$, partial $\eta^2 = 0.40$), as latencies were slower in children ($M = 207.24$ ms) than adults ($M = 183.24$ ms, 95% CI of the difference = [15.37 ms, 32.62 ms]). No other main effects or interactions reached significance. Similarly, our analysis of the N170 peak latency comparing 5–7 and 8-10 year-olds similarly revealed only a main effect of participant age ($F(1,33) = 9.05$, $p = 0.005$, partial $\eta^2 = 0.22$). This effect was driven by faster latencies in older children ($M = 196.10$ ms) relative to younger children ($M = 208.77$ ms, 95% CI of the difference = [4.10 ms, 21.24 ms]). Similar results were found when estimating the overall effect of age as a 3-level factor (5-7-year-olds, 8-10-year-olds, and adults), with only a significant main effect of age ($F(2,47) = 22.23$, $p < 0.001$, partial $\eta^2 = 0.49$). No other main effects or interactions reached significance.

In summary, the analysis of ERPs (P100, N170) revealed a main effect of orientation on several aspects of the data (mean P100 amplitude, P100 latency, and N170 amplitude), although the direction of the effect of orientation on the N170 amplitude differed in children and adults. In addition, a main effect of animacy was found on the mean amplitude of the N170, in which doll faces evoked larger (more negative) N170 amplitudes then real faces, regardless of age group or the faces' orientation.

3.6. Time-series of decoding accuracies

We next examine the time-course of the representation of face orientation and animacy over posterior (occipitotemporal) channels, as evidenced by time-resolved decoding (as opposed to differences in component latencies and amplitudes). Time-series of decoding accuracies exhibited similar temporal profiles in both children age groups compared to the adult group (Fig. 5). Animacy (dolls versus real faces) could not be reliably decoded from the posterior channels at any point post-onset, in either group (no significant cluster after cluster correction). In contrast, face orientation (inverted versus upright faces) could be decoded with about 60% accuracy in both children groups from posterior channels, significantly above chance in the 5-7 year-old group (significant cluster: 248–316 ms, $p < 0.05$) and marginally so in the 8-10 year-old group (marginally significant cluster: 272–316 ms, $0.05 < p < 0.1$). In adults, classification accuracy also rose above chance for orientation (significant clusters, $p < 0.05$; Fig. 5), and marginally above chance for animacy (marginally significant cluster: 240–276 ms, $0.05 < p < 0.1$). Thus, face orientation information could be reliably decoded both in children and adults from posterior channels. Animacy could not be decoded in any children age group and could marginally be decoded in adults from posterior channels. Similar analyses using the same number of channels distributed across the whole calp (Supplementary Fig. 5) yielded similar results, with the decoding of animacy rising significantly above chance in adults (significant cluster, $p < 0.05$, 244–300 ms) but not in either of the children groups (cluster $ps > 0.1$).

