The Neural Correlates of Infant and Adult Goal Prediction: Evidence for Semantic Processing Systems

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The sequential nature of action ensures that an individual can anticipate the conclusion of an observed action via the use of semantic rules. The semantic processing of language and action has been linked to the N400 component of the event-related potential (ERP). The authors developed an ERP paradigm in which infants and adults observed simple sequences of actions. In one condition the conclusion of the sequence was anticipated, whereas in the other condition the conclusion was not anticipated. Adults and infants at 9 months and 7 months were assessed via the same neural mechanisms—the N400 component and analysis of the theta frequency. Results indicated that adults and infants at 9 months produced N400-like responses when anticipating action conclusions. The infants at 7 months displayed no N400 component. Analysis of the theta frequency provided support for the relation between the N400 and semantic processing. This study suggests that infants at 9 months anticipate goals and use similar cognitive mechanisms to adults in this task. In addition, this result suggests that language processing may derive from understanding action in early development.

Keywords: action perception, semantic processing, infants, N400, theta

Observed human actions are complex and intricate streams of continuous information. As adults, we readily process and interpret this information in terms of intentions, beliefs, and desires (Decety & Grezes, 2006; Heider & Simmel, 1944). Recently, the neural basis of this ability has been investigated in adults (Zacks et al., 2001). In a previously unrelated line of research, cognitive neuroscientists have investigated the properties of language processing in the adult brain. This work has shown that specific neural responses exist for processing semantic information in sentences, with prediction of a terminal verb dependent on prior sentence content (Kutas, 1997). In order to investigate the development of

semantic processing, we developed a paradigm based on language-processing research whereby infants and adults viewed simple streams of action and were assessed in terms of a neural mechanism that has been found in adults to relate to the violation of predictions, based on prior semantic information.

It has long been known that humans tend to process actions in terms of intentions and beliefs (e.g., Heider & Simmel, 1944); however, this knowledge has not translated into an understanding of how or why transitions occur in the understanding of others throughout early development. Advances in philosophical thought by Dennett (Dennett, 1987; Griffin & Dennett, 2008) have fed through to empirical studies with infants (e.g., Csibra, 2008; Csibra, Gergely, Bíró, Koós, & Brockbank, 1999). It is now suggested that observed actions displayed in three dimensions are not thought of simply in the present tense but also in terms of future goals and desires by infants from 6.5 months of age (Kamewrai, Kato, Kanda, Ishiguro, & Hiraki, 2005), although this is not the case for stimuli depicted in two dimensions (e.g., Csibra et al., 1999).

The current level of understanding related to the development of the neural basis of social goal perception is highly limited. This is particularly the case when this knowledge is compared with the current knowledge of infant understanding of goals that has been derived from behavioral studies. For example, using a habituation technique, Woodward (1998) showed that infants are sensitive to a change in goal from 5 months of age. However, of key importance for the present study, this pattern of findings could not be replicated when infants watched unfamiliar movements, such as contact between an object and the back of the experimenter's hand (Woodward, 1999). This work shows that while infants understand

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the concept of goals during early development, the refinement of that understanding becomes more nuanced throughout the first postnatal year.

Work on the cognitive neuroscience of social development is relatively less advanced (see Grossmann & Johnson, 2007, for a review). Even though much work has been conducted on specific topics within social perception such as face- and eye-gaze processing (e.g., de Haan & Nelson, 1997), joint attention (e.g., Striano, Reid, & Hoehl, 2006; Parise, Reid, Stets, & Striano, 2008), and biological motion processing (Hirai & Hiraki, 2005; Reid, Hoehl, & Striano, 2006), only one study has investigated the infant's perception of goals (Reid, Csibra, Belsky, & Johnson, 2007). In this study, 8-month-old infants were presented with video clips showing complete and incomplete goal-directed actions (pouring liquid from a bottle into a glass). In an initial experiment, it was found that infants looked longer at the incomplete action than at the complete action, indicating a discrimination of the two actions. In a second experiment, the neural correlates of perceiving complete and incomplete actions were examined by measuring induced gamma oscillatory brain activity. The results showed a significant difference between complete and incomplete actions over left frontal channels, with an increase of gamma activity in the incomplete condition (Reid et al., 2007). These findings can be related to the detection of a mismatch between anticipated actions (goal completion) and perceived actions (the incompletion of goals). This interpretation is based on a phenomenon called *forward mapping*, suggesting that humans continuously predict possible motion trajectories and the future actions of others on the basis of their own motor representations (Shiffrar & Freyd, 1990).

In comparison with current understanding of the neural correlates of infant perception of goal-directed action, work on the neural correlates of attention is highly advanced. One component of the infant event-related potential (ERP) is the midlatency *negative central* (Nc) component. The Nc occurs approximately 300–700 ms after stimulus onset, is most prominent at frontocentral electrodes, and is thought to reflect attentional orienting to salient stimuli (Courchesne, Ganz, & Norcia, 1981; Nelson, 1994; Webb, Long, & Nelson, 2005) and/or a general attentional arousal (Richards, 2003a).

In isolation to work on goal-directed actions or on neural correlates to infant attention, there is evidence to suggest that structures involved in the processing of language and certain actions are tightly bound. Mechanisms involved in the perception of action sequences may be similar to those associated with the processing of semantic understanding found within language research (Iacoboni, 2005; Miller & Johnson-Laird, 1976). In research investigating the neural correlates of the processing of grammar and syntactic structure, sequence processing has been investigated. One ERP component, the N400, has been paired with the lack of a semantically congruent sentence ending when compared with the content of the prior sentence (e.g., Friederici, 2002). Initially described over 20 years ago (Kutas & Hillyard, 1980a, 1980b), the N400 has been instrumental in refining linguistic theory and has proved foundational for an understanding of the relationships among language, semantics, structure, and neurophysiological correlates to these cognitive processes (Kutas, 1997). In language research, the N400 has been related to the building of a semantic context, with the N400 produced whenever a word does not fit a

context. For example, when adults read the sentence "The pizza was too hot to cry," they manifest a larger N400 amplitude response than when they read the sentence "The pizza was too hot to eat" (Kutas & Hillyard, 1980b).

