10 Investigating event-related oscillations in infancy

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Two general approaches have been taken to the electrophysiological study of infant brain function: event-related and evoked potentials (see Chapters 2–8 of this volume) and resting EEG (see Chapters 8 and 9). In this chapter, we introduce a third (intermediate) approach that we term “event-related oscillations”. Briefly, event-related oscillations (EROs) are bursts of EEG at particular frequencies that are approximately time-locked to task or stimulus presentation events. For this reason, they are taken to reflect oscillatory activity in the brain related to specific task-relevant computations. While there is a growing literature on EROs in adults, particularly with respect to high-frequency (gamma-band) bursts, the approach has only just begun to be applied to infants. In the first section of this chapter we initially describe (1) how EROs can be analyzed from raw EEG data, (2) the potential pitfalls and sources of artefact with EROs, and (3) issues of experimental design. Following this, we review evidence from two areas where we have adopted the ERO approach to study infants’ perception and processing of objects. Finally, we discuss potential future avenues for research on infant cognition with EROs.

ERO ANALYSIS AND METHODS

Neurons have the inherent capacity to spontaneously produce oscillatory activity at frequencies above 20 Hz (Llinás, 1988). Sensory stimuli in several modalities (visual, auditory, olfactory) can elicit such oscillations in the gamma-band frequency range (20–80 Hz, most commonly around 40 Hz). When a large number of neurons fire synchronously at the same frequency, these oscillations can be recorded from the scalp by conventional EEG techniques. Recently several laboratories have started to analyze human EEG signals in terms of bursts of oscillatory activities and interpret them in relation to the cognitive functions that the participants performed while their brainwaves were recorded (e.g., Tallon-Baudry & Bertrand, 1999).

The EEG signal can be analyzed both in the time domain and in the frequency domain. Analysis in the frequency domain (see Chapters 8 and 9)
yields a description of the signal in terms of relative power or amplitude in various frequency bands, each associated with different brain states. Analysis of EEG in the time domain reveals dynamics of brain activity in the millisecond timescale and its relation to cognitive and/or neural events. However, oscillatory neural activities are usually restricted in both time and frequency content; therefore, analyses only in the time or frequency domain tend to be blind to them. To reveal task-related bursts of oscillatory activities, especially if they occur at higher frequency ranges, we need to perform a time–frequency analysis that tracks how amplitude (or power) varies at different frequencies over time. The relations among time domain, frequency domain, and time–frequency analyses are illustrated in Figure 10.1.

There are several ways to perform a time–frequency analysis on EEG signals. From a mathematical point of view, the best method is to perform a wavelet analysis (Samar, Bopardikar, Rao, & Swarz, 1999). The most

![Figure 10.1](image-url)  
**Figure 10.1** Time–frequency analysis. A segment of EEG recording can be analyzed both in the time domain (horizontal trace) and in the frequency domain (vertical trace). However, time–frequency analysis of the same recording (contour map) reveals oscillatory activities that are restricted both in time and in frequency domain.
commonly used technique in human EEG research involves a continuous wavelet transformation, with Morlet wavelets appropriately scaled within the frequency range to be explored (Tallon-Baudry, Bertrand, Delpuech, & Pernier, 1996). The result of this transformation is a time-varying function of amplitude power along the frequencies of interest. When these time–frequency functions are interpreted in relation to cognitively important events whose timing can be determined accurately (e.g., stimulus onset, eye-movements), they are called event-related oscillations (EROs).

There are two types of EROs: evoked EROs are oscillations that are phase-locked to the corresponding event and can be recovered from averaged, non-filtered event-related potential (ERP) waveforms; induced EROs are not phase-locked and are obtained from raw EEG before averaging (Figure 10.2). Evoked oscillations are usually short-latency responses, while induced oscillations can occur both close to and farther away from the corresponding events (Herrmann & Mecklinger, 2000). Time–frequency analyses can also be applied to explore connectivity across brain regions (Lachau, Rodriguez, Martiniere, & Varela, 1999). Long-range phase synchrony between oscillatory activities at two recording sites probably reflects temporary functional connectivity (Varela, Lachaux, Rodriguez, & Martiniere, 2001). Coherence analyses that take temporarily restricted oscillatory activities into account are being developed in various laboratories (e.g., Lachau et al., 2002) but, to our knowledge, have not been applied to infant EEG yet.

