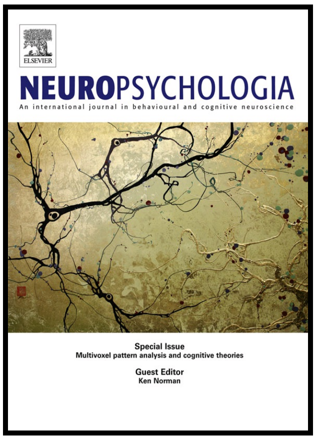
Links between action perception and action production in 10-week-old infants

Vincent M. Reid, Katharina Kaduk, Judith Lunn



www.elsevier.com/locate/neuropsychologia

PII: S0028-3932(17)30418-9
DOI: https://doi.org/10.1016/j.neuropsychologia.2017.11.005
Reference: NSY6561

To appear in: *Neuropsychologia*

Received date: 16 November 2016
Revised date: 6 October 2017
Accepted date: 3 November 2017

Cite this article as: Vincent M. Reid, Katharina Kaduk and Judith Lunn, Links between action perception and action production in 10-week-old infants, *Neuropsychologia,* https://doi.org/10.1016/j.neuropsychologia.2017.11.005

Links between action perception and action production in 10-week-old infants

Vincent M. Reid*, Katharina Kaduk, Judith Lunn
Department of Psychology, Lancaster University, UK
*Correspondence to:Department of Psychology, Lancaster University, Fylde College, Bailrigg, Lancaster LA1 4YF, England. Tel.: +44 (0)1524592915. v.reid@lancaster.ac.uk

Abstract

In order to understand how experience of an action alters functional brain responses to visual information, we examined the effects of reflex walking on how 10-week-old infants processed biological motion. We gave experience of the reflex walk to half the participants, and did not give this experience to the other half of the sample. The participant's electrical brain activity in response to viewing upright and inverted walking and crawling movements indicated the detection of biological motion only for that group which experience the reflex walk, as evidenced by parietal electrode greater positivity for the upright than the inverted condition. This effect was observed only for the walking stimuli. This study suggests that parietal regions are associated with the perception of biological motion even at 9-11 weeks. Further, this result strongly suggests that experience refines the perception of biological motion and that at 10 weeks of age, the link between action perception and action production is tightly woven.

Keywords
Infant, social cognition; Biological motion; ERPs, effects of experience

1.0 Introduction

Humans interact with the social environment from birth. It is therefore surprising that the understanding of the development of social abilities is still highly limited, including those relationships between action perception and action production. How infants process goals and intentions has become key to action perception and action production research (Longo & Bertenthal, 2006; Hauf & Prinz, 2005). Recent work, however, on the perception of biological motion has opened the possibility of investigating action perception-production relations in very young infants without the need for infants to understand goals or to produce imitative behaviours.

A large literature suggests that infants first must acquire a specific level of reasoning about their own actions in order to be able to understand the actions of others. Further, infants do so by analogy to self-produced actions (e.g. Barresi & Moore, 1996; Meltzoff, 1995; Tomasello, 1995, 1999). Despite these claims, only one study has investigated such issues in infants younger than 6 months of age. Sommerville, Woodward, and Needham (2005) provided experience of object contact for 3-month-old infants by providing them with 'sticky mittens' that allowed object engagement during a developmental period far earlier than would normally occur naturally. It was found that only those infants who were given the prior experience of object contact were able to focus on the relation between an experimenter and her object-directed goal during a subsequent habituation task. Control infants, who did not have the experience with sticky mittens, did not process the difference in stimuli when the observed object directed goal was modified.

However, the issue of influence of action production on action perception can be addressed without requiring the infant to discriminate others' goals. Intentional action is a highly complex form of movement (Elsner, 2007). By investigating the role of action experience in the perception of biological motion (BM), we can examine this issue at an earlier age in development which reduces the number of complex processes that are involved in the task. This allows us to index a more ‘pure’ relationship between perception and production – without the need for the infant to detect goals.

Behavioural research dating from the 1980s using point-light displays (PLDs; where points of light are superimposed on key joints of an otherwise unseen figure), suggests that infants detect biological motion and discriminate it from other forms of motion, such as drifting dots, from 3-4 months of age (Bertenthal, 1993). However, Simion, Regolin and Bulf (2008) demonstrated that two-day-old infants were capable of distinguishing a BM stimulus from random motion. Critically, in an additional experiment, these authors showed that the infants had a sensitivity to upright over inverted presentations of BM. Previous work has shown that inversion of BM severely disrupts the perceived biological nature of the stimuli in adults, with the recent suggestion that the basis for this orientation preference may be associated with characteristic motion patterns of the feet (Troje & Westhoff, 2006). The conclusion of Simion et al. (2008), that the detection of BM is an inborn component of the visual system, stands in stark contrast to the earlier work that had indicated sensitivity for biological motion only from 3-4 months of age (e.g., Fox & McDaniel, 1982; Bertenthal, Proffitt, Kramer, & Spetner, 1987; Bertenthal, Proffitt, & Cutting, 1984).