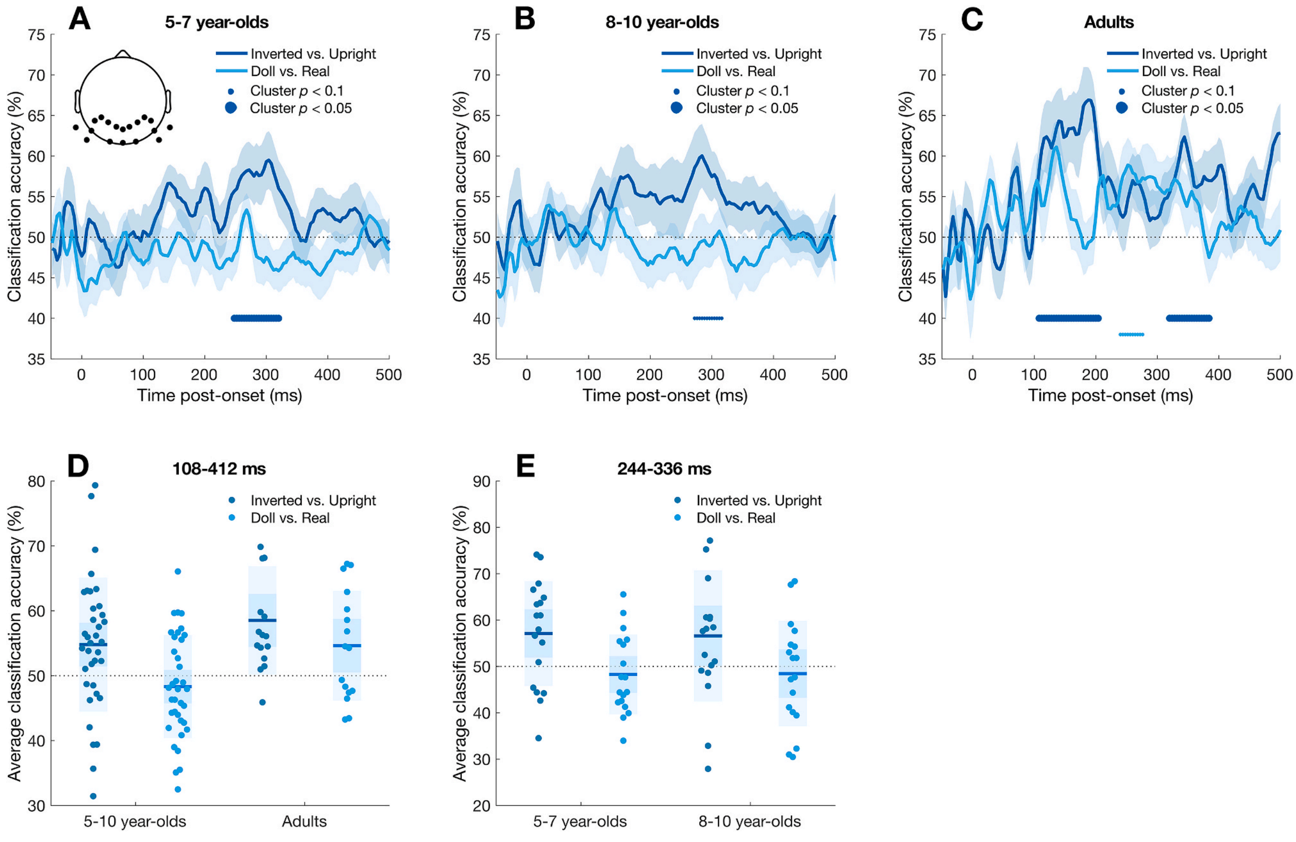

Fig. 5. (A–C) Average classification accuracy time-series (±s.e.m.) for decoding face orientation (inverted vs. upright) and animacy (doll vs. real) by age group. **(D–E)** Average and individual classification accuracy time-series over time windows, by age group and classification type.

3.7. Comparison of average decoding accuracies between adults and children

We next examine whether classification accuracy significantly varied as a function of age group (adults vs. all children) and classification type (orientation vs. animacy). Pooling classification time-series from both children age-groups as well as the adult group yielded one significant cluster ($p < 0.05$) from 108 to 412 ms for the classification of orientation, but none for animacy. To test whether the observed classification accuracy significantly differed between age groups and classification type (orientation or animacy), mean classification accuracy over the 108–412 ms time-window (as identified above) for each classification type and participant were subjected to post-hoc mixed-effects analyses of variance with classification type as a within-subjects factor and age group (adults vs. all children) as a between-subjects factor.

This analysis revealed a main effect of classification type ($F(1,100) = 16.14$, $p = 0.001$, $\beta = -6.47$, 95% CI [-9.66, −3.27], $d = -0.61$) with no significant effect of age group either as a main effect (adults vs. children; $F(1,100) = 1.62$, $p = 0.206$) or in interaction with classification type ($F(1,100) = 0.79$, $p = 0.377$). The main effect of classification type held when controlling for the total number of valid trials available for each of the two classified classes (main effect of classification type: $F(1,99) = 16.14$, $p = 0.001$, $\beta = -6.47$, 95% CI [-9.66, −3.27], $d = -0.60$; all other $ps > 0.05$), or the minimum and maximum number of trials available from the two classes (main effect of classification type: $F(1,98) = 16.81$, $p < 0.001$, $\beta = -6.27$, 95% CI [-9.31, −3.24], $d = -0.60$; all other $ps > 0.05$). Similar results were found when estimating the overall effect of age as a 3-level factor (5-7 year-olds, 8-10 year-olds, adults), showing a main effect of classification type ($F(1,98) = 7.64$, $p = 0.007$, $\beta = -6.36$, 95% CI [-10.92, −1.79], $d = -0.59$), with no significant effect of age group either as a main effect or in interaction with classification type ($ps > 0.05$), whether or not the total number of valid trials in each class or the minimum and maximum number of valid trials in each class were added as covariates to the model.

