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# Human infants dissociate structural and dynamic information in biological motion: evidence from neural systems

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**This study investigates how human infants process and interpret human movement. Neural correlates to the perception of (i) possible biomechanical motion, (ii) impossible biomechanical motion and (iii) biomechanically possible motion but nonhuman 'corrupted' body schema were assessed in infants of 8 months. Analysis of event-related potentials resulting from the passive viewing of these point-light displays (PLDs) indicated a larger positive amplitude over parietal channels between 300 and 700 ms for observing biomechanically impossible PLDs when compared with other conditions. An early negative activation over frontal channels between 200 and 350 ms dissociated schematically impossible PLDs from other conditions. These results show that in infants, different cognitive systems underlie the processing of structural and dynamic features by 8 months of age.**

**Keywords:** infants; Event related potentials; biological motion; body schema; parietal cortex; frontal cortex

Humans have an early capacity to detect biological motion (Bertenthal *et al.*, 1987). This is shown by a preference to attend to biological motion over other forms of motion, such as drifting dots (Bertenthal, 1993). However, no work exists that investigates the development of neural systems involved in processing differences in the biomechanical structure underlying the biological motion. One such distinction is the detection of biological motion and infants' sensitivity for disruption of typical human body schema.

Much behavioural research has been conducted on infants' perception of biological motion (see Bertenthal, 1993, for a review). This work has shown early sensitivities in humans to biological aspects of movement. For example, 3- and 5-month-old infants discriminate point-light displays (PLDs) of human movement from ones in which the temporal patterning of the lights are perturbed, even when the perturbation includes the same mathematical translations as undisrupted PLDs (Proffitt and Bertenthal, 1990). It is thus not simply an issue of the amount of movement that allows infants to discriminate biological from non-biological movement. Rather, the movement within the PLD conveys information that suggests coherent underlying schematic representations.

Developing neural mechanisms associated with the perception of biological motion have been previously investigated. One study utilizing event related potential (ERP) techniques found that 8-month-old infants process biological motion in parietal regions of the brain when contrasted with scrambled motion (Hirai and Hiraki, 2005). These authors found differences between conditions from 100 ms after presentation. This effect was later confirmed in an ERP study where upright and inverted biological motion PLDs of walking and kicking were presented to infants (Reid *et al.*, 2006), indicating that the preference of 4–6-month-old-infants to upright PLDs found by Fox and McDaniel's (1982) may be related to activation in parietal networks.

In contrast to developmental research, much neuroimaging work has focussed on adult processing of biological motion. Work with event-related potentials and source analysis has indicated an early processing network of right posterior extrastriate cortex (Jokisch *et al.*, 2005; Thierry *et al.*, 2006). fMRI studies indicate a more complex picture, with parietal, posterior fusiform gyrus and inferior temporal areas involved (Wheaton *et al.*, 2004; Peelen *et al.*, 2006).

In isolation to biological motion research, work has investigated infant processing of human body structure. Gliga and Dehaene-Lambertz (2005) found in their ERP study that infants by 3 months detect distortions in human body configuration. These authors found a reduction in a P400-like component in bilateral posterior regions for static images of distorted bodies and faces. Behavioural work by Slaughter *et al.* (2002), indicated that infants did not differentiate between corrupted and normal static images of body schema until 18 months of age. In later work (Heron and Slaughter, 2004), when movement was added to the human bodies, infants at 9 months differentiated corrupted and normal human body schema. This suggests that

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movement assists the detection of the parameters of the human body, together with its biomechanical constraints.

The neural basis of the perception of body schema in adults has also been investigated in studies utilizing fMRI. One study found that those aspects of their paradigm indexing body schema activated the inferior parietal cortex and the insula (Chaminade *et al.*, 2005). In their task, the participant had to move the same limb as seen on a computer screen. During this activity, Chaminade *et al.* (2005) also found activation in ventromedial prefrontal cortex. Other work has also indicated that anterior regions are involved in body schema processing. McCrea (2007) found that the right superior frontal gyrus was activated when participants were required to identify images of body parts in a viewed image. In contrast to identification tasks, the left inferior frontal lobe has been implicated in processing the specific content of biological motion, such as hand actions (Baumgaertner *et al.*, 2007). Dorsolateral frontal regions have also been implicated in the failure of stroke patients to identify body posture (Schwoebel and Branch Coslett, 2005). The evidence therefore suggests that frontal regions are involved in the detection and processing of human body shape.

