Attentional dynamics of infant visual foraging

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Young infants actively gather information about their world through visual foraging, but the dynamics of this important behavior is poorly understood, partly because developmental scientists have often equated its essential components, looking and attending. Here we describe a method for simultaneously tracking spatial attention to fixated and nonfixated locations during free looking in 12-week-old infants using steady-state visual evoked potentials (SSVEPs). Using this method, we found that the sequence of locations an infant inspects during free looking reflects a momentary bias away from locations that were recently the target of covert attention, quickly followed by the redirection of attention—in advance of gaze—to the next target of fixation. The result is a pattern of visual foraging that is likely to support efficient exploration of complex environments by facilitating the inspection of new locations in real time.

steady-state visual evoked potential amplitude modulation | inhibition of return

From birth onward, infants gather information about their world through aggressive visual foraging, a behavior with obvious adaptive significance that provides important visual input during a period of rapid brain development (1–3). Despite its importance, early visual foraging remains poorly understood, partly because developmental scientists have often equated its essential components, looking and attending. That is, the target of spatial attention is generally inferred from the direction of gaze, and the magnitude of attention is inferred from the duration of fixation.

For more than half a century, these simplifying assumptions linking gaze and attention have led to enormous progress in understanding the minds of infants (4). However, looking and attending are not the same. In fact, the standard experimental paradigm used to study attention in adults requires them to maintain visual fixation at a central location while directing attention to peripheral locations (5). In infants, changes in heart rate following the onset of a visual stimulus reflect systematic changes in attention manifested by variation in distractibility during continuous fixation of the stimulus (6). Importantly, adaptations of Posner's spatial cueing paradigm for adults (7), in which a brief visual cue at a peripheral location influences the latency of subsequent eye movements to that location, indicate that shifts of attention can occur without shifts of gaze by 4 mo of age (8–11).

The distinction between looking and attending is critical in visual foraging. That is because the heart of visual foraging lies precisely in the dynamic coupling, on a short time scale, between the spatial allocation of attention and the redirection of foveal vision in a way that facilitates discovery and learning in a complex environment. If we are to understand infant visual foraging, we must discover how the allocation of covert attention to multiple peripheral locations changes during free looking, and whether those changes in covert attention are related to where gaze will be directed next. To do this, we must simultaneously track attention to nonfixated locations, as well as fixated locations, in relation to spontaneous shifts of gaze.

Research with adults suggests that attentional modulation of ongoing, stimulus-driven brain activity might provide a way to track the allocation of covert attention during infant visual foraging. In adults, flickering visual stimuli drive oscillations in the EEG called steady-state visual evoked potentials (SSVEPs) (12). SSVEPs driven by spatially localized stimuli are most prominent in posterior regions over visual cortex where they are generated (13). Importantly, attention directed to a fixated or nonfixated stimulus increases the amplitude of the associated SSVEP (14, 15). Attentional modulation of SSVEP amplitude is correlated with changes in early components of the event-related potential, especially N1 (16), and is strongest over temporooccipital and parietooccipital regions (14, 17). The increase in SSVEP amplitude is thought to be mediated by top–down effects of attention on the contrast gain, response gain, and response synchronization of visual neurons (18–20).

SSVEPs are also detectable in young infants. They have been used to study visual acuity and cortical function (21, 22), the behavioral and brain response to variation in stimulus temporal frequency (23), the detection of optic flow (24), and the consequences of perinatal brain damage (25). However, to date, there have been no reports of attentional modulation of SSEVPs in infants.

Therefore, in this report we first show that attention rapidly modulates SSVEP amplitude in 12-wk-old infants (experiment 1). We then use SSVEPs to expose the attentional dynamics of infant visual foraging by tracking the allocation of covert attention to nonfixated objects before spontaneous gaze shifts during free looking (experiment 2).

