

Distinct Processing of Objects and Faces in the Infant Brain

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Abstract

■ Previous work has shown that gamma-band electroencephalogram oscillations recorded over the posterior cortex of infants play a role in maintaining object representations during occlusion. Although it is not yet known what kind of representations are reflected in these oscillations, behavioral data suggest that young infants maintain spatiotemporal (but not featural) information during the occlusion of graspable objects, and surface feature (but not spatiotemporal) information during the occlusion of faces. To further explore this question, we presented infants with an occlusion paradigm in which they would, on half of the trials, see surface feature violations of either a face or an

object. Based on previous studies, we predicted higher gamma-band activation when infants were presented with a surface feature violation of a face, but not of an object. These results were confirmed. A further analysis revealed that whereas infants exhibited a significant increase in gamma during the occlusion of an object (as reported in previous studies), no such increase was evident during the occlusion of a face. These data suggest markedly different processing of objects and faces in the infant brain and, furthermore, indicate that the representation underpinned by the posterior gamma increase may contain only spatiotemporal information. ■

INTRODUCTION

Since early studies revealed the remarkable object knowledge that young infants appear to possess (e.g., Spelke, Kestenbaum, Simons, & Wein, 1996; Spelke, Breinlinger, Macomber, & Jacobson, 1992; Baillargeon, Spelke, & Wasserman, 1985; Bower & Wishart, 1972), a huge number of studies have further advanced our understanding of what infants know about objects and the constraints that govern their behavior. Recent studies have begun to explore the underlying neural correlates of object processing in infancy (e.g., Wilcox, Bortfeld, Woods, Wruck, & Boas, 2005; Kaufman, Csibra, & Johnson, 2003, 2005; Baird et al., 2002; Csibra, Davis, Spratling, & Johnson, 2000) and revealed possible neural markers of object retention in 6-month-olds. For example, during periods of brief occlusion, an increase in gamma-band oscillatory activity was found in infants over the right posterior temporal cortex (Kaufman et al., 2005; Kaufman, Csibra, et al., 2003). With similar findings in adults (Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998), these studies implicate oscillations in the gamma-band (~40 Hz) frequency as playing a role in the maintenance of object representations during occlusion.

It is not yet known what kind of information is maintained in these representations. However, many behavioral studies suggest that during the first year of

life, infants can only retain a limited amount of object information during both short and long periods of occlusion. For example, infants of 6.5 months and younger appear only able to hold a single item in short-term memory (Káldy & Leslie, 2005; Ross-Sheehy, Oakes, & Luck, 2003). Ross-Sheehy, Oakes, and Luck (2004) and Ross-Sheehy et al. (2003) showed that infants detected changes in one featural dimension (color) or spatial location only if the display contained a single item, but they failed to detect the change if the displays contained multiple items. Other studies have found that although infants may be able to process both surface feature¹ and spatiotemporal information during the first year of life, they fail to bind this information together (Oakes, Ross-Sheehy, & Luck, 2006; Mareschal & Johnson, 2003; Simon, Hespos, & Rochat, 1995). Thus, they may be able to correctly deduce that there must be two objects present behind a screen based on the fact that they saw two distinct objects appearing and disappearing behind an occluder, but they do not appear to expect these two objects to be, in terms of their surface features, the *same* two objects that they had previously seen until they reach 12 months of age (Tremoulet, Leslie, & Hall, 2000; Xu & Carey, 1996).

It has been suggested that the visual processing of manipulable objects is primarily concerned with aspects relevant for action affordance, such as location in space, distance, and size and shape information that is relevant for grasping (Gibson, 1979). This information is thought

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to be predominantly processed in the dorsal cortical visual route (Jeannerod, 1997), and studies with adults have shown that even passively viewing objects that invite actions (e.g., household utensils) activates the dorsal pathway (Grèzes & Decety, 2002). Infants, too, appear to process objects in terms of whether or not they afford action (Yonas & Hartman, 1993). Given the evidence that infants are unable to integrate both identity and location information during periods of occlusion, and based on the assumption that viewing objects automatically activates the dorsal pathway, Mareschal and Johnson (2000, 2003) hypothesized that by varying the type of stimuli presented to the infant, the kind of information that infants will encode or retain should differ. By presenting infants with objects that afforded action, Mareschal and Johnson found that 4-, 6-, and 9-month-old infants retained information that would be relevant for interacting with that object (e.g., the location of the object). However, these same infants did not remember the surface features of the object and were not surprised when one object was substituted for another one in the same location during occlusion. However, when infants in a different group were presented with stimuli that did not afford action (human faces) and which are thought to be processed via the ventral visual stream (Kanwisher, McDermott, & Chun, 1997; Gross, 1992), they selectively retained surface feature, but not location information, and so were able to detect a change in the identity of the stimulus, but not its location.