In relative isolation from BM research, developmental research involving the assessment of electrophysiological brain responses has proved to be a valuable source of novel insights into cognitive and perceptual processing during early development (see e.g. Stets, Stahl & Reid, 2012, for a review). Investigating neural correlates related to the perception of external events can yield knowledge on information processing even in the absence of an overt behavioural response by the participant. To date, relatively few studies have investigated the neural correlates of BM processing in infants (Hirai & Hiraki, 2005; Marshall & Shipley, 2009; Reid, Hoehl, & Striano, 2006; Reid, Hoehl, Landt & Striano, 2008). In one event-related potential (ERP) study (Hirai & Hiraki, 2005), the differential neural response to upright BM and scrambled motion (SM) in 8-month-old infants suggested that the averaged amplitude for BM between 200-300 ms was significantly larger than that for SM in these infants and in adults. Further, this activity was detected on right parietal electrodes, in a fashion similar to that seen in adults during the processing of biological motion. Another ERP study examining 8-month-old infants' processing of upright and inverted PLDs depicting human movement (Reid et al., 2006; replicated in Reid et al., 2008) found that upright compared with inverted motion elicited a greater right posterior amplitude in the infants' ERPs, suggesting differential processing of these conditions. Similar effects were found by Marshall and Shipley (2009) in bilateral posterior locations in 5-month-old infants. This suggests that earlier ages are capable of differentiating different forms of motion as measured by ERPs, but with more diffuse neural correlates than at older ages.

Thus far the focus of this introduction has been on ERP studies with infants related to the perception of biological motion. Even though there are relatively few of these studies, there has been a wealth of research investigating neural mechanisms related to biological motion production during development in humans (MEG Mu frequency analysis - Berchicci et al., 2011) and how this may relate to action observation in primate infants (EEG Mu frequency analysis - Ferrari et al., 2012; Vanderwert et al., 2015). The Mu frequency in particular has also been explored in a number of studies to examine relationships between action perception and production (e.g., van Elk, van Schie, Hunnius, Vesper & Bekkering, 2008; Reid, Striano & Iacoboni, 2011).

It is difficult to relate frequency based literature to the current study due to the differences in methods involved. ERPs typically require a number of presentations of the stimulus, with the presentation tightly timelocked to the EEG. This allows for the examination of time course dynamics related to the processing of the stimulus. EEG frequency based studies do not require such precise timing. The dynamics related to time are not relevant for the majority of frequency studies related to action perception and/or action production (e.g., Reid, Striano & Iacoboni, 2011). It is therefore difficult to relate ERP-based studies to EEG studies investigating frequency. Similar putative mechanisms may be present in an ERP analysis of data and in a frequency assessment of the same dataset (e.g., ERP: Striano, Reid & Hoehl, 2006, frequency: Hoehl, Michel, Reid, Parise & Striano, 2014) but the relationship between the two different approaches to understanding perceptual and cognitive systems is not always clear. Despite this, some associations can be made. One key study by Gerson, Bekkering and Hunnius (2015) utilized an EEG approach to examine relationships between action perception and action production during early development. Infants at 10 months of age received a short period of training over a number of days that was related to a specific novel action that resulted in a sound. The infants also observed a novel action that resulted in a sound. An assessment of the 6-9Hz band was conducted with the infants during the presentations of the sounds from the two conditions. Gerson and colleagues (2015) found that there was suppression of this frequency band for the sound that was present for the active action condition and this was not present for the observation condition. Further, the amount of suppression was correlated with the amount of motor learning during the training phase. Via this innovative paradigm, this study shows that relationships between action perception and action production exist and that this is manifested in the motor systems of the infant at 10 months of age.

The present study investigates the behavioural and neural correlates of action perception and action production in 10-week-old human infants. We will first provide the experience of walking via the walking reflex with one group whereas the other group will experience a control activity. We will then index the familiarity of these actions by assessing posterior ERP activity in order to investigate the effects of walking experience on the perception of walking movements. In so doing, we will investigate possible mechanisms via which action perception and action production are interrelated at a perceptual level. The Directed Attention Model (Reid & Striano, 2006) suggests that infants filter extraneous information from the environment in order to process social information. Within this framework, motor experience may help to facilitate the refinement of sensory mechanisms by providing a perceptual skew to motorically aligned movements. Based on prior literature (van Elk et al., 2008, Gerson, Bekkering & Hunnius, 2015), we hypothesise that infants who have had experience of walking will produce a differential waveform between upright and inverted walking conditions in posterior scalp regions, similar to the ERP studies of infants at older ages (e.g., Reid et al., 2006). This effect has been classified as being related to the N290 component (Grossmann &

Johnson, 2007), although it likely varies as a function of age in terms of latency and morphology. We anticipate that there would be no effect or a reduced effect for the crawling stimuli, given the lack of motor experience for this form of movement. We also hypothesise that there would be little or no difference between conditions for a sample of infants with no experience of producing stepping actions. Further, the exact time-window of the N290-like component will likely be at a delayed latency when contrasted with studies featuring older infants. Latency effects for the present study are difficult to predetermine due to the extremely young sample tested in the current investigation when contrasted with prior studies. This study will also help to understand the ERP correlates of BM processing in early development, which thus far are not known.