The N400 ERP has been found to be sensitive to the perception of semantic information in paired words and visual stimuli (Nigam, Hoffman, & Simons, 1992). Recent research with adults has suggested that a differential N400 response is produced following observation of meaningful and meaningless hand postures, such as the "thumbs up" emblem when compared with a hand position with no symbolic meaning (Gunter & Bach, 2004). The N400 has also been observed when sequences of words are followed by congruent or incongruent gestures (Wu & Coulson, 2005). N400 responses to photographs are delayed in latency and more anterior in topography when compared with N400 components derived from language studies, potentially due to the complexity of the visual stimulus. It is most likely that generators of the N400 are located in the superior temporal sulcus (STS; e.g., magnetoencephalography [MEG], Halgren et al., 2002; intracranial ERPs, Guillem, N'Kaoua, Rougier, & Claverie, 1995; MEG/magnetic resonance imaging [MRI], Simos, Baslie, & Papanicolaou, 1997). Importantly, the STS is the same region that has been implicated in action processing and goal direction understanding in adults (e.g., Allison, Puce, & McCarthy, 2000; Blakemore & Decety, 2001; Blakemore et al., 2003).

Research with infants suggests that by 9 months, infants process action from two-dimensional scenes in terms of future goals and the efficient means to achieve these goals (Csibra et al., 1999). Other research suggests that 8-month-old infants do not require the presentation of the end state of an action in order to attribute a goal to an action (Reid et al., 2007). What these studies do not address is whether similar mechanisms are used between infants and adults when they are making these attributions to observed action.

Should adults and 9-month-old infants predict specific goals to actions using similar cognitive systems, we reasoned, then both groups would produce an N400 response to the final component of an action sequence in which the final component of the action is not expected. For action sequences in which the final component is expected, we anticipated that, comparatively, no N400 component would be observed. We further predicted that 7-month-old infants would not produce N400-type responses as a result of viewing actions in two-dimensional scenes, as there is no behavioral evidence to suggest that infants at this age have developed these social-cognitive skills in relation to sequences of action. We also predicted that the Nc component would be evident in the ERP resulting from these stimuli due to their high social salience and engaging nature. To further support a semantic interpretation of any N400 response, we also predicted that our data would contain frequency responses in the theta range to semantic violations, as has been previously seen in adults by Hald and colleagues (Hald, Bastiaansen, & Hagoort, 2006). To test these predictions, we showed adult participants and infants at 9 and 7 months of age short sequences of actions in which three images were presented on a screen consecutively. The first image displayed the general context of the action. The second displayed the initiation of the action. The third image showed the conclusion of the action, either as a semantically anticipated or unanticipated goal.

Method

Participants

Fifteen adults participated (7 men and 8 women), with an average age of 24.6 years (range 21–30 years). All participants were from a Caucasian middle-class background from a midsized city in Germany and had normal or corrected-to-normal vision. For inclusion in the grand average, participants were required to have at least 50 artifact-free trials across conditions. Fourteen infants (8 boys and 6 girls) were also tested, at the age of 9 months ± 12 days. Another 16 infants were tested but were excluded from the final sample as a result of fussiness ($n = 4$) or failure to reach the minimum requirements for adequate averaging of the ERP data ($n = 12$). Thirteen infants (7 boys and 6 girls) were tested at the age of 7 months ± 12 days. For 7-month-old infants, 30 further infants were tested but were excluded from the final sample as a result of fussiness ($n = 9$) or failure to reach the minimum requirements for adequate averaging of the ERP data ($n = 21$). All infants were from a Caucasian middle-class background from a midsized city in Germany, born full term (37–41 weeks) and in the normal range for birth weight. Infants were included in the final sample, provided that a minimum of 10 artifact-free trials per condition were obtained for their average; however, each 9-month-old infant contributed a mean of 17 ($SD = 3$) trials to their average for each condition. Each 7-month-old infant contributed a mean of 21 ($SD = 5$) trials to their average for each condition. There were no differences in the number of trials in the final average between the two conditions for any age group. This experiment was conducted with the understanding and the written consent of each participant or his or her parent in accordance with institutional protocols.

Materials

Adult stimuli. Sets of photographs depicting a male actor were made, depicting eating (twice—once with a spoon and once holding the food).[1] For the presented sets, each contained three photographs. The first photograph displayed the general context of the action. The second displayed the initiation of the action. The third photo displayed either the anticipated conclusion of the action or an unanticipated conclusion to the action (see Figure 1).

Infant stimuli. Two further sets of photographs of a female actor were made, depicting different eating actions with action content similar to those shown to adults. These actions were chosen for presentation to infants as they were judged to be readily interpretable and salient for this age range. The male actor sequences of eating were presented to infants and adults. We included new eating stimuli for infants featuring a female agent in order to counter potential habituation to what would otherwise be limited stimuli, which would result in an unacceptably high dropout rate. As their action content was the same as the stimuli shown to adults, we rationalized that this would not affect results.[2] All other parameters were the same as those for adult stimuli (see Figure 1).

Procedure

The parameters for the infant and adult procedure were the same. Infants sat on their mother's lap in a dimly lit, sound-

Figure 1. All stimuli sets used in the study. Column A = context of action; Column B = initiation of action; Column C = anticipated conclusion of action; Column D = unanticipated conclusion of action. Adults saw only stimuli of the top two rows. Note that these stimuli were presented in color.

attenuated, and electrically shielded cabin. Viewing distance was 90 cm away from a 70-Hz, 17-inch stimulus monitor. The stimuli were presented at 16×13 cm and were thus 8.26 degrees of visual angle. The experiment consisted of one block with 200 trials (100 anticipated sequences and 100 unanticipated sequences). Infants therefore saw a maximum of 200 stimuli sequences, with a division of male–female stimuli of exactly half each.

The two conditions were presented to the subject utilizing the software ERTS (Version 3.18, BeriSoft Corporation, Frankfurt, Germany) in a random order, with the constraints that the same condition not be presented three times consecutively and that the number of presentations of each sequence of stimuli be balanced in every 20 trials presented. Each image was presented on the screen for 1 s. Between the presentations of the sequences, the screen was blank for a random period of between 800 ms and 1000 ms (see Figure 2 for an example of the stimulus presentation sequence). If an infant became fussy or 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. Electroencephelographic (EEG) activity was recorded continuously, and infant behavior was also video recorded throughout the session for off-line, 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 activity was recorded continuously with Ag/AgCl electrodes from 23 scalp locations of the 10-20 system, referenced to

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[1] Other stimuli were presented to adult participants, although data relating to these stimuli are not presented here. The presence of these stimuli was in order to enhance the attention of the participants and to ensure that resulting data did not contain alpha waves, which are an artifact associated with boredom or fatigue. These additional stimuli included photographs depicting putting on sunglasses, combing hair, putting on shoes, and holding a pen.