Given that young infants are limited in the amount of object information they are able to maintain during periods of occlusion, and that the kind of stimulus presented modulates what information is maintained, the current study aimed to find evidence that the infant brain detects surface feature changes of faces following occlusion, but not of objects. We draw our hypotheses from a recent study by Kaufman, Csibra, et al. (2003) in which an initial burst of gamma-band oscillatory electroencephalogram (EEG) activity during the occlusion of an object was followed by a further increase in gamma-band activity when the infant was shown that an object had magically disappeared. Whereas the gamma increase during occlusion was interpreted as a neural correlate of the infant maintaining a representation of the occluded object, the further gamma increase was taken as reflecting the infant brain attempting to reconcile what it had expected to see with the contrary evidence now presented. We reasoned that if infants maintain the features of faces during occlusion, but not of objects (Mareschal & Johnson, 2000, 2003), then infants may exhibit an increase in gamma-band activity when presented with a surface feature change of a face, but not of an object. If infants do not maintain the surface feature information for occluded objects, when presented with a change in surface features, there is no reconciling to be done because the infant has no expectations about the properties of the object.

A further aim of the current study was to explore whether the increase in gamma-band activity found during the occlusion of an object in Kaufman et al. (2005) and Kaufman, Csibra, et al. (2003) would also be present during the occlusion of a face. Much evidence exists suggesting that not only does the human brain process faces and objects differently (e.g., Allison, Puce, & McCarthy, 2000; Kanwisher et al., 1997), but the infant brain may treat faces (or people) and objects quite differently during periods of occlusion. In the study already described, Mareschal and Johnson (2000, 2003) found that the spatiotemporal properties of faces are not maintained during occlusion. Furthermore, in a recent study by Kuhlmeier et al. (2004), it was found that 5-month-old infants looked longer towards an event that violated the spatiotemporal properties of an object, but not of a human agent. The authors of the latter study espouse the view that initially, infants may apply quite different constraints to people and objects, and that although they know that objects cannot move on discontinuous pathways, they do not appear to have the same expectations for people. Thus, it is possible that infants have different expectations about occluded objects and faces. Furthermore, given that the type of information retained is modulated by the type of stimulus presented, it is possible that the increase in gamma-band activity observed over the posterior cortex supports a specific type of representation. Presenting infants with stimuli that are known to predominantly elicit either featural or spatiotemporal processing will help to address this question.

We presented two groups of infants with visual stimuli that disappeared as a screen went up to occlude them (occlusion period), and then as the screen was lowered, the infant saw either the same stimulus that was occluded or a different exemplar of the same stimulus category (visible period). The stimuli were objects (toys) for one group of infants and faces for the other. In order to maximize the likelihood that infants would retain either location (for those in the object group) or featural (for those in the faces group) information, a design was chosen whereby infants saw only brief presentations of the stimuli (500 msec) and were required to retain information in memory for brief occlusion periods (500–800 msec). Such brief presentation times have been shown to be sufficient to allow 6-month-old infants to encode and retain either featural or spatiotemporal information, but not both (Oakes et al., 2006), and are also conducive to an infant EEG study in which data from many trials have to be collected in a short time.

METHODS

Participants

Twenty 6-month-old infants (aged 170–198 days, mean age of 188.5 days) participated in this experiment. An

additional 38 infants were tested but excluded from further analysis due to fussiness or movement that resulted in recording artifacts ($n = 35$) and procedural error ($n = 3$).² This study was carried out in accordance with human subjects ethical guidelines mandated by the National Institutes of Health (USA) and the Medical Research Council (UK).

Design and Stimuli

All experimental stimuli were presented on a computer screen with MATLAB using the Psychophysics Toolbox extension. Two faces (both female) and two objects (a toy train and a similarly sized transparent toy with balls inside) were used as stimuli. The toys were chosen to be of a similar size to the faces when filmed behind the occluder.

Infants were assigned to two conditions, which differed only with respect to the class of stimuli (faces, $n = 10$, or objects, $n = 10$) that the infant viewed. Each trial began with the face or object fully visible on the screen for 500 msec. The screen then rose for 500 msec until the stimulus was completely occluded. The duration of the occlusion period varied randomly between 500 and 800 msec. The screen was then lowered for 500 msec and revealed either the same stimulus that was occluded (“no change” trials), or the other exemplar of the same category (face or object, “change” trials). The stimulus was revealed for 500 msec, and this 500 msec also comprised the first 500 msec of the subsequent trial. The two trial types (change and no change) were randomly presented to the infant. Infants watched the stimuli for as long as they were willing, and, if needed, an experimenter attracted the infants’ attention back to the screen by calling their name through a microphone. Infants in the faces condition viewed between 60 and 194 trials (median = 136) and infants in the objects condition viewed between 99 and 259 trials (median = 149). An independent samples t test confirmed there was no significant difference in the number of trials viewed between the two groups, $t(18) = 1.5$, $p = .14$.