In order to further understand the neural mechanisms related to the perception of PLDs during infancy, the current experiment investigates ERPs associated with the task of observing PLDs of human movement which have been modified in some conditions to display biomechanically impossible movement or to contain biomechanically possible movement delivered via a corrupted nonhuman schema. Through manipulating human movement to create a nonhuman biological motion, we can investigate the developing sense of canonical body structure for the first time at the neural level. Such an approach is suggested by the results of Heron and Slaughter (2004), where dynamic information lowered the age from 18 to 9 months at which infants discriminated schematically possible from impossible human body configurations. Based on previous research (e.g. Hirai and Hiraki, 2005), we hypothesized that the perception of biological facets of the stimuli would manifest themselves in a parietal location with an increase in positivity for the biological motion compared to the biomechanically impossible motion. In addition, to further investigate infant perceptual processing of movement, we presented infants with stimuli that were biologically possible in their movement but contained a corrupted human body schema. Based on adult research (e.g. Chaminade *et al.*, 2005) should infants discriminate normal human from nonhuman corrupted body schema, we predict differential processing in parietal and frontal regions.

## MATERIALS AND METHODS

### Participants

Fifteen infants (10 males and 5 females) were tested, with an average age of 8 months ± 12 days. All infants were born full term (37–41 weeks) and were in the normal range of birth weight. Another 40 infants were tested but were excluded from the final sample as a result of fussiness ($n = 12$), or failing to reach the minimum requirements for adequate averaging of the ERP data ($n = 28$). This relatively high attrition rate was due to three experimental conditions in the present study when compared to the standard two conditions in most infant ERP studies (see de Haan, 2007 on how the number of conditions are constrained in infant EEG/ERP research). The minimum criteria for inclusion was 10 trials per condition, however, each infant contributed 31–76 (mean of 40.7) trials to their average across conditions, leading to a mean of 13.6 trials per condition. This experiment was conducted with the understanding and the written consent of each participant's parent.

### Stimuli

Two videos of a male actor were produced using a digital video camcorder. The video was transferred to the software Quicktime (5.0) where individual frames were extracted from the video. The frames were individually modified in Photoshop so that joints were depicted as white squares. All other aspects of the image were removed and replaced by a black background. There were 15 points of light in total, comprising the spatial locations for toes (two), ankles (two), knees (two), hips (two) elbows (two), hands (two), shoulders (two) and nose (one). One sequence featured a PLD of kicking, whereas the other depicted walking, translating from right to left (see Figure 1, top). These stimuli were modified twice: once to create biomechanically impossible movement and once to create biologically possible human movement with corrupted underlying body schema. All stimuli were matched for overall movement, as assessed by the number of white pixels utilised across time over the black background.

For the creation of biomechanically impossible motion, frame-by-frame alterations of video of human movement were modified in Adobe Photoshop (7.0) whereby the kicking PLD was transformed into an impossible biological movement by rotating the knee, ankle and toe of the kicking leg 360° in proportional time with the kicking action. The end perceptual result was a PLD of the human form where the leg appeared to detach, spin around in a circle and reattach to the leg during the course of a kicking movement (see Figure 1, bottom left). Overall this produced a percept of a biologically possible person performing a biomechanically impossible movement with their leg. This particular manipulation, we reasoned, produced an action that was matched in movement parameters to the normal kicking action while displaying impossible biological activity.

