Oscillatory activity in the infant brain reflects object maintenance

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The apparent failure of infants to understand ''object permanence'' by reaching for hidden objects is perhaps the most striking and debated phenomenon in cognitive development. Of particular interest is the extent to which infants perceive and remember objects in a similar way to that of adults. Here we report two findings that clarify infant object processing. The first is that 6-mo-old infants are sensitive to visual cues to occlusion, particularly gradual deletion. The second finding is that oscillatory electroencephalogram activity recorded over right temporal channels is involved in object maintenance. This effect occurs only after disappearance in a manner consistent with occlusion and the object's continued existence.

object permanence | infancy | gamma oscillations | electroencephalogram

One of the most striking phenomena in human cognitive development is that, for young infants, objects that are out of view appear to cease to exist (1). This phenomenon was first revealed by Piaget's observations that infants <9 mo of age do not reach for hidden objects and led him to conclude that ''object permanence'' emerges late during infant development. More recently, however, studies that measure infants' looking behavior have suggested that infants can, in fact, keep in mind occluded objects at an earlier age than Piaget thought (2–4). For example, infants look longer at events that violate the permanence and solidity of objects than they do at perceptually similar events that do not include such violations (2).

One view that accounts for infants' success in maintaining a representation of hidden objects derives from perceptual routines that track objects in space and time (5). The adult human visual system appears to maintain visual ''indices'' (6) or ''object files'' (7), which individuate visual entities by their spatial location or motion path. The mechanisms that track objects through space and time implicitly implement the principle of spatio-temporal continuity that governs our intuition and infants' reasoning about the continuing existence of occluded objects (8). Crucially, if an object becomes temporarily occluded behind another object, its index survives this transient invisibility while it points to the space hidden from view (9). This preservation of the index to an invisible object may last for seconds (10) and depends on whether the object has disappeared from view in a way that is consistent with occlusion. Invisible objects are less likely to be maintained, i.e., their ''object file'' is more likely to be discarded, when they disappear instantaneously or gradually but not consistently with the presence of a continuous occluding surface (9).

If this explanation of young infants' ability to represent hidden objects is correct, infants should be sensitive to the visual cues that indicate gradual occlusion in 3D space. Indeed, it has been demonstrated in behavioral studies that infants can recover depth information from deletion/accretion pattern of moving objects (11, 12) and may be able to interpolate trajectories of objects while they are behind visible occluders (4, 13). However, it is not known whether infants' tendency to maintain the representation of an invisible object is modulated by these cues. The present study was designed to address this question by building on preliminary evidence for the neural correlates of object processing (14). Although open to some alternative explanations, this correlate was an increase in γ-band (20–60 Hz) electroencephalogram (EEG) oscillations over right temporal cortex at times when an object was hidden from view.

We presented infants with visual stimuli that disappear either via occlusion (consistent with continued existence) or via disintegration (inconsistent with continued existence). If infants, like adults, are truly sensitive to cues of gradual occlusion and maintain or discard object files according to these cues, we would expect to see increased γ-band oscillations over right temporal cortex after an occlusion event but not after a disintegration event. Because we directly compare two types of disappearance, of which only one is compatible with an object's continued existence, we can directly assess neural activity related to object maintenance.

Methods

Thirty-six full-term 6-mo-old infants (aged 158–195 d and mean age of 171.2 d) participated in this experiment. We chose 6-mo-olds because this was the age group that displayed γ activity in right temporal areas in our previous work (14). An additional 25 infants were tested but were excluded from further analysis because of eye or body movements that resulted in recording artifacts (n = 20) or procedural error (n = 5). This study was carried out in accordance with human subjects ethical guidelines mandated by the United States National Institutes of Health and the United Kingdom Medical Research Council. Informed consent was obtained from the parents of all infant participants.

