

How do bodies become special? Electrophysiological evidence for the emergence of body-related cortical processing in the first 14 months of life

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Highlights:

- Unlike for faces, it is still unclear in the literature when and how images of bodies evoke specialised neural activations in the infant brain.
- Infant P400 reflects adult-like patterns of face inversion more than N290 suggesting that P400 may be a relatively stronger precursor of the adult N170.
- Face and body perception may follow different developmental trajectories, as we show little evidence for body specialisation within the first 14 months.
- Body representations are established by domain-general learning mechanisms that follow emerging infant motor development and visual exposure to entire bodies.

Abstract

There is general consensus that the representation of the human face becomes functionally specialised within the first few months of an infant's life. The literature is divided, however, on the question whether the specialised representation of the remainder of the human body form follows a similarly rapid trajectory or emerges more slowly and in line with domain-general learning mechanisms. Our study investigates visual ERPs in adults (P1 and N170) and infants (P1, N290, P400, and Nc) of three age groups (3.5, 10, and 14 months) to compare the emergence of face- and body-structural encoding. Our findings show that visual ERPs were absent (P1, N290, P400) or smaller (Nc) for bodies than for faces at 3.5 months. At older ages, P400 was smaller (10 months) and peaked later (14 months) for bodies than for faces. Effects of stimulus orientation were not reliably found until 14 months, where they were more broadly distributed for faces than for bodies. Inverted faces, but not bodies, produced an adult-like pattern for P400 at 14 months, emphasising the role of P400 as the precursor of the adult N170. Importantly, our findings argue that structural encoding of the human body form emerges later in infancy and is qualitatively different from the structural encoding for faces. This is commensurate with infant motor development and the experience of viewing complete body shapes later than faces.

Keywords: body representation, face inversion, body inversion, ERPs, infants.

Introduction

Face processing in infants has been studied extensively, revealing it as a rapidly emerging ability present from birth (Buiatti et al., 2019; Farroni et al., 2013) and quantitatively mature by early childhood (McKone, Crookes, Jeffrey, & Dilks, 2012). This, together with evidence that newborns orient preferentially towards faces (Johnson, Dziurawiec, Ellis, & Morton, 1991), has led to the suggestion that face recognition is the result of an innate 'social brain', with genetically pre-specified pathways (Baron-Cohen et al., 1999). One of the most influential developmental accounts, the *interactive specialisation framework* advanced by Johnson (2000), suggests that face recognition emerges as a result of changes in the interactions between brain regions that were already partially active before birth. Therefore, by virtue of initial biases that make newborns orient preferentially towards faces, some cortical pathways are then engaged more than others by these particular stimuli.

In stark contrast to faces, very little is known about the development of body perception. Like faces, bodies and body parts (e.g., hands) are important social and communicative tools. Bodily stimuli are also represented in specialised neural networks and enjoy privileged processing in adults (e.g., de Gelder et al., 2010; Downing & Peelen, 2016).

Event-related potential (ERP) studies are critical for investigating the neural time course at early stages of face and body processing and before such skills can be observed in overt behaviour (Richards, 2000). One of the most studied ERP components in adult face and body processing is the posterior (occipitotemporal) N170, which is enhanced in response to faces or bodies relative to other items including inanimate objects (e.g., Bentin et al., 1996; Stekelenburg & de Gelder, 2004). ERP studies have also shown that changes in stimulus orientation and the relation between individual stimulus features enhance and delay the N170 for faces as well as for bodies, due to the concomitant recruitment of additional neural resources (for reviews see de Gelder et al., 2010; Eimer, 2011; Piepers & Robbins, 2012; Rossion, 2014).

Thus, there are similarities in the structural encoding of faces and bodies: both are processed optimally when they are upright and normally configured. Configural structural representation is considered to be the hallmark of functional specialisation (e.g., for upright faces; Tanaka & Farah, 1993), and the templates underpinning such representations are based on canonical viewpoints acquired through expertise (e.g., Lee et al., 2011).

Configural analysis for faces comprises holistic processing (of the face as an integrated entity), first-order structural processing (of the spatial arrangements of individual features), and second-order structural processing (of the metric distances between individual features; Maurer, Le Grand, & Mondloch, 2002). For bodies, configural analysis is driven by

an additional type, hierarchical structural processing (of the position of features relative to the overall structure of the stimulus; e.g., where arms attach to the trunk), which is thought to take place after first-order and before holistic processing (Reed, Stone, Grubb, & McGoldrick, 2006).

While face inversion affects first-order structural analysis, body inversion affects both first-order and hierarchical structural analyses, suggesting that these processing types are necessary for the structural encoding of bodies (e.g., Reed et al., 2006; Soria Bauser & Suchan, 2013).

Infant ERP studies have suggested that the processes underlying the N170 are evident as two distinct occipitotemporal components; a negative peak around 290 ms (N290) and a positive deflection around 400 ms (P400) after the presentation of a face stimulus (Halit, de Haan, & Johnson, 2003). These components are thought to represent the N170 infant precursors because of their gradual reflection of face sensitivity across different ages. This has been shown in terms of heightened or faster responses to faces vs. objects (N290 in 4.5-month-olds; Guy, Zieber, & Richards, 2016), human vs. monkey faces (N290 in 3-, 6- and 12-month-olds; P400 in 12-month-olds; de Haan, Pascalis, & Johnson, 2002; Halit et al., 2003), upright vs. inverted faces (P400 in 6-month-olds; de Haan et al., 2002), inverted vs. upright human faces (N290 and P400 in 12-month-olds; Halit et al., 2003; see also Parise, Handl, & Striano, 2010, for similar findings with scrambled versus intact faces in 4-month-olds). In sum, infant ERP studies show that there is increasing

neural sensitivity to, and structural encoding of, human faces during the first year of life (for a recent review see also Hoehl, 2016).

Preceding the occipitotemporal N290 and P400 components, infant ERP waveforms also exhibit a P1 component at the same location. While this component has not been shown to be face-sensitive in infancy, face inversion can affect P1 in addition to N170 in adults and children (e.g., Itier & Taylor, 2002, 2004a, 2004b, 2004c; Jacques, d'Arripe, & Rossion, 2007). A few infant ERP studies have also identified a later component, the Negative central (Nc) component, which peaks between 400 and 800 ms after stimulus onset over frontal and central midline electrodes and shows some sensitivity to faces (Parise et al., 2010; Courchesne, Ganz, & Norcia, 1981; Marinovic, Hoehl, & Pauen, 2014; Guy et al., 2016). de Haan and Nelson (1997) suggested that the Nc is enhanced in response to a familiar stimulus, and thus reflects processes related to attention and stimulus recognition for information stored in long-term memory.

Infants may be sensitive, not just to faces, but to the whole human body form from relatively young ages, and in fact infants as young as 3.5 months can recognize the human form in dynamic point light displays (Bertenthal, Proffitt, & Cutting, 1984; Bertenthal, Proffitt, & Kramer, 1987; see also Fox & Daniel, 1982). Using a preferential looking paradigm, Heron-Delaney, Wirth, and Pascalis (2011) found that 3.5- and 6-month-olds exhibit a preference for static images of human bodies over other primate bodies even in the absence of faces. For newborns, however, this species preference was restricted to faces, suggesting that

the sensitivity for human body structure develops later than that for human faces but does so within the first few months of life. Infants may also be sensitive to typical (hierarchical structural) body configurations in photographs or line drawings of human bodies much earlier (3.5 months; Gliga & Dehaene-Lambertz, 2005; Zieber et al., 2014; 5 months; Hock, White, Jubran, & Bhatt, 2016; for review see Bhatt, Hock, White, Jubran, & Galati, 2016) than had previously been assumed (15-18 months; Slaughter & Heron, 2004; Slaughter, Heron, & Sim, 2002). For example, Gliga and Dehaene-Lambertz (2005) directly compared face and body stimuli and found that the P400 component was enhanced by stimuli whose first-order structure had been changed relative to intact stimuli, suggesting structural encoding of the human body form from 3 months of age. However, it is possible that infants responded to the implied bodily dynamics or to other low-level differences in intact and scrambled configurations rather than encoding these configurations as bodies (see Heron-Delaney et al., 2011; Slaughter, Heron-Delaney, & Christie 2011). While this study shows that the infant P400 may denote the structural encoding of bodies, at present, there are too few ERP studies to know whether other infant components related to face processing (N290, Nc) are also sensitive to the human body form.