[2] To confirm this, we conducted a 2×2 repeated-measures ANOVA with the factors Action (expected, unexpected) by Stimuli (male stimuli, female stimuli) with the same parameters as the final N400 dataset for 9-month-old infants. No significant effects related to stimuli were found.
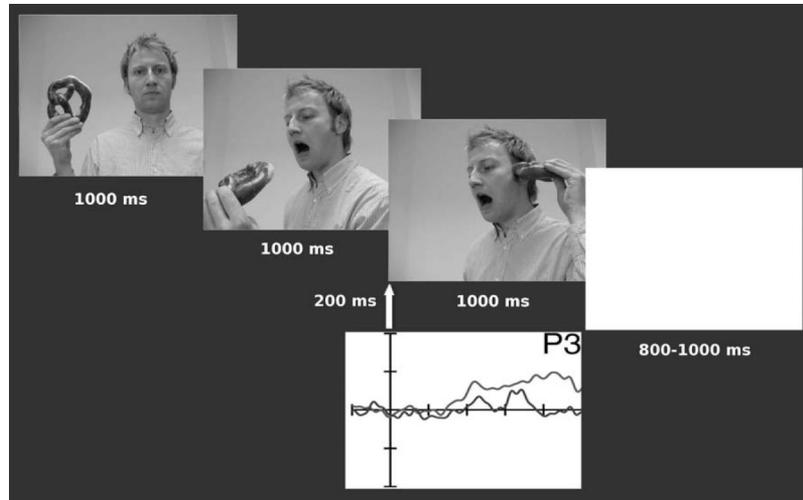
Figure 2. An example of the stimuli sequence and time line presented to the participants. Note that the ERP is time locked to the presentation of the final image in the sequence. The data are from the grand average of the 9-month-old infants.

the vertex (Cz). Data were amplified via a Twente Medical Systems 32-channel REFA amplifier. Horizontal and vertical electrooculograms were recorded bipolarly. Sampling rate was set at 250 Hz (every 4 ms), although we resampled the data every 12 ms in our analysis in accordance with the suggested guidelines for our analysis technique (see Hoorman, Falkenstein, Schwarzenau, & Hohnsbein, 1998). EEG data were rereferenced off-line to the linked mastoids. Off-line filters were set from 0.3–30 Hz.

The EEG recordings were segmented into epochs of waveform that comprised a 200-ms baseline derived from the last 200 ms of the second picture in the sequence and 1000 ms of the image displaying the action conclusion. The technique of utilizing the prior sequence image as the baseline was adopted from Wu and Coulson (2005) as this procedure ensures that no unnecessary disruption of the observed sequence occurs, which in turn could potentially conflict with the sequential processing of semantic information. For the elimination of electrical artifacts caused by eye and body movements, EEG data were rejected off-line whenever the standard deviation within a 200-ms gliding window exceeded 80 μV at any electrode. Data were also visually edited off-line for artifacts and to ensure that included trials were those in which the infant was attending to the screen.

For statistical analysis of adult data, a clear negative peak was observed in the unanticipated condition in the general time window expected for an N400 component, whereas this was not the case for the anticipated condition. A time window was chosen around the amplitude peak of the N400 component in frontal (F3, Fz, F4), central (C3, Cz, C4), and parietal regions (P3, Pz, P4), from 420–548 ms after stimulus onset. The window analysis technique of Hoorman et al. (1998) was utilized as one condition displayed a defined peak in the window of interest, whereas the other did not. Therefore analysis of the waveform could not be conducted using standard statistical techniques for ERP analysis, such as peak amplitude or mean amplitude of the effect of interest as the expectations of these tests were violated. For peak amplitude analysis, all conditions should have a defined peak in the time

window of interest. This was not the case for the current data. Mean amplitude analysis, conversely, is suitable when no peak is present in the data. This was also not the case for the current data, as one condition contained a defined peak whereas the other did not. The window analysis technique devised by Hoorman et al. (1998) is based on a conventional analysis of variance (ANOVA), with time as an additional within-subjects factor. The significance of differences between conditions can be determined by the interaction of condition with time. Variances of ERPs were analyzed by a $2 \times 3 \times 11$ general linear model analyzing condition (anticipated, unanticipated), location (frontal: the average of F3, Fz, F4; central: the average of C3, Cz, C4; parietal: the average of P3, Pz, P4), and time (11 samples at one sample per 12 ms).

An N400-like effect was also seen in data from the 9-month-old infants, with a similar morphology to that seen in adults, although delayed in time by around 200 ms. As the negative peak was observable only in parietal regions for 9-month-old infants due to masking by the Nc component, for statistical analysis a time window was chosen in parietal regions (P3, Pz, P4) around the amplitude peak of the infant N400 effect from 600–800 ms after stimulus onset. Variances of ERPs were analyzed by a 2×17 general linear model analyzing condition (anticipated, unanticipated) and time (17 samples at one sample per 12 ms) as suggested for such data by Hoorman et al. (1998). In addition, the peak negativity of the Nc was assessed in frontocentral channels in a time window between 300–800 ms in congruence with other studies investigating this waveform (e.g., Hoehl, Reid, Mooney, & Striano, 2008).

We also considered time–frequency analyses of these data. Theta induced power activity was computed by averaging across frequency bins in the theta frequency band (3–7 Hz for adults; 3–4.5 Hz for infants). The time windows were 1: 0–250 ms, 2: 250–500 ms, and 3: 500–750 ms. Values were baseline corrected inside each time window. In both samples three regions of interest (ROIs) were considered by averaging electrodes in the following three areas: frontal (F3, Fz, F4), central (C3, Cz, C4), and parietal

region (P3, Pz, P4). Data were analyzed inside each region by using the nonparametric Friedman's ANOVA for within measures. Nine different ANOVAs (3 time windows × 3 ROIs) were conducted out for each sample with the expected–unexpected conditions as the within-subjects factor.

Results

Adults displayed an N400 component broadly across frontal, central, and parietal regions of the scalp in the unanticipated condition but not in the anticipated condition as displayed in a condition by time interaction in the ANOVA, $F(1, 10) = 3.449$, $p < .001$. This comparison of conditions indicated that the effect was a result of significant differences between anticipated and unanticipated conditions; variation in ERP amplitude was evident only in the unanticipated condition. This indicated an N400 component only in this condition (see Figure 3; note that negative is plotted upward). There was no effect of location, suggesting that the effect was across frontal, central, and parietal regions, as shown in the grand average.

For 9-month-old infants, the analysis across parietal scalp regions indicated that there was an interaction between condition and time, $F(1, 16) = 3.161$, $p < .001$, also highlighting variation in ERP amplitude in the unanticipated condition but not in the anticipated condition (see Figure 4; note that negative is plotted

upward). A t test investigating frontocentral channels (F7, F3, FC3, C3, Cz, Fz, F8, F4, FC4, C4) in a time window between 300 and 800 ms indicated that the Nc peak negativity of the two conditions was significantly different, $t(13) = 2.78$, $p = .016$, with the anticipated condition more negative than the unanticipated condition.