In order to create coherent biological motion with altered underlying body schema, the stimuli depicting walking were also altered from video, frame-by-frame, utilising Adobe Photoshop (7.0). The dots for the knee joints were modified so that they circumflexed backwards rather than forwards

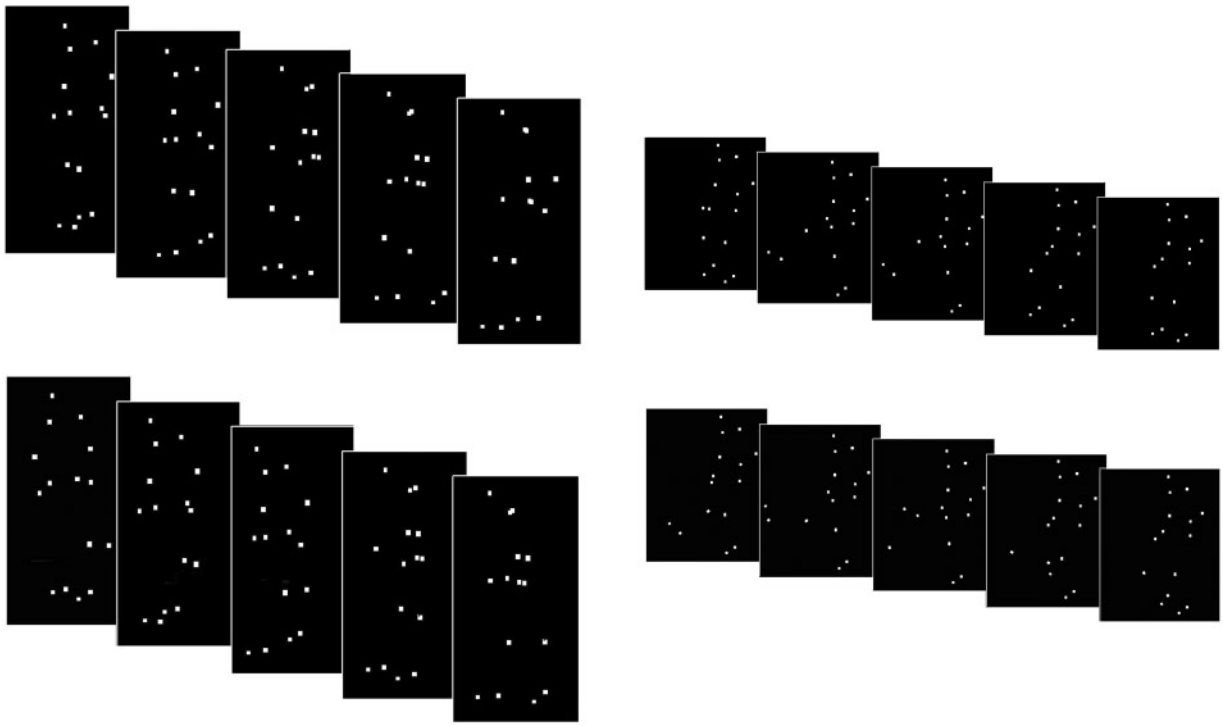

**Fig. 1** Top left: Point-light display stimuli depicting normal walking biological motion. Bottom left: PLD stimuli displaying biologically possible motion with a schematically impossible representation of the human form with the knees shifted to circumflex backwards. Top right: PLD stimuli depicting normal kicking biological motion. The first and last frames are the same between the possible and impossible stimuli. Bottom right: PLD stimuli depicting impossible biomechanical motion.

during the walking motion. The perceptual result was structurally coherent biological motion containing legs that appeared to belong to the rear of a horse, analogous to the body schema of the mythical race fawns and the Roman god Pan (see Figure 1, bottom right). This manipulation, we reasoned, created normal biological motion but with an incorrect body schema for a human agent.

In summary, we created three conditions. These were (i) biomechanically impossible motion (a kicking action), (ii) biologically possible motion with corrupted body schema (a walking action) and (iii) biologically possible motion. This last condition was based on both kicking and walking PLDs. We chose these two sets of stimuli and analysed them as one condition as no differences were found between ERP responses at any location to either action by Reid *et al.* (2006). In their study, both sets produced greater positivity in parietal sites when displayed upright and when compared with inverted presentation. In merging the results of these two forms of action, we hoped to gain a clearer measure of biological motion that indexed this form of motion inherent in both manipulated conditions. No impossible walking stimuli were presented, or corrupted body schema stimuli involving kicking.