In summary, while researchers generally agree that face representation is a rapidly emerging skill, there is currently no similar consensus about the developmental trajectory of body representation. Given that both faces and bodies are crucial social and communicative tools for engagement

with conspecifics, it is of profound importance to investigate the developmental changes of body structural encoding in comparison to faces.

In the present study, three groups of infants aged 3.5, 10, and 14 months and an additional group of adults were shown images of upright and inverted faces as well as upright and inverted bodies (without heads). The youngest and oldest infant age groups were chosen based on previous evidence for the emergence of body specialisation (3.5 months, Gliga & Dehaene-Lambertz, 2005; Zieber et al., 2014; 14 months, Slaughter et al., 2011). An additional in-between age was included to shed further light on the developmental changes of the neural signatures for face and body processing. Visual ERPs were extracted to investigate the emergence and development of infant components P1, N290, P400, and Nc, as well as adult components P1 and N170. The overall aim of this study was to understand whether the emergence of privileged processing for human bodies is driven by a similar developmental programme as that for faces (neonatal orienting plus rapid learning) (Gliga & Dehaene-Lambertz, 2005; Zieber et al., 2014), or whether it is instead gradually learnt and abstracted from visual exposure and motor control as part of more domain-general learning mechanisms (Slaughter et al., 2011). We expected visual P1, N290, P400, and Nc components to be present in response to both faces and bodies from the youngest age group (Gliga & Dehaene-Lambertz, 2005). We also expected evidence for face configural encoding (differential responses to upright and inverted images) to

increase with age, starting with orientation effects over P400 from 3 months and affecting also the N290 from 10 or 14 months (de Haan et al., 2002; Halit et al., 2003). Since body structural encoding may follow a similar trajectory as faces (Gliga & Dehaene-Lambertz, 2005; Zieber et al., 2014), we may expect the same pattern of orientation effects for bodies. Alternatively, since visual ERPs may express the cortical precursors of infants' looking responses, which arise between 12 and 15 months (Slaughter et al., 2011), we may therefore only expect to see orientation effects for bodies over N290 and P400 no earlier than 10 months. We further tested whether differences in the infant Nc to faces and bodies might denote differential developmental changes for these two classes of stimuli, reflecting the effects of differential familiarity.

Methods

Participants

As common in developmental ERP research (e.g. Lunghi, Piccardi, Richards, & Simion, 2019; Verneti et al., 2018; Geangu, Quadrelli, Lewis, Cassia, & Turati, 2015), we aimed to test between 15 and 20 infants in each age group. Based on this, we identified a target final sample size of 54 infants (stopping rule), i.e. average of 18 infants in each group.

Overall 54 healthy, full-term infants participated in the study (16 3.5-month-old infants, 20 10-month-old infants, 18 14-month-old infants). Of these, 13 were excluded due to fussiness and 2 for technical errors. The final sample included 13 3.5-month-old infants (9 female), aged between

84 and 133 days (mean age 108 days, $SD = 11.8$), 15 10-month-olds (7 females), aged between 273 and 332 days (mean age 297 days, $SD = 17.6$), and 11 14-month-old infants (8 females) aged between 400 and 443 days (mean age 421 days, $SD = 11.8$). Testing commenced only if the infant was awake and in an alert state. Fourteen (7 females) healthy adults volunteered as participants. Their ages ranged from 21 to 27 years (mean age 22.7 years, $SD = 2.1$), they all had normal or corrected-to-normal vision and were right-handed. Informed written consent, which was approved by the Science and Health Faculty Ethics Sub-Committee of the University of Essex (approval no.: SR1402; project name: The development of cognitive and social skills from infancy to adulthood), was obtained from the parents of infants and from adult participants.

Stimuli

Participants viewed colour images of six different face identities (3 male, 3 female) and six body identities (3 male, 3 female) of different ethnicities, with neutral facial expressions or in neutral postures, each displayed in an upright or inverted orientation. The face stimuli were selected from the NimStim set (Tottenham et al., 2009; available at <http://www.macbrain.org/resources.htm>), while the body stimuli were created in our lab as part of a separate project. Written consent was obtained from the models for the use of the images of their body, with the head cropped, in other experiments. The face stimuli occupied 17.2° vertical x 11.1° horizontal visual angle and the bodies occupied 17.2°

vertical x 5.6° horizontal visual angle. While smaller in horizontal visual angle, the luminosity of the body stimulus displays (including grey background) had a slightly higher mean intensity (157.5 / 256) than that of face stimulus displays (145.8 / 256). Cartoon pictures were used as inter-trial stimuli in order to keep the infants engaged in the study (see Figure 1 for examples of stimuli).

-- Figure 1 about here --

Procedure

Infants sat on their parent's lap 60 cm away from a 23-inch computer monitor in a quiet and dimly lit room. Each trial started with a colour cartoon image displayed in the middle of the screen, which lasted between 1400 and 1800 ms. Following this, a face or a body stimulus replaced the cartoon image for 1000 ms (see Figure 1). Sounds were occasionally used to re-direct infants' attention toward the screen and were played during cartoon presentation. Upright and inverted face and body stimuli were presented in a random order for a total of 240 trials (60 trials for each stimulus type) or until the infant became fussy and inattentive. The minimum criterion for inclusion was 10 trials per condition (e.g., Kobiella, Grossman, Reid, & Striano, 2007; Leppänen, Moulson, Vogel-Farley, & Nelson, 2007). There were no significant differences between the infant age groups in the number of trials included for analyses for each condition, $F(2,36)=.428$, $P>.6$. The average number

of trials considered for the analysis for the 3.5-month-old infants was 13.5 ($SD=6.8$) for face upright, 15.4 ($SD=6.7$) for face inverted, 14.9 ($SD=7.6$) for body upright, and 14.6 ($SD=6.1$) for body inverted conditions. The average number of trials considered for the analysis for the 10-month-old infants was 18.4 ($SD=5.4$) for face upright, 17.6 ($SD=4.9$) for face inverted, 19.7 ($SD=6.1$) for body upright, and 19.3 ($SD=3.6$) for body inverted conditions. The average number of trials considered for the analysis for the 14-month-old infants was 20.4 ($SD=10.3$) for face upright, 20 ($SD=8.6$) for face inverted, 22 ($SD=9.5$) for body upright, and 20.8 ($SD=9.7$) for body inverted conditions. The average number of trials considered for the analysis for the adults was 49.4 ($SD=4.1$) for face upright, 47.3 ($SD=8.1$) for face inverted, 47.1 ($SD=5.8$) for body upright, and 47.4 ($SD=6.5$) for body inverted conditions.