2.0 Method

2.1 Participants

32 infants aged 9-11 weeks (mean age 10.6 weeks) participated in the study. All infants were born full term (37-41 weeks) and were in the normal range for birthweight. Following data editing we had 13 participants in the experience and 13 in the no experience groups due to too few trials for the formation of adequate individual average ERPs from 6 participants. Our a priori lower limit was 8 trials per condition, in order to be broadly in line with prior studies in this field (e.g., Reid, Hoehl & Striano, 2006). Participants contributed the following number of trials (range) per condition: Experience group: Walking upright, 13.6(10-19), Walking inverted, 13.4(9-22), Crawling upright, 12.9(8-19), Crawling inverted, 14.2(8-24); No experience group: Walking upright, 14.3(8-

.24), Walking inverted, 13.3(8-28), Crawling upright, 13.8(8-31), Crawling inverted, 13.5(8-25).

This study was approved by the Durham University Department of Psychology Ethics Committee and the study conformed to the guidelines of the Declaration of Helskini.

2.2 Procedure

This study comprised a pretest element, where walking experience was or was not given to infants, and a second component, where ERP measures related to the perception of biological movements were recorded.

Prior to taking part in the ERP component of the study, half the sample was induced to produce the stepping reflex for a period of three minutes. We conjectured that this experience may alter the perception of related BM. As the walking reflex is enhanced from 10.4 to 20.3 steps per minute at this age by submerging the legs in water (and thereby reducing leg mass; Thelen, Fisher & Ridley-Johnson, 1984), we provided a warm bath expressedly for this purpose. The bath was made to the same specifications as were used by Thelen et al. (1984), being a 32 gallon rectangular aquarium (92cm X 32cm X 45cm), with the water level rising to the middle torso. The same methodology reported in Thelen et al., (1984) was used, with the infant held under the arms and lowered into the water. Step frequency was recorded via a camera positioned outside the bath, with the step period commencing once the feet made contact with the bottom of the bath. An average of 23.25 steps occurred (SD 8.63, range 8-39). The other half of the sample, the “no experience group” also experienced the bath. However, their legs did not touch the ground and the reflex walk did not take place.

We therefore predict that the preference for walking and crawling BM in the no experience group will not be significantly different from each other. The number of steps was calculated for each infant, with “steps” defined as per Thelen, Fisher & Ridley-Johnson (1984), whereby downward pressure of the leg is applied and a translation motion from leg to leg is observed. For an example of such behaviour, see Figure 1.

All infants’ walking behaviour was coded. A second coder, who was not aware of the aims of the study, assessed the number of steps produced by nine participants. Cohen’s Kappa for reliability of the coding for the walking steps was 0.79. Once this pre-test phase was completed, two forms of biological motion depicting walking and crawling in upright and inverted positions were presented to infants in a standard ERP paradigm.

2.3 Stimuli

Half the stimuli were the same as those reported in Reid et al., (2006), where a PLD was displayed showing a human walking, translating from right to left on the screen. An additional video of a male actor was filmed using a digital video camcorder, depicting crawling movements. Individual frames were extracted from the video and were modified using Photoshop Pro 7 in order that key joints were depicted as white squares. All other aspects of the images were removed and replaced by a black background. There were 15 points of light in total for the walking and crawling stimuli sets, comprising the spatial locations for toes (2), ankles (2), knees (2), hips (2) elbows (2), hands (2), shoulders (2) and nose (1). The resultant PLD depicting crawling showed a person translating from right to left across the screen. These stimuli were presented in an upright and in an inverted plane, in order to create the upright and inverted conditions. For all stimuli, movement translated the screen from right to left.

2.4 ERP Procedure

Infants sat on their mother's lap in a dimly lit room at a viewing distance of 40 cm away from a 70Hz 19-inch stimulus monitor. The experiment consisted of one block with 200 trials (50 upright walk, 50 upright crawl, 50 inverted walk, 50 inverted crawl). Should the infant view all trials, the block looped to a further 200 trials. The four conditions were presented to the infant in a random order.