Procedure and Analysis

Infants sat in a darkened room on a parent’s lap, 60 cm from the stimulus monitor. EEG was recorded using a Geodesic Sensor Net composed of 62 electrodes distributed evenly across the scalp. EEG was recorded and analyzed with respect to the vertex electrode³ and sampled at 250 Hz. We recorded the EEG and videotaped the infants’ looking behavior for as long as they were willing to watch the screen. Trials in which infants did not look at the entire sequence were excluded from the analysis on the basis of coding looking behavior on the videotapes. Induced gamma-band oscillatory activation was analyzed using an established procedure (Kaufman et al., 2005; Kaufman, Csibra, et al., 2003; Csibra et al., 2000). We employed a continuous wavelet transform to

single trials of EEG in each channel using Morlet wavelets at 1-Hz intervals in the 20- to 60-Hz range, and average wavelet coefficients within infants were calculated by taking the mean across trials.

Infants were included in the analysis if they provided 10 or more artifact-free trials per condition. Two separate analyses were carried out from these data. First, we were interested in the effect of the change versus no-change outcomes for each stimulus. For this analysis, each infant contributed between 40 and 105 (median 64, out of a mean of 164 presentations) and 40 and 74 (median 58, out of a mean of 136 presentations) trials to their average, in the object and face conditions, respectively.

Second, we were interested in the effect of occlusion for each of the two stimulus types. For this analysis, each infant contributed between 16 and 68 (median 53.5, out of a mean of 164 presentations) and 33 and 81 (median 41, out of a mean of 136 presentations) trials to their average, in the objects and faces conditions, respectively. There were no significant differences between groups in the number of artifact-free trials available for either the change or occlusion analysis: change, $t(18) = 1.1$, $p = .27$; occlusion, $t(18) = 1.8$, $p = .1$.

RESULTS

Two separate analyses were conducted. First, we investigated whether there were differences in gamma activity depending on whether or not a stimulus changed following occlusion. Second, we investigated whether we could see a similar increase in gamma-band oscillatory activity during occlusion that was evident in a number of previous studies (Kaufman et al., 2005; Kaufman, Csibra, et al., 2003).

Change Analysis

As no previous research has explored EEG correlates of recognizing changes in a stimulus, an initial visual inspection identified areas of interest for further analyses. A cluster of six left frontotemporal electrodes (12, 15, 16, 17, 20, 21) and six right frontotemporal electrodes (2, 53, 54, 56, 57, 61) appeared to show greater gamma-band activity during the change trials than the nonchange trials for infants in the face condition. These two areas together with the same posterior cluster analyzed for the occlusion analysis (below) were included in the analysis.

We then calculated the average gamma-band (20–60 Hz) activation over the aforementioned six left frontotemporal region electrodes, six symmetrically equivalent right frontotemporal electrodes, and seven posterior channels. The average gamma-band activation over these channels was calculated for a 100-msec baseline period (when the stimulus was fully occluded) and for the duration of stimulus visibility (from the time at which the face or object began to be visible (100 msec after the

screen began to lower) until it had been fully visible for 500 msec, a total duration of 900 msec.

A repeated measures analysis of variance (ANOVA) with Time (baseline vs. stimulus presentation), Change (old vs. new), and Region (left frontal, right frontal and posterior) as within-subjects factors and Condition (faces vs. objects) as a between-subjects factor was carried out. This analysis revealed a significant main effect of Time, $F(1,18) = 12.6, p = .002$, a significant main effect of Region, $F(2,17) = 22.8, p = .0001$, and significant interactions between Time and Change, $F(1,18) = 4.76, p = .04$, and Time, Change, and Condition, $F(1,18) = 4.82, p = .04$. In order to resolve these interactions, we first ran separate ANOVAs for each of our conditions (faces and objects) with Time (baseline vs. stimulus presentation), Change (change vs. no change), and Region (left frontal, right frontal, and posterior) as within-subjects factors.

Analysis of data from the “faces” group revealed a significant main effect of Region, $F(2,8) = 16.8, p = .001$, and significant interactions between Time and Change, $F(1,9) = 7.07, p = .03$, and Time and Region, $F(2,8) = 17.3, p = .001$. Separate analyses by Region revealed significant interactions between Time and Change in both the left frontal, $F(1,9) = 6.95, p = .03$, and right frontal, $F(1,9) = 8.25, p = .02$, regions, but no significant effects in the posterior region. Follow-up paired-samples t tests showed that there was a significant decrease in gamma-band activation from the baseline period to the stimulus presentation period over both left and right frontal electrodes, but only when the revealed stimulus was old: left, $t(9) = 3.51, p = .007$; right, $t(9) = 4.09, p = .003$. There was no effect of the variable Time when the stimulus revealed was new.