Results

Experiment 1: Attentional Modulation of SSVEPs. In experiment 1, we manipulated infants' attention while they looked at a yellow toy duck that flickered at 8 Hz. The flicker drove SSVEPs that were readily detected in the EEG by scalp electrodes in temporo- and parietooccipital regions (Fig. 1). While infants looked at the duck, we increased attention to it by rotating it back and forth for 2 s. We used stimulus motion because its effect on attention in early infancy is well documented (26). Active events (object rotation) and control events (no object rotation) occurred in a random order at variable intervals. We measured (*i*) the relative amplitude of the SSVEPs driven by the flickering object (EEG amplitude at the flicker frequency divided by the amplitude interpolated between the adjacent frequencies); (*ii*) the phase delay of SSVEP peak amplitude with respect to flicker onset; and (*iii*) amplitude-independent phase locking between SSVEP and object flicker (27) in the 2-s period before event onsets and the 2-s period after event offsets (not during events). Based on the attentional modulation of SSVEPs found in adults, we expected that the relative amplitude of infants' SSVEPs would increase following active but not control events.

Event type (active, control) × period (2-s period preceding event onset, 2-s period following event offset) × hemisphere × sex analyses of variance were conducted on SSVEP relative amplitude, phase delay, and phase locking. There were no main or interaction effects involving sex (all $P > 0.05$). Therefore, sex was not included in the analyses reported below.
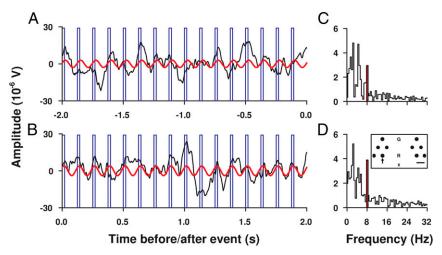
Fig. 1. Representative EEG, amplitude spectra, and SSVEPs from one infant before the onset and after the offset of an active event in experiment 1. (*A* and *B*) EEG (thin black lines) recorded from a temporooccipital electrode (arrow in boxed inset in *D*) during the 2-s period before the onset (*A*) and after the offset (*B*) of an active event, and a sinusoidal representation of the SSVEP (thick red lines) derived from Fourier analysis of the EEG. Square waves (thin blue lines) indicate the timing and duration of the LED on-states that generated the object flicker. (*C* and *D*) Amplitude spectra for the EEG in *A* and *B*, respectively. Filled red bars indicate the amplitude at the flicker frequency (8 Hz). The boxed inset in *D* indicates the location of the recording electrodes (filled circles), the reference (R) and ground (G) electrodes, and the inion (x); the scale bar is 2.3 cm. The most anterior recording electrodes correspond approximately to P3 and P4 in the 10–20 system (49); the most lateral electrodes correspond approximately to T5 and T6.

SSVEP relative amplitude increased more in the 2-s period following the offset of active than control events (Fig. 2*A*), as indicated by a significant event type × period interaction, $F(1,14) = 9.11$, $P = 0.009$. SSVEP relative amplitude increased substantially following the offset of active events (1.50 ± 0.28–2.35 ± 0.43, mean ± SE), $t(14) = 3.25$, $P = 0.006$, but not following the offset of control events (1.50 ± 0.28–1.51 ± 0.16), $t(14) = 0.02$, $P = 0.98$. There were no other significant main or interaction effects for relative amplitude, all $P > 0.05$.

SSVEP phase locking to the flicker also increased more in the 2-s period following the offset of active than control events (Fig. 2*C*), as indicated by a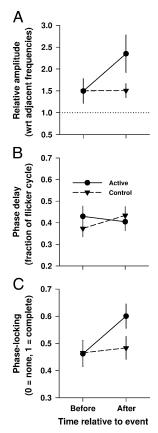 significant event type × period interaction, $F(1,14) = 5.01$, $P = 0.042$. Phase locking increased following the offset of active events (0.46 ± 0.05–0.60 ± 0.04), $t(14) = 2.97$, $P = 0.01$, but not following the offset of control events (0.47 ± 0.05–0.48 ± 0.04), $t(14) = 0.41$, $P = 0.69$. The increased phase locking after active events also resulted in a main effect of period, $F(1,14) = 4.80$, $P = 0.046$. In addition, there was an event type × hemisphere interaction, $F(1,14) = 5.66$, $P = 0.032$, which was due to a difference in phase locking between the right and left hemispheres before the onset of active events (0.53 ± 0.05 in the right hemisphere vs. 0.40 ± 0.06 in the left), $t(14) = 2.60$, $P = 0.021$, but not after (0.63 ± 0.05 in the right vs. 0.57 ± 0.06 in the left), $t(14) = 0.91$, $P = 0.38$, which was likely a spurious effect. There were no other significant main or interaction effects for phase locking, all $P > 0.05$. There were no significant main or interaction effects for SSVEP phase delay (Fig. 2*B*), all $P > 0.05$.

