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## **Electrophysiological Methods in Studying Infant Cognitive Development**

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**Abstract**

The measurement of the electroencephalogram (EEG) provides a rich source of information about the neural mechanisms underlying ongoing cognitive events. Various ways of analysing the neural markers recorded non-invasively from the scalp have been successfully applied to study developmental populations. The goal of this chapter is to give an introduction and to provide an overview of how electrophysiological methods can be used to elucidate brain and cognitive development in infancy. To this end, we begin by briefly describing the physiological basis of the EEG, and then review the components observed in event-related potentials (ERPs) to auditory, visual, multimodal stimuli and saccades. We also discuss recent work investigating event-related oscillations (EROs) and its role in cognitive development. We conclude by reflecting upon the future directions of the field.

Cognitive neuroscience, through its various neuroimaging techniques, enables us to look at the living brain at work, and thus provides us with tools to investigate the neural underpinnings of developmental behavioural change. One class of these neuroimaging methods relies on the non-invasive and painless recording of brain electrical activity measured by electrodes placed on the scalp. The recorded signal, the *electroencephalogram* (EEG), carries information about the ongoing brain activation at the millisecond time-scale, and derived measurements, like the event-related potentials (ERPs) and the event-related oscillations (EROs), allow us to relate this information to the cognitive processes that the brain is engaged in. This technique is especially popular for measuring functional brain activation in developmental populations because it is relatively easy to record and the signal is relatively robust. For example, it is less sensitive to artefacts created by movement than is fMRI, and thus is better suited for studying awake, attentive children and infants (de Haan and Thomas, 2002). Furthermore, there is a longstanding tradition in its use with infants and young children, and its excellent temporal resolution can reveal information about the timing of neurocognitive processes that occur while an infant or child is engaged in some cognitive activity rather than providing information only about the final behavioural outcome of these processes.

### **The electroencephalogram**

The ongoing electrical brain activity can be recorded simultaneously from a number of electrodes attached to the scalp. These electrodes pick up the voltage changes that occur when a large number of cerebral neurons are activated in close proximity and in high synchrony. The electrical potential changes measured on the scalp primarily reflect the postsynaptic depolarization of cell dendrites and not the action potentials generated by the neurons. It is also important to note that in order to generate a large enough electrical field to

be measurable on the scalp, the depolarization has to occur on many synapses that are more or less aligned in the same direction. The closer the activated neuron population to the surface of the cortex, the more likely its activation is reflected in the ongoing EEG.

The placement of electrodes on the scalp conventionally follows the international 10/20 system (Jasper, 1958), in which electrodes are placed at certain distances from each other along the anterior-posterior and the lateral axes. The electrodes in this system are labelled according to cerebral lobe (frontal, temporal, parietal) under the location, odd numbers assigned to the left and even numbers to the right hemispheres, whereas Z indicating the midline. The relationships of the standard 10/20 system to the infant cerebral cortex differs slightly from that to adult (Blume, 1974) due to different relative proportions of parietal and frontal lobes in infants and adults and incomplete opercularization of the temporal lobe in infants.

Although being most frequently used, the 10/20 system offers relatively poor spatial resolution of the signal. Over the years, this system has been extended to a 10/10 (Nuwer et al., 1998) and a 10/5 system (Oostenweld and Praamstra, 2001) to provide better spatial sampling on the surface of the head. Recently high-density electrode systems, such as caps or nets comprising 64 or 128 electrodes have become popular. A relatively new technique, the Geodesic Sensor Net (GSN) allows a large number of electrodes to be quickly applied to the scalp surface (Tucker, 1993), which is especially useful in studies with infants, children, and special populations (Johnson et al., 2001). Even a 64-electrode GSN recording yields a sampling density of less than 3 cm with infants.

The ongoing EEG is traditionally analyzed in the frequency domain. One of the main parameters which modulates the rate and amplitude of the EEG waves is the general alertness of the person. The alpha-band activity (8-13 Hz) can be measured from the occipital region in an awake and resting person when the eyes are closed. Beta waves (13-30 Hz) are

characteristic of strong mental activation and are detectable over the parietal and frontal lobes. Delta-band waves (0.5-4 Hz) are detectable in infants and sleeping adults, while theta activity (4-8 Hz) is obtained from children and sleeping adults. The EEG also contains activation in the gamma-band (24-100 Hz) in both children and adults. However, the magnitude of this activity is so small compared to other frequency bands that it cannot normally be detected without special signal analysis techniques.