EEG recording and analysis

Brain electrical activity was recorded continuously using a Hydrocel Geodesic Sensor Net consisting of 128 Ag–AgCl electrodes evenly distributed across the scalp (Figure 2) and referenced to the vertex. EEG was amplified with a 0.1 to 100 Hz band-pass filter and digitized at 500 Hz. Off-line analysis was conducted using NetStation 4.5.1 analysis software (Electrical Geodesic Inc.). Continuous EEG data were low-pass filtered at 30 Hz using digital elliptical filtering and segmented in epochs from 100 ms before until 700 ms after stimulus onset. Segments with eye

movements and blinks were detected manually and rejected from further analysis. Artefact-free data were then baseline-corrected to the average amplitude of the 100 ms pre-stimulus interval and re-referenced to the average potential over the scalp. Finally, individual and grand averages were calculated.

-- Figure 2 about here --

Statistical analyses of the ERP data targeted the examination of stimulus type (face, body) and orientation (upright, inverted) effects over right and left occipitotemporal electrode sites and over right, left, and medial frontocentral electrodes. Groups of electrodes were initially selected for analysis based on previous studies of infant face and body perception (e.g., de Haan et al., 2002; Rigato, Farroni, & Johnson, 2010) and this selection was adjusted following visual inspection to find where the components of interest were maximal in the present dataset. For the analyses of the occipitotemporal components, this resulted in a slightly different selection for the three age groups tested (Figure 2). For the 3.5-month-old infants, the electrodes included in the analyses were: 76, 77, 83, 84, 90, 91 (right hemisphere); 59, 65, 66, 70, 71 (left hemisphere). For the 10- and 14-month-olds, the electrodes included in the analyses were: 83, 84, 90, 91, 96 (right hemisphere); 58, 59, 65, 66, 70 (left hemisphere). For the adults, the electrodes included in the analyses were right hemisphere electrodes 83 (O2), 84, 85, 90 (PO8), 91, 92 (P4), 95 (P10), 96 (P8), 97 and left hemisphere electrodes 52 (P3), 59, 60, 65

(PO7), 66, 70 (O1). Waveforms from these electrodes were averaged to create left-hemisphere and right-hemisphere clusters for each condition.

For the analyses of the Nc in infants, the following frontocentral electrodes were selected: 103, 104, 110 (C4, right hemisphere); 35, 36, 41 (C3, left hemisphere), Cz and 11 (Fz) for medial sites.

Over the occipitotemporal clusters, we detected the expected P1, N290, and P400 infant components in most conditions, however, they peaked at different latencies for the younger and older age groups. The latencies of peak amplitudes were determined for each individual participant by visual inspection, and time windows were then chosen to include the temporal spread of peaks across participants. This resulted in the following time-window selection. For the 3.5-month-olds, the P1 was analysed between 160 and 290 ms, the N290 between 290 and 400 ms, and the P400 between 440 and 550 ms. For the 10- and 14-month-old infants, the P1 was analysed between 170 and 340 ms, the N290 between 240 and 360 ms, and the P400 between 350 and 550 ms. Over the frontocentral clusters, we identified the expected Nc which was analysed for the time window 400-700 ms after stimulus onset. For adults, we detected the expected occipitotemporal P1 and N170 components and selected time windows centred on their peaks (P1: 110-160 ms; N170: 160-230 ms). The amplitudes of the occipitotemporal ERP components in different conditions were compared with t-tests at each point within these time windows, controlling for type I error using Monte Carlo simulations (Guthrie and Buchwald, 1991; see Supporting Information). We were

specifically interested in the differences between face and body processing, and in the effects of stimulus orientation. Therefore, we tested for main effects of stimulus type (face and body), for main effects of orientation (upright and inverted) across both stimulus types, and for main effects of orientation separately for each stimulus type (upright and inverted faces; upright and inverted bodies). All analyses were run separately for each hemisphere (RH, LH).

The peak latencies of the ERP components were analysed by multiple t-tests, corrected using the method described by Benjamini & Hochberg (1995), which controls the false discovery rate. Corrections were applied for multiple comparisons across components and hemispheres within each age group and within each analysis (overall effects of stimulus type, overall effects of orientation, and effects of orientation separately for each stimulus type).

Results

Table 1 shows a summary of the results of Monte Carlo simulations (amplitude effects) and Benjamini-Hochberg corrected t-tests (latency effects) for overall effects of stimulus type (1a, 1b), for overall effects of orientation (1c), and for effects of orientation separately for each stimulus type in each hemisphere (1d).

--Table 1 about here --

Adults

Face and body stimuli elicited clear P1 (peak latencies: faces: M=137 ms, SD = 10.4; bodies: M=147 ms, SD = 6.6) and N170 (faces: M=190 ms, SD = 11.1; bodies: M=205 ms, SD = 11.3) components in all conditions (see Figure 3).

There were no main effects or interactions in the analysis of P1 amplitudes, however P1 latencies were affected by stimulus type, with P1 peaking earlier to faces (M=134 ms, SD = 13.3) than to bodies (M= 147 ms, SD = 9.5) in the LH ($t(13)=-4.7$, $p<.001$), and similarly in the RH (faces: M=140 ms, SD =8.3; bodies: 148 ms, SD = 6; $t(13)=-4.9$, $p<.001$).

N170 amplitudes were affected by orientation and stimulus type. In the RH there was an overall effect of orientation (176-230 ms; autocorrelation: 0.92; sequence length: 14 ms), and of stimulus type (160-190 ms and 206-230 ms; autocorrelation: 0.95; sequence length: 16 ms). Further, we identified an orientation effect for both faces (172-226 ms; upright: M=-.3 μ V, SD=2.5; inverted: M=-3.1 μ V, SD=1.9; autocorrelation: 0.90; sequence length: 14 ms) and bodies (192-212 ms; upright: M=-.7 μ V, SD=1.8; inverted: M=-1.6 μ V, SD=1.9; autocorrelation: 0.95; sequence length: 16 ms). Similarly, in the LH there was an overall effect of orientation (190-230 ms; autocorrelation: 0.96; sequence length: 18 ms) and stimulus type (160-178 ms; autocorrelation: 0.93; sequence length: 16 ms). There was an orientation

effect for both faces (194-230 ms; upright: $M=-.2 \mu\text{V}$, $SD=2.4$; inverted: $M=-1.3 \mu\text{V}$, $SD=2.4$; autocorrelation: 0.94; sequence length: 16 ms) and for bodies (200-230 ms; upright: $M=.2 \mu\text{V}$, $SD=2$; inverted: $M=-.5 \mu\text{V}$, $SD=2.4$; autocorrelation: 0.97; sequence length: 20 ms). Corrected t-tests showed that for N170 latencies there were no effects of orientation overall or within each stimulus type. Instead, there were overall effects of stimulus type showing earlier N170 latencies to faces than to bodies in each hemisphere (LH, faces: $M=190$ ms, $SD=16.2$, bodies: $M=206$ ms, $SD=16$, $t(13)=-5.0$, $p<.001$; RH, faces: $M=190$ ms, $SD=14.2$, bodies: $M=204$ ms, $SD=11.7$, $t(13)=-5.1$, $p<.001$).

-- Figure 3 about here --

Infants

The expected occipitotemporal components were present at all ages for faces (peak latencies: *P1*, 3.5mo: $M=226$ ms, $SD=18.9$, 10mo: $M=243$ ms, $SD=31.4$, 14mo: $M=227$ ms, $SD=9.6$, ; *N290*, 3.5mo: $M=341$ ms, $SD=19.6$, 10mo: $M=301$ ms, $SD=23.7$, 14mo: $M=309$ ms, $SD=4.9$; *P400*, 3.5mo: $M=489$ ms, $SD=27.4$, 10mo: $M=459$ ms, $SD=31.8$, 14mo: $M=447$ ms, $SD=6$), but only from 10 months for bodies (*P1*, 10mo: $M=266$ ms; $SD=33.9$, 14mo: $M=250$ ms, $SD=8.6$; *N290*, 10mo: $M=290$ ms, $SD=25.4$; 14mo: $M=308$ ms, $SD=6.5$; *P400*, 10mo: $M=465$ ms, $SD=36.5$; 14mo: $M=482$ ms, $SD=8.8$) (see Figure 4).