In sum, briefly increasing infants' attention to an object while they looked at it resulted in increased amplitude of the SSVEP driven by the object and increased phase locking of the SSVEP to the object flicker.

Experiment 2: Dynamic Allocation of Covert Attention to Nonfixated Objects. Having demonstrated that attention modulates the amplitude of infant SSVEPs, we next used SSVEPs to track the dynamic allocation of covert attention to multiple, nonfixated objects in the seconds before spontaneous shifts of gaze during free looking. In contrast to experiment 1, we did not manipulate attention in experiment 2. The stimulus objects were three yellow toy ducks, arranged horizontally, which flickered at different rates (8, 10, or 12 Hz) so that the corresponding SSVEPs could be distinguished. EEG was recorded as in experiment 1 (Fig. 1). The relative amplitude, phase delay, and phase locking of the SSVEPs driven by each object were measured in the four 500-ms

Fig. 2. SSVEP measures (mean ± SEM, n = 16) during the 2-s periods before the onset and after the offset of active and control events in experiment 1. (*A*) Relative amplitude of SSVEP driven by object flicker. (*B*) Phase delay of SSVEP with respect to object flicker. (*C*) Phase locking between SSVEP and object flicker.

intervals preceding spontaneous gaze shifts from the fixated center object to the left or right peripheral objects. Based on the results from adults and monkeys cited above, we expected to find evidence of covert attention to the nonfixated objects, including increased attention to the target of upcoming gaze shifts shortly before the onset of eye movement.

Peripheral object (to-be-fixated, other) × interval (successive 500-ms intervals) × hemisphere × sex analyses of variance were conducted on SSVEP relative amplitude, phase delay, and phase locking. Because visual sensitivity varies with retinal eccentricity (28), the SSVEP driven by the fixated object was analyzed separately with interval × hemisphere × sex analyses of variance. There were no main or interaction effects involving hemisphere or sex (all $P > 0.05$) in either set of analyses. Therefore, hemisphere and sex were not included in the analyses reported below. Where relevant, the reported P values reflect the Greenhouse–Geisser correction for nonsphericity.

The relative amplitude of the SSVEPs driven by the peripheral to-be-fixated and other objects showed opposite curvilinear changes in the 2 s before gaze shifted from the center object (Fig. 3A), as indicated by a peripheral object × interval interaction, $F(3,96) = 4.12$, $P = 0.01$, with a strong quadratic component, $F(1,32) = 9.98$, $P = 0.003$. There were no main effects of peripheral object or interval, both $P > 0.05$. There was no effect of interval on SSVEP relative amplitude for the fixated object, $P > 0.05$. There were no significant effects on SSVEP phase delay
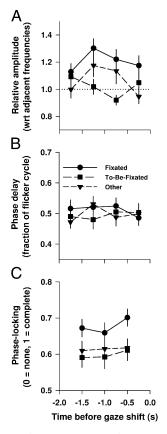
(Fig. 3B) or phase locking (Fig. 3C) for either the fixated or peripheral objects, all $P > 0.05$.

Notably, the relative amplitude of the SSVEP driven by the to-be-fixated object first decreased (1–2 s before gaze shifted), while that of the other object increased, as indicated by a peripheral object × interval interaction over the first two intervals, $F(1,32) = 5.53$, $P = 0.025$, with no main effects of object or interval, $P > 0.05$. Then, in the last 500 ms before gaze shifted the trends reversed, and the amplitude of the SSVEP driven by the to-be-fixated object increased while that of the other object decreased, as indicated by a peripheral object × interval interaction over the last two intervals, $F(1,32) = 7.37$, $P = 0.011$, with no main effects of object or interval, $P > 0.05$. Between these changes, the amplitude of the SSVEP driven by the other object exceeded that of the to-be-fixated object, as indicated by a main effect of object during the middle two intervals, $F(1,32) = 8.15$, $P = 0.008$, with no main effect of interval and no object × interval interaction, $P > 0.05$.

In sum, during free looking, infants covertly attended to peripheral objects before they spontaneously shifted gaze to one of them. Their covert attention to the next target of fixation increased before eye movement began, and they looked away from the object that was recently the dominant target of covert attention.

