Neural correlates of the perception of goal-directed action in infants

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Abstract

We investigated the neural correlates of the perception of human goal-directed action by 8-month-old infants. Infants viewed video loops of complete and incomplete actions, which they could discriminate according to our pilot study, while we recorded their electrophysiological brain activity. Analysis of bursts of gamma-band oscillations resulting from passive viewing of these stimuli indicated increased gamma-band activity over left frontal regions when viewing incomplete actions as compared with complete actions. These results suggest that by 8 months infants are sensitive to the disruption of perceived goal-directed actions.

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1. Introduction

Human action is continuous, dynamic and complex. The ability to parse this ongoing movement into segments or units of action is vital for the interpretation of other’s intentions (Zacks et al., 2001). Whereas the work to date has addressed topics such as when in development infants detect segments within action sequences (Baldwin, Baird, Saylor, & Clark, 2001) or discriminate alterations of intentions (Woodward, 1999), investigators have yet to examine neural systems of the infant brain associated with observing action sequences.

The issue of what cues infants use to parse perceived sequences of human action has generated debate (see e.g., Baird & Baldwin, 2001) with recent research suggesting that markers of intentionality throughout human action may be critical to understanding boundaries in goal directed action (Baldwin et al., 2001). Other works also suggest that by 9 months of age, infants can understand action in terms of future goals and the efficient means to achieve these goals (Gergely, Nádasdy, Csibra, & Bíró, 1995), with this skill evident even at 6.5 months (Kamewrai, Kato, Kanda, Ishiguro, & Hiraki, 2005).

The current study seeks to illuminate infants’ perceptual abilities by examining the neural correlates of observing human action. A significant advantage of neurophysiological measurements with good temporal resolution is that they allow investigators to examine with great precision the critical time points at which infants or adults parse continuous sequences of action into chunks. Investigating the neural correlates of action perception by infants is consequently the primary goal of the current study.

2. Pilot experiment

In order to study the neural activation related to complete and incomplete goal-directed actions, we needed to know what actions would infants see as being complete and goal-directed. We presented 8-month-old infants with three types of actions in complete and incomplete versions. We measured infants’ looking times to these actions to ascertain whether their expectation was violated, and thus their looking times increased, upon observing an incomplete action.

2.1. Method

Twenty-one infants (8 males and 13 females) were tested, with an average age of 243 days. Infant’s looking times were measured while they were watching looped videoclips on a computer monitor. First, they were presented with a familiarization trial, which involved an actress seated at a table reaching for, grasping and examining a toy before replacing the toy on the table. Then they were shown six test trials in random order, in which the same actress manipulated an object, and either did or did not complete a familiar action (see Fig. 1).

The ‘pouring’ video clip showed the actress unscrewing the top of a clear glass bottle containing orange juice and then pouring some of the juice into a clear glass cup. In the ‘eating’ action the actress used a spoon to eat from a soup bowl, and in the ‘drinking’ action she drank orange juice from a clear glass. The incomplete versions of these actions differed from the complete versions in that the clip froze before completion, i.e., before liquid would have left the bottle, or before the spoon or glass would have touched the actresses lips. Following the still frame, the video was reversed to ensure a symmetric action sequence, and to ensure
that no visual jolt related to editing the video occurred at this crucial point in the film. Thus each infant was effectively seeing the same video frames, but in reverse order. To ensure similarity with incomplete films, the complete condition films were also reversed so that they reversed from the point of completion of the goal.

Test trials were terminated when the infants looked away from the monitor for at least one second, and after watching the event for at least 4 s. Looking times were measured on-line, and reliability was checked through recoding the infants’ video-taped behaviour.