Participants viewed the following number of trials (range) per condition: Experience group: Walking upright, 37.2(20-63), Walking inverted, 36.2(17-63), Crawling upright, 37.8(21-67), Crawling inverted, 37.9(22-65); No experience group: Walking upright, 38.5(16-57), Walking inverted, 36.8(16-54), Crawling upright, 37.8(16-57), Crawling inverted, 37.5(16-57).

Each trial lasted 1 second in total. Each trial was preceded by a small triangular fixation cross presented in the middle of the screen for 500 ms. Between the presentations of the stimuli, the screen was blank for a period of between 800 ms and 1000 ms. The session ended when the infant's attention could no longer be attracted to the screen. EEG and the behaviour of the infant were recorded continuously throughout the session in order that trial by trial editing of the data could take place. This ensures that included trials were when the infant fixated the screen.

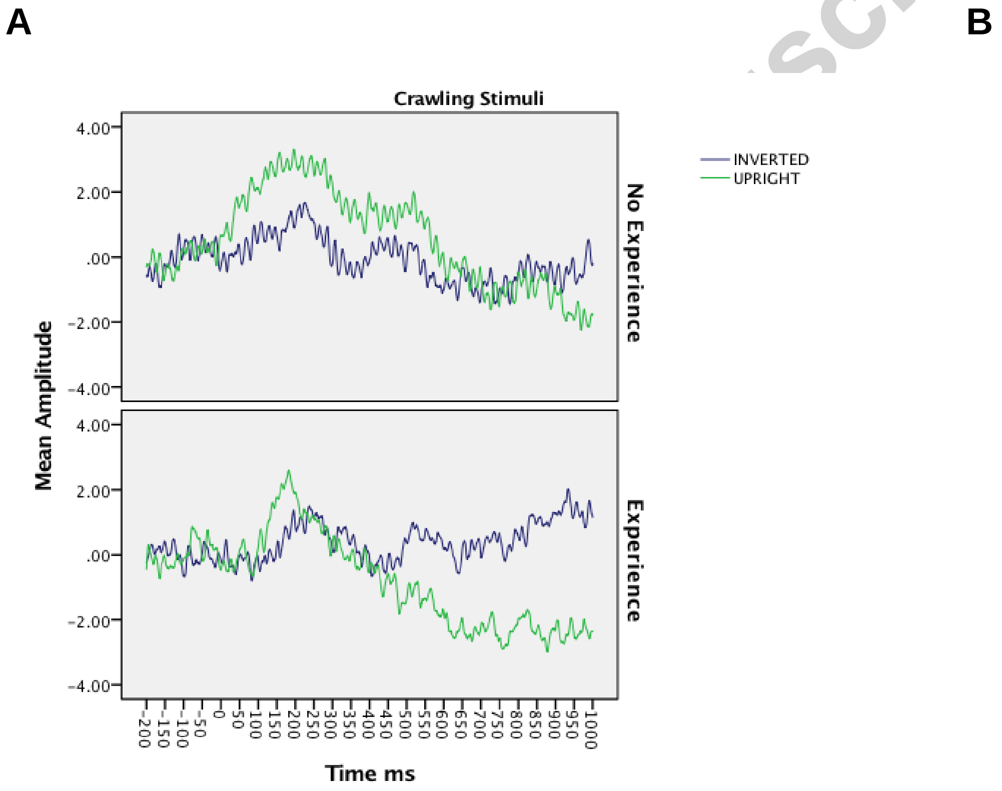
2.5 EEG Recording and Analysis

EEG was recorded continuously with Ag–AgCl electrodes from 32 scalp locations of the 10–20 system, referenced to the vertex (Cz). Data was amplified via a Neuroscan 32-channel amplifier. Horizontal and vertical electro-oculargram were recorded bipolarly. Sampling rate was set at 250 Hz. EEG data was re-referenced offline to the linked mastoids. The EEG recordings were segmented into epochs of waveform that comprised a 100 ms baseline featuring a central fixation object and 1000 ms of upright or inverted biological motion comprising walking or crawling. For the elimination of electrical artifacts caused by eye and body movements, EEG data was rejected offline by visual editing of trial by trial data. Edited data were subjected to a 0.3-30Hz bandpass filter. No channel interpolation took place due to too few electrodes in the montage.

Figure 1: Examples of experience group bath behaviour, displaying a walking reflex action (left) and the no experience group bath behaviour (right). Infants were submerged to the same degree and for the same amount of time across the two groups.