Discussion

The results of experiment 1, in which 12-wk-old infants' attention to an object was manipulated while they looked at the object, demonstrate that attention modulates ongoing, stimulus-driven brain activity in the early stages of visual processing during continuous looking. The finding that attention enhanced SSVEP phase locking to the stimulus flicker suggests that attentional modulation of SSVEP amplitude in infants, as in adults, may in part reflect increased response synchrony among neurons in visual cortex. However, some of the measured phase locking associated with increased SSVEP amplitude after active events may also reflect proportionally less interference from variable-phase background activity not driven by the stimulus but fluctuating at the flicker frequency. It is unclear whether other mechanisms by which attention influences early visual processing, such as changes in the contrast and response gain of visual neurons (29–31), which are thought to mediate the effects of attention on SSVEP amplitude in adults (18–20), also contribute to the attentional modulation of SSVEP amplitude in infants. Regardless of the specific mechanisms involved, the demonstration of attentional modulation of SSVEP amplitude in infants allowed us to examine the attentional dynamics of visual foraging in experiment 2.

The results of experiment 2, in which SSVEPs driven by nonfixated objects were measured, reveal two previously unknown components of attentional dynamics during infant visual foraging. First, infants' covert attention to the target of an upcoming saccadic eye movement begins to increase in the 500 ms before gaze shifts. This redirection of spatial attention in advance of actual eye movement is consistent with extensive evidence from human and nonhuman adults, which has shown attentional effects on visual neurons whose receptive fields contain the not-yet-fixated target and enhanced perceptual performance at the location (32–38). Similar effects on perception in young infants, if they occur, are likely to facilitate the inspection of new locations during visual foraging. Furthermore, increased responsiveness of visual neurons to input from a peripheral location during free looking might help overcome the difficulty infants at this age have unlocking gaze from its current location ("sticky fixation") (9, 39, 40) by facilitating the disinhibition of saccadic eye movements (41).

The second component of attentional dynamics revealed by experiment 2 is the link between the allocation of covert spatial

Fig. 3. SSVEP measures (mean ± SEM, $n = 33$) during the 2-s period before spontaneous shifts of gaze in experiment 2. (A) Relative amplitude of SSVEPs driven by the center (fixated) object and the peripheral (to-be-fixated, other) objects during successive 500-ms intervals. (B) Phase delay of SSVEPs with respect to object flicker during successive 500-ms intervals. (C) Phase locking between SSVEPs and object flicker calculated across sequential pairs of 500-ms intervals.

attention 1–2 s before the end of a look and the direction of the upcoming gaze shift. When infants spontaneously shift their gaze, they look away from the previously nonfixated peripheral object that 1–2 s earlier had been the primary target of covert attention and toward the previously nonfixated peripheral object that had not been the target of covert attention. That is, spontaneous shifts of gaze during free looking by 12-wk-old infants are consistent with the mechanism of inhibition of return (IOR). IOR has been reported in older infants when gaze shifts are triggered by the appearance of a peripheral stimulus following exogenous cues (11, 42, 43), but not during free looking when shifts of gaze are endogenously triggered. IOR has been extensively studied in adults and animal models, and there is compelling evidence that it facilitates visual foraging by increasing the likelihood that new locations will be inspected (7, 44, 45).

Taken together, the present experiments reveal the dynamic integration of basic mechanisms linking attention and gaze during free looking in young infants. The sequence of locations an infant inspects reflects a momentary bias away from locations that were recently the target of covert attention, quickly followed by the redirection of attention to the next target of fixation before eye movement begins. The result is a pattern of visual foraging that is likely to support efficient exploration of complex environments by facilitating the inspection of new locations in real time.

Efficient visual foraging, in turn, is likely to have important consequences for young infants learning about their world during this period of rapid brain maturation. In particular, the early integration of IOR and the redirection of attention ahead of gaze during free looking may provide a foundation for the development of more general foraging behavior, which demands the coordination of body movement with attention and gaze. For example, the efficient integration of attention and gaze by 12 wk may provide key support for the rapid emergence of skilled reaching and grasping in the following weeks (46, 47), as infants extend their exploration of the environment and increase the multisensory richness of their experience in it. More generally, the dynamic coupling of motor activation with attention and gaze appears to reflect the embodied nature of early cognition (48) and may facilitate the development of adaptive behavior more broadly, possibilities that merit investigation with methods that allow attention, gaze, and body movement to be tracked simultaneously under natural conditions.