In order to confirm the content of the modified stimuli, the stimuli were also displayed to 40 adults (mean age 24.3) who were not briefed as to the content of the stimuli and did not know the nature of the study. They were asked to verbally identify the content of the movie. An experimenter noted each response. Ninety-eight percent of adults identified the walking and kicking PLDs as those actions with one adult failing to identify the kicking action as a kicking action. Ninety-two percent described the biologically impossible PLD as a kicking action that was impossible. Common phrases included: 'The leg is coming off and flipping', and 'It's a person kicking, but it's all wrong'. Ninety-four percent described the schematically corrupted PLD as a walking non-human with a human upper body. Common statements included: 'It's a person walking but the legs are not human', or 'This is someone walking but the legs are not right'.

## Procedure

Infants sat on their mother's lap in a dimly lit sound-attenuated and electrically-shielded cabin, at a viewing distance of 90 cm away from a 70 Hz 17-in. stimulus monitor. The stimuli were presented at 16 by 13 cm and were thus 8.26° of visual angle. The experiment consisted of one block with 198 trials (66 biologically possible, 66 biomechanically impossible and 66 schematically impossible).

The three conditions were presented to the infant utilizing the software ERTS (BeriSoft Corporation, Germany) in a random order with the constraint that the same condition was not presented three times consecutively and that the number of presentations of each set of stimuli was balanced in every 22 clips presented. Each clip lasted 1 s in total. Each trial was preceded by a small triangular fixation object presented in the middle of the screen for 500 ms. Between the presentation of the stimuli, the screen was blank for a random period of between 800 and 1000 ms. If the infant became fussy or

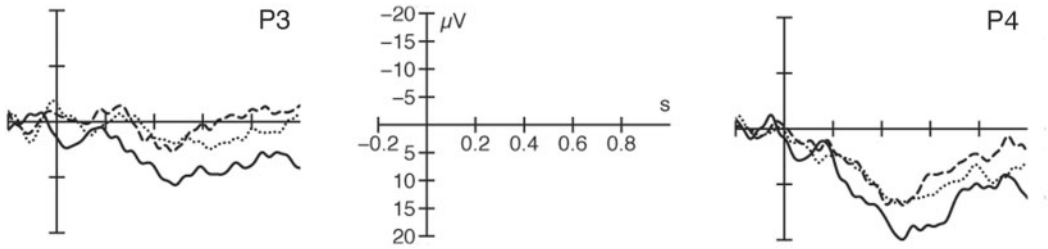


**Fig. 2** Parietal electrodes displaying the effect of increased positive amplitude in the stimuli depicting biologically impossible motion when compared with biologically possible motion and biologically possible motion with corrupted body schema, from 300 to 700 ms. Note that the 200 ms baseline consists of 100 ms of baseline and 100 ms of PLD. Key: dashes = biologically possible; black = biologically impossible; dots = biologically possible with corrupted body schema.

uninterested in the stimuli, the experimenter gave the infant a short break. The session ended when the infant's attention could no longer be attracted to the screen. EEG was recorded continuously and the behaviour of the infants was also video-recorded throughout the session for offline trial-by-trial editing of the EEG to ensure that the infant was looking at the screen for all included trials.

### EEG recording and analysis

EEG was recorded continuously with Ag-AgCl electrodes from 23 scalp locations of the 10–20 system, referenced to the vertex (Cz). Data were amplified via a Twente Medical Systems 32-channel REFA amplifier. Horizontal and vertical electrooculargram were recorded bipolarly. Sampling rate was set at 250 Hz. EEG data were baseline corrected and re-referenced offline to the linked mastoids. Data were filtered with high and low-pass filters from 0.1 to 35 Hz.

The EEG recordings were segmented into epochs of waveform that comprised a 100 ms period of a triangular central fixation object and 1100 ms of PLD. The baseline was selected to include 100 ms of the central fixation object and 100 ms of the PLD as movement within the first 100 ms was not detectable across all conditions. This ensured that differences in the ERP were due to factors associated with motion rather than a reaction to observed differences between the conditions in the initial configuration of the point lights. For the elimination of electrical artefacts caused by eye and body movements, EEG data were rejected off-line whenever the s.d. within a 200 ms gliding window exceeded 80 μV at any electrode. Data were also visually edited offline for artefacts.