Infants were assigned to two conditions. In the visible-occluder condition (n = 21), each trial began with a stationary digital color photo of an object (visual angle = 3.8°) in the center of an otherwise uniformly gray screen (Fig. 1a). Directly to the left or the right of this photo was a black square (visual angle = 4.1°). The items remained stationary for between 600 and 1,100 ms (randomly determined). This was followed by the disappearance event that took two alternative forms: occlusion or disintegration. The occlusion event consisted of the black square moving laterally until it entirely covered the object (600 ms). The object remained occluded for 600–1,000 ms, and then the black square moved laterally away (left or right determined randomly), revealing the object (600 ms). The object remained the same on each trial unless the participant lost interest in the stimulus, in which case a new object was displayed as the occluder moved away. A sound was also played when the experimenter judged that it was needed to reengage an infant's attention to the monitor. In the disintegration event, the black square moved laterally as it did during occlusion; however, the square appeared to move behind the object rather

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Abbreviation: EEG, electroencephalogram.

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than over it. Meanwhile, as the black square moved, the object appeared to disintegrate (with pixels randomly blinking out) over 600 ms.

The invisible-occluder condition ($n = 15$) differed from the visible-occluder condition in several ways (Fig. 1b). First, there was no visible black square adjacent to the object. Second, the background was gray and had dots (<0.1° of visual angle) spaced evenly throughout the screen (0.45° apart from one another). The object appeared to be on top of these dots. As in the visible-occluder condition, each trial consisted of either an occlusion or disintegration event. The occlusion event consisted of a portion of the dotted background appearing to lift up and move laterally to cover the object. In the disintegration event, the object disappeared gradually the same way as in the visible-occluder condition, with only the dotted background remaining by the end. The time course of the invisible-occluder condition was identical to that of the visible-occluder condition with the single exception that after the period of occlusion, the next trial began with the object simply reappearing in the center of the screen (instead of an occluder appearing to move away from it). All experimental stimuli were presented with MATLAB (Mathworks, Natick, MA) by using the psychophysics toolbox extensions (15, 16).

Infants sat in a darkened room on a parent's lap, 60 cm from the stimulus monitor. The sequences were shown to the participants in a semirandom order with no event being shown more than three times consecutively. EEG was recorded by using a Geodesic Sensor Net (17) comprised of 62 electrodes distributed evenly across the scalp. The vertex electrode served as reference, and the EEG was sampled at 250 Hz. We recorded the EEG and videotaped the infants' looking behavior as long as they were willing to watch the computer screen. Trials in which infants did not look at the entire sequence were excluded from the analysis. Induced γ-band oscillatory activation was analyzed by using established procedure (18). We used a continuous wavelet transformation to single trials of EEG in each channel by 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. Unlike the calculation of evoked γ-band activation, this procedure preserves the induced high-frequency oscillatory brain activity that is time-locked but not necessarily phase-locked to the eliciting event. Because continuous occlusion is unlikely to evoke γ-band oscillations that are phase-aligned at the millisecond time range, in the present study we focused only on induced γ-band activations. Each infant contributed 26–145 (median 47) trials to their average (of a mean 90 presentations). Time-frequency activations were baseline-corrected by subtracting the average activity during the last 100 ms before the object began to disappear. We selected this time period as the baseline because it preceded any differences between the conditions and because it did not contain any occlusion or partial-occlusion events.

We compared induced oscillations over right temporal areas among the four conditions during disappearance and the ensuing 600 ms when no object was visible but either the occluder (visible-occluder condition) or the background only (invisible-occluder condition). We quantified the γ-band oscillations as the average activity at the nine electrodes over the right and left posterior temporal cortex (see Fig. 2). Electrode sites were selected based on previous work by Kaufman *et al.* (14) and on previous studies with human and nonhuman primates (19, 20).

Results

We calculated the average γ-band activation over the left and right posterior temporal region in 12 100-ms bins from the moment the object started to disappear until 600 ms after
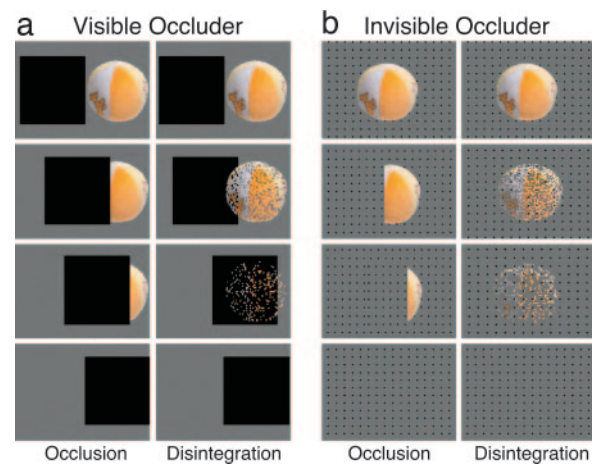