EROs are particularly useful tools to study infants’ cortical responses for several reasons. Induced EROs may be less sensitive to latency variability than conventional ERPs, and infants’ electrophysiological responses to stimuli are known to vary more than those of adults. Also, unlike ERPs, EROs can reflect relatively sustained activation in situations where cognitive processing of certain events cannot be expected to be time-locked well to the event. For example, in a study on “object permanence” that we will discuss later, we found a sustained gamma-band response recorded over temporal regions while 6-month-old infants watched a display in which an object was occluded.

Time–frequency analyses are similarly, if not more, sensitive to electrical and behavioural EEG artefacts than conventional ERPs. Changes in electrical connectivity or sudden eye-movements that create sharp voltage jumps in the recording produce high-amplitude transient responses in a wide range of frequencies. Similarly, muscular artefacts and mains electrical noise may add sustained high-frequency component to the signal, which is usually filtered out in ERP analyses. Thus, any activity that extends widely in either the temporal or the frequency domain should be treated with suspicion. To avoid such potential artefacts in our own data (1) we video record participants’ faces during sessions to allow later rejection of trials with eye or jaw movement, (2) we record EOG from electrodes around the eye to allow identification of saccades, and (3) we have created time–frequency plots from experiments in which we actually induce saccades from infants (see, e.g., Csibra, Tucker, & Johnson, 2001) and we have simulated possible artefacts from mains and
Figure 10.2 Calculating evoked and induced EROs. Induced EROs are computed from raw EEG segments and therefore they are insensitive to phase variability across trials. In contrast, evoked EROs are calculated from averaged ERPs and retain only phase-locked oscillations.
video screens. From the latter approach we have gained experience of the time–frequency signatures of these sources of activity.

**PERCEPTUAL “BINDING”**

Our perception of coherent, unified objects depends crucially on the brain’s ability to ‘bind’ together various features coded by early stages of vision (Treisman & Schmidt, 1982). One promising recent line of research with adults has demonstrated a close association between gamma-band oscillations of neural activity and visual binding, pointing to a central role for oscillatory neural circuits. This link between oscillations and binding was first evident in recordings from single cells in monkey and cat cortex (Singer & Gray, 1995), but more recent studies have employed electroencephalography (Müller et al., 1996; Tallon-Baudry et al., 1996) and behavioural techniques (Elliott & Müller, 2000) to reveal similar phenomena within the adult human brain. Psychophysical experiments have demonstrated that presentation of stimuli in synchrony with a 40 Hz oscillation helps temporal binding, while electrophysiological studies provided evidence for gamma-band bursts of neural activity contingent on the experience of object perception.

In a previously unrelated line of research, experimenters have sought to determine the extent of object-processing abilities in young infants, and the features and cues they rely on when parsing visual scenes into objects (Kellman & Banks, 1998). One of the ways in which infants’ object-processing abilities have been probed is to assess whether or not they are able to perceive static illusory objects composed from a number of separate elements (Bertenthal, Campos, & Haith, 1980; Kavsek, 2002). Results from behavioural studies indicated that while infants of 7 months and older perceive static illusory objects such as the Kanizsa figures, infants of 5 months or less may not. However, more recent studies have suggested that the developmental transition at around 6 months of age is related more to the emerging ability to complete partly occluded objects and to recover depth in illusory figures than to perceiving illusory figures per se (Csibra, 2001; Ghim, 1990; Kavsek, 2004). Studies of object processing in infants have relied on behavioural paradigms such as habituation or preferential looking. Gamma-band electrophysiological responses may provide a more direct measurement for perceptual binding and/or object completion in the infant brain.