For statistical analysis a time window was chosen in parietal regions (P3, P4) around the amplitude peak of the effect from 300–700 ms after stimulus onset. For assessment of differences in frontal electrodes, we considered the mean amplitude in the three conditions from 200–350 ms after stimulus onset. Variances of ERPs were analysed in an ANOVA with three within-subject conditions: biomechanically possible PLDs (human); biomechanically impossible PLDs (human); and biomechanically impossible PLDs (nonhuman).

## RESULTS

We assessed the ERP difference in normal biological motion, biomechanically impossible motion and possible biological motion with corrupted body schema by considering the mean amplitude in the three conditions. Analysis was performed over parietal regions as previous research with infants has suggested that this location may be related to the processing of biological information (Hirai and Hiraki, 2005; Reid *et al.*, 2006). Furthermore, analyses were conducted on frontal channels based on findings from adult neuroimaging research. The grand average did not indicate significant effects at any other sites.

The analysis of mean amplitude in the parietal area from 300-700 ms indicated that there was a main effect of condition, $F(2,28) = 3.535$, $P = 0.043$. Follow up paired-samples *t*-tests comparing conditions indicated that the effect was primarily due to significant differences between biologically possible and biomechanically impossible PLDs, $t(14) = 2.312$, $P = 0.036$, reflecting a greater positivity in parietal regions for biomechanically impossible PLDs ($M = 13.35$ microvolts, SE 2.85) than for possible PLDs ($M = 6.28$ microvolts, SE 2.57); see Figure 2. A statistical trend was also found indicating differences between biologically possible but schematically corrupted PLDs and impossible PLDs, $t(14) = 1.803$, $P = 0.093$, reflecting a trend towards greater positivity in parietal regions for biomechanically impossible PLDs (*M* and SE as above) than for biologically possible PLDs with corrupted schematics ($M = 7.04$ μV, SE 2.69).

For frontal regions, a time window was chosen around the peak of a clearly defined component from 200–350 ms after stimulus onset (shown as 100–250 ms after the zero point in Figure 3 due to the inclusion of 100 ms of PLD in the baseline epoch). ERPs were evaluated statistically by assessing the following frontal and central channels: F7, F3, Fz, F4, F8, FC3, FC4, C3, Cz and C4.

The results of the ANOVA indicated that there was a main effect of condition, $F(2,28) = 5.517$, $P = 0.01$. Follow up paired-samples t-tests comparing conditions indicated that the effect was a result of significant differences between schematically corrupted PLDs and the other two conditions, namely biologically possible and biomechanically impossible motion. The paired samples *t*-tests displayed the following results: schematically corrupted PLDs *vs* biologically possible PLDs, $t(14) = 2.142$, $P = 0.05$; schematically corrupted PLDs*vs* biomechanically impossible PLDs,

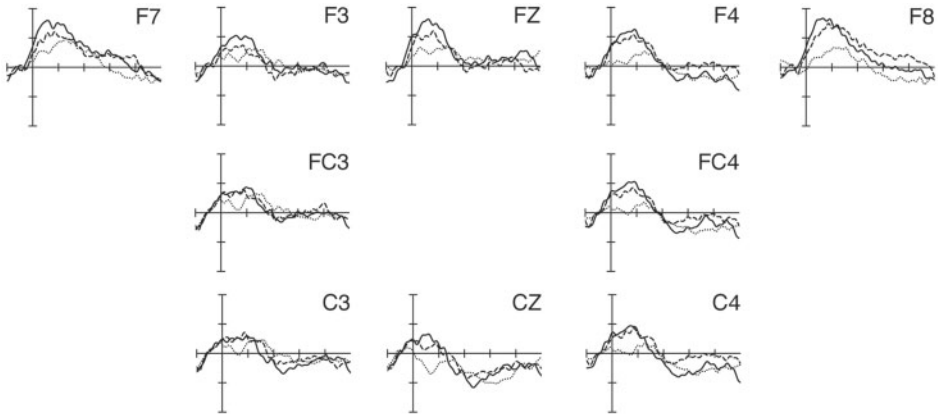


**Fig. 3** The ERP at frontal and central electrode sites displaying the effect of decreased negative amplitude in the stimuli depicting biologically possible motion with corrupted body schema when compared with biologically possible motion and biologically impossible motion, from 100–250 ms post baseline. Note that the 200 ms baseline consists of 100 ms of baseline and 100ms of PLD. Key: dashes = biologically possible; black = biologically impossible; dots = biologically possible with corrupted body schema.