2.2. Results and discussion

The looking times to the six test events are reported in Table 1. Statistical analyses (within subjects $t$-tests) were performed on log-transformed looking times. These tests indicated a reliable looking time difference between complete and incomplete actions only in the ‘pouring’ action. The failure to demonstrate discrimination within the other two action pairs does not entail that the infants did not understand the goal of eating or drinking. It is possible, for example, that infants at this age are familiar with the pretend eating and drinking actions, or that the completion of the pouring action (the transfer of

<table>
<thead>
<tr>
<th>Action</th>
<th>Looking time (s) (SE) Complete</th>
<th>Incomplete</th>
<th>$t$-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pouring</td>
<td>4.70 (1.35)</td>
<td>8.04 (1.45)</td>
<td>2.613*</td>
</tr>
<tr>
<td>Eating</td>
<td>8.66 (1.94)</td>
<td>6.46 (0.86)</td>
<td>0.101</td>
</tr>
<tr>
<td>Drinking</td>
<td>7.61 (1.53)</td>
<td>8.31 (1.55)</td>
<td>0.039</td>
</tr>
</tbody>
</table>

The asterisk indicates significant difference ($p < .05$).
substance) was more salient in our clips than the other two actions (see Onishi, Baillargeon, & Leslie, 2007, for a thorough overview of pretend actions). On the basis of this pilot study we decided to use the pouring action in our electrophysiological study.

3. EEG experiment

In adults, parsing of action sequences is partly based upon understanding the goal of the action. One study that has investigated neural activity associated with action parsing found bilateral activation in the posterior regions of the cortex (Brodmann’s areas 19/37) and in a small region in the right frontal cortex, the precentral sulcus (Zacks et al., 2001). It has also been suggested that the right Superior Temporal Sulcus (STS) is vital to the processing of human movement and action understanding (see Blakemore & Decety, 2001, for a review). Frontal regions have also been shown to play a role in taking an intentional stance towards an agent in a visual display (Gallagher, Jack, Roepstorff, & Frith, 2002).

We recorded electrophysiological activity from the scalp while infants viewed video clips containing complete and incomplete pouring actions. Gamma-band activity, and especially gamma-band event-related oscillations (EROs) in adults have been associated with top-down attentional processing and object perception (e.g., Debener, Herrmann, Kranczioch, Gembris, & Engel, 2003; Gruber & Müller, 2005; Rodriguez et al., 1999). In the infant brain, these oscillations may play a fundamental role in binding separately coded perceptual information together to form a unified percept (Csibra, Davis, Spratling, & Johnson, 2000).

Recent theories on the role of gamma-band oscillations conjecture that their function is not limited to the establishment of binding (Engel, Fries, & Singer, 2001). Rather, these authors suggest that coherence changes in the gamma frequency may be the means of grouping and selecting distributed neural elements in order to form dynamic networks with which to complete a cognitive task. More generally, this suggests that gamma oscillations may be a means by which the human brain forms new associations and retrieves stored knowledge.

3.1. Methods

3.1.1. Participants

Thirteen infants (6 females and 7 males) participated, with an average age of 242 days (range 235–254 days). All infants were born full term (37–41 weeks) and were in the normal range for birth weight (>2500 g). These infants had not previously seen the experimental stimuli and did not participate in the pilot experiment. Another 19 infants were tested but were excluded from the final sample as a result of fussiness (n = 5), failing to reach the minimum requirements for adequate averaging of the ERO data (n = 11), or technical failures (n = 3).

3.1.2. Procedure

The complete and incomplete pouring actions were presented to the infant in a random order with the constraint that the same clip was not presented three times consecutively and that the number of presentations of each set of stimuli was balanced in every 20 clips presented. Each clip lasted 8 s. Between each action, 800 ms of black screen was inserted. A train noise was present throughout each trial in order to orient the infant to the screen. The sound started anew with each trial, and was selected to be not interpretable as biolog-
ical in nature nor time-locked to any specific part of the visual stimuli. If the infant became fussy or uninterested in the stimuli, a short break was taken. The session ended when the infant’s attention could no longer be attracted to the screen. The infants’ behaviour was video-recorded throughout the session.

3.1.3. EEG recording and analysis

EEG was recorded continuously by a Geodesic Sensor Net comprising 62 channels referenced to the vertex (Tucker, 1993). A ground electrode was positioned at the rear of the head, and horizontal electrooculogram was recorded from electrodes positioned at the outer canthi of the eyes. All bioelectrical signals were recorded using Electrical Geodesics Inc. amplifiers (Eugene, OR) with an input impedance of less than 100 MΩ. The sampling rate was 250 Hz, the band pass was 0.1–100 Hz, and the gain was set to 10,000 times. A time–frequency analysis of the data was performed using a continuous wavelet transform. The detailed methods used for recording and time–frequency analysis of EEG are described in Csibra et al. (2000).