With these factors in mind, we (Csibra, Davis, Spratling, & Johnson, 2000) investigated binding-related gamma oscillations in infants while they viewed static illusory objects. To elicit binding-related activation, we presented infants with a Kanizsa subjective-figure pattern (see left side of the first row of Figure 10.3), known to yield the percept of an illusory square, that is sensitive to the binding of the separate “pacmen” elements within the stimulus into a coherent object (Kanizsa, 1976). The Kanizsa Square is therefore an ideal candidate for measuring binding effects and has formed the basis
Figure 10.3 Induced gamma-band oscillations to Kanizsa Squares and control stimuli in 8- and 6-month-old infants. Both the increased and reduced activations were restricted to the left frontal area. Adapted from Csibra et al. (2000).
of several previous studies of gamma oscillations in adults (Herrmann, Mecklinger, & Pfeifer, 1999; Tallon-Baudry et al., 1996). Furthermore, this pattern has featured prominently in previous behavioural studies of perceptual development, such that the current findings can be viewed in the context of a substantial body of other data.

We compared brain activation elicited by the Kanizsa Square to that elicited by a control stimulus (see left side of the bottom row of Figure 10.3) comprising precisely the same “pacmen” elements as the Kanizsa Square. However, in the control stimulus, the pacmen were rearranged so as not to elicit perceptual grouping and consequently no percept of an illusory figure. Any binding-related activation should thus pertain only to the Kanizsa Square, and not to the control stimulus.

Infants aged 6 months and 8 months viewed Kanizsa Squares and control stimuli on a computer screen while EEG was recorded. The recording was then subjected to the time–frequency analysis discussed earlier to yield a measure of induced oscillatory brain activation. Given the results of previous behavioural studies, we predicted that the 8-month-old infants, like adults in previous studies, would show induced gamma-band activations to the Kanizsa Square. In adults, illusory objects induce a burst of 40 Hz oscillations at about 250–300 milliseconds after stimulus onset. This characteristic gamma burst would not be expected following presentation of the control stimulus. In contrast to our predictions for the 8-month-olds, we anticipated that infants of 6 months would not show binding-related gamma oscillations.

In 8-month-olds we found an enhancement of induced gamma-band activity in response to the Kanizsa Square over the left frontal scalp in the 240–320 ms time window, corresponding in time course to results found in adults (Figure 10.3A). No equivalent gamma enhancement was seen in response to the control stimulus. However, intriguingly, the response to the control stimuli showed a significant decrease in activity within the gamma band over the same scalp areas and at slightly earlier latency (around 200 ms). This effect has never been reported in adults. Note, however, that in contrast to studies with adults, our test stimuli were preceded by attractive colourful pictures (a cartoon figure, an animal, or a geometric shape), which might also have engaged feature-binding processes. Thus, one plausible interpretation of the suppression of gamma-band activity is that it is a response to the removal of a foveated object that no longer requires active representation. We suggest that the gamma-band activity during presentation of the Kanizsa Square did not show this suppression because the Kanizsa Square acts as an occluder and infants maintain a mental representation of the occluded stimulus. A similar dissociation of gamma-band activation when an occluded object is present or not was also found in our other further studies (see later in this chapter). Kanizsa figures have been shown to be able to act as occluding surfaces (Davis & Driver, 1998), and this account is consistent with evidence from experiments in human adults showing a similar left frontal scalp pattern of 40 Hz oscillation in task situations that require subjects to maintain an
object representation while it is not directly visible (Tallon-Baudry, Bertrand, Perronnet, & Pernier, 1998) and with single-cell studies in primates showing activity of neurons in the frontal cortex during “object permanence” tasks (Graziano, Hu, & Gross, 1997).

The time–frequency analysis for the group of 6-month-old infants yielded quite different results from those observed in the older group (Figure 10.3B). While there were some fluctuations in amplitude in the gamma band over the left frontal cortex after presentation of the Kanizsa Squares, these did not come in bursts similar to those observed in adults, but were smeared over long time intervals. The absence of adult-like binding-related gamma oscillation in 6-month-olds is consistent with partial activation of gamma-band oscillatory responses, and probably binding processes, but with a much higher variability in latency, both between and within subjects. This finding suggests that the neural development at around 6 to 8 months of age that allows infants to perceive static illusory objects involves a decrease in variability of gamma range bursts of oscillatory activity in the frontal cortex. It is also conceivable that, at this transitional age, a subset of the 6-month-old infants in our sample were able to bind the visual elements into a Kanizsa figure.