The EEG of children varies with age. During the first weeks of life, low-amplitude, poorly defined activity has been observed, composed of random-frequency waves in the delta, theta, and alpha ranges. The dominant activity in resting state is 4-6 Hz in 6-month-olds and 5-7 Hz by 1 year of age. At 4 years of age, the 7-8 Hz waves predominate, and by 8 years, the majority of children show alpha-band activity within adult frequency range. Distinct runs of beta activity are seldom observed in children, whereas episodic theta activity may be observed in frontal lobes until the age of 20 (Kooi, 1971).

Some researchers have attempted to relate cognitive and brain development by correlating activity in certain frequency bands with behavioural variables in infants (Bell and Fox, 1992; Bell, 2001; Mundy, Card, and Fox, 2000). The majority of studies using electrophysiological measures, however, attempt to link cognitive processes to brain activations not via inter-individual variability but by directly manipulating those cognitive processes. Studies with adult participants normally require them to solve various cognitive tasks, and then compare the brain electrical activation during the short time periods while they are engaged in the different conditions. For obvious reasons, preverbal infants cannot be assigned tasks to solve, but they can be exposed to different stimuli that require different cognitive processes to deal with.

In this chapter, we discuss some techniques that have been used to analyze the EEG data collected during such cognitive studies with human infants. All the methods employ the

same general idea for extracting the signal from the continuous EEG that is related to specific cognitive processes: repetition. Inducing the replication of the same cognitive event several times can help us to separate the electrical signal reflecting brain activation related to those events from other ongoing neural activity. We do not discuss in detail a class of techniques called *steady-state* and *sweep evoked potentials*, which employ rapid repetitions of stimuli at regular intervals and assesses their effect by frequency analysis. Although they are rarely used in developmental cognitive neuroscience research, they provide a good example of how to use electrophysiological techniques to answer developmental questions that do not aim at infant cognition directly but are essential to resolve in order to know the constraints that determine what young infants can see and can hear. *Event-related potentials* (ERPs) and *event-related oscillations* (EROs) also rely on repeated events, and reduce the effect of background or non-related brain activations by time-locked averaging of the EEG. We do not discuss the methodological details of these techniques here (for methodological guidance, see recent excellent handbooks: e.g., Handy, 2005; de Haan, in press). Instead, we summarize how these techniques have been used to answer questions of cognitive development in human infants.

### **Event-Related Potentials**

Event-related potentials are calculated as time-locked averages of the EEG signal. The event that defines the EEG segment must be defined with millisecond-range accuracy, and can be a stimulus of any modality, an omission of an expected stimulus, or a response generated by the participant. ERPs also differ from traditional stimulus-evoked potentials in that the brain activation related to the event may also precede, and not just follow, the event. This is frequently the case when the event is a response, or an external stimulus with well predictable timing.

The averaged ERPs are composed of a series of negative-going and positive-going waves. An ERP component, according to definition of Näätänen and Picton (1987) is the contribution of a generator process to the ERP waveform. If temporally overlapping components are of opposite polarities, they cancel one another either partially or totally. Traditionally, ERP components are divided into two categories: exogenous and endogenous. Exogenous (or sensory, or obligatory) components can be elicited by any detectable stimulus and represent brain response to the occurrence of the stimulus. Exogenous components typically occur within the first 100-200 ms after stimulus onset and are, to a limited extent, sensitive to the physical features of the stimulus, such as intensity, frequency, rate of stimulus presentation (Näätänen, 1992). Endogenous components mainly reflect internally generated mental events related to the cognitive assessment of the stimulus. The endogenous components, occurring after 100-200 ms from stimulus onset, reflect the processing not only of physical stimulus features, but also, depending on the paradigm and task, can index several stimulus-related cognitive processes. Because more and more recent studies suggest that even the early ERP responses can be modulated by top-down processes, like selective attention, the distinction between exogenous and endogenous components is not as meaningful as it once seemed to be.

The majority of ERP waves are thought to reflect the synchronous activity of neural systems generated by excitatory and inhibitory post-synaptic potentials. Thus, the maturational changes in ERP morphology might to a large extent involve changes in intracortical synaptic organization and synaptic density (Eggermont, 1988; Vaughan and Kurtzberg, 1992). Vaughan and Kurtzberg (1992) suggested that the ERP amplitude is proportional to the magnitude of synaptic activation. Indeed, the sequence of changes in synaptic density parallels changes in the ERP amplitude, which follow an inverted U-shape function, with rapid increase of the ERP amplitudes during infancy followed by a gradual



decline during childhood. The sequence of synaptogenesis has been described as following a similar U-shape function: rapid increase in synaptic density during infancy is followed by gradual decline to the mature adult levels at puberty (Huttenlocher, 1979). The striking parallel between the course of synaptogenesis previously reported by Huttenlocher and Dabholkar (1997) and the ERP-peak amplitudes was observed for auditory (Kushnerenko et al., 2002a) and visual modality in infants (Vaughan and Kurtzberg, 1992), for auditory modality in children (Ponton et al., 2000), and for both the visual and auditory modalities together (Courchesne, 1990). The increase in consistency of brain response with age (Thomas and Crow, 1994), resulting in decrease of the trial-to-trial latency variability also contributes to the shortening of the ERP peak latencies. The latency changes in one ERP peak might also be affected by the maturational changes in another, overlapping peak (Ponton et al., 2000; Kushnerenko et al., 2002a).