For each trial, EEG data were segmented to create an epoch from 200 ms before the difference between conditions was presented, to 1000 ms after the complete and incomplete films had diverged. Data were visually edited for artefacts offline. For each individual, if the total number of trials of data came to less than 10 trials, that individual was discarded from further analyses. Missing data from individual electrodes were interpolated, using spherical spline interpolation, provided that the interpolation did not exceed 10% of the data gained from a single trial (six electrodes from the 62 channel sensor net). Finally the data were referenced to the average before being transformed using the Morlet wavelet to investigate the frequency range from 20 to 60 Hz. After wavelet transformation, 100 ms was cut from both ends of these epochs to exclude an artefact associated with wavelet transformation. The average activation of the 100 ms before the two clips diverged served as baseline. We calculated the gamma-band EROs as the average amplitude in the 32–48 Hz frequency range, since no task-related effects were observed outside this frequency range (and within 20–60 Hz).

3.2. Results

Preliminary visual inspection of the time–frequency plots across the scalp revealed two main differences between the video clips. First, a left frontal effect was observed from 216 to 284 ms after the point where the complete and incomplete clips first deviated. Two channels close to the sites F3 and F7 on the international 10–20 system (Jasper, 1958) were selected to represent this effect and the data on them were averaged to create an aggregate measure. Second, effects over left occipital leads were observed early (72–128 ms) and late (816–880 ms) in the epoch. This site of interest corresponded to channels 32, 33 and 36 of the infant geodesic sensor net and were averaged together to create an aggregate score.

3.2.1. Frontal effects

In order to demonstrate that the effects seen in frontal regions were not accounted for by baseline differences in gamma power between conditions, we conducted a $2 \times 2$ ANOVA with epoch (baseline period, ERO) and condition (complete, incomplete) as within subject factors. The ANOVA indicated an interaction between epoch and condition, $F(1,12) = 5.95, p < 0.05$. A follow-up paired samples $t$-test indicated higher
gamma-band EROs in the incomplete than in the complete condition in the latency range of 216–284 ms, \( t(12) = 2.55, p < 0.05 \). This can be seen as a lighter region across left frontal sites in Fig. 2, which topographically displays the differences in gamma activation between the conditions within this time window. A follow-up \( t \)-test did not indicate a significant difference between conditions in the baseline period, \( t(12) = 0.97, p = 0.35 \). Other frontal effects were either more transient, could not be dissociated from potential artifacts, or occurred over single channels only.

3.2.2. Occipital effects

We conducted a similar assessment of occipital regions for the two epochs of interest as we did for frontal regions, where we performed a 2 \( \times \) 2 ANOVA with epoch (baseline period, ERO) and condition (complete, incomplete) as within subject factors. For the assessment of the early phase of gamma activation (72–128 ms), the ANOVA indicated an effect of epoch, \( F(1,12) = 19.23, p < 0.01 \) and an interaction between epoch and condition, \( F(1,12) = 14.54, p < 0.05 \). A follow up paired samples \( t \)-test indicated greater gamma activity in the complete condition relative to the incomplete condition, \( t(12) = 3.34, p < 0.01 \) (see Fig. 3, left side, for the scalp topography of the effect). In the later phase (816–880 ms) a similar ANOVA indicated an effect of epoch, \( F(1,12) = 13.98, p < 0.01 \) and a trend towards significance for the interaction between epoch and condition, \( F(1,12) = 3.24, p < 0.09 \). A follow up paired samples \( t \)-test indicated greater gamma activity in the complete condition relative to the incomplete condition, \( t(12) = 4.79, p < 0.01 \) (see Fig. 3, right side). A follow-up \( t \)-test did not indicate a significant difference between conditions in the baseline period, \( t(12) = 0.97, p = 0.35 \).

3.3. Discussion

In order to investigate neural correlates of the perception of action, we presented 8-month-old infants with video sequences that produced an increase in looking time towards
the incomplete condition in the preceding pilot study. Analysis of gamma-band EROs revealed a significant difference between the complete and incomplete action conditions over certain left frontal channels. This significant frontal difference occurred within the latency range of 216–284 ms after the two versions of the video diverged. This time window is similar to that which had previously been implicated in gamma-band oscillatory burst involving infant cognitive processes related to visual perception (Csibra et al., 2000). The direction of the difference indicated that the incomplete condition elicited greater power than did the complete condition.