No N400-like effects were found for infants of 7 months (see Figure 5). However, a similar Nc effect was seen with 7-month-old infants, as was observed in 9-month-old infants. A t test investigating the same channels and time window as conducted for the assessment of the Nc in 9-month-old infants indicated that for infants at 7 months, the peak negativity of the two conditions was significantly different, $t(12) = -2.992$, $p = .011$, with the anticipated condition more negative than the unanticipated condition.

Time–frequency ANOVAs revealed five significant comparisons in the adult group: In the central region in Windows 1 and 2, $\chi^2(1, N = 18) = 5.56$, $p < .02$, for both; in the parietal region for all time windows, $\chi^2(1, N = 18) = 8.00$, $p < .005$; $\chi^2(1, N = 18) = 10.89$, $p < .001$; $\chi^2(1, N = 18) = 5.56$, $p < .02$, respectively. In all comparisons, the unexpected condition had higher induced theta power when compared with the expected condition. In contrast, no significant results were present in the infant group. The theta oscillatory activity displayed by the adult sample is in
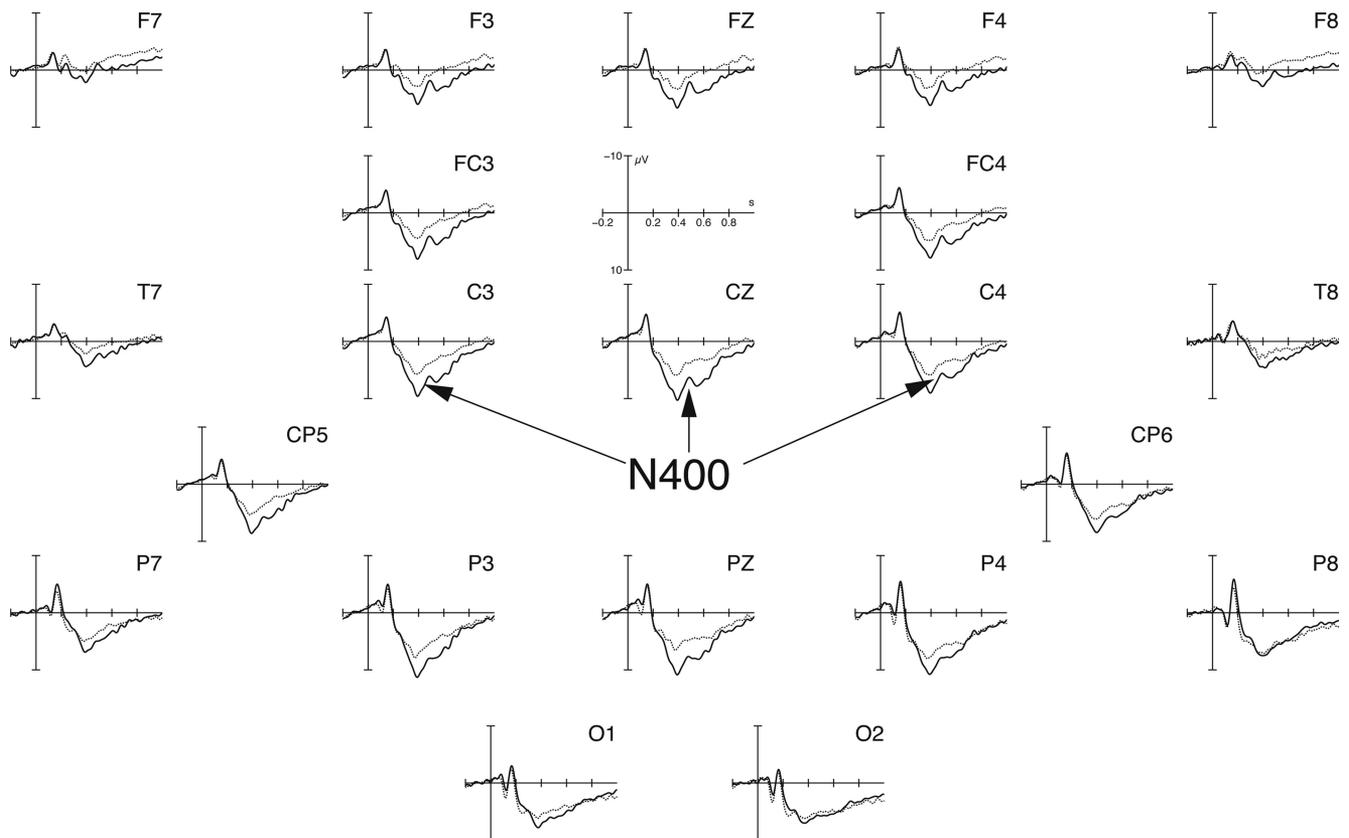