-- Figure 4 about here --

P1

In 3.5-month-olds, the P1 amplitude was affected by stimulus type, with larger amplitudes for faces than bodies, in the RH (160-186 ms; faces: $M=12.3 \mu\text{V}$, $SD=1.7$; bodies: $M=11.7 \mu\text{V}$, $SD=2.3$) and in the LH (160-192 ms; faces: $M=12.4 \mu\text{V}$, $SD=2.3$; bodies: $M=9.2 \mu\text{V}$, $SD=2.3$; autocorrelation: 0.96; sequence length: 22 ms). P1 latency was also affected by stimulus type showing earlier peaks for faces ($M=218 \text{ ms}$, $SD=5.9$) than for bodies ($M=247 \text{ ms}$, $SD=7.3$; $t(12)=-3.9$, $p=.002$) in the RH.

In 10-month-olds, the amplitude and latency of the P1 were not affected by any factor (Figure 5). There were no stimulus-general or stimulus-specific P1 effects of orientation until 14 months, where we found an effect of orientation overlapping both P1 and N290 time-windows (see Figure 6). This was found between 240 and 334 ms (autocorrelation: 0.99; sequence length: 40 ms) in the LH, and between 244 and 308 ms (autocorrelation: 0.98; sequence length: 36 ms) in the RH. There was a greater positivity over P1 time-window for inverted ($M=9.2 \mu\text{V}$, $SD=2.1$) compared to upright ($M=4.7 \mu\text{V}$, $SD=1.8$) stimuli, and a greater negativity over N290 time-window for upright ($M=-8.1 \mu\text{V}$, $SD=1.6$) compared to inverted ($M=-3.6 \mu\text{V}$, $SD=1.3$) stimuli. For faces, an orientation effect was found over the LH between 248 and 310 ms (P1, upright: $M=4.8 \mu\text{V}$, $SD=2.2$; inverted: $M=8.7 \mu\text{V}$, $SD=1.9$; N290, upright: $M=-8.7 \mu\text{V}$, $SD=2.3$; inverted: $M=-3.3 \mu\text{V}$, $SD=1.5$) (autocorrelation:

0.99; sequence length: 36 ms). For bodies, an orientation effect was found in the LH between 248 and 276 ms for N290 only (upright: $M=-5.8 \mu\text{V}$, $SD=3.3$; inverted: $M=1.4 \mu\text{V}$, $SD=4$; autocorrelation: 0.96; sequence length: 26 ms). No effects of latency were found in 14-month-old infants.

--Figure 5 and 6 about here --

N290

For N290 amplitude, an effect of stimulus type, with larger amplitudes for faces than bodies, was found in 3.5-month-olds in the RH only (290-332 ms; faces: $M=-1.3 \mu\text{V}$, $SD=2.4$; bodies: $M=-.03 \mu\text{V}$, $SD=2.9$; autocorrelation: 0.94; sequence length: 20 ms). In 10-month-olds, the N290 amplitude was affected by orientation in the LH, but not in the RH, (242-274 ms; upright: $M = -7.5 \mu\text{V}$, $SD=2$; inverted: $M = -1.9 \mu\text{V}$, $SD=2.1$; autocorrelation: 0.98; sequence length: 32 ms). As described in the previous section, at 14 months, the amplitude of the N290 was affected by orientation effects which were also overlapping with the amplitude of the P1 component. There were no effects of latency in either group.

P400

No amplitude effects were found for this component at 3.5 months of age. However, at 10 months, P400 amplitude was affected by stimulus type, with larger amplitudes for faces than bodies, in the LH (422-482 ms;

faces: $M = 16.8 \mu\text{V}$, $SD=2.3$; bodies: $M = 11.8 \mu\text{V}$, $SD=2.2$;
autocorrelation: 0.96; sequence length: 30 ms), and by orientation at 14
months in both the LH (404-550 ms; autocorrelation: 0.97; sequence
length: 34 ms) and in the RH (438-550 ms; autocorrelation: 0.99;
sequence length: 40 ms). P400 was enhanced for inverted ($M=15.1 \mu\text{V}$,
 $SD=2.6$) compared to upright ($M=8.6 \mu\text{V}$, $SD=1.9$) stimuli. For faces,
orientation effects were identified over the LH (406-550 ms; upright:
 $M=7.9 \mu\text{V}$, $SD=3.4$; inverted: $M= 16.4 \mu\text{V}$, $SD=4.4$; autocorrelation:
0.98; sequence length: 40 ms) and the RH (422-550 ms; upright: $M=7.3$
 μV , $SD=3.2$; inverted: $M= 19.2 \mu\text{V}$, $SD=4.1$; autocorrelation: 0.97;
sequence length: 32 ms). However, there were no orientation effects for
bodies.

While latency effects were not found at 3.5 or 10 months of age, there
were overall effects of stimulus type at 14 months, such that faces
evoked earlier P400 peaks than bodies over the LH (faces: $M=445$ ms,
 $SD=4.9$, bodies: $M=476$ ms, $SD=11.7$, $t(10)=-3.2$, $p=.010$) as well as
over the RH (faces: $M=449$ ms, $SD=9.4$, bodies: $M=488$ ms, $SD=8.1$,
 $t(10)=-4.1$, $p=.002$).

Nc

The analyses of the frontocentral *Nc* revealed a statistically reliable effect
of stimulus type in the 3.5-month-olds from 406 to 556 ms with larger
amplitudes for faces ($M=-6.9 \mu\text{V}$, $SD=1.5$) than bodies ($M=-1.5 \mu\text{V}$,
 $SD=1.2$; see Figure 7) (autocorrelation: 0.99; sequence length: 66 ms).

However no significant differences between face and body were found at older ages (10 months, faces: $M=-4.4 \mu V$, $SD=1.2$; bodies: $M=-3.1 \mu V$, $SD=1$; 14 months, faces: $M=-3.4 \mu V$, $SD=1.4$; bodies: $M=-3.5 \mu V$, $SD=1.7$).

-- Figure 7 about here --

Discussion

The aim of the present study was to chart the development of early visual cortical responses to human faces and bodies, and their sensitivity to stimulus inversion, over three infant ages (3.5, 10, and 14 months) and in adults.

Our findings for adults mirror those reported in the literature of face and body processing with P1 and N170 peaking earlier for faces than for bodies (e.g., Thierry et al., 2006). We also confirm that, for both bodies and faces, inverted versus upright stimuli evoke an enhanced N170 component (for reviews see Eimer, 2011; de Gelder et al., 2010).

Similarly to Stekelenburg & de Gelder (2004), N170 inversion effects for faces were much larger than those for bodies (about three times larger in our study). Unlike previous reports, however, N170 was not found to be delayed by stimulus inversion.

Our infant findings show that structural encoding of the human body form emerges later and is qualitatively different from structural encoding for faces. We concluded this from two lines of findings:

(1) Infant electrophysiological markers of visual processing (frontocentral Nc, occipitotemporal P1, N290, P400) were visible from 3.5 months of age when infants viewed faces but only from 10 months of age when they viewed bodies. The Nc, P1 and N290 components were found to have larger amplitudes for faces than for bodies at 3.5 months. Face sensitivity over Nc is consistent with an interpretation of this component as reflecting stimulus familiarity (de Haan and Nelson, 1997). By 10 months, the Nc waveform no longer differentiated between faces and bodies, possibly indicating bodies either gaining greater familiarity and/or attracting increasing interest due to their novelty at this age. At 10 months, P400 was found to be larger to faces than bodies, and at 14 months, it peaked earlier in response to faces than bodies.