There are at least two types of explanation for this effect. The first of these is based on the view that increased gamma-band activity in the incomplete condition reflects greater attention to that sequence. Müller, Gruber, and Keil (2000) suggested that an increase in induced gamma-band activity in adults might be related to task demands involving visual attention. In the present experiment, infants’ increase in looking towards the incomplete condition is consistent with an interpretation that they encountered a violation of expectation. The consequence of the expectancy violation might have been an increase in attention, which in turn may have led to the greater gamma oscillations in frontal regions.

Another potential explanation for this finding is that the infant brain attempts to continue the action despite visual cues suggesting that the action has ceased (‘‘forward mapping’’). There is considerable evidence that when adults watch videos of human action they continuously predict possible trajectories of motion (e.g., Chatterjee, Freyd, & Shiffrar, 1996; Shiffrar & Freyd, 1990, 1993), though such forward mapping has not yet been tied to greater gamma-band activation. The oscillatory brain activity in the gamma frequency band may be related to the mismatch between anticipated and perceived actions, and it is increased in situations where an action is terminated before an apparent goal is achieved.

The occipital activity that was observed in this study suggests that the visual cortex responded to the changes to the visual scene related to the pouring event. The early time period matches the onset of liquid exiting the bottle and entering the cup. The later time
period matches the cessation of liquid exiting the bottle. During both epochs, the occipital gamma-band activation was higher than during the baseline, suggesting that the infants paid close attention to this event. Additionally, gamma-band activity was stronger in the complete than in the incomplete condition, possibly indicating visual activity related to the motion stimulus of liquid flow. The pouring event was located to the right in the visual scene, and the observed effect was located in the contralateral occipital hemisphere.

This EEG study provides support for previous behavioural work indicating that infants use markers of “intentionality” to determine coherent action segments (e.g., Baldwin et al., 2001). Specifically, the increased gamma activity in the incomplete action indicates that infants were sensitive to the disruption of the intended goal of the action. Also, these data may reflect a specific increase of attention associated with the parsing of sequences of human behaviour into segments of goal-directed actions. However, the mechanisms by which intentionality is detected are still far from understood (see Rochat, 2007).

4. Conclusions

The aim of the present research was to investigate the neural correlates of parsing of human goal-directed actions by 8-month-old infants. We found that when the expected goal of an action was not achieved, infants responded with increased looking times (pilot study) and increased gamma activity to the incomplete action.

When the current electrophysiological data are considered in light of previously reported results showing that infants at 8 months do discriminate possible from impossible biological actions (Reid, Belsky, & Johnson, 2005), it appears that infants at this age may be on the cusp of adult-like perception of human action in at least some respects. At this age, a sub-set of infants with good fine motor skills are sensitive to the biological possibility or otherwise of perceived human action (see Reid et al., 2005), and the infants in the current study were sensitive to at least one goal-directed action sequence. The issue of how closely motor skills are related to the perception of action must remain open. The current study does, however, suggest that infants have a neurocognitive system for detecting goal-directed actions that is at least partially established prior to the infant’s own ability to produce the observed action. In this instance, infants at 8 months would be unable to pour liquid from a bottle into a glass, yet they appeared to discriminate complete from incomplete actions as assessed by both behavioural and neural measures.

Recent research suggests that by 8 months, infants process some aspects of biological motion in a manner similar to adults (Reid, Hoehl, & Striano, 2006). The current study also demonstrates a sensitivity by 8 months to at least some components of human goals. Importantly, the results of this study suggest that infants are capable of processing goal directed actions in the absence of the ability to perform that action themselves. This suggests that some associations are made between the infant and the actions of an adult, despite the lack of a mature system for a proprioceptive schema of the infant’s own body. Further work will determine what role, if any, gamma-band activity has in the detection of others’ goals.

Whatever the precise explanation of the neural correlates of the effect observed in our experiment, the overall finding of increased gamma-band activity in frontal regions to an incomplete action when compared with a complete action provides an important first step in neurocognitive research into the perception of human action during infancy.
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References