Figure 3. Grand average across all electrodes for the adult participants (gray = anticipated; black = unanticipated). The N400 component is maximal in the ERP at 500 ms in the unanticipated condition in frontal (F3, FZ, F4) and central (C3, CZ, C4) locations. Note that negative is plotted up.
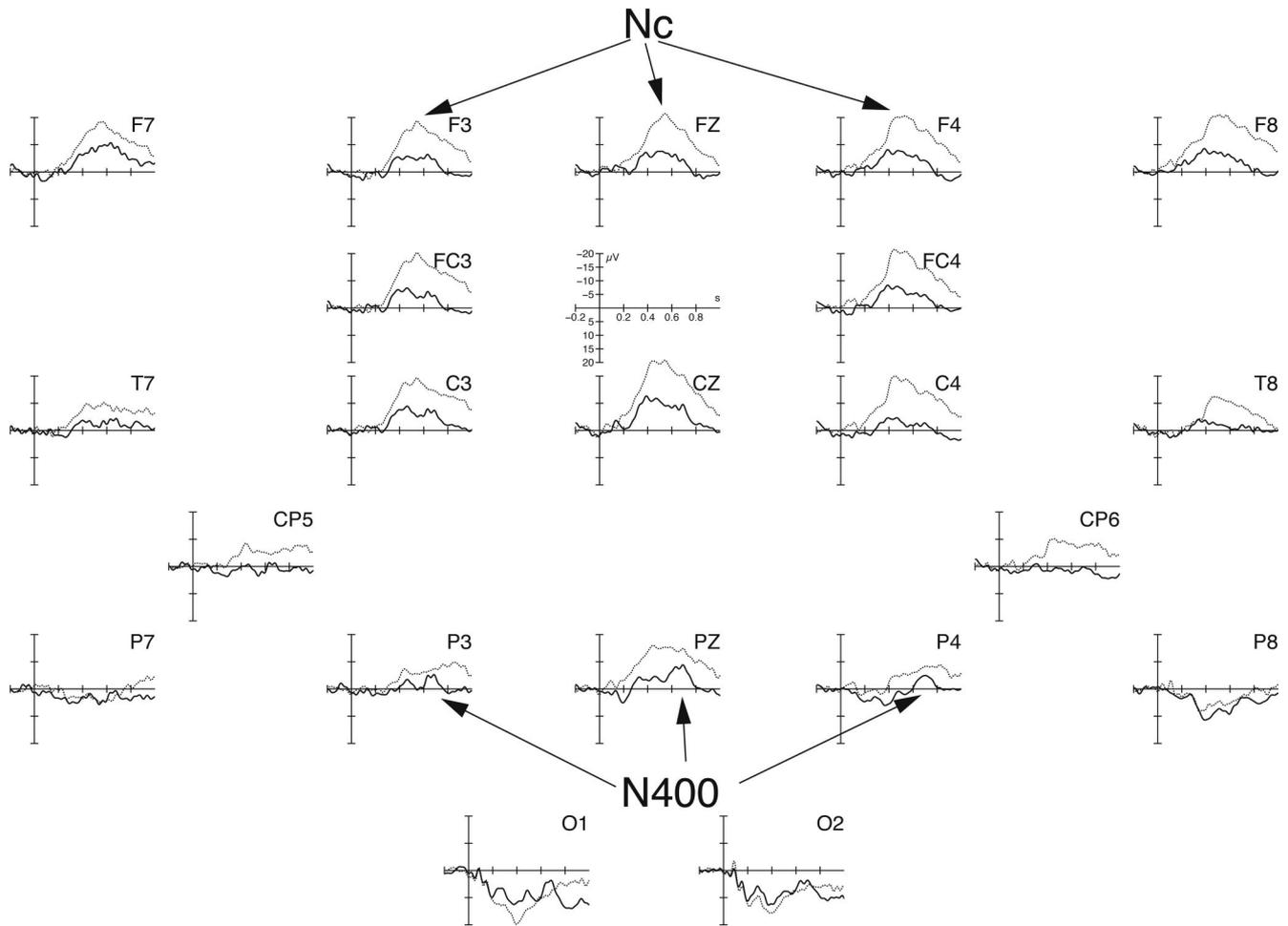
Figure 4. Grand average across all electrodes for 9-month-old infant participants (gray = anticipated; black = unanticipated). The N400 component was analyzed as the negative deflection in the ERP at 700 ms in the parietal locations (P3, PZ, P4). An Nc effect was also present in frontal and central areas, larger in amplitude for the anticipated condition. Note that negative is plotted up.

line with Hald et al. (2006), who showed increased theta for semantic violation during sentence processing.

Discussion

This study was designed to investigate electrophysiological responses in infants and adults to the perception of anticipated and unanticipated action outcomes. We showed participants sequences of three photographs, with the first two conveying context and the final photograph depicting the completion of an action. If goals were detected by both adults and infants utilizing similar predictive systems, then we expected an N400 response to the final component of an unanticipated action sequence for both groups. For action sequences in which the final component was anticipated, we predicted that no N400 component would be observed. These predictions were confirmed, with the production of components that appeared to be consistent across older infants and adults. Further, adults produced theta activations that were analogous to the N400 response in the ERP data. Infants did not produce this

effect; however, this was due to the infant theta resting at a comparably lower frequency (2–5 Hz), which is in the range for low frequency distortion during the creation of the frequency wavelet. Despite this, from eight out of nine cases (3 regions of interest $\times$ 3 time windows), the unexpected condition was higher than the expected. This result was comparable with the adult results but lacking in power due to the frequency distortion. The N400 results provide evidence that adults and infants at 9 months use similar semantic processing systems to predict the actions of others, although no such N400 component or theta response was seen in younger infants at 7 months of age.

It is possible that the N400-like effect observed may have the same neural basis in infants and in adults, despite differences in waveform morphology and topography. Those differences include the temporal differences between populations in the observed negative effect. The N400 produced by infants was delayed in time (around 700 ms after stimulus onset) when compared with the adult N400 component (around 500 ms after stimulus onset). Such
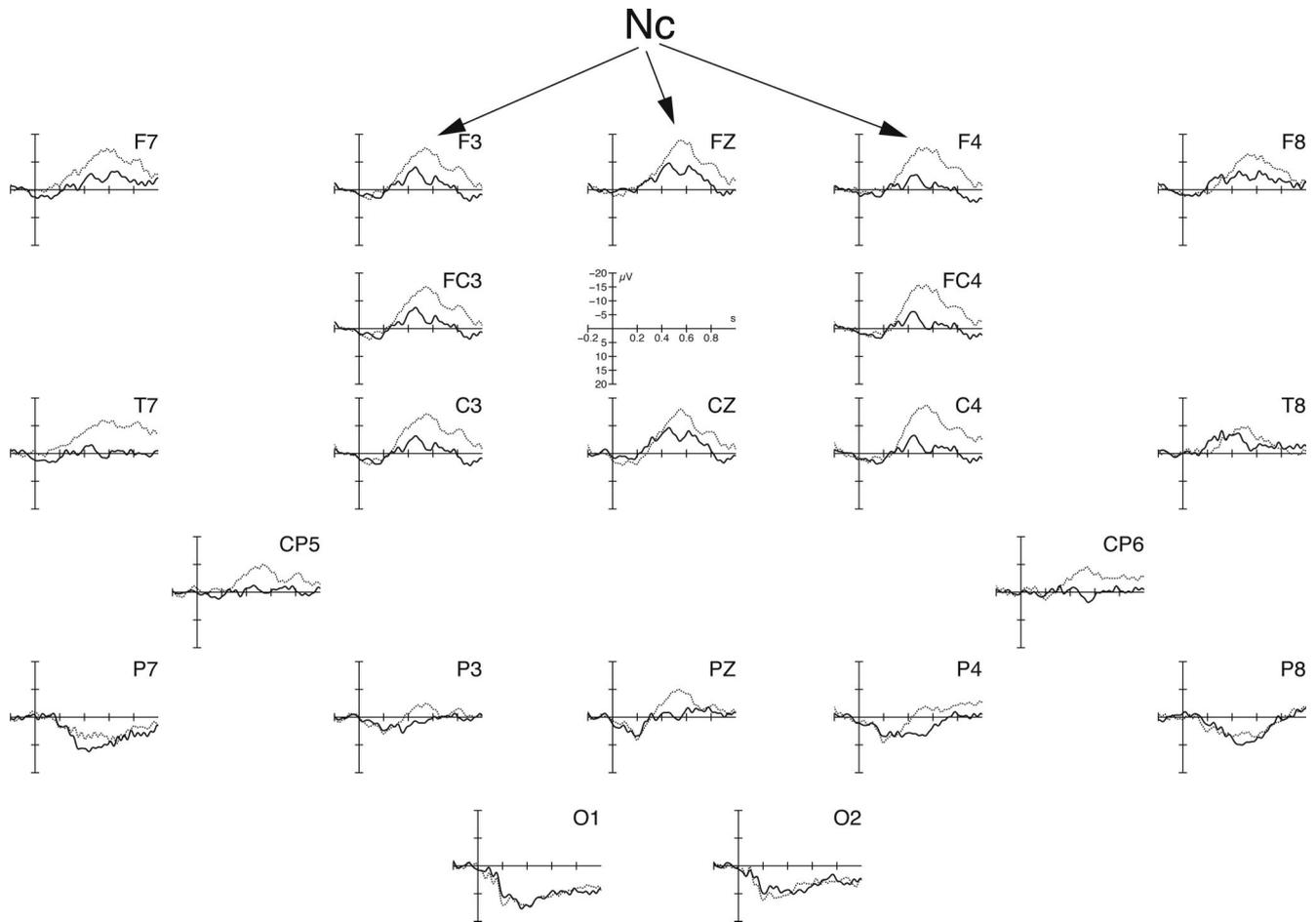
Figure 5. Grand average across all electrodes for 7-month-old infant participants (gray = anticipated; black = unanticipated). No N400 component was evident at any location. An Nc effect was also present in frontal and central areas, larger in amplitude for the anticipated condition. Note that negative is plotted up.