Analysis of data from the “objects” group revealed a significant main effect of Time, $F(1,9) = 9.33, p = .01$, and a significant main effect of Region, $F(2,8) = 8.35, p = .01$, but no effects of the variable Change. Separate analyses by Region revealed main effects of Time in both the left frontal channels, $F(1,9) = 6.48, p = .03$, and the posterior channels, $F(1,9) = 9.02, p = .02$, and a similar but non-significant pattern of results in the right frontal channels, $F(1,9) = 2.69, p = .1$. Follow-up t tests, with data collapsed over the Change factor, showed that in both the left frontal and the posterior region, the gamma activity decreased from baseline to stimulus presentation: left frontal, $t(9) = 2.55, p = .03$; posterior, $t(9) = 3.00, p = .02$. There was also a nonsignificant decrease in gamma-band activity in the right frontal region, $t(9) = 1.64, p = .13$ (see Table 1 for a summary of data from the change analysis).

Overall, these results show greater modulation of gamma-band activity in response to a change in face following occlusion, driven by a significant decrease in activity when infants see a face they saw before occlusion. This effect was most pronounced over the left frontotemporal region, with a similar pattern of activity in right frontotemporal electrodes. Infants in the objects condition showed a similar decrease in gamma-band activity

when they saw an “old” object revealed, but showed the same decrease also when the object was “new”.

Occlusion Analysis

Previous research has implicated gamma-band activity over temporal posterior electrodes during the occlusion of an object (Kaufman et al., 2005; Kaufman, Csibra, et al., 2003; Tallon-Baudry et al., 1998). We therefore expected to find increased activity relative to baseline in posterior channels during the period of occlusion, at least for the infants who viewed objects as stimuli. A visual inspection of the data suggested a markedly different pattern of results depending on the condition. For infants in the objects condition, a fairly widespread increase in gamma-band activity spanning a large number of posterior channels was revealed, in which the gamma-band activity during the period of occlusion increased relative to baseline. In contrast, for infants in the faces condition, there was a widespread *decrease* in gamma-band activity relative to baseline, which was not restricted to any particular region. In accord with previous findings and our visual analysis of the data, we selected seven channels (33, 34, 37, 38, 40, 41, 45) spanning a cluster of occipital electrodes (see Figure 1). As a comparison, we analyzed the same 12 frontal channels used for the Change analysis (6 from the left hemisphere [12, 15, 16, 17, 20, 21] and six from the right [2, 53, 54, 56, 57, 61]) (Figure 2). The average gamma-band activation (20–60 Hz) over these regions was calculated for a 100-msec baseline period (when the stimulus was fully visible) and for the duration of stimulus occlusion (from the time at which the face or object started to become occluded (100 msec after the screen began to raise) until it had been fully occluded for 500 msec, a total duration of 900 msec).

A repeated measures ANOVA was carried out with Time (baseline vs. occlusion) and Region (left frontal, right frontal, and posterior) as within-subjects factors and Condition (faces vs. objects) as a between-subjects factor. This analysis revealed significant main effects of Time, $F(1,18) = 5.16, p = .036$, and Region, $F(2,17) = 29.7, p = .0001$, and a significant interaction between Time and Condition, $F(1,18) = 5.71, p = .028$. There were also marginally significant interactions between Region and Condition, $F(2,17) = 2.98, p = .08$, and Time and Region, $F(2,17) = 3.33, p = .06$.

In order to resolve these interactions, separate analyses by Condition were carried out. First, for infants from the faces condition, a repeated measures ANOVA with Time (baseline vs. occlusion) and Region (left frontal, right frontal, and posterior) as within-subjects factors revealed significant main effects of Time, $F(1,9) = 6.67, p = .03$, and Region, $F(2,8) = 17.4, p = .001$. Follow-up paired-sample t tests showed a significant decrease in gamma-band activity from baseline (full visibility) to occlusion in both the left frontal region, $t(9) = 2.31, p = .05$, and the posterior region, $t(9) = 3.65, p = .005$.