Fig. 1. Visible and invisible occluder stimuli over time. The object first appears whole and disappears via either occlusion or disintegration over 600 ms.

complete disappearance. We analyzed these activations in a four-way multivariate ANOVA with condition (invisible vs. visible occluder) as a between-subject factor, and event (occlusion vs. disintegration), hemisphere (left vs. right), and latency (12 bins) as within-subject factors. This analysis yielded only a significant interaction between hemisphere and event factors: $F (1, 34) = 4.765, P < 0.05$. To resolve this interaction, we conducted three-way multivariate ANOVAs within the two hemispheres. On the left side, no significant effect was found. In contrast, we found a significant main effect of event [$F (1, 34) = 6.608, P < 0.02$] on the right side, indicating that the γ-band activation at right temporal leads was higher during occlusion than it was during disintegration. There was no interaction with condition, suggesting that the effect was equally strong in both conditions.

Although this statistical analysis did not indicate variation of the γ-band activation difference over time, we were interested in the temporal progression of the effect. Separate two-way ANOVAs in the 12 time bins yielded significant main effect of events during 7 of the 12 time bins, strongest within the 200 ms right after complete disappearance ($Fs > 7.5$, $Ps < 0.01$), weaker in earlier and later time bins ($Fs > 4.3$, $Ps < 0.05$; see Fig. 2).

Discussion

The results of this study are consistent with the idea that infants' perception of objects relies on the same visual cues as the object tracking mechanisms described in adults (9). Right temporal γ-band oscillatory activity was affected differently when the visual cues indicated the continuing presence of an object from when they signaled disintegration. This difference was also evident when the occluder responsible for the disappearance of the object was itself invisible. Crucially, the difference in levels of oscillatory activity was strongest during a period in which there were no visible differences between the two conditions. In other words, infants' oscillatory brain activity after complete disappearance responded not to the current state of the object but to its perceptual history.

In addition to the above conclusion, the present study significantly extends the preliminary report of an association between γ-band EEG activity and object maintenance in infants (14). Specifically, the present results address the question of whether infants in the previous studies would best be characterized as exhibiting "object permanence" or object memory. This previous work showed that there was a clear neural correlate of object
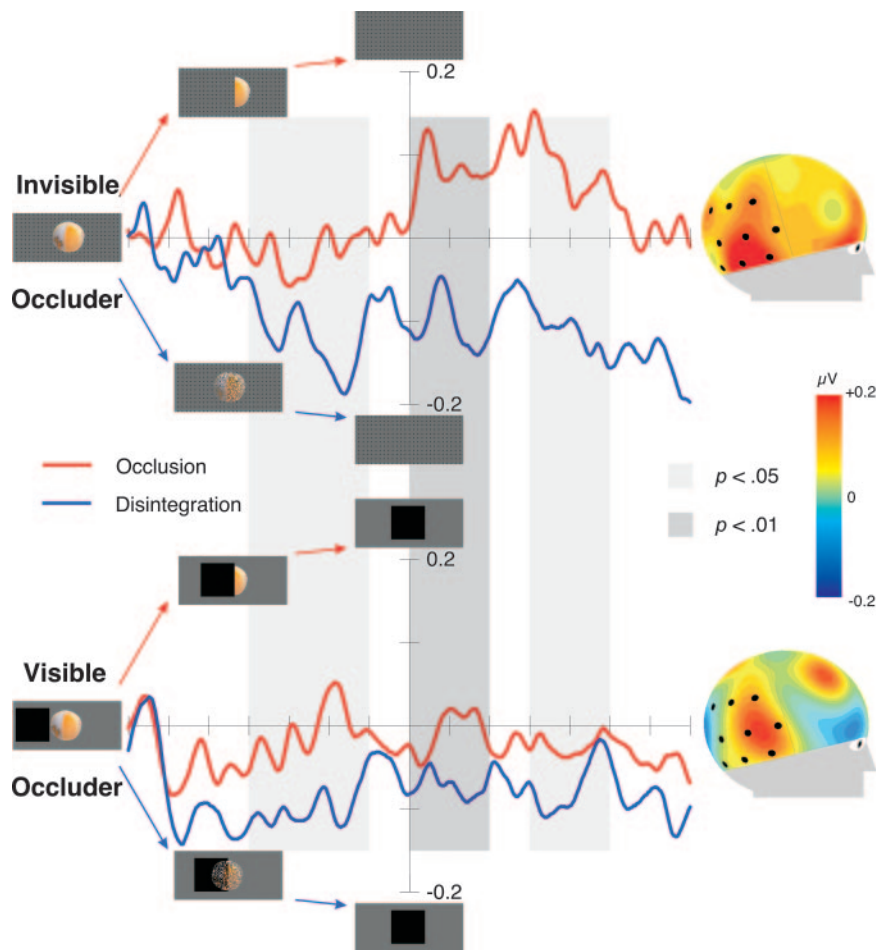
Fig. 2. γ-Band activity. (*Left*) Time-frequency analysis of the average EEG at four electrodes over the right temporal cortex during and after the object's disappearance. Gray depicts areas of significant statistical difference. There was significantly greater γ activity in the occlusion event than in the disintegration event before and just after disappearance. (*Right*) Topographical map the between-event difference (occlusion–disintegration) of γ-band (20–60 Hz) activity in the period after the disappearance of the object.