a temporal delay in components is typical in infant ERP data when compared with adult data (Friedrich & Friederici, 2006; Webb et al., 2005). Further, there are at least two explanations for the topographical differences that were observed between the populations. It is possible that the N400 component in infants was masked in frontal and central sites by the large Nc component that was induced by the stimuli. The clear negative amplitude effect of the N400 was therefore observed in parietal regions only for the unanticipated condition, although if the Nc component could be factored out via techniques such as independent components analysis (ICA), then it may be possible that the N400 component could be observable in frontal and central sites in infants. However, the current data were not suitable for ICA due to the study's violations of the assumptions made by ICA, such as the lack of electrodes in our recording montage when compared with what is optimal for ICA (see Anemueller, Sejnowski, & Makeig, 2003).

An alternative explanation for the topographical differences found between adult and infant N400 components in the present study is related to the stimulus type and the relative experience of adults and infants. In studies of the N400 component utilizing photographic images, the N4 is maximal at frontal and central sites

in adults (e.g., West & Holcomb, 2002; Wu & Coulson, 2005) and in children (Coch, Maron, Wolf, & Holcomb, 2002). However, with auditory stimuli or visually presented single words, an N4-type component is maximal at central and parietal regions in adults (e.g., Kutas, Van Petten, & Besson, 1988; Nobre & McCarthy, 1994) and in toddlers (Friedrich & Friederici, 2006). Some researchers have suggested that the N400 might be an index of lexically based semantic processes, such as a lexical search. This results in the observation of an N400 during tasks that require activation of semantic networks (e.g., Fischler & Raney, 1991). From this perspective, the N400 is smaller in response to anticipated stimuli because spreading activation has already partially activated the representation of the stimuli on exposure to prior information. Conversely, the N400 is larger in response to unanticipated stimuli because prior information is not congruous. The net result is the requirement of relatively more resources for activation of the representation of the stimuli, such as the goal of the action. On the basis of this hypothesis, it is possible that picture stimuli, such as those in the present study, are processed in infancy with the generators typical for the N400 for semantic processing of language observed in older ages. As infants have had little expe-

rience with the observation of either language or action structure, it is possible that the more posterior network is utilized when stimuli are relatively novel and complex. A more frontally distributed N400 may be related to relatively effortless processing of stimuli as well as to task demands. These factors may also explain the diffuse topography of the N400 component across frontal, central, and parietal electrodes that was produced by adult participants.

Issues with the development of the ERP waveform are also raised by the results of the present study. Friedman (1991) suggested that the ontogenetically unique Nc component present in the infant ERP is a precursor to the N400 component observed in the adult. Such a supposition was based on the cognitive properties of the Nc because it is elicited by novel or attention-getting stimuli that require further processing (see Webb et al., 2005, for a brief review). However, in the current study an Nc effect is evident in both anticipated and unanticipated conditions in frontal and central locations in addition to a posterior N400 component for the unanticipated condition. Further, the N400-like negative component is observed only in the condition in which an N400 response would be predicted. It is also at approximately the correct temporal and topographical location for an N400 response. In further support of this interpretation of the infant waveform, other studies that have investigated the Nc effect from visual stimuli have not produced any negative deflection at the same latency or location as the putative infant N400 that is described here (e.g., Reynolds, & Richards, 2005; Striano et al., 2006). The results of the present study therefore indicate that the Nc and the N400 are two distinct components in the infant ERP and that the Nc is not a precursor to the N400. Further, the N400-like component cannot be related to attentional processing of the stimuli as the Nc component, itself an index of attentional allocation, was significantly larger for the anticipated condition when compared with the unanticipated condition. This is to be expected as infants find food consumption to be a highly salient event. For this reason, it is therefore likely that the N400-like component is indeed related to the processing of the semantic violation of the unanticipated stimuli and is not related to attentional allocation per se.

It is interesting that for both 9-month-old infants and adults, anticipated outcomes generated more negative ERPs than did unanticipated outcomes, despite the anticipated condition failing to display any N400-like components. This difference cannot be attributed to differences in psychophysical characteristics of the two conditions, as differences in contrast and in other aspects of the images, such as luminance, were controlled. Rather, as the ERP reflects only lower frequencies of the EEG (see Taylor & Baldeweg, 2002, for a brief review) the continuous difference between conditions may reflect the degree to which low-frequency neuronal activity is in phase, with less coherent phasic activity in the anticipated condition depicted by a constantly more negative ERP than in the unanticipated condition.