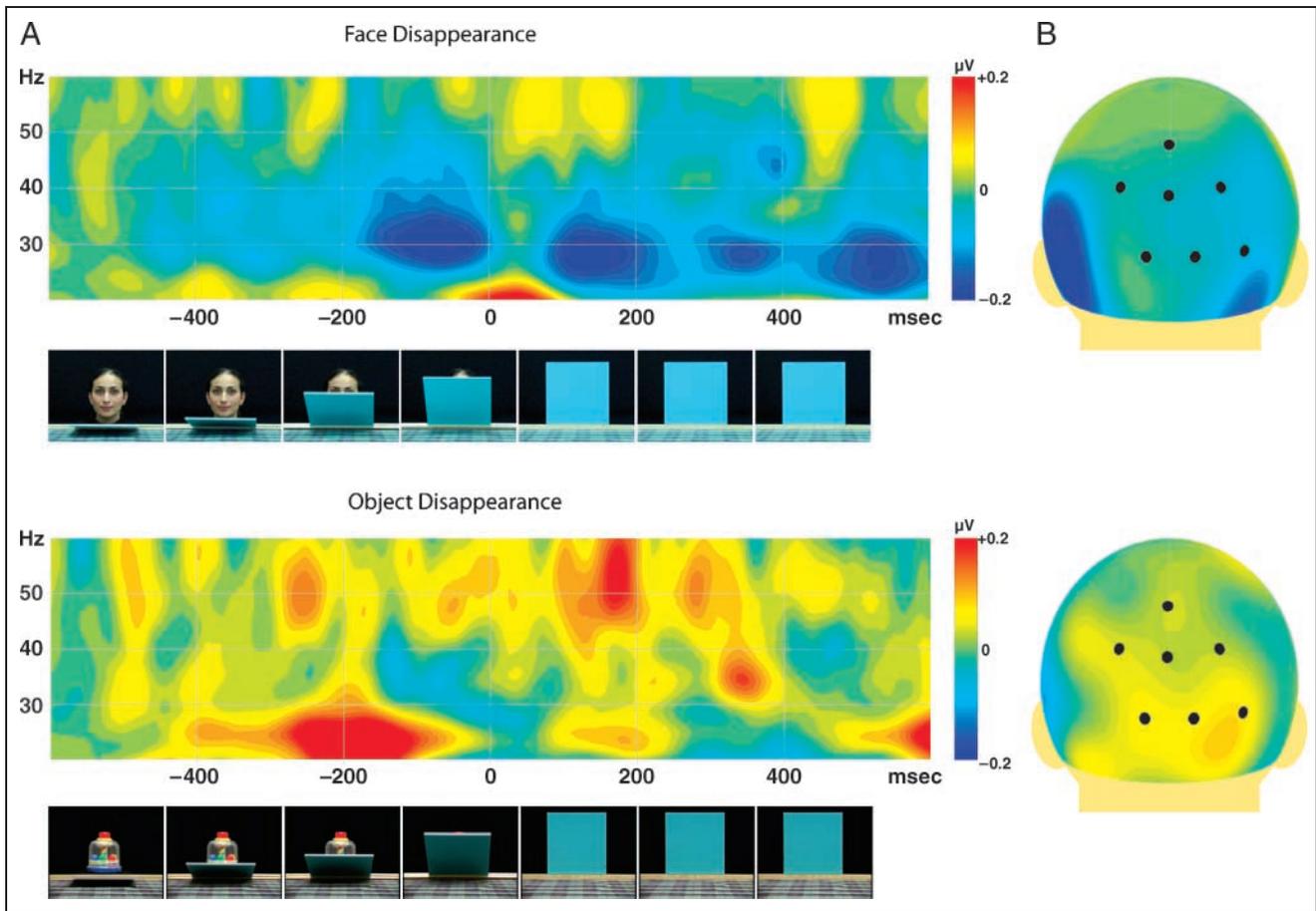


Figure 1. Baseline-corrected gamma-band activity during stimulus occlusion. (A) Time frequency analysis of the average EEG at seven electrodes over the posterior region showed higher activations relative to a baseline period of full visibility in infants who saw objects, but not in infants who saw faces. (B) A topographical map of the gamma-band (20–60 Hz) activity during occlusion (compared to baseline) for each of the two groups of infants.

There was no effect of Time in the right frontal region, $t(9) = 1.22, p = .25$. Second, for infants from the objects condition, another repeated measures ANOVA with Time (baseline vs. occlusion) and Region (left frontal, right frontal, and posterior) as within-subjects factors revealed a significant main effect of Region, $F(2,8) = 10.8, p = .005$, and an interaction between Time and Region that approached significance, $F(2,8) = 2.89, p = .1$. Follow-up paired-sample t tests showed that there was a significant increase compared with baseline in gamma-band activity over posterior channels, $t(9) = 2.22, p = .05$, but no significant differences from baseline in either the left or right frontal regions (see Table 2 for a summary of data from the occlusion analysis).

Overall, these results show that there is an increase in gamma-band activity over posterior channels during the occlusion of an object, but a decrease during the occlusion of a face.