memory as evidenced by an increase of γ oscillatory activity after an object's occlusion (i.e., a train entering a tunnel). Yet, the findings of that study could not definitively distinguish between object permanence (a persistent representation of continued existence for an unseen object) and a memory trace for an object that had simply disappeared. That is, it could plausibly be argued that infants did not represent the train's continued existence, but rather simply remembered the most interesting element of the stimulus array after its disappearance. The present study demonstrates that the neural activity arising after an object's disappearance is specifically related to its mode of disappearance. Objects that disappear in a manner inconsistent with occlusion induce decreased γ oscillations relative to objects that disappear in a way that is consistent with occlusion.

We observed no significant difference between the visible and invisible occluder conditions, which is consistent with the perceptual "tunnel effect" observed in adults (21). This result suggests that, under our testing conditions, 6-mo-old infants will maintain objects (or not) on the basis of their deletion pattern: disappearing via a single linear boundary is important, but a visible occluding object or surface is not required. This conclusion is consistent with behavioral studies indicating that, although 2 mo after birth infants have difficulty in perceiving occlusion of any form, by 6 mo (3) or earlier (4), the perception of object continuity after occlusion is robust and occurs under a wide range of conditions. With further development and expe-

rience of everyday objects, infants may go on to develop more abstract representations of objects under occlusion, such as identity (22). Future studies could determine whether object maintenance in infants depends on disappearance via a single coherent edge by examining "reverse occlusion" conditions (9).

One issue raised by the present findings is whether the γ-band EEG effect is a correlate of object processing or a neural basis for it. By the former account, the observed γ-band EEG changes could reflect differences in attention in the different conditions. By the latter account, high-frequency oscillations in the temporal region may support active representations of objects that are not currently directly visible (20).

We suggest that the findings of the present study and of previous work support the view that γ oscillations provide a basis for active representations. First, the results of Tallon-Baudry's work (20, 23) with adults are analogous to our results in that there was greater γ-band oscillatory activity in right-temporal cortex when adult subjects were told to keep an object in mind despite the fact that their task required them to attend to both the object-memory condition and the condition in which no object memory was necessary. Second, the results of Kaufman *et al.* (14) did include attentional differences, but in a way that was inconsistent with the observed γ-band effects being related to attention. In the behavioral part of that study, infants were most interested in an impossible disappearance event. However, in the EEG portion of the study, γ activity increased as soon as the train entered the tunnel and before

the infants were shown the outcome of the event. That is, regardless of whether the event turned out to be an impossible disappearance or a possible appearance, γ-band activity increased whenever a hidden object was present.

Thus, we suggest that γ-band EEG over right temporal leads reflects underlying neural mechanisms that are important for the tracking of objects in infants. Future work may determine the role, if any, of γ EEG in maintaining detailed representations of objects, including their identity.

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