Our results also indicated a larger peak amplitude of the Nc when infants at both 9 and 7 months viewed the conclusion of anticipated actions relative to the peak amplitude of the Nc for the conclusion of unanticipated actions. These results suggest that the consumption of food is of high interest to infants. An alternative explanation may be that the Nc indicates a familiarity effect for the expected condition. In previous studies the Nc was found to be enhanced for highly familiar stimuli, such as known faces,

relative to novel ones (e.g., de Haan & Nelson, 1997). The stimuli featuring food directed to the mouth may therefore be more familiar than stimuli depicting food directed to locations other than the mouth. This suggests that infants at 7 and 9 months process what "should be" when people hold food and direct it to the head; however, only at 9 months do infants detect that incongruous actions are "wrong."

In terms of cognitive abilities, these results indicate that infant perception of goals may be more fully advanced at 9 months than was previously realized. Research investigating infant sensitivity to the parsing of goal-directed action has found differences in looking time to paused images of completed actions when compared with pauses in actions in the midst of action flow. However, these differences were found by 10–11 months of age (Baldwin, Baird, Saylor, & Clark, 2001) and have not to date been investigated at younger ages. It is possible that one interpretation of the current study is related to action parsing and the prediction of events. Our stimuli were effectively depicting key components of an action sequence. The presentation of unexpected action outcomes effectively mirrors the effects of action interruption that were demonstrated by Baldwin et al. (2001). Other recent research has indicated that infants at 8 months can detect differences in videos in which actions are complete or incomplete; however, this was the case only when very simple actions were displayed (Reid et al., 2007).

The present study raises the issue of when in development infants begin to predict the goals of others. What underlies those changes in action processing with age also requires further investigation. Past research (e.g., Halgren et al., 2002) suggests that the generator of the N400 is the STS. One possibility may be that between 7 and 9 months of age the STS matures and becomes capable of processing semantic information. Further work is needed to resolve this possibility.

An alternative explanation that may account for these findings is that changes occur in working memory capacities from 7 to 9 months of age. These changes may allow an older infant to maintain information about the action sequence for the duration of the task, whereas this may not be the case for infants at 7 months of age. Specifically, three images were displayed in each sequence, with information-conveyed factors including people, objects, gaze direction, and relations between people and objects. Research on the development of working memory capacities is limited but suggests a small but appreciable capacity by 7 months of age (e.g., Pelphrey & Reznick, 2002; Reznick, Morrow, Goldman, & Snyder, 2004; Ross-Sheehy, Oakes, & Luck, 2003). Working memory capacities may thus account for the differences seen between processing of these stimuli between infants at 7 and at 9 months of age.

The results of the present study suggest that 9-month-old infants in the present study are capable of discerning semantic information within actions utilizing neural systems that have previously been associated with language processing at later stages of development. It is possible that a fundamental prerequisite of complex language development may be the ability to process and interpret the actions of others. At the ontogenetic and cognitive level, this study converges with evolutionary theory to suggest that the processing of language may derive from the ability to make sense of others' actions or gestures (e.g., Arbib, 2005; Corballis, 2003; 2004; Rizzolatti & Arbib, 1998). Therefore, in order to understand

language, which is inherently goal directed on multiple levels (Arbib, 2005), it may make sense to first understand basic aspects of goal-directed action early in development, which can act as a scaffold for later language development.

In sum, the current ERP data provide new insights into the cognitive and brain mechanisms underlying adult and infant capacities to detect goals within action, in which the N400 component appears to be involved. Through taking an existing paradigm in adult cognitive neuroscience and adapting it in a developmentally appropriate manner, we have provided new insights into the relation between adult and infant processing of the same social information. Thus, the current findings suggest that infants at 9 months may process goals in a manner similar to that of adults.

References

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences, 4,* 267–278.

Anemueller, J., Sejnowski, T. J., & Makeig, S. (2003). Complex independent component analysis of frequency-domain EEG data. *Neural Networks, 16,* 1313–1325.

Arbib, M. A., (2005). From monkey-like action recognition to human language: An evolutionary framework for neurolinguistics. *Behavioral and Brain Sciences, 28,* 105–124.

Baldwin, D. A., Baird, J. A., Saylor, M. M., & Clark, A. (2001). Infants parse dynamic action. *Child Development, 72,* 708–717.

Blakemore, S. J., Boyer, P., Pachot-Clouard, M., Meltzoff, A., Segebarth, C., & Decety, J. (2003). The detection of contingency and animacy from simple animations in the human brain. *Cerebral Cortex, 13,* 837–844.

Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews Neuroscience, 2*(1), 561–567.

Coch, D., Maron, L., Wolf, M., & Holcomb, P. J. (2002). Word- and picture-processing in children: An event-related potential study. *Developmental Neuropsychology, 22*(1), 373–406.

Corballis, M. C. (2003). From hand to mouth: The gestural origins of language. In M. H. Christiansen & S. Kirby (Eds.), *Language evolution* (pp. 201–218). Oxford, England: Oxford University Press.

Corballis, M. C. (2004). FOXP2 and the mirror system. *Trends in Cognitive Science, 8*(2), 95–96.

Courchesne, E., Ganz, L., & Norcia, A. M. (1981). Event-related brain potentials to human faces in infants. *Child Development, 52,* 804–811.

Csibra, G. (2008). Goal attribution to inanimate agents by 6.5-month-old infants. *Cognition, 107,* 705–717.

Csibra, G., Gergely, G., Bíró, S., Koós, O., & Brockbank, M. (1999). Goal attribution without agency cues: The perception of "pure reason" in infancy. *Cognition, 72,* 237–267.

Decety, J., & Grezes, J. (2006). The power of simulation: Imagining one's own and other's behaviour. *Cognitive Brain Research, 1079,* 4–14.

de Haan, M., & Nelson, C. A. (1997). Recognition of the mother's face by six-month old infants: A neurobehavioral study. *Child Development, 68,* 187–210.

Dennett, D. C. (1987). *The intentional stance.* Cambridge, MA: MIT Press.

Fischler, I., & Raney, G. E., (1991). Language by eye: Behavioral and psychophysiological approaches to reading. In J. R. Jennings & M. G. H. Coles (Eds.), *Handbook of cognitive psychophysiology: Central and autonomic nervous system approaches* (pp. 511–561). New York: Wiley.

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Science, 6,* 78–84.

Friedman, D., (1991). The endogenous scalp-recorded brain potentials and their relation to cognitive development. In J. R. Jennings & M. G. H.

Coles (Eds.), *Handbook of cognitive psychophysiology: Central and autonomic nervous system approaches* (pp. 621–656). New York: Wiley.

Friedrich, M., & Friederici, A. D. (2006). Early N400 development and later language acquisition. *Psychophysiology, 43,* 1–12.

Griffin, R., & Dennett, D. C. (2008). What does the study of autism tell us about the craft of folk psychology? In T. Striano & V. M. Reid (Eds.), *Social cognition: Development, neuroscience and autism.* Oxford, England: Blackwell.