(2) Orientation effects which indicate functional specialisation for processing images of upright faces and bodies were present from 10 months as an overall effect (N290), but only from 14 months as stimulus-specific effects (P1, N290, P400). However, most of these orientation effects (P1, P400) were driven by face stimuli only. Separate analyses of P1 and N290 time windows in 14-month-olds (which overlapped to cover all individuals' peaks in all conditions) identified the same overall orientation effect, starting around 240 ms (see Table 1c and d). Figure 6 shows that this time point falls before the P1 peak for some conditions (inverted faces and bodies in LH, inverted bodies in RH). Given the temporal lag for body components, this effect may thus be interpreted as a P1 enhancement for inverted bodies. For faces, however, this effect is

likely to reflect an enhancement of N290 for upright compared to inverted faces. Visual inspection of the waveforms shows that a similar pattern (stimulus-general N290 effects of orientation starting over P1) is present already in 10-month-olds over the LH, suggesting that this orientation sensitivity develops between 10 and 14 months. A more robust orientation effect for faces was found over the P400 component in 14-month-olds, where inverted faces elicited larger amplitudes than upright faces. This pattern of results suggests that the P400, rather than the N290, may be the strongest contributor to the adult N170 because it reflected adult-like patterns of inversion more than the N290¹. However, the N290 clearly contributes to the structural encoding of faces and bodies in the left hemisphere, albeit in a non-adult like manner. Given that this is the first study to observe the orientation effect for both faces and bodies in the same infants, further studies, and in particular longitudinal studies, are necessary to explore the relative contributions of these two infant components.

Overall, this suggests that infants are sensitive to stimulus orientation at substantially later developmental stages than previously observed, starting between 10 and 14 months of age. In fact, our findings confirm

¹ To substantiate the suggestion that P400 is a relatively stronger candidate as a precursor for the adult N170 than N290, we ran a repeated measures analysis of variance on the peak amplitude data with the factors age, stimulus type, and orientation for both components. This revealed a stimulus x orientation x age interaction for P400 amplitudes ($F(2,36)=3.803, p=.032$), and a stimulus x age interaction for P400 latencies ($F(2,36)=5.925, p=.006$). There were no such age-related changes for the N290.

some, but not all, orientation effects previously reported for faces (see de Haan et al., 2002; Halit et al., 2003). We also report an orientation effect (N290 in 10-month-olds) which is in the opposite direction to Halit et al.'s (2003) findings. It is known, however, that the direction of infant orientation effects does not always remain stable across age (see McKone et al., 2012).

While at 14 months the structural encoding for faces is well-developed, it is only just emerging for bodies. In fact, at this age, orientation effects were wider-ranging, and more adult-like, for faces (P1 and N290 in LH, P400 in LH and RH) than for bodies (N290 in LH). Moreover, the body orientation effect was significant for a smaller time window (about 30 ms) than the equivalent N290 effect for faces (about 60 ms) (see Table 1d).

This is unlike previous ERP studies of face and body processing using stimulus scrambling instead of inversion (Gliga & Dehaene-Lambertz, 2005), but is in line with behavioural evidence indicating that functionally specialised body representations emerge slowly and gradually (Slaughter & Heron, 2004; Slaughter et al., 2002).

There are a number of differences between Gliga and Dehaene-Lambertz's (2005) and our study that make it difficult to compare our disparate findings directly. One concerns the electrophysiological responses in our youngest group of infants (3.5-month-olds). Unlike Gliga and Dehaene-Lambertz, we could not observe the expected N290-P400 complex in response to body stimuli. This might be due to low-level visual differences between the stimuli in the two studies, including the presence

of cues that imply body movement, which younger infants might be more sensitive to. Another substantial difference resides in the categories of visual stimuli that were compared (upright vs. inverted bodies, intact vs. scrambled bodies). Changing the first-order relationships between elements of the body (or the face) may affect emerging representations earlier in life than inversion. This could be because orientation effects depend on a hierarchical structural representation of the entire body form (though not necessarily on a complete template match; see Reed et al., 2006, Experiment 3), while scrambling effects could conceivably occur on the basis of representing a partial body (e.g., upper body only, lower body only). This speculation would be in line with age-related changes in visual exposure to, and motor control of, increasing proportions of the body, that is, from individual body parts to the body as one whole unit. Similar to ERP findings, the behavioural infant literature also reports discrepancies between age of acquisition for body-structural representations. Like Gliga and Dehaene-Lambertz (2005), one study suggested that structural body representations are already available at 3.5 months (Zieber et al., 2014; see also Bertenthal et al., 1984). However, other studies that have used stimuli and methodologies very similar to Zieber et al.'s do not echo their findings with similar-age and older infants (for review see Slaughter et al., 2011). Instead, most studies find that infants do not show visual preferences for images of intact body configurations until 15 to 18 months of age, which is consistent with our findings in the present study.

This suggests that, unlike face representations, body representations emerge slowly and gradually, in line with domain-general learning mechanisms (see Slaughter et al., 2011). It is worth noting that the absence of clear ERP signals and effects does not necessarily imply the absence of an ability or that the underlying mechanism is not operational (Hood, 2001). The ability to structurally encode bodies is also highly stimulus-dependent (Slaughter et al., 2011), ranging from real-life, moving bodies in 4-6 month-olds to abstract body representations (mannequins, dolls, photographs, drawings) in 9-month-old infants. The ability to represent the body in a configural and increasingly abstractable manner might depend on the level of visual exposure to own or others' entire bodies, the developing motor abilities, or the interactions among these factors. Typically, all of these are rather limited at birth and increase with age in the following months.

When an infant is able to sit or stand up, the opportunities of being exposed to different types of visual stimuli, including whole bodies, increases. Similarly, when the infant becomes more mobile, there are increased opportunities for using their whole body in a coordinated fashion (e.g. crawling, walking). One possibility is that infants gradually learn about body structure through integrated visuomotor exposure, perhaps as a corollary of the preferential orienting toward faces and biological motion they show at birth (e.g., Simion, Regolin, & Bulf, 2008). For example, a recent study showed that periods of intensively looking at faces are replaced by periods of intensively looking at hands manipulating

objects at around 12 months of age (Fausey, Jayaraman, & Smith, 2016). It was suggested that the integration of face and hand information as belonging to one person may be established through their spatio-temporal proximity. Similarly, configural representations of entire bodies may depend on the close coupling of visuomotor or, more generally, sensorimotor experience of the structural elements of the human body in time and space. Slaughter et al. (2004) showed that 12-month-olds who were able to walk discriminated typical from scrambled body configurations, compared to non-walking 12-month-olds (but see also Christie & Slaughter, 2009). Future research should seek to delineate how emergent face and body representations are interrelated with one another and with a range of sensorimotor learning at the neural level. More specifically, infant visual ERP studies could include measures of gross and fine motor development, perhaps distinguishing between object-related behaviours and body-exploratory or self-other discriminatory behaviours.

In conclusion, our study contributes to understanding how the human body becomes more than the sum of its parts. This has important implications for society and health, primarily because our body is central to our self-experience and to our identity as individuals. Knowing how configural structural representations are acquired is an essential step in identifying early markers of later-life failures of configural processing, for example in eating or body dysmorphic disorders (e.g., Groves, Gillmeister, & Kennett, 2019; Mundy & Sadusky, 2014; Urgesi, Fornasari,

Canalaz, Perini, Cremaschi et al., 2014). It may also inform how primary caregivers could interact with infants in ways that promote beneficial sensorimotor inputs in order to alleviate developmental conditions related to the processing of human stimuli (e.g., autism; Marco, Hinkley, Hill, & Nagarajan, 2011; Klin, Lin, Gorrindo, Ramsay, & Jones, 2009).