3.0 Results

Previous research with older infants suggested that effects would be present in parietal electrodes (Hirai & Hiraki, 2005, Reid, Hoehl, & Striano, 2006, Reid, Hoehl, Landt & Striano, 2008, Marshall & Shipley, 2009). An average amplitude for each 50 ms time bin from 350-550ms for each trial was calculated and analyzed in a 2 (group: experience, no experience) X 2 (motion type: walking, crawling) X 2 (orientation: upright, inverted) mixed model with participant as a random effect. The mixed linear model that we employed accounts for the variability between the 50 ms averaged epochs for each child (level 1) and estimates of the group, orientation and motion factors (level 2) taking account of this level 1 individual child variance. We did not test for mean differences between 50 ms bins as a fixed factor as this would be too difficult to interpret. Electrodes in each location were averaged together for analysis purposes. The alpha level for all pairwise comparisons was Bonferroni adjusted. The mixed model showed no significant main effects, a significant group x motion interaction $F(1,1216) = 22.77, p < 0.001$ and a significant group x motion x orientation interaction $F(1,1216) = 43.0, p < 0.001$. The Infants with experience of walking produced parietal region activity from 350ms-550ms after stimulus onset that was significantly more positive in mean amplitude for the upright walking when contrasted with the inverted walking stimuli (Upright M=1.5, 95% CI [-0.4, 3.4] Inverted M=-0.5, 95% CI [-2.4, 1.4], $p < 0.001$). Whereas, in infants who had no experience of walking the mean amplitude was significantly more positive for upright crawling contrasted with the inverted crawling stimuli (Upright M=1.4, 95% CI [-0.5, 3.2] Inverted M=-0.8, 95% CI [-2.0, 1.8], $p=0.002$). The inverse relationships were also significant. Infants in the walk experience group produced a mean amplitude more positive for inverted crawling contrasted with upright crawling (Inverted M=-0.1, 95% CI [-2.0, 1.8], Upright M=-1.2, 95% CI [-3.1, 0.7], *p=0.021*), whereas infants in the no experience group produced a mean amplitude more positive for inverted walking contrasted with upright walking (Inverted M= 0.42, 95% CI [-1.5, 2.3], Upright M= -1.47, 95% CI [-3.7, 0.4] *p < 0.001*). Figure 2 displays the parietal activity recorded in the two groups for each of the four stimuli conditions.



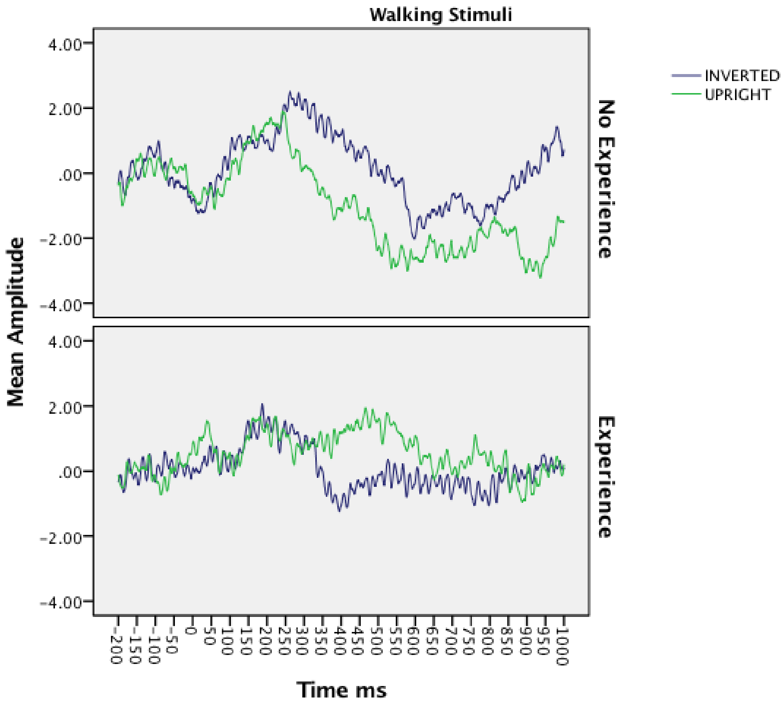


Figure 2A: Parietal electrodes for the no experience (top) and experience group (bottom) in response to the depiction of upright (green) and inverted (blue) inverted stimuli. Figure 2B: Parietal electrodes for the no experience (top) and experience group (bottom) in response to the depiction of upright (green) and inverted (blue) walking stimuli.

4.0 Discussion

This study was designed to investigate the effects of a limited amount of experience on how 10-week-old infants perceive biological motion, as measured by electrophysiological correlates. Infants participated in one of two groups, with one experiencing reflex walking prior to observing PLD stimuli of biological motion, with the other not experiencing the reflex walk prior to recording their electrophysiological response to the observation of PLD stimuli. Infants were presented with stimuli depicting walking and crawling in upright and inverted positions. Based on these ERP results, we found that only those infants who had encountered walking experience produced ERP results that were similar to effects found in older ages (Reid et al., 2006). During the perception of crawling stimuli, those infants who had no experience produced morphologies that were more similar to older ages. The group of infants with walking experience did not produce this effect. This suggests that the limited period of experience encountered prior to the ERP procedure altered the infant's perception of walking, indicating a link between action perception and action production in early infancy. This result strongly suggests that experience refines the perception of biological motion during early infancy.