Grossman, T., & Johnson, M. H. (2007). The development of the social brain in infancy. *European Journal of Neuroscience, 25,* 909–919.

Guillem, F., N'Kaoua, B., Rougier, A., & Claverie, B. (1995). Intra-cranial topography of event-related potentials (N400/P600) elicited during a continuous recognition memory task. *Psychophysiology, 32,* 382–392.

Gunter, T. C., & Bach, P., (2004). Communicating hands: ERPs elicited by meaningful symbolic hand postures. *Neuroscience Letters, 372,* 52–56.

Hald, L. A., Bastiaansen, M. C. M., & Hagoort, P. (2006). EEG theta and gamma responses to semantic violations in online sentence processing. *Brain and Language, 96,* 90–105.

Halgren, E., Dhond, R. P., Christensen, N., Van Petten, C., Marinkovic, K., Lewine, J. D., & Dale, A. M. (2002). N400-like magnetoencephalography responses modulated by semantic context, word frequency, and lexical class in sentences. *Neuroimage, 17*(3), 1101–1116.

Heider, F., & Simmel, M. (1944). An experimental study of apparent behavior. *American Journal of Psychology, 57,* 243–259.

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

Hoehl, S., Reid, V. M., Mooney, J., & Striano, T. (2008). What are you looking at? Infants' neural processing of an adult's object-directed eye gaze. *Developmental Science, 11*(1), 10–16.

Hoorman, J., Falkenstein, M., Schwarzenau, P., & Hohnsbein, J. (1998). Methods for the quantification and statistical testing of ERP differences across conditions. *Behavioral Research Methods: Instruments & Computers, 31,* 103–109.

Iacoboni, M. (2005). Understanding others: Imitation, language, and empathy. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (Vol. 1, pp. 77–99). Cambridge, MA: MIT Press.

Kamewrai, K., Kato, M., Kanda, T., Ishiguro, H., & Hiraki, K. (2005). Six-and-a-half-month-old children positively attribute goals to human action and to humanoid-robot motion. *Cognitive Development, 20,* 303–320.

Kutas, M. (1997). Views on how the electrical activity that the brain generates reflects the functions of different language structures. *Psychophysiology, 34,* 383–398.

Kutas, M., & Hillyard, S. A. (1980a). Event-related potentials to semantically inappropriate and surprisingly large words. *Biological Psychology, 11,* 99–116.

Kutas, M., & Hillyard, S. A. (1980b, January 11). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science, 207,* 203–205.

Kutas, M., Van Petten, C., & Besson, M. (1988). Event-related potential asymmetries during the reading of sentences. *Electroencephalography and Clinical Neurophysiology, 69,* 218–233.

Miller, G. A., & Johnson-Laird, P. N. (1976). *Language and perception.* Cambridge, MA: Harvard University Press.

Nelson, C. A. (1994). Neural correlates of recognition memory in the first postnatal year of life. In G. Dawson & K. Fischer (Eds.), *Human behavior and the developing brain* (pp. 269–313). New York: Guilford Press.

Nigam, A., Hoffman, J. E. & Simons, R. F. (1992). N400 and semantic anomaly with words and pictures. *Journal of Cognitive Neuroscience, 4,* 15–22.

Nobre, A. C., & McCarthy, G. (1994). Language related ERPs: Scalp distributions and modulation by word-type and semantic priming. *Journal of Cognitive Neuroscience, 6,* 233–255.

Parise, E., Reid, V. M., Stets, M., & Striano, T. (2008). Direct eye contact influences the neural processing of objects in 5-month-old infants. *Social Neuroscience, 3*(2), 141–150.

Pelphrey, K. A., & Reznick, J. S. (2002). Working memory in infancy. *Advances in Child Development and Behavior, 31,* 173–227.

Reid, V. M., Csibra, G., Belsky, J., & Johnson, M. H. (2007). Neural correlates of the perception of goal-directed action in infants. *Acta Psychologica, 124,* 129–138.

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

Reynolds, G. D., & Richards, J. E. (2005). Familiarization, attention, and recognition memory in infancy: An ERP and cortical source localization study. *Developmental Psychology, 41*(4), 598–615.

Reznick, J. S., Morrow, J. D., Goldman, B. D., & Snyder, J. (2004). The onset of working memory in infants. *Infancy, 6*(1), 145–154.

Richards, J. E. (2003a). Attention affects the recognition of briefly presented visual stimuli in infants: An ERP study. *Developmental Science, 6,* 312–328.

Rizzolatti, G., & Arbib, M. (1998). Language within our grasp. *Trends in Neuroscience, 21,* 188–194.

Ross-Sheehy, S., Oakes, L. M., & Luck, S. J. (2003). The development of visual short-term memory capacity in infants. *Child Development, 74*(6), 1807–1822.

Shiffrar, M., & Freyd, J. J. (1990). Apparent motion of the human body. *Psychological Science, 1,* 257–264.

Simos, P. G., Baslie, L., & Papanicolaou, A. (1997). Source localization of the N400 response in a sentence-reading paradigm using evoked magnetic fields and magnetic resonance imaging. *Brain Research, 762,* 29–39.

Striano, T., Reid, V. M., & Hoehl, S. (2006). Neural mechanisms of joint attention in infancy. *European Journal of Neuroscience, 23,* 2819–2823.

Taylor, M. J., & Baldeweg, T. (2002). Application of EEG, ERP, and intracranial recordings to the investigation of cognitive functions in children. *Developmental Science, 5,* 328–334.

Webb, S. J., Long, J. D., & Nelson, C. A. (2005). A longitudinal investigation of visual event-related potentials in the first year of life. *Developmental Science, 8,* 605–616.

West, W. C., & Holcomb, P. J. (2002). Event-related potentials during discourse-level semantic integration of complex pictures. *Cognitive Brain Research, 13,* 363–375.

Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. *Cognition, 69,* 1–34.

Woodward, A. L. (1999). Infants' ability to distinguish between purposeful and non-purposeful behaviors. *Infant Behavior and Development, 22,* 145–160.

Wu, Y. C., & Coulson, S. (2005). Meaningful gestures: Electrophysiological indices of iconic gesture comprehension. *Psychophysiology, 42*(6), 654–667.

Zacks, J. M., Braver, T. S., Sheridan, M. A., Donaldson, D. I., Snyder, A. Z., Ollinger, J. M., Buckner, R. L., & Raichle, M. E. (2001). Human brain activity time-locked to perceptual event boundaries. *Nature Neuroscience, 4*(6), 651–655.