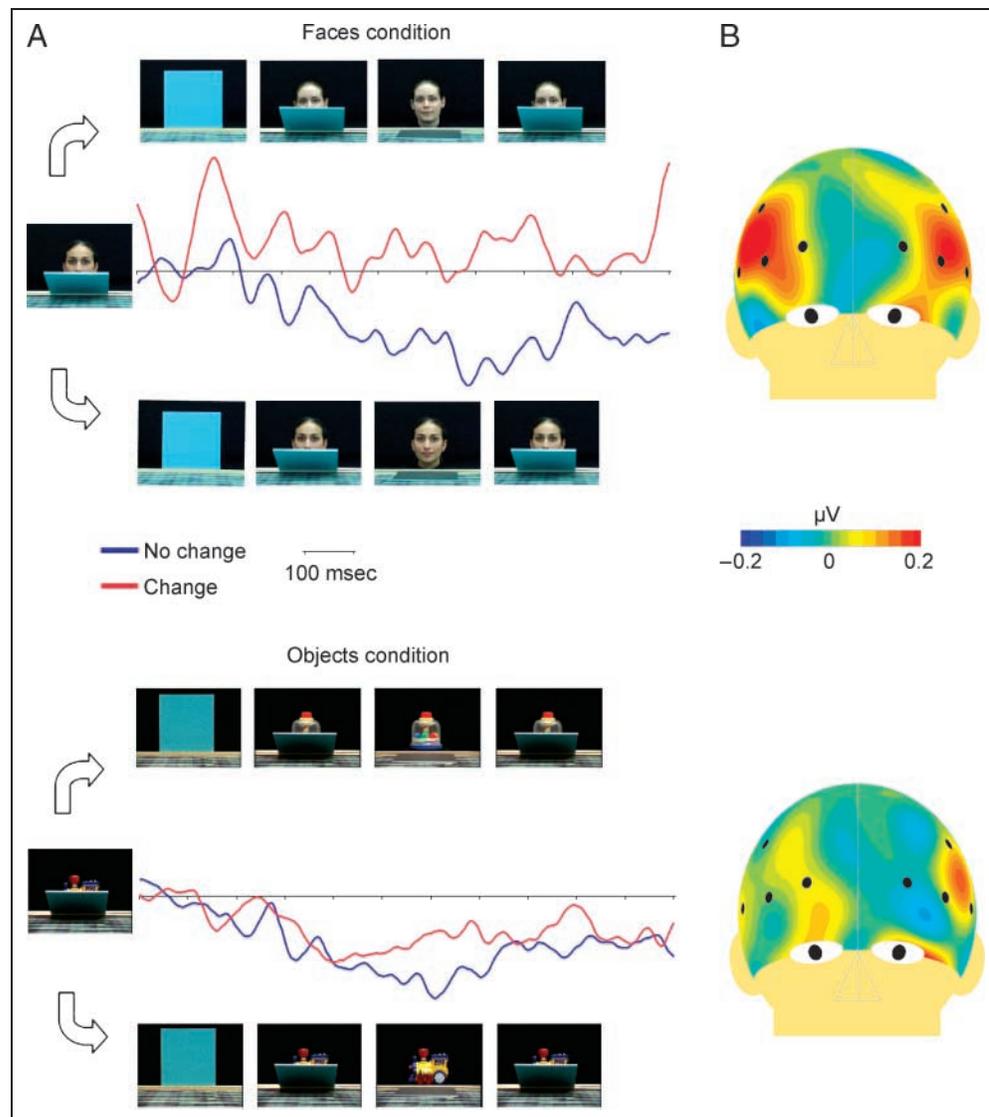
DISCUSSION

The present results suggest a striking dissociation between the way that 6-month-old infants process faces

and objects. First, we demonstrate that 6-month-olds exhibit a decrease in gamma-band activity when they see the same face revealed but not when they see a different face, indicating that they detected the change in face after occlusion and do maintain surface feature information for faces. However, we found no such differences in the response of the infant brain to the old and new object, suggesting that, at least in the context of this paradigm, 6-month-old infants do not maintain the surface features of the object during occlusion. Second, whereas our data provide support for previous work by demonstrating that 6-month-olds exhibit an increase in gamma-band activity over a similar area of the posterior cortex during the occlusion of an object, we found no such corresponding increase during the occlusion of a face. In fact, we found a significant decrease in activity during the occlusion of a face.

The decrease in gamma-band activity in response to an old (i.e., present before occlusion) face but not in response to a new face suggests that infants detected the change in face. The decrease in gamma-band activity in response to both the old and new object, however, suggests that they did not detect the change in object.

Figure 2. Baseline-corrected gamma-band activity as the stimulus is revealed. (A) Time frequency analysis of the average EEG at 12 electrode sites (6 left frontal and 6 right frontal electrodes) as the stimulus was revealed to the infant after occlusion, with no change (blue line) or with change (red line). There was a significant decrease in gamma-band activity as the object was revealed (whether it had changed or not), but only a significant decrease in gamma-band activity when the face had not changed, indicating that infants recognized the change in face. (B) A topographical map of the between-condition difference (change – no change) of gamma-band (20–60 Hz) activity during the visible stimulus phase for infants in each group (faces and objects).