Prior EEG research with infants has indicated relationships between action perception and action production in terms of motor systems (e.g., van Elk et al., 2008; Gerson, Hunnius & Bekkering, 2015). The current study indicates that the relationships extend beyond motor systems and may be indexed in fundamental perceptual mechanisms related to biological motion processing. As such, the integration and association of action perception and action production is clearly more multifaceted than has been previously reported.

Meltzoff has proposed in his 'like me' developmental framework (Meltzoff, 2005, 2007; Meltzoff & Gopnik, 1993) that infants' fundamental interpersonal relations are based on their representation of action. The 'like me' framework proposes that infants monitor their bodily acts and detect cross-modal equivalents between their own acts-as-felt and the acts-as-seen in others (Meltzoff, 2007). Drawing on imitation research, the 'like me' hypothesis requires functional action perception and action production linkages in order to function. For example, in order to imitate, infants must watch actions performed by others, use this visually provided information as a source for an action plan, and then complete the corresponding motor output by themselves. Thus, imitation taps action perception, cross-modal coordination, action production, and memory. Not only must learning actions by observation occur, but the action knowledge must be transferred to the production of ones' own actions. The range of investigated imitative behaviours thus far covers facial and body movements, as well as actions on objects, intended actions, and social goals (Meltzoff, 1995). Critically, support to date for the 'like me' hypothesis has only derived from paradigms that employ imitation. The results of the present study suggest that the 'like me' hypothesis is not restricted to imitative capacities and is related to fundamental social processing as seen in biological motion processing, as well as in goal monitoring and imitation. Specifically, the walking experience group produced ERPs to observing walking that were similar to those found for older ages, but not for crawling stimuli. The no experience group produced those effects for crawling but not for walking. The motor repertoire of the infant at ten weeks is naturally more aligned to the crawling, gross motor movement when contrasted with the walking action. The act of walking has therefore shifted the percept of biological motion for those infants who had experienced self produced stepping behaviour. Here we refer to infants at 8 months when outlining results from older ages (Hirai & Hiraki, 2005; Reid, Hoehl, & Striano, 2006; Reid, Hoehl, Landt & Striano, 2008). The experience of walking and any relationship with point light display processing was not documented in the prior literature. Therefore it should be highlighted that the link between walking experience and the perception of point light displays of walking remains unclear at this older age. It should also be noted that the "like me" hypothesis, and the newborn imitation data that act as its foundation, continue to be controversial in their own right (see, e.g., Oostenbroek et al., 2016; Meltzoff et al., 2017).

The role of the infant N290 component has been suggested to cortical processes underlying the detection of “humanness” independent of the nature of the stimulus (Grossmann & Johnson, 2007). This component, which is also that which was significantly different between conditions in the current study, suggests that this is the case. Prior work has indicated its presence in inverted compared with upright human motion (Reid et al., 2006) and inverted human faces compared with upright human faces (Halit et al., 2003). As a result of this, it has been suggested that the N290 may be driven by familiarity (Grossmann & Johnson, 2007). The results of the present study align with this notion. The walking motion was more familiar than the crawling motion for the experience group but the motor repertoire more closely matched crawling in the no experience group.

An alternative explanation is that perceptual narrowing of different aspects of biological motion have been artificially facilitated in the present study. This is similar to perceptual narrowing seen in face processing, where younger infants can individuate monkey faces from each other but older infants cannot (Pascalis, de Haan & Nelson, 2002). Therefore infants at 10 weeks detect the biological motion seen in crawling, with four limbs bearing load and locomoting, but they do not detect it as readily for walking. The opposite is true for the experience group, who have had their attention skewed to elements of the stimuli that more closely match their own motor experience.

We predicted that we would encounter an enhanced positivity that will be evident for the upright walking stimuli for those infants who had experienced reflex walking. Even though we could not claim that reflex walking is the same as walking as seen in adults, it was conjectured that any difference in ERPs would be due to the underlying schematic nature of the PLD becoming more salient for infants as a result of their experience. We predicted that this will not be the case for the upright crawl condition as no such movement had been executed by the infant. It is important to note that we are suggesting that this brief experience has altered perceptual characteristics of these infants, such that they perceive the walking motion. It is this alteration in perception that has produced these identified neural correlates. We are not claiming that the brief experience of walking has reorganized infant brain anatomy. To our knowledge, no such work has been conducted where brief experience causes rapid changes to neural architecture.