The minimum, maximum, and total number of trials available over each of the two classes did not significantly differ based on classification type or the interaction of classification type and age (all $ps > 0.6$) but did differ according to age group (all $ps < 0.05$) as adults tended to contribute more trials than children. Overall, it does not appear likely that the significantly accurate classification of orientation but not animacy reflects differences in the number of trials available for these two classifications. Classification accuracies for the classification of face orientation or animacy were comparable between children and adults when adjusting for trial numbers, despite animacy classification being marginally above chance in adults but not in children.

3.8. Comparison of average decoding accuracies between 5-7- and 8-10-year-old children

We next examined whether classification accuracy significantly varied as a function of children's age group (5–7 vs. 8-10-year-olds) and classification type (orientation vs. animacy). Pooling classification time-series from both children age-groups yielded a significant cluster ($p < 0.05$) from 244 to 336 ms for the classification of orientation, but none for animacy. Children's mean classification accuracies over the 244–336 ms time-windows (as identified above) for each classification type and participant were subjected to post-hoc mixed-effects analyses of variance with classification type as a within-subjects factor and age group (5–7 vs. 8-10-year-olds) as a between-subjects factor.

This analysis revealed a main effect of classification type ($F(1,68) = 9.53$, $p = 0.003$, $\beta = -8.83$, 95% CI [-14.54, −3.12], $d = -0.64$) but no effect of child age either alone (5–7 vs. 8-10-year-olds; $F(1,68) = 0.02$, $p = 0.903$), or in interaction with classification type ($F(1,68) = 0.03$, $p = 0.862$). The results held when controlling for the total number of valid trials available for each of the two classified classes (main effect of classification type: $F(1,67) = 9.53$, $p = 0.003$, $\beta = -8.83$, 95% CI [-14.55, −3.12], $d = -0.64$; all other $ps > 0.05$), or the minimum and maximum number of trials available from the two classes (main effect of classification type: $F(1,66) = 9.31$, $p = 0.003$, $\beta = -8.87$, 95% CI [-14.67, −3.07], $d = -0.64$; all other $ps > 0.05$).

Thus, classification accuracy for face orientation in the 244–336 ms time-window did not significantly differ between the two children age groups, despite being significantly above chance in the 5-7-year-old group but only marginally above chance in the 8-10-year-old group. Again, the minimum, maximum, and total number of trials available over each of the two classes did not significantly differ based on classification type or the interaction of classification type and age (all $ps > 0.6$), but did differ according to children age group (all $ps < 0.05$) as 8-10-year-olds tended to contribute more trials than 5-7-year-olds.

4. Discussion

In the current study, we used EEG to assess the development of the perceptual sensitivity to face animacy in childhood. More specifically, we presented real or doll faces, upright or inverted, to adults and children of either 5–7 years or 8–10 years of age. We find multiple effects of facial orientation on the P100 and N170 ERP components, as previously reported in children (Itier and Taylor, 2004) and adults (Rossion and Gauthier, 2002; Rossion et al., 2000). In particular, N170 amplitudes were larger (more negative) for inverted than upright faces in adults, as has classically been reported. In 5-10 year-old children, mean N170 amplitudes were larger (more negative) for upright than inverted faces while P100-corrected N170 amplitudes were similar for upright and inverted faces, in line with similar findings in school-aged children (Hileman et al., 2011; Itier and Taylor, 2004). In addition, we observed an a medium-sized effect of face animacy on the N170 amplitude across the three studied age groups (adults, 5-7-year-olds, and 8-10-year-olds), where the amplitude of the N170 was larger (more negative) for doll than real faces. Importantly, there was no significant interactive effect of orientation and animacy on the P100 or N170. That is, the sensitivity of the N170 to animacy was not affected by face inversion, and vice versa. The fact that the effect of animacy was not affected by inversion is particularly notable because it suggests that the N170 sensitivity to face animacy may not depend on face-specific, expert configural processing that face inversion is known to disrupt (Cashon and Holt, 2015; Maurer et al., 2002; Yovel and Kanwisher, 2005).