$t(14) = -2.735$, $P = 0.016$. This analysis reflected a reduced negativity in frontal regions for schematically corrupted PLDs ($M = -2.72\,\mu V$, SE 2.07) than for possible PLDs ($M = -7.67\,\mu V$, SE 3.21) and biomechanically impossible PLDs ($M = -9.95\,\mu V$, SE 2.93); see Figure 3.

No other effects were evident at any scalp location at any time.

## DISCUSSION

We investigated the neural mechanisms in infancy associated with the perception of possible biological motion and biomechanically impossible motion. We also assessed infant processing of normal and corrupted human body schema. The present experiment found that parietal regions were involved in the perception of biological aspects of the stimuli. Frontal activity dissociated corrupted human body schema from biomechanically impossible biological motion and normal biological motion, suggesting infant sensitivity to schematic information within motion that is mediated by frontal systems.

The bilateral parietal activity is consistent with prior research into the perceptual parameters of biological motion discrimination. This study effectively replicates the amplitude effects seen for normal, upright biological motion in Reid *et al.* (2006) in the right hemisphere. Additionally, the increased bilateral parietal positive amplitude component for biomechanically impossible stimuli found in the present experiment suggests that infants at this age discriminate the biologically possible from biomechanically impossible motion. However, it is of interest that the effect in the current study was located bilaterally as indicated by the grand average ERP, rather than to the right parietal hemisphere. Research into the perception of PLDs with adults has previously indicated a right hemisphere bias (Wheaton *et al.*, 2001; Jokisch *et al.*, 2005). One possibility is that the neural mechanisms in infants for the perception of the biological nature of movement in a PLD have not yet matured to the point where the focus of neural activation is specific to the right hemisphere. However, this explanation does not sit well with previous work suggesting a right hemisphere location during the perception of biological motion in infants (Hirai and Hiraki, 2005; Reid *et al.*, 2006). An alternative explanation is that the current study contains stimuli with a more subtle manipulation of only a few points in the scene (e.g. the knee points) whereas manipulations in previous studies modified the entire scene. Due to the complexity of the manipulations in the present study, they may require more sustained processing when compared with previous tasks. This in turn may be indexed as bilateral parietal activation, where additional visuospatial resources are recruited to process the fundamental differences between conditions. Such a hypothesis has support from fMRI studies that indicate bilateral activations in posterior regions when dealing with complex visual information containing biological motion (e.g. Peelen *et al.*, 2006).

The finding of frontal effects associated with the perception of corrupted schematics of the human body relative to normal and impossible human movement have implications for our understanding of infant perceptual processes. The corruption to human body schema in this experiment follows similar corruptions used by Slaughter *et al.* (2002), where alterations were made to body schema without disrupting the location of the trunk and other fundamental constructs of the human body. These authors did not find differences in infant looking between corrupted and normal static images of body schema until 18 months of age. Our data suggest that infants at 8 months do discriminate normal from corrupted body schema. However, there is a fundamental difference between the present study and those of Slaughter *et al.* (2002). We presented dynamic stimuli rather than static images. Heron and Slaughter (2004) presented dynamic stimuli and found that infants at 9 months could disambiguate their stimuli. Therefore the dynamic factor most likely emphasised the biomechanical construct of

the represented agent. In doing so, this may highlight to infants the biomechanical components of the agent and thus provide grounds for discrimination of normal and corrupted schema.