We predicted effects in parietal regions. The results confirmed the prediction. However, the effect is bilateral in nature rather than restricted to one location. This fits with Marshall and Shipley's (2009) results, where bilateral effects were found in five-month-old infants. Work with older infants has consistently pointed to effects only in right parietal electrodes (Hirai & Hiraki, 2005; Reid, Hoehl, & Striano, 2006; Reid, Hoehl, Landt & Striano, 2008). The present results are therefore congruent with Marshall and Shipley (2009) and suggest that diffuse activity is present in relation to biological motion processing during the first few postnatal months, with specialization to right regions restricted to the latter half of the first postnatal year.

4.1 Conclusion

In conclusion, the results of the present study suggest that even at 10 weeks the link between action perception and action production is present at the level of motion processing. Further, it is likely that this link is a fundamental component of the development of social information processing mechanisms. It is therefore suggested that BM processing is a foundational element of social-cognitive development upon which other elements of social cognition are built. The Directed Attention Model (Reid & Striano, 2007, Hoehl, Reid, Parise, Handl, Palumbo & Striano, 2009) may account for how these mechanisms may be evidenced throughout early development.

Acknowledgements

This research was funded by an ESRC Small Grant (Project number: RES-000-22-3277). We thank the parents and infants for taking part in this study and Manuela Stets for assistance with testing some infants.

References

Barresi, J., & Moore, C. (1996). Intentional relations and social understanding. *Behavioural & Brain Sciences, 19*(1), 107-154.
Berchicci M., Zhang T., Romero L., Peters A., Annett R., Teuscher U., et al. (2011). Development of mu rhythm in infants and preschool children. *Developmental Neuroscience*, 33, 130–143.
Bertenthal, B. I. (1993). Infants' perception of biomechanical motions: Intrinsic image and knowledge-based constraints. In C. Granrud (Ed.), *Carnegie symposium on cognition: Visual perception and cognition in infancy* (pp. 175-214). Hillsdale, NJ: Erlbaum.
Bertenthal, B. I., Proffitt, D. R., & Cutting, J. E. (1984). Infant sensitivity to figural coherence in biomechanical motions. *Journal of Experimental Child Psychology, 37*, 213-230.
Bertenthal, B. I., Proffitt, D. R., Kramer, S. J., & Spetner, N. B. (1987). Infants' encoding of kinetic displays varying in relative coherence. *Developmental Psychology, 23*, 171-178.
Cannon E. N., Yoo K. H., Vanderwert R. E., Ferrari P. F., Woodward A. L., Fox N. A. (2014). Action experience, more than observation, influences mu rhythm desynchronization. *PLoS ONE* 9:e92002.
Dannemiller, J.T. & Freedland, R.L. (1991). Detection of relative motion by human infants, *Developmental Psychology,* 27, 67–78.
Elsner, B. (2007). Infants' imitation of goal-directed actions: the role of movements and action effects. *Acta Psychologica, 124,* 44-59.

Ferrari, P.F., Vanderwert, R.E., Paukner, A., Bower, S., Suomi, S.J., Fox, N.A. (2012). Distinct EEG amplitude suppression to facial gestures as evidence for a mirror mechanism in newborn monkeys. *Journal of Cognitive Neuroscience*, 24, 1165–72.

Fox, R., & McDaniel, C. (1982). The perception of biological motion by human infants. *Science, 218*, 486-487.

Gerson, S., Bekkering, H. and Hunnius, S. (2015). Short-term motor training, but not observational training, alters neurocognitive mechanisms of action processing in infancy. *Journal of Cognitive Neuroscience* 27(6), pp. 1207-1214.

Grossmann, T. and Johnson, M.H. (2007). The development of the social brain in human infancy. *European Journal of Neuroscience*, 25, 909-919.

Halit, H., de Haan, M. & Johnson, M.H. (2003). Cortical specialisation for face processing: face-sensitive event-related potential components in 3- and 12-month-old infants. *Neuroimage*, 19, 1180–1193.

Hauf, P., & Prinz, W. (2005). The understanding of own and others' actions during infancy: “You-like-me” or “Me-like-you”? *Interaction Studies, 6:3,* 429-445.

Hirai, M., & Hiraki, K. (2005). An event-related potentials study of biological motion perception in human infants. *Brain Research. Cognitive Brain Research, 22*(2), 301-304.

Hoehl, S., Reid, V.M., Parise, E., Handl, A., Palumbo, L & Striano, T. (2009). Looking at eye gaze processing and its neural correlates in infancy – implications for social development and Autism Spectrum Disorder. *Child Development,* 80(4), 968-985.

Longo, M. R., & Bertenthal, B. I. (2006). Common Coding of observation and execution of action in 9-month-old infants. *Infancy, 10*(1), 43-59.

Marshall, P. J., & Shipley, T. F. (2009). Event-related potentials to point-light displays of human actions in 5-month-old infants. *Developmental Neuropsychology*, *34*, 368-377.