The N170 amplitude, but not P1 amplitude, was exaggerated in response to artificial (doll) compared to real human faces irrespective of age group or the face's orientation (i.e., there was no significant animacy by age or animacy by orientation interaction). These findings suggest that a sensitivity of the N170 to facial animacy emerges developmentally as early as 5 years of age and exhibits a relative stability from childhood through adulthood. Such developmental trajectory is consistent with the developmental time-course of the sensitivity to other facial dimensions, such as race (Balas et al., 2011; Stahl et al., 2008; Wiese et al., 2014). The robustness of the N170 sensitivity to face animacy with respect to inversion is more difficult to interpret, although it is in line with similar findings in adults (Balas and Pacella, 2015; Balas et al., 2017a, 2017b). Several potential mechanisms may theoretically account for the sensitivity of the N170 amplitude to animacy. For example, relative lack of experience of children and adults with artificial compared to human faces could lead to an "out-group effect" for animacy that is reflected on the amplitude of the N170; Doll faces might be more efficiently detected as faces than real faces (e.g. due to the simplified facial features and impoverished superficial texture), leading to an exaggerated N170; Alternatively, modulation of N170 by face animacy might be driven by another, confounded facial dimension, such as femininity (Balas, 2013). However, these potential mechanisms are difficult to reconcile with the observed absence of an inversion by animacy effect, which would be expected if the sensitivity of the N170 to face animacy required face-specific, configural processing (but see e.g. Sekuler et al., 2004) typically understood to be disrupted by face inversion (Cashon and Holt, 2015; Maurer et al., 2002; Yovel and Kanwisher, 2005). Thus, another possibility is that the sensitivity of the N170 to face animacy as reported in the current study could be driven by low-to mid-level properties of the stimuli, such as texture. Visual texture could affect the amplitude of the N170 (but not P100) irrespective of face inversion, and is known to systematically differ between animate (or natural) and inanimate (or artificial) faces (Balas and Conlin, 2015; Long et al., 2017). Indeed, recent fMRI work in adults suggests that high-level vision areas might be more sensitive to shape or texture than the abstract dimension of animacy per se (Bracci et al., 2019; Long et al., 2018). The current EEG findings generally align with these existing results, extending them to the middle childhood age range. More research is needed to determine the extent to which the observed sensitivity of the N170 to face animacy reflects sensitivity to low-, mid-, or high-level visual properties. Regardless of the specific mechanism responsible, the current findings suggest that in 5–10-year-old children and adults the N170, but not P100, component exhibits some sensitivity to face animacy that is not disrupted by face inversion.

We found that the effect of animacy on the N170 amplitude was already present by 5–7 years of age, at the onset of middle childhood. A previous ERP analysis of the current adult sample failed to evidence an effect of face animacy on the N170 either as a main effect or in interaction with face orientation (Balas et al., 2017a, 2017b). It is conceivable that the effect of animacy on the N170 simply failed to reach significance in the adult group when it was considered in isolation. Alternatively, there might be a genuine but relatively small (i.e., too small to be reliably detected in the current study) decrease in the sensitivity of the N170 of animacy between childhood and adulthood, perhaps during the course of puberty and adolescence which are known to remodel social processing networks and thus might modify the processing of face animacy (Blakemore, 2008). Future research examining the developmental trajectory of face animacy and artificial face processing in infants, children and adults over a range of behavioral and neuroimaging tasks will help disambiguating these two possibilities.

We additionally used time-resolved multivariate pattern analysis ("decoding") of the EEG signal to examine whether and when, after stimulus onset, information about face orientation or animacy could be reliably extracted from the occipitotemporal EEG signal in children and adults (Grootswagers et al., 2017; Holdgraf et al., 2017; Isik et al., 2014). We observed that information about face orientation could be reliably decoded (i.e., was possibly represented) from occipitotemporal channels within 500 ms post-onset at all ages (significant clusters were identified from about 250 to 350 ms in children, and both 100–200 ms and 320–380 ms in adults). Overall, decoding accuracy for the classification of face orientation was comparable across all age groups after adjusting for numbers of valid trials. In contrast, information about face animacy could not be significantly decoded from occipitotemporal channels at any age in children and could only marginally be decoded in adults (a marginally significant cluster emerged at about 240–275 ms). Average classification accuracy for animacy did not significantly differ between children and adults. In other words, there was no evidence that face animacy was reliably represented at posterior channel locations in children, and only limited evidence in adults, at least within 500 ms post-onset during a task (mushroom oddball detection) that only necessitated minimal face processing. Robust decoding of face animacy was observed from whole-scalp channels in adults, but not in either of the children age groups, in line with prior findings that cortical areas beyond the high-level visual cortex may be involved in representing the abstract dimension of animacy (Bugatus et al., 2017). It is of course possible that more robust representations of face animacy would have been uncovered at occipitotemporal locations by a different neuroimaging method, or in a different task requiring deeper face processing or the explicit extraction of animacy, as reported by at least one fMRI study in adults using an odd-one-out face detection task (Looser et al., 2013). Activation-based (e.g. ERP) and information based (e.g. decoding) analyses differ in their methods, objectives, and interpretation (Hebart and Baker, 2018). Any of the methodological differences between ERP and decoding analyses (such as the difference in electrodes used) may account for the different results obtained from the ERP and decoding analyses, although importantly the electrodes used for decoding included those used for ERPs. Taken together, these decoding results remain to be replicated, but are generally in line with the notion that robust sensitivity to face orientation is mostly in place by childhood (Cashon and Holt, 2015).