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Table 1. Overview of significant time windows for each age group, ERP component and hemisphere for amplitude (a) and latency (b) differences between faces and bodies, amplitude differences between upright and inverted orientations overall (c) and separately for each stimulus type (d). (+) and (-) after each time window indicate the direction of the effect in line with the heading of each table (+) or in the reverse direction (-).

a)

| Amplitude effects | | Stimulus type: Faces > Bodies | |
|-------------------|---------------|----------------------------------|-------------------------------|
| Age group | ERP component | Left hemisphere | Right hemisphere |
| 3.5 months | P1 | 160-192 ms (+) | 160-186 ms (+) |
| | N290 | | 290-332 ms (+) |
| | P400 | | |
| | Nc | 406-556 ms (+) | |
| 10 months | P1 | | |
| | N290 | | |
| | P400 | 422-482 ms (+) | |
| | Nc | | |
| 14 months | P1 | | |
| | N290 | | |
| | P400 | | |
| | Nc | | |
| Adults | P1 | | |
| | N170 | 160-178 ms (+) | 160-190 ms; 206-230 ms (+) |

b)

| Latency effects | | Stimulus type: Faces earlier than Bodies | |
|-----------------|---------------|---|--------------------|
| Age group | ERP component | Left hemisphere | Right hemisphere |
| 3.5 months | P1 | | <i>p</i> =.002 (+) |
| | N290 | | |
| | P400 | | |
| 10 months | P1 | | |
| | N290 | | |
| | P400 | | |
| 14 months | P1 | | |
| | N290 | | |
| | P400 | <i>p</i> =.010 (+) | <i>p</i> =.002 (+) |
| Adults | P1 | <i>p</i> <.001 (+) | <i>p</i> <.001 (+) |
| | N170 | <i>p</i> <.001 (+) | <i>p</i> <.001 (+) |

c)

| Amplitude effects | | Orientation: Inverted > Upright | |
|-------------------|---------------|------------------------------------|------------------|
| Age group | ERP component | Left hemisphere | Right hemisphere |
| 3.5 months | P1 | | |
| | N290 | | |
| | P400 | | |
| 10 months | P1 | | |
| | N290 | 242-274 ms (-) | |
| | P400 | | |
| 14 months | P1 | 240-334 ms (+) | 244-308 ms (+) |
| | N290 | 240-334 ms (-) | 244-308 ms (-) |
| | P400 | 404-550 ms (+) | 438-550 ms (+) |
| Adults | P1 | | |
| | N170 | 190-230 ms (+) | 176-230 ms (+) |

d)

| Amplitude effects | | Orientation: Faces inverted > Faces upright | | Orientation: Bodies inverted > Bodies upright | |
|-------------------|---------------|--|------------------|--|------------------|
| Age group | ERP component | Left hemisphere | Right hemisphere | Left hemisphere | Right hemisphere |
| 3.5 months | P1 | | | | |
| | N290 | | | | |
| | P400 | | | | |
| 10 months | P1 | | | | |
| | N290 | | | | |
| | P400 | | | | |
| 14 months | P1 | 248-310 ms (+) | | | |
| | N290 | 248-310 ms (-) | | 248-276 ms (-) | |
| | P400 | 406-550 ms (+) | 422-550 ms (+) | | |
| Adults | P1 | | | | |
| | N170 | 194-230 ms (+) | 176-226 ms (+) | 200-230 ms (+) | 192-212 ms (+) |

Figure legends:

Figure 1. Example of a trial sequence showing an inverted body stimulus (A), and examples of face and body stimuli (B), which were presented upright and inverted in separate trials. (Examples of face stimuli are adapted with permission from: Tottenham, N., Tanaka, J., Leon, A.C., McCarry, T., Nurse, M., Hare, T.A., Marcus, D.J., Westerlund, A., Casey, B.J., Nelson, C.A. (2009). The NimStim set of facial expressions: judgments from untrained research participants. *Psychiatry Research*, 168(3):242-9.)

Figure 2. Electrode layout of the Hydrocel Geodesic Sensor Net. Occipitotemporal electrodes used for analysis are highlighted for 3.5-month-olds (A), 10- and 14-month-olds (B) and adults (C). Frontocentral electrodes used for all infant Nc analyses are highlighted in (D).

Figure 3. ERP waveforms to bodies (black) and faces (grey) in upright (solid) and inverted (dashed) orientations over left (left panel) and right (right panel) occipitoparietal sites in adult participants. Components P1 and N170 are indicated. The solid lines underneath the graphs show the continuous time points of the waveforms for which comparisons between faces and bodies (Stimulus type: dark grey), upright and inverted

presentations (Orientation: dark grey), and between upright and inverted presentations specific for each stimulus type (Orientation: Faces: light grey; Orientation: Bodies: black) were significant. See text for analysis details.

Figure 4. ERP waveforms to bodies (black) and faces (grey) in upright (solid) and inverted (dashed) orientations over left (left panel) and right (right panel) occipitotemporal sites in 3.5-month-olds. Components P1, N290 and P400 are indicated. The solid lines underneath the graphs show the continuous time points of the waveforms for which comparisons between faces and bodies (Stimulus type: dark grey), upright and inverted presentations (Orientation: dark grey), and between upright and inverted presentations specific for each stimulus type (Orientation: Faces: light grey; Orientation: Bodies: black) were significant. See text for analysis details.

Figure 5. ERP waveforms to bodies (black) and faces (grey) in upright (solid) and inverted (dashed) orientations over left (left panel) and right (right panel) occipitotemporal sites in 10-month-olds. Components P1, N290 and P400 are indicated. The solid lines underneath the graphs show the continuous time points of the waveforms for which comparisons between faces and bodies (Stimulus type: dark grey), upright and inverted presentations (Orientation: dark grey), and between upright and

inverted presentations specific for each stimulus type (Orientation: Faces: light grey; Orientation: Bodies: black) were significant. See text for analysis details.

Figure 6. ERP waveforms to bodies (black) and faces (grey) in upright (solid) and inverted (dashed) orientations over left (left panel) and right (right panel) occipitotemporal sites in 14-month-olds. Components P1, N290 and P400 are indicated. The solid lines underneath the graphs show the continuous time points of the waveforms for which comparisons between faces and bodies (Stimulus type: dark grey), upright and inverted presentations (Orientation: dark grey), and between upright and inverted presentations specific for each stimulus type (Orientation: Faces: light grey; Orientation: Bodies: black) were significant. See text for analysis details.

Figure 7. ERP waveforms to bodies (black) and faces (grey) in 3.5-month-olds (left panel), 10-month-olds (middle panel) and 14-month-olds (right panel) over frontocentral sites. Component Nc is indicated. The solid lines underneath the graphs show the continuous time points of the waveforms for which comparisons between faces and bodies (Stimulus type: dark grey) were significant. See text for analysis details.