The finding of dissociations between the perception of normal and corrupted body schema are in line with the results of Gliga and Dehaene-Lambertz (2005) who investigated infant structural encoding of human bodies. These authors found via ERP techniques that infants by 3 months are capable of perceptually discriminating distortions in human body configuration. The present study suggests a similar sensitivity by at least 8 months of age. The current study, however, did not find similar electrophysiological effects in terms of topography and latency to those of Gliga and Dehaene-Lambertz (2005), despite results suggesting similar cognitive processing. This is most likely due to (i) their use of static images whereas the present study utilized dynamic stimuli and (ii) the difference in location of the electrical reference between the two studies.

A fundamental question that arises from the results of the present study is whether there is any significance to the frontal topography of the differences found between normal and corrupted (nonhuman but biomechanically possible) schema. The functional implications of the frontal effect include the possibility that this particular task involves skill learning on the part of the infant (Johnson, 2001). As the observation of others is a component of the social world that is learned, it is possible that infants at 8 months are in the process of learning about body schema. Various studies have indicated that frontal regions are employed during skill learning in adults. For example, novice chess players display frontal activity during chess games, but highly experienced players process chess problems by using more posterior regions of the brain (Amidzic *et al.*, 2001). An alternative explanation for the frontal activity is that it is similar to the frontal effects found by Chaminade *et al.* (2005), where they interpreted this in terms of the feeling of 'rightness' of a response or a perception. One final possibility is that the infants may perceive the PLDs depicting corrupted schema as 'nonhuman'. As frontal regions have been implicated in tasks that involve large amounts of social-cognitive information (e.g. Grossmann *et al.*, 2007; Sabbagh and Flynn, 2007), the perception of 'nonhuman-ness' may lead to reduced negativity in frontal regions relative to the two 'human' PLD conditions.

The early latency of the difference in ERP amplitude between conditions in frontal regions can be interpreted in relation to previous research where the identification of human movement is highly rapid. For example, Johansson (1973) found that when naïve adults were presented with a PLD for 200 ms, they reported the perception of a walking human. In a study comparing typical and atypical samples of children and adolescents, when presented with 120 ms of a PLD, more than half the subjects identified human movement from object movement (Moore *et al.*, 1995). This was despite the sequence of presented stimuli corresponding to only three frames presented at 25 frames per second. It is therefore reasonable to assume that differences seen in the present study between PLDs depicting corrupted body schema and PLDs of normal body schema should be produced by the infant brain from 200 to 350 ms. Methodologically, frontal peaks are found at a similar latency in adults in studies that have utilized dynamic visual stimuli (e.g. Wu and Coulson, 2005) although no such frontal peaks were detected in infant research utilizing dynamic stimuli (Hirai and Hiraki, 2005; Reid *et al.*, 2006). When combined, the behavioural and ERP data thus far suggest that the effects seen in frontal regions are related to the identification of differences seen between PLDs of schematically corrupted and normal human movement.

This study raises issues associated with the developmental time course for perceiving and interpreting human movement. It is not possible to conclude from this study when in development those skills associated with the perception of *specifically human* biological motion begin to be evidenced. At this stage it is entirely possible that there is dissociation at some age earlier than 8 months between the ability to detect biomechanically possible motion derived from schematically nonhuman body and the ability to detect biologically impossible motion produced by an intact human schema. More advanced models of infant social-cognitive processing need to be developed (e.g. Reid and Striano, 2007). Such models will allow predictions to be made on the appropriate ages where social skills will be acquired. In this sense, these models are akin to models of social cognition that have been produced within the cognitive neurosciences (e.g. Satpute and Lieberman, 2006). Once a robust understanding of the parameters of social development exists, predictions can be made about the developing infant's ability to determine the nature and meaning of different variables present in biological motion.

In summary, the results of this study demonstrate that for human infants, parietal regions are involved in the detection and assessment of motion, including its biological nature. Frontal activity was found relating to the detection of biological motion containing corrupted human body schematics. The present data suggest that infants by 8 months are capable of detecting and discriminating possible from biomechanically impossible motion and that they are sensitive to at least some components of the schematic construction of represented agents. This study should allow a more complete understanding of how visual systems are utilized for processing complex stimuli, above all on how the developing system utilizes and interprets rich visual information.

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