Materials and Methods

Experiments were approved by the Cornell University Institutional Review Board for Human Participants. Informed consent was obtained from a parent for each infant participant.

Experiment 1: Attentional Modulation of SSVEPs. *Participants.* Usable data were obtained from 16 healthy infants (9 males) with no known sensory or motor problems. Birth weights were 2.47–4.45 kg (median = 3.32 kg), gestational ages were 37–42 postmenstrual weeks (median = 40 wk), and postnatal ages at the time of study were 81–90 d (median = 84 d). An additional 16 infants were studied but did not provide usable data due to fussiness (*n* = 8), insufficient looking (*n* = 4), poor EEG signals (*n* = 2), or technical errors (*n* = 2).
Stimulus. The stimulus object was a commercially available soft plastic yellow toy duck mounted in front of a black felt screen 64 cm from the infant's face. The object subtended 7 × 6 degrees of visual angle (horizontal × vertical) and contained four light-emitting diodes (LEDs; Radio Shack, 276–320). Two of the LEDs (left and right sides of the body) were always on. To drive the SSVEP, the other two LEDs in the object (center of the body and head) cycled continuously and synchronously between on and off at 8 Hz with a duty cycle of 0.17. Pilot testing indicated that this duty cycle was less distracting than longer duty cycles while effectively driving oscillations in the EEG at the flicker frequency without strong harmonics. The luminance difference between the on and off states (the effective flicker) was 58 cd/m², and the ambient light level at the infant's face was 10 lx.
Procedure. Infants sat upright in an infant seat with lateral and back support as needed. While infants looked at the object, the data acquisition program

generated active and control events in a random order at variable 8–12-s intervals and stored their onsets and offsets along with the other acquired data for later analysis. Active events generated by the data acquisition program triggered back-and-forth rotation of the stimulus object (±45 deg in the plane perpendicular to the infants' line of sight) for 2 s at 3 cycles per s. Control events generated by the data acquisition program did not trigger rotation of the stimulus object, but identified segments of the data against which to compare any changes in the SSVEP measures following active events. Data collection continued until the infant became disinterested or fussy, which occurred after 108–923 s (median = 267 s). For 3 infants, more than one attempt was required to obtain usable data.
Data acquisition. A small cloth cap containing the scalp electrodes (Compumedics Ag/Ag/Cl sintered Quik-Cap electrodes) and conductive gel (Electro-Gel, Electro-Cap International) was held in place on temporo- and parietooccipital regions (see inset in Fig. 1*D*) with a latex-free gauze head band (Surgilast 5.5). The scalp was not abraded. Five recording electrodes were used on each hemisphere to increase the chance of obtaining usable EEG. Impedance was below 10 K ohms for electrodes that provided usable signals. EEG signals were amplified with a gain of 50,000 and band-pass filtered with 12 db per octave cutoffs at 1 and 100 Hz and a notch filter at 60 Hz (Grass Model 15), then digitized at 256 Hz with 12-bit resolution (National Instruments 6023E). Corneal reflections of the stimulus object were video recorded (Cohu 4910) at 59.94 fields per s for offline confirmation of visual fixation.
Data reduction. Events were used if the infant fixated the object continuously from at least 2 s before event onset to at least 2 s after event offset, and usable EEG was available from both hemispheres. Continuous fixation was indicated when the object's corneal reflection remained centered over the infant's pupil in each successive field of the video recording. Leads were excluded if EEG amplitude exceeded ±100 μV for more than 5% of the 2 s preceding event onset or the 2 s following event offset. Because many infants lost interest in the object quickly, we analyzed the first usable active and control events, all of which had at least two usable leads from each hemisphere (median = 4.5).
Data analysis. EEG amplitude and phase spectra were calculated separately for each usable lead during the 2 s preceding event onset and the 2 s following event offset using the fast Fourier transform implemented in LabVIEW 8.5 (National Instruments). SSVEP relative amplitude was defined as EEG amplitude at the flicker frequency (8 Hz) divided by the interpolated (linear) amplitude between the frequencies adjacent to the flicker frequency (7.5 and 8.5 Hz), which corrects for changes in baseline EEG amplitude and differences in signal strength between recording sites. SSVEP phase delay was defined as the fraction, φ, of a flicker cycle ($0 < \varphi \leq 1$) by which peak SSVEP amplitude followed flicker onset. Phase locking between SSVEP and object flicker was calculated across the four 500-ms intervals in the 2 s before event onset and the four 500-ms intervals in the 2 s after event offset using the method of Tallon-Baudry et al. (27), which yields an estimate between 0 (no phase locking) and 1 (complete phase locking) that does not depend on signal amplitude and is robust against artifacts. By this method, phase locking is calculated as the magnitude of the complex average over intervals of the normalized complex amplitude in each interval. The amplitude, phase-delay, and phase-locking results from each usable lead were averaged separately for the left and right hemispheres.