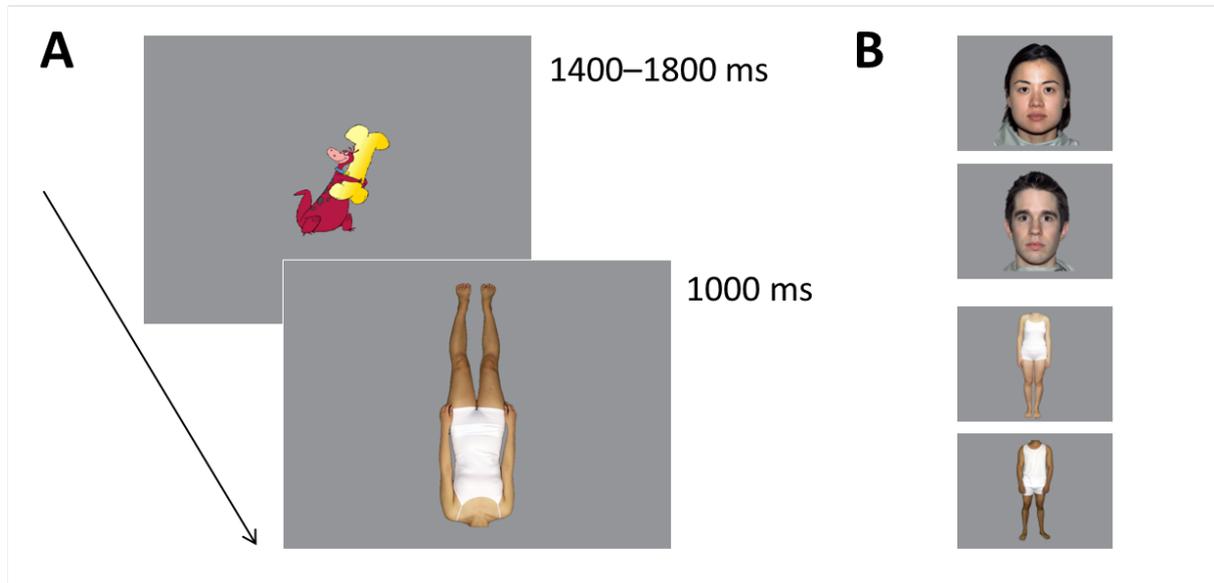


Figure 1

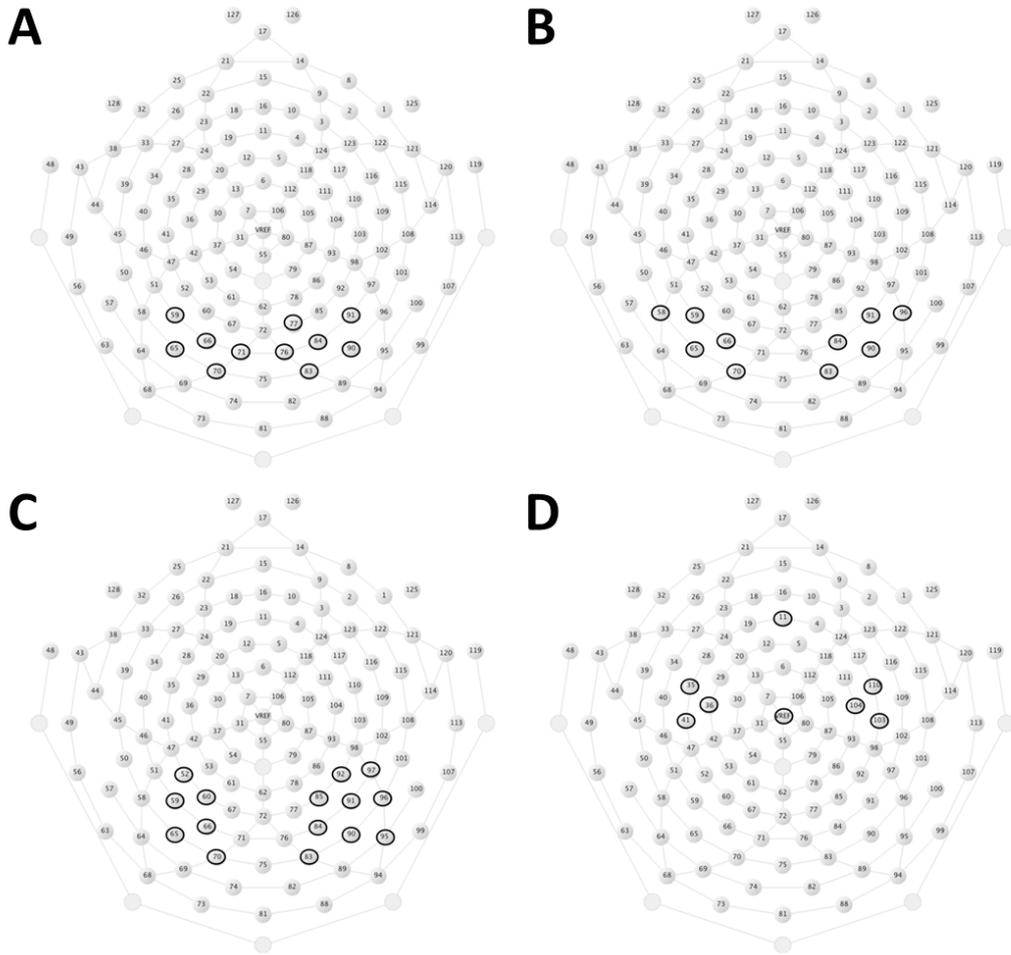


Figure 2

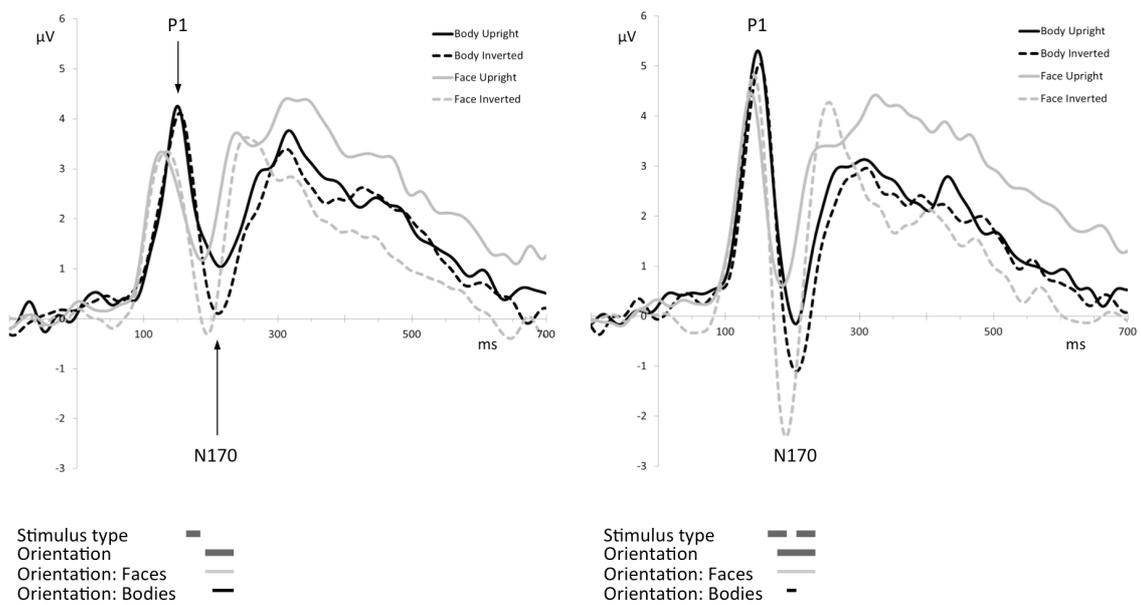
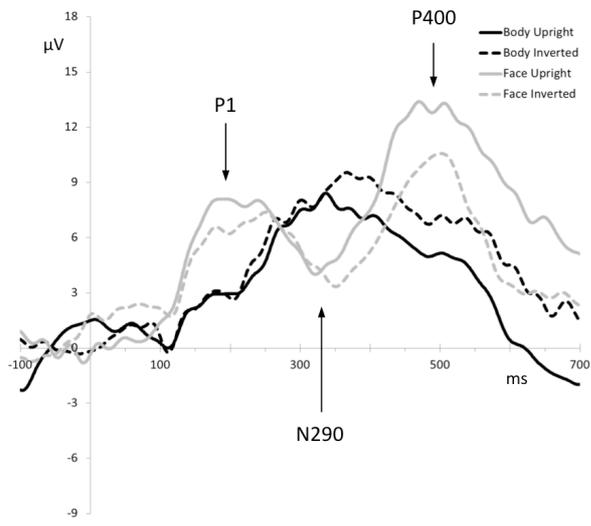
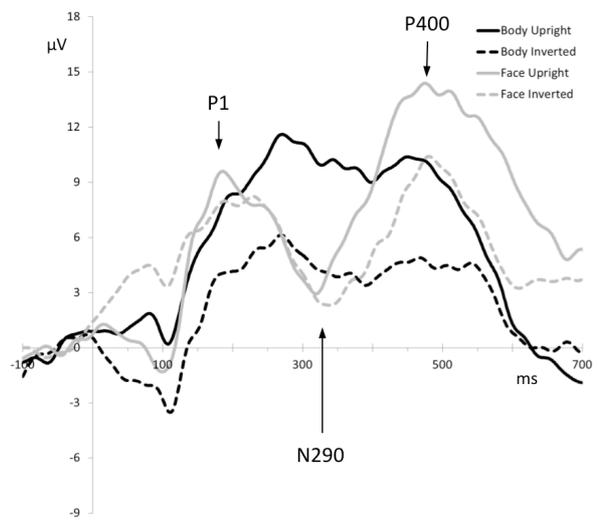