These data fit with the findings by Mareschal and Johnson (2000, 2003), who demonstrated that 4-, 6- and 9-month-old infants look longer when shown a featural violation following the occlusion of a face, but not when they are shown a spatiotemporal violation. It is possible that the decrease in gamma-band activity evident when infants see an old face (but not a new face)

Table 1. Regions in Which There Was a Significant Increase or Decrease in Gamma-band Activity during Occlusion of the Stimulus, Relative to a Baseline Period of Full Visibility, for Each Stimulus Type

Stimulus	Posterior	Right Frontal	Left Frontal
Face	Decrease, $p < .005$	No difference	Decrease, $p < .05$
Object	Increase, $p < .05$	No difference	No difference

and when they see both an old and a new object reflects something akin to a repetition suppression effect, which has been reported in a number of studies of high-frequency oscillations (Gruber & Muller, 2002, 2005).

Table 2. Regions in Which There Was a Significant Increase or Decrease in Gamma-band Activity Relative to Baseline When the Stimulus Had Either Changed or Not Changed after Occlusion

Stimulus	Condition	Posterior	Frontal
Face	Change	No difference	No difference
	No change	No difference	Decrease, $p < .01$
Object	Change	Decrease, $p < .02$	Decrease, left, $p < .03$
	No change	Decrease, $p < .02$	Decrease, left, $p < .03$

infants at this age are unable to maintain object features across periods of occlusion, the new object will not be differentiated from the old object, and a repetition effect would be expected in response to each unocclusion event, irrespective of whether the stimuli revealed is old or new. However, inferring repetition suppression from high-frequency oscillations depends on the relationship between these oscillations and action potentials, and so should be interpreted with caution. As induced gamma-band responses are known to be modulated by attention (Muller, Gruber, & Keil, 2000), it is also possible that the decrease in gamma-band activity in response to the old and new object and the old face reflect lower levels of attention paid to repetitions of a stimulus seen before occlusion. Further studies are needed to address the important question of what such decreases in gamma-band activity reflect.

Infants' inability to detect changes in the featural identity of potentially graspable objects also fits with several studies suggesting that infants below 12 months of age do not consistently rely on the surface features of objects in object individuation tasks when those features are not relevant for action on the object (Kaufman, Csibra, et al., 2003; Wilcox, 1999; Xu & Carey, 1996). These results have been explained in terms of differences in the way that objects and faces are visually processed. Whereas faces are processed via the ventral visual stream, favoring surface feature information, graspable objects are additionally processed by the dorsal stream, which privileges spatiotemporal information. While the brain is still developing, it is possible that information from the two visual pathways is not fully integrated such that infants cannot maintain both featural and spatiotemporal information, and the type of processing involved in the particular pathway that is dominant for that particular stimulus will be privileged (Johnson, 2005). Such a lack of integration may persist until even into the second year of life (DeLoache, Uttal, & Rosengren, 2004).

There is considerable debate concerning whether infants are able to use features to individuate objects during the first year of life (Wilcox, Schweinle, & Chapa, 2003). It is likely that the perceived "graspability" of the object is an important factor that may influence what kind of information is prioritized (Kaufman, Mareschal, & Johnson, 2003). The amount of time infants are given to encode the stimulus may also influence what information can be retained about the stimulus, and the complexity of the objects involved is known to influence the number of objects that can be remembered (Alvarez & Cavanagh, 2004). It is also known that brief presentation times (<500 msec) of objects and faces results in a processing advantage for objects, probably due to the greater complexity of faces and the configural processing that they elicit (Curby & Gauthier, 2007). Considering that infants in this study did detect the face change following occlusion, but not the object change, our

results are unlikely to be due to the short presentation times, but rather our results fit better with the idea that infants fail to integrate and bind together information from separate pathways.

With regard to the occlusion period, although the topographic distribution of the increase in gamma in this paradigm was somewhat more posterior than that reported in Kaufman, Csibra, et al. (2003), we interpret the predicted increase as functionally equivalent, reflecting the maintenance of the representation of the object now that it is no longer visible. A broad posterior increase in gamma has also been reported in a number of adult studies in which subjects were required to maintain information during either occlusion or retention intervals (Jokisch & Jensen, 2007; Tallon-Baudry et al., 1998). Such activation ensures that out of sight is not out of mind, and would enable the infant to demonstrate the surprise that they exhibit when they are subsequently shown that, following occlusion, no object is revealed (Kaufman, Csibra, et al., 2003; Wynn & Chiang, 1998). However, this effect did not hold for infants who viewed faces as stimuli. On the contrary, a significant decrease in gamma-band activity relative to a baseline period was evident when a face was occluded. One possible explanation for this decrease of gamma during the occlusion of a face is that it reflects attentional modulation. Upright faces elicit higher levels of gamma activity than do other stimuli (e.g., inverted faces, Keil, Muller, Ray, Gruber, & Elbert, 1999) and so the decrease when the face is no longer visible may reflect a response to the disappearance of a particularly interesting stimulus class. Alternatively, a decrease in posterior gamma during the occlusion of a stimulus that engages the ventral stream may reflect inhibition of the dorsal stream, as recently proposed by Jokisch and Jensen (2007).