The present results must be interpreted in the light of the following limitations. One of the main limitations of this work lies in the relatively limited sample size (N = 18 per children age group, and N = 16 adults). On a similar note, numbers of trials were relatively low, but adequate for decoding (about 40–80 trials per class when decoding face orientation or animacy separately within-subjects, using 18 channels as features with a linear SVM). This characteristic of the data, along with the typically low signal to noise ratio of EEG signals collected from developmental populations, could have limited the accuracy that could be achieved. However, these factors cannot account for the observed difference in accuracy for decoding face orientation versus face animacy. A second limitation of the study is the use of doll faces, which are arguably familiar to many children, and a relatively limited stimulus set. Idiosyncrasies in the stimuli, or the specific status of dolls, could have contributed to the current results. Further research will determine whether the current results extend to all human versus artificial faces equally. A third limitation is the use of a cross-sectional design, which renders the results susceptible to cohort effects. As the use of technology has evolved over the last decades, adults and children of varying ages likely had different levels of exposure to artificial faces (e.g., artificial cartoon or game characters, robots, or avatars) in their lifetime. A fourth limitation lies in the absence of concurrent behavioral data, precluding us from relating the observed differences in N170 amplitude between inanimate and animate faces with relative behavioral difficulties in processing inanimate faces. Finally, a fifth limitation concerns the restriction to time-locked voltages recorded from occipitotemporal electrodes during passive viewing, and on ERPs associated with visual processing (P100, N170). The current study focuses on the role of visual experience in shaping, or "tuning", expert face perception in visual areas, specifically on the effects of animacy and inversion on visual processes. However, face animacy may rather be represented by brain areas beyond the visual areas, such as the prefrontal cortex, that can represent abstract categories as a function of task demands (Bugatus et al., 2017). Indeed, MVPA analyses from whole scalp electrodes yielded significant decoding of animacy in the adult group, but not in any of the children's groups. It is also conceivable that animacy representations, whether in occipitotemporal or other regions, may not be adequately captured by time-locked voltages. Future studies may examine the developmental trajectory of face animacy representation in a wider range of brain areas during a categorization task, including representation-based analyses that do not rely on temporal synchrony between trials.

In conclusion, we investigated the time-course of the neural sensitivity to face animacy in children, as a function of face inversion. We found that the amplitude of the N170 component, a well-described component related to face processing, was sensitive to face animacy in 5–10-year-old children. This sensitivity to animacy did not appear to rely on face-specific configural processing as indexed by the inversion effect, suggesting that it may reflect a sensitivity to of animate versus inanimate textures rather than the attunement of expert face processing to animate rather than inanimate faces. In addition, multivariate pattern analyses of the EEG signal did not yield any evidence that face animacy information was robustly represented during passive viewing in children. In adults, face animacy information could be extracted from whole scalp channels, but only marginally so from occipitotemporal channels.

Author contributions

Laurie Bayet: Formal analysis, Figures, Writing – original draft, Writing – Reviewing & Editing. Alyson Saville: Data Collection and Management. Benjamin Balas: Conceptualization, Methodology, Data Collection and Management, Formal analysis, Writing – original draft, Writing – Reviewing & Editing.

Data accessibility

The primary, de-identified data supporting the reported analyses is available online at https://osf.io/ef6gw/.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

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