Figure 3



Stimulus type —
 Orientation
 Orientation: Faces
 Orientation: Bodies



Stimulus type —
 Orientation
 Orientation: Faces
 Orientation: Bodies

Figure 4

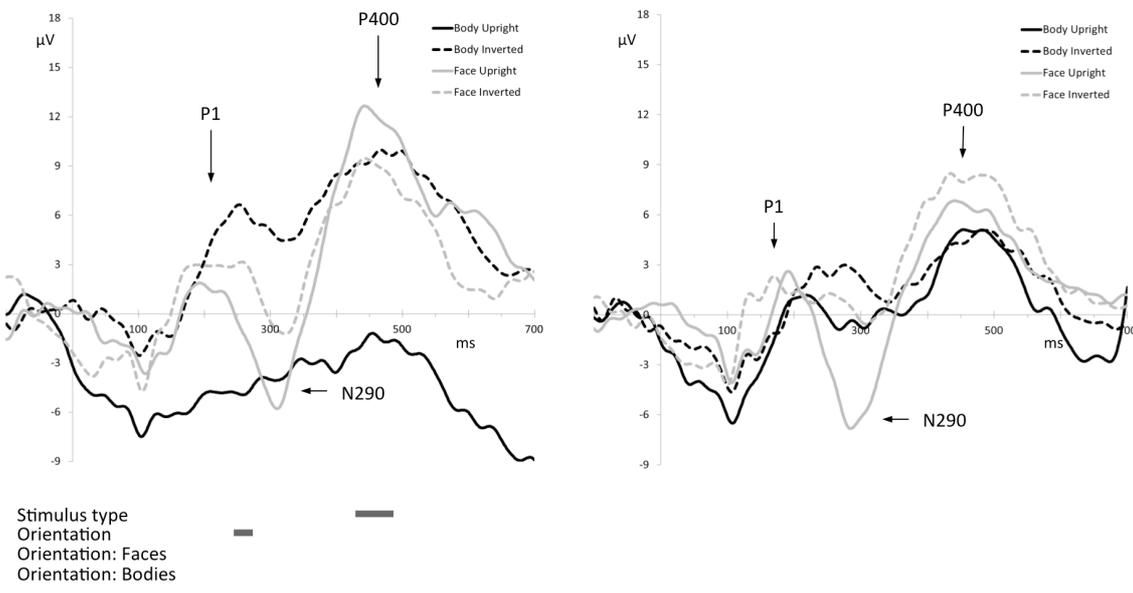


Figure 3

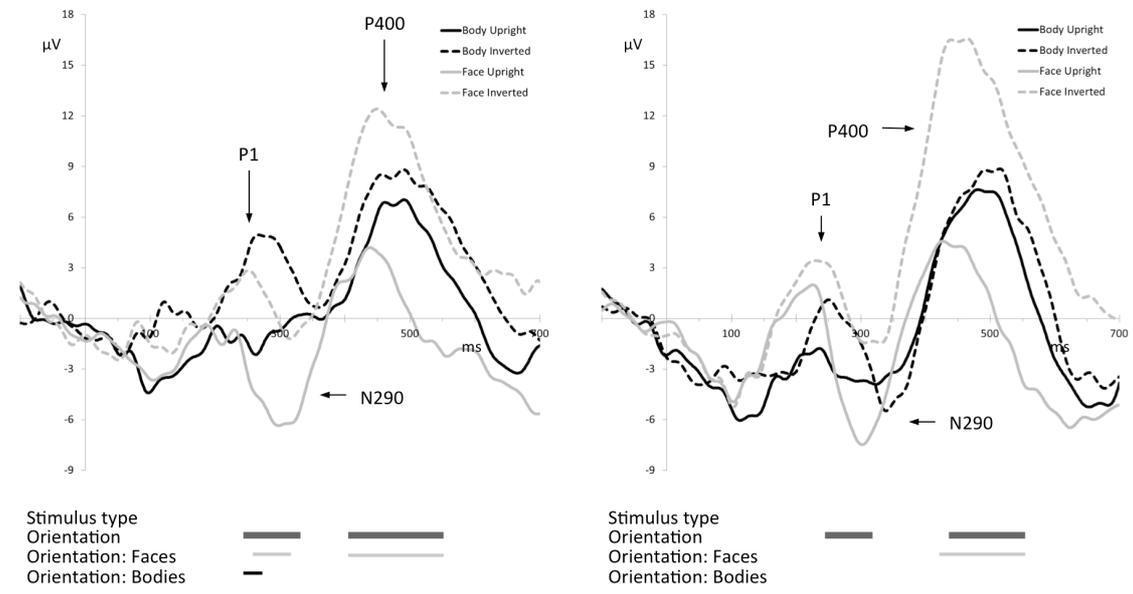


Figure 4

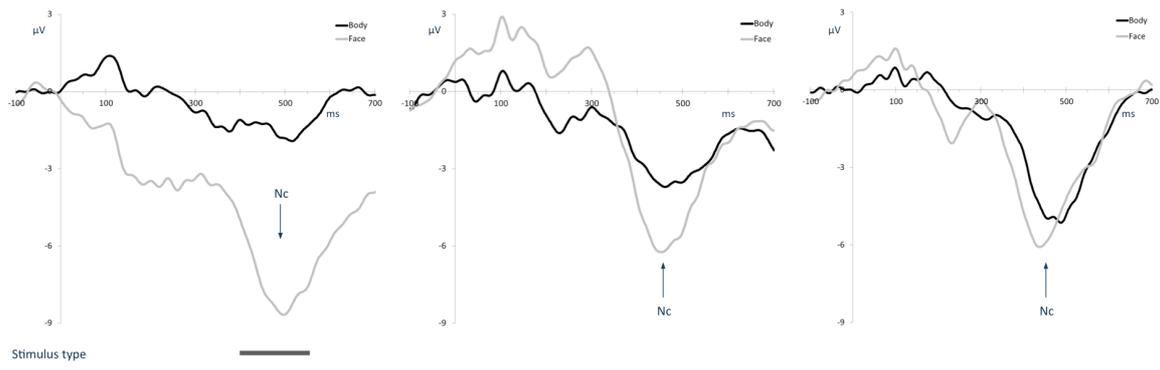


Figure 7