Considering the gamma-band activation that we found in response to occlusion and stimulus change together, an interesting picture emerges. On the one hand, 6-month-old infants appear not to detect a change in the features of an object following occlusion. However, the increase in posterior gamma-band activity during the occlusion of an object suggests that infants are representing *something* about the object during this period. On the other hand, despite not displaying an increase in posterior gamma-band activity during the occlusion of a face, infants nonetheless appear to detect changes in features of a face following a period of occlusion. This paradoxical finding suggests that the increase in posterior gamma-band activity during the occlusion of an object is not related to maintaining surface feature information.

What is then the role of the increase in posterior gamma-band activity during occlusion in both the present and the previous studies? We propose that the gamma-band activity evident during occlusion reflects the maintenance of a representation of the stimulus, but that this representation contains only spatiotemporal information. A recent finding by Jokisch and Jensen (2007) provides

support for this proposal. In this study, adult participants were required to maintain either featural or spatiotemporal information about a face during a retention interval. An increase in gamma-band activity over the posterior cortex was evident during retention of spatiotemporal information, but not during retention of featural information. Whereas in the study by Jokisch and Jensen, adults were instructed which dimension to attend to, the absence of gamma-band activity in the infant brain during the occlusion of a face likely reflects infants' inability to maintain spatiotemporal information for a stimulus for which recognition, hence retaining identity information, is more important. This explanation posits well-documented processing limitations (Káldy & Leslie, 2005; Ross-Sheehy et al., 2003, 2004) as the cause of this failure to maintain spatiotemporal information for faces.

A slightly different explanation is that the absence of posterior gamma-band activity during the occlusion of a face (interpreted as a spatiotemporal representation) reflects differences in the expectations that young infants may have about the continued existence of people and objects. Infants appear to hold different expectations of persistence depending on whether an object is shown to be inert or self-propelled (Wu & Baillargeon, 2006), or human or nonhuman (Kuhlmeier, Bloom, & Wynn, 2004; but see Saxe, Tzelnic, & Carey, 2006). A recent hypothesis proposes that human infants may have entirely distinct modes of construal for inanimate objects and humans, and that, for young infants, some of the laws that govern inanimate objects may not yet apply to people (Bloom, 2004). It is therefore possible that infants in this study do not show an increase in posterior gamma-band activity because they do not hold specific expectations about the spatial and temporal continuity of faces. Whereas objects tend to be enduring features of the infants environment, people come and go. The suppression of gamma-band activation during the occlusion of a face may plausibly reflect a response to the disappearance of a stimulus that elicits a strong gamma-band response (Keil et al., 1999) and is no longer perceived as requiring active representation (Csibra et al., 2000). One implication of this explanation is that, despite detecting the change in face, infants may not find this incongruent. A lack of "surprise" to the change in face may account for the difference between the gamma response to the violation outcome in Kaufman, Csibra, et al. (2003) (an increase in gamma compared with baseline) and the lack of increase in response to the new face in the current study, a change that they nevertheless did detect. Whether this is a plausible explanation remains to be determined, but caution should be applied in interpreting looking-time responses to face identity changes following occlusion (e.g., Bertenthal, Longo, & Michalska, 2005).

We have proposed that the markedly different pattern of neural activation depending on whether infants view faces or objects could reflect the fact that, whereas infants

represent spatiotemporal information during object occlusion, they do not represent this same information during the occlusion of a face. This discrepancy arises either because 6-month-olds are limited in their capacity to bind together and therefore retain both location and identity information, or because they simply do not apply to people the same rigid permanence constraints that are appropriate for inanimate objects.

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Notes

1. In accord with the object processing literature (e.g., Mareschal & Johnson, 2003), we use the phrase "surface feature" to refer to the color, texture, and local configuration of features of a stimulus. This is contrasted with the term "spatiotemporal information" that refers to the spatial location, trajectory, and action-relevant shape of an object.
2. Such a high attrition rate is common in electrophysiological studies with young infants (e.g., Quinn, Westerlund, & Nelson, 2006; Csibra et al., 2000).
3. Similar results were obtained using average referenced data.

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