Meltzoff, A. N. (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. *Developmental Psychology, 31,* 838-850.

Meltzoff, A. N. (2005). Imitation and other minds: The “Like Me” hypothesis. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science* (2, pp. 55-77). Cambridge, MA: MIT Press.

Meltzoff, A. N. (2007). The ‘Like Me’ framework for recognizing and becoming an intentional agent. *Acta Psychologica, 124,* 26-43.

Meltzoff, A. N., & Gopnik, A. (1993). The role of imitation in understanding persons and developing a theory of mind. In S. Baron-Cohen, H. Tager-Flusberg, & D. J. Cohen (Eds.), *Understanding other minds: Perspectives from autism* (pp. 335-366). New York: Oxford University Press.

Meltzoff, A.N., Murray, L., Simpson, E., Heimann, M., Nagy, E., Nadel, J., Pedersen, E.J., Brooks, R., Messinger, D.S., de Pascalis, L., Subiaul, F., Paukner, A., Ferrari, P.F. (2017). Re-examination of Oostenbroek et al. (2016): evidence for neonatal imitation of tongue protrusion. *Developmental Science*, DOI: 10.1111/desc.12609

Oostenbroek, J., Suddendorf, T., Nielsen, M., Redshaw, J., Kennedy-Constantini, S., Davis, J., …Slaughter, V. (2016). Comprehensive longitudinal study challenges the existence of neonatal imitation in humans. *Current Biology*, 26, 1334-1338.

Pascalis, O., de Haan, M., & Nelson, C.A. (2002). Is face processing species-specific in the first year of life? Science, 296, 1321-1323.

Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology, 9*(2), 129-154.

Reid,V.M., Hoehl, S., Landt, J. & Striano, T. (2008). Human infants dissociate structural from dynamic information in biological motion: Evidence from neural systems. *Social, Cognitive and Affective Neuroscience,* 3, 161-167.

Reid, V. M., Hoehl, S., & Striano, T. (2006). The perception of biological motion by infants: an event-related potential study. *Neuroscience Letters, 395*(3), 211-214.

Reid, V.M. & Striano, T. (2008) The directed attention hypothesis of infant social cognition: Further evidence. In Striano, T., & Reid, V.M. (eds) (2008). *Social Cognition: Development, Neuroscience and Autism*. Oxford: Wiley-Blackwell.

Reid, V.M., Striano, T. & Iacoboni (2011). Neural correlates of dyadic interaction during infancy. *Developmental Cognitive Neuroscience*, 1(2), 124-130.

Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Sciences of the United States of America, 105*(2), 809-813.

Sommerville, J. A., Woodward, A. L., & Needham, A. (2005). Action experience alters 3-month-old infants' perception of others' actions. *Cognition*, 96, B1-B11.

Stets, M., Stahl., D., & Reid, V.M. (2012). A meta-analysis investigating factors underlying attrition rates in infant ERP-studies. *Developmental Neuropsychology*, 37, 226-252.

Striano, T. & Reid, V.M. (2006). Social cognition in the first year. *Trends in Cognitive Science* 10(10), 471-476.

Thelen, E., Fisher, D.M., & Ridley-Johnson, R. (1984). The relationship between physical growth and a newborn reflex. *Infant Behavior and Development,* 7, 479-493.

Tomasello, M. (1995). Joint attention as social cognition. In C. Moore & P. J. Dunham (Eds.), *Joint attention: Its origins and role in development* (pp. 103-130). Hillsdale, NJ: Lawrence Erlbaum.

Tomasello, M. (1999). Having intentions, understanding intentions, and understanding communicative intentions. In P. D. Zelazo, J. W. Astington, & D. R. Olson (Eds.), *Developing theories of intention: social understanding and self-control* (pp. 63-75). Mahwah, NJ: Erlbaum.

Troje, N.F. & Westhoff, C. (2006) The inversion effect in biological motion perception: evidence for a ‘life detector’? *Current Biology*, 16, 821–824.

Vanderwert, R., Simpson, E.A., Paukner, A., Suomi, S.J., Fox, N.A., & Ferrari, P.F. (2015). Early social experience affects neural activity to affiliative facial gestures in newborn nonhuman primates. *Developmental Neuroscience,* 37(3), 243-252.

van Elk, M., van Schie, H.T., Hunnius, S., Vesper, C. & Bekkering, H. (2008). You’ll never crawl alone: Neurophysiological evidence for experience-dependent motor resonance in infancy. *Neuroimage, 43*, 808-814.

Woodward, A. L. (1998). Infants selectively encode the goal of objects of an actor’s reach. *Cognition,* 69, 1-34.

Highlights

- Processing biological motion induces positive amplitude ERPs at 10 weeks of age
- Experience of reflex walking altered the perception of biological motion
- Action perception and action production are linked at a fundamental level