Our results also indicate that the frontal cortex may play a crucial role in the development of feature binding or object completion. Along with other findings (Csibra, Tucker, & Johnson, 1998; Johnson, Tucker, Stiles, & Trauner, 1998), this suggests a critical role for the frontal cortex in infant visual cognition, although more studies are needed to determine whether the frontal activation is directly related to the binding process, or reflects further attentional processing on the object “bound” elsewhere in the infant brain.

**OCCLUDED OBJECTS AND “OBJECT PERMANENCE”**

Since Piaget’s (1954) original observations, one of the most striking phenomena in cognitive development has been the apparent failure of infants to show “object permanence”. When an object is occluded by a cover, infants often behave as if it is no longer present: out of sight is out of mind. In contrast, studies measuring looking times reveal quite sophisticated reasoning about hidden objects even in young infants (for a review see Baillargeon, 2001). In a previously separate line of research, sustained responses in neural circuits have been identified as a mechanism for maintaining representations of objects during a period of occlusion (Rainer & Miller, 2000). In particular, in human adults gamma-band (~40 Hz) activity has been associated with maintaining an object/location in mind (Tallon-Baudry et al., 1998). We (Kaufman, Csibra, & Johnson, 2003) measured infants’ electrophysiological responses to occlusion events at the age where reaching behaviour does not yet show evidence of understanding “object permanence”.

Prior to examining EROs, it was necessary to determine that our experimental stimuli were realistic enough to be perceived as real objects to the
infant participants. Therefore, we created digital video sequences of real objects involved in expected and unexpected events and measured infants’ looking time to them in a traditional “violation of expectation” paradigm (von Hofsten & Spelke, 1985). Each infant was shown sequences of video-recorded and digitally edited events depicting an object (a train engine) appearing or failing to appear from under a tunnel when it should or should not have been there. Infants were first familiarized with the situation by watching a repeating event in which the engine entered the screen and then went into, and reversed out from, the tunnel. Following the single familiarisation trial, four test events (Expected Appearance, Unexpected Appearance, Expected Disappearance, Unexpected Disappearance) were then presented in counterbalanced order. Each event cycle was 6 seconds (which did not vary across the four video types). Looking time was measured from the point at which infants began to look continuously from the start to the end of the event sequence (thus providing certainty that they had witnessed the expected or unexpected aspects of the event). The event was repeated until infants looked away from the video monitor for 2 seconds. Longer looking times are thought to reflect greater information processing in infant behavioural research (von Hofsten & Spelke, 1985).

Our results were consistent with earlier findings (Wynn & Chiang, 1998) that infants are highly sensitive to the unexpected disappearance of an object (consistent with object permanence) but are less sensitive to an unexpected appearance. A number of possible explanations for the appearance/disappearance discrepancy have been offered—including the idea that infants can infer the existence of two objects behind an occluder (Aguiar & Baillargeon, 2002; Baillargeon, 1994). Whatever the correct explanation for this result, this experiment demonstrated that infants react to our computerized stimuli as if they were watching real objects.

Subsequently, we measured EROs while infants watched the events that we used in the behavioural paradigm. We hypothesized that gamma-band oscillatory activity may be present in the infant brain during object occlusion. Results and analyses are illustrated in Figure 10.4. Statistical analyses on the average gamma-band (20–60 Hz) activity in six consecutive 200-ms windows revealed higher activity in the Unexpected than in the Expected Disappearance condition both before and after a hand lifted the tunnel. Comparing gamma power in each of the two conditions to the preceding baseline revealed that, prior to the tunnel being lifted, gamma power was reduced in the Expected Disappearance condition (Figure 10.4A). After the tunnel was lifted, there was significant enhancement of gamma-band activity in the Unexpected Disappearance condition relative to the baseline. These activity changes were largely restricted to the right, rather than the left, temporal area.