What has emerged as a general finding from developmental ERP studies is that young infants do not show as many well-defined peaked ERP responses as adults, but do show greater slow wave activity (Nelson and Luciana, 1998). The greater slow wave activity during the first two years of life has been attributed to reduced synaptic efficiency. ERP waveforms with well-defined peaks over the frontal cortex, which are typical for adults, begin to emerge around 4 years but do continue to develop well beyond that age (Nelson and Luciana, 1998; Taylor, Batty, and Itier, 2004).

We discuss the typical findings of ERP research in infants grouped by the events that are used to elicit those potentials. First we review infant ERPs to auditory and visual stimuli, then we briefly summarize some studies with multimodal stimuli and eye-movement related analyses.

## **ERPs to auditory stimuli**

The P1-N1-P2 complex. In adults, auditory ERPs start with a small P1 (or P50) deflection that peaks at about 50 ms. The P1 is followed by a usually larger N1 response, peaking at about 100 ms and further by a P2 component peaking at approximately 180-200 ms from stimulus onset (Näätänen, 1992; Ponton et al., 2000). The P2 peak is often followed by a negativity, labelled N2 (Picton et al., 1974). This peak has an adult latency of 220-270 ms (Ponton et al., 2000). The N2 elicited by frequent repetitive stimuli was reported mostly in children (Ceponiene, Cheour, and Näätänen, 1998; Enoki et al., 1993; Karhu et al., 1997; Korpilahti and Lang, 1994), but it was also shown in adults (Ceponiene et al., 2001; Karhu et al., 1997; Kushnerenko et al., 2001; Picton et al., 1974; Ponton et al., 2000).

The adult P50-N100-P200 (P1-N1-P2) complex is not readily identifiable in infants and children before about 10 years of age (Ponton et al., 2000; Courchesne, 1990). Most of the ERP studies in infants have reported a large positive deflection at midline electrodes, with a maximum amplitude at about 300 ms, followed by a negativity at about 600 ms (Barnet et al., 1975; Graziani et al., 1974; Ohlrich et al., 1978; Pasma et al., 1992; Rotteveel et al., 1987; Shucard et al., 1987).

Novak et al. (1989) followed the maturation of the auditory ERPs to speech stimuli (/da/ and /ta/ syllables) from birth to 6 months. The P2-N2 complex recorded at birth changed in morphology by the age of 3 months. The authors discerned two positive peaks in the latency range of the infantile P2 (P1m and P2m) with different scalp predominance: the P1m was larger frontally than centrally, whereas the P2m was largest centrally. A discontinuity (negative trough) between these two positive peaks, at about 160-200 ms, was termed N1m by the authors. The N1m became prominent by the age of 6 months. During the first 6 months of life, the P1m and P2m increased in amplitude and gradually decreased in latency. Further, peak amplitudes did not increase linearly, but followed an inverted-U function with a

maximum at 3 months in Barnet et al.'s (1975) study and at 6 months in the studies by Vaughan and Kurtzberg (1992) and Kushnerenko et al. (2002a). The amplitude of the second major positive peak (P2m or P350) markedly decreased between 6 and 9 months, while the amplitude of the preceding negativity (N1m or N250) increased (Kurtzberg et al., 1986, Kushnerenko et al., 2002a).

A longitudinal study performed in the same infants from birth to 12 months of age employing spectrally rich harmonic tone showed that an analogue to the N1m (labelled N250 according to its peak latency) could be identified already at birth and consolidates by the age of 6 months. By the age of 1 year, the waveform morphology observable through early childhood is attained (Figure 1). However, as can be seen in Figure 1, the N250 in newborns appears to be sensitive to stimulus duration and probability. A negative peak within the N1 latency range was obtained by Wunderlich et al. (2006) from birth in response to words but not to tones. Thus, tones do not seem to be perfect stimuli for auditory ERP research with very young infants (see also Kushnerenko et al., 2006). The P350 (P2) is also dependent upon stimulus probability and interstimulus interval (for compatible evidence in older children see Ceponiene et al., 2002b; Kurtzberg et al., 1995).

Throughout early school years, children's ERP in response to auditory stimuli presented at a fast rate consists of the P100, N250 and N450 peaks (Ceponiene et al., 1998, 2001, 2002b). With a slower presentation rate, however, an adult-like P1-N1-P2-N2 pattern can be observed (Ceponiene et al., 1998, 2002b; Karhu et al., 1997). The N1 can be elicited from the age of 3 years with a slow stimulation rate (Paetau et al., 1995; Sharma et al., 1997), which suggests longer refractory periods of N1 generators in children.

Mismatch responses. In order to study the capacity to discriminate or categorize auditory stimuli, many researchers employ the so-called auditory "oddball" paradigm. In this paradigm one stimulus (the "standard") is repeated frequently (about 60 to 90 % of trials) and

another (the “deviant”) occurs infrequently. The oddball paradigm can either be passive (unattended), when no response is required from the participant, or active (attended), when subject is supposed to react to the deviant, “target” stimuli. The most extensively studied ERP component, the P3b ( or P300), is elicited in response to such target stimuli under attended oddball conditions. Among the endogenous components elicited in passive auditory oddball paradigms in adults are the mismatch negativity peaking about 150-200 ms, the P3a (250-350 ms), and the late negativity, Nc (commencing at about 500 ms).

The *mismatch negativity* (MMN) was isolated from the N2 wave by Näätänen and colleagues (1978). The MMN is generated by a neural matching process between a deviant sensory input and the neural representation, or ‘sensory memory trace’, formed by the repetitive standard sound. This auditory-cortex activation presumably reflects an automatic pre-attentional change-detection process, comparing the new auditory input with information stored in auditory sensory memory (Näätänen, 1992).

Several auditory-change detection components have been described in infants. In the majority of the studies, a positivity peaking at about 300 ms was observed (Dehaene-Lambertz and Pena, 2001; Dehaene and Gliga, 2004; Friedrich et al. 2004; Dehaene-Lambertz et al., 2000; Dehaene-Lambertz and Baillet, 1998; Dehaene-Lambertz and Dehaene, 1994; Winkler et al., 2003). An early negativity peaking at about 150 ms was obtained only in response to frequency change with grossly deviating stimuli (Ceponiene et al., 2002a; Morr et al., 2002; Kushnerenko et al., 2002b) and was suggested to be related to spectral change of acoustic parameters (Kushnerenko et al., 2006).

A broad long-lasting later negativity (270-400 ms) was found in response to relatively small auditory contrasts in newborns and even prematurely born infants (e.g., to the difference between Finnish vowels /y/ and /i/, Cheour-Luhtanen et al., 1995, 1996; Cheour et al., 1999). Leppanen et al. (2004) attempted to explain the discrepancy between the polarity

of the change-detection response in infants and adults by the maturational level of the newborn, because it had been established that immature neonates display inverse polarity ERPs (Kurtzberg et al., 1985). Thus, the broad negativity obtained in prematurely born infants may be due to an immature neural response. In full term newborns, however, no immature ERPs were found in response to broadband stimuli and large spectral changes (Kushnerenko et al., 2006). In contrast, both a large-amplitude early negativity and a central positivity were elicited reliably across neonates in response to these stimuli. The requirement of large spectral deviation suggests an incomplete refinement of frequency-specific pathways, and is consistent with evidence showing that frequency resolution and fine frequency tuning improves during the first 6 months of life (Abdala and Folsom, 1995; Werner, 1996).

Further in development, negative and positive mismatch responses appear to overlap and mask each other, resulting in a predominantly positive deflection before 1 year of age, and even in the absence of deviant-standard difference between 1 and 4 years of age with relatively small acoustic contrasts (Morr et al., 2002). Accordingly, it was shown that the relative strength of positive and negative mismatch responses varied from age to age and from infant to infant (Kushnerenko et al., 2002b).

Another component that can be obtained in the passive oddball paradigm is the P3a, a fronto-centrally maximal positivity elicited by stimuli that catch attention. Squires et al. (1975) proposed that the P3a was the central electrophysiological marker of the orienting response (see also Sokolov et al., 2002). 'Novel' sounds (random mixture of mechanical or environmental noises) among pure tones are often used to elicit the P3a. Such grossly deviating stimuli typically elicit a large P3a response in children (Gumenyuk et al., 2004; Ceponiene et al., 2004) and adults (Escera et al., 2000). Surprisingly, newborns also show a similar pattern of response to 'novel' sounds (Kushnerenko et al., 2002b, 2006). It has been argued, however, that the major part of the P3a in newborns is elicited by the spectral

richness of the novel sounds, which recruit new afferent neurons into the response pool.

The P3a is sometimes followed by a frontal negativity at 500-600 ms latency in children's and infants' auditory ERPs (Gumenyuk et al., 2004; Ceponiene et al., 2004; Kushnerenko et al., 2002b, 2006). This late negativity is larger in amplitude