Experiment 2: Dynamic Allocation of Covert Attention to Nonfixated Objects.
Participants. Usable data were obtained from 33 healthy infants (16 males) with no known sensory or motor problems. Birth weights were 2.38–4.34 kg (median = 3.52 kg), gestational ages were 37–41 postmenstrual weeks (median = 40 wk), and postnatal ages at the time of study were 78–88 d (median = 84 d). An additional 13 infants were studied but did not provide usable data due to fussiness (*n* = 4), insufficient looking (*n* = 5), poor EEG signals (*n* = 2), or technical errors (*n* = 2).
Stimuli. The stimulus objects were three commercially available soft plastic yellow toy ducks mounted in a horizontal array in front of a black felt screen 56 cm from the infant's face. The center object subtended 11 × 10 deg visual angle (horizontal × vertical). The left and right objects subtended 7 × 6 deg and their inside edges were 11 deg from the outside edges of the center object. The center object was larger to maximize infants' looking time to it. Each object contained five LEDs (Radio Shack 276–320). Three of the LEDs (left and right sides of the body and center of the head) were always on. The additional LED (compared with experiment 1) was used to enhance the corneal reflections of the objects to facilitate coding of gaze. To drive the SSVEPs, the other two LEDs in each object (center of the body and head) cycled continuously and synchronously between on and off with a duty cycle of 0.17. Each object flickered at a different rate (left and right objects at 8 or 10 Hz, randomly assigned; center object at 12 Hz) so the corresponding

SSVEPs could be distinguished. The luminance difference between the on and off states was 58 cd/m^2 for the left and right objects and 35 cd/m^2 for the center object, and the ambient light level at the infant's face was 13 lx.

Procedure. Infants sat upright in an infant seat with lateral and back support as needed. Infants were allowed to look freely at the three objects until they became disinterested or fussy, which occurred after 73–515 s (median = 222). For seven infants, more than one attempt was required to obtain usable data.

Data acquisition. Data acquisition methods were the same as experiment 1.

Data reduction. Looks at the center object that ended with a spontaneous gaze shift to the left or right object were used if visual fixation of the center object was continuous (i.e., its corneal reflection remained centered over the infant's pupil) for at least 2 s preceding the gaze shift, the shift to one of the peripheral objects took no more than 500 ms, and usable EEG was available from both hemispheres. Leads were excluded if EEG amplitude exceeded ±100 µV for more than 5% of any of the four 500-ms intervals in the 2-s period preceding the gaze shift. The timing of the gaze shifts was determined independently by two coders. The difference between their determinations was 0 or 1 video field (17 ms) for 95% of the shifts (median = 0, mean = 0.8). Differences were resolved before the data were analyzed. Across all infants, the number of center looks meeting the above criteria ranged from 1 to 14 (median = 4); 97% of those center looks had at least 2 usable leads from each hemisphere (median = 5).

Data analysis. EEG amplitude and phase spectra were calculated separately, as in experiment 1, for each usable lead during each of the four 500-ms intervals in the 2-s period preceding usable gaze shifts from the center to the left or right object. For each object, SSVEP relative amplitude was defined as EEG amplitude at the flicker frequency (8, 10, or 12 Hz) divided by the interpolated (linear) amplitude between 6 and 14 Hz (the frequencies adjacent to the flicker frequencies). SSVEP phase delay was defined as in experiment 1. Phase locking between SSVEP and object flicker was defined as in experiment 1 and calculated across the three sequential pairs of four 500-ms intervals. For each center look, the amplitude, phase delay, and phase-locking results from each usable lead were averaged separately for the left and right hemispheres. The contralateral hemisphere was used for the right and left objects; both hemispheres were used for the center object. The results from multiple center looks by an infant were averaged.

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