These results demonstrate a sustained period during which gamma power over the right temporal region was consistently higher during an event where infants represented an object despite it being occluded. This response persisted
Figure 10.4 Induced gamma-band oscillations to occluded objects in 6-month-old infants. A right temporal activation was elicited both when an object had been hidden and failed to reappear (A), and during hiding before reappearance (B).
despite initial visual evidence to the contrary. We propose that this gamma activity provides a neural basis for object permanence in infants. Just before the tunnel was lifted there was a relative (to baseline) decrease in gamma power in the Expected Disappearance condition. This suggests that the visual presence of the engine during the baseline phase partially activated gamma activity, which was then further strengthened during the later periods of occlusion in the Unexpected Disappearance condition. The maximal point of gamma power increase in the Unexpected Disappearance condition occurred around 500 ms after the initial lifting of the tunnel. One interpretation of this finding is that the infant’s brain attempts to strengthen further the representation of the “hidden” object to better compete with the (now) direct visual evidence to the contrary. By this view, object permanence is the ability to maintain a sufficiently strong representation of the object, despite competing evidence from visual input (Munakata, 2001).

If this sustained gamma activity is related to representation of non-visible objects, it should also be evident in an ordinary event of temporary hiding, like the Expected Appearance event described above. Furthermore, an alternative explanation for the increase in gamma activity following the uncovering event is that it is correlated with the perception of an impossible event—and not directly related to object representation. In order to test these hypotheses we conducted another EEG experiment using only the appearance events.

As in the Unexpected Disappearance condition above, an increased gamma power was evident at right temporal channels during the time and condition where the train should be hidden underneath the tunnel. There was no significant increase in gamma activity time-locked to the Unexpected Appearance event. As before, the differences in oscillatory activity by condition were specific to right temporal channels.

These results bolster the earlier findings, in that infants showed an increase in gamma activity at right temporal leads when the train should have been underneath the tunnel. However, and in contrast to the earlier experiment, following the tunnel being lifted there were no significant differences in gamma power either between the two conditions or from the baseline. This supports the notion that the increase in gamma power following the lifting of the tunnel in the first EEG experiment is related to representing an object in the face of contradictory visual input.

In the latter EEG experiment, because the train was always revealed, there was no need to maintain a representation of the object independent of visual input. These results further advance the interpretation that gamma power in the right temporal area reflects active maintenance of occluded objects.

In a recent experiment we have also demonstrated that the right temporal gamma-band activation does not simply reflect a memory trace of the disappearing object but rather its active maintenance (Kaufman, Csibra, & Johnson, 2005). Six-month-old infants displayed a higher activation when an object disappeared by deletion (consistent with being occluded) than when it disappeared by disintegration. This result supports the view that derives
CONCLUSIONS AND FUTURE PROSPECTS

In this chapter we have discussed two applications of ERO to the study of infant cognition. However, this effort to date probably only scratches the surface of the possible applications of the ERO approach for studying typical and atypical brain function. For example, the fact that induced ERO does not require the extent of time-locking to stimulus events that conventional ERPs do, means that it can be used in a wider range of experimental paradigms. With Vincent Reid (see Reid, Csibra, Belsky, & Johnson, in press), we have begun to explore the significance of bursts of gamma activity when infants view dynamic video sequences of humans performing actions such as reaching for an object in either an intentional or an accidental manner.

Another potential line of experimentation with EROs concerns the atypical brain responses observed in some developmental disorders. For example, we (Grice, de Haan, Halit, Johnson, Csibra, & Karmiloff-Smith 2003) have observed that adults with Williams syndrome and autism do not show the same patterns of gamma bursts as adults do in a Kanizsa figure paradigm similar to that described for infants earlier in this chapter. It will be intriguing to see whether these atypical patterns of ERO can be observed in young children or infants “at risk” for autism.

A number of challenges lie ahead for the ERO approach. The first of these is to develop adequate methods for assessing coherence between different regions of the brain in order to determine their patterns of functional connectivity. Another challenge will be to attempt to localize the underlying neural generators of oscillatory activity, since EEG has typically proved harder to localize than conventional ERPs because they do not necessarily occur in coherent clusters on the scalp (Tallon-Baudry, Bertrand, & Pernier, 1999). On a more positive note, high-frequency neural oscillations are more likely to map directly onto regions that show changes in the BOLD signal as detected by functional MRI techniques (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). Thus, we are more likely to find correspondences between results obtained with fMRI and EROs than we are with ERP and fMRI. Despite the challenges of this new approach, we believe that EROs will become a major new thrust in the study of infant brain electrophysiology.
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REFERENCES


Tallon-Baudry, C., Bertrand, O., & Pernier, J. (1999). A ring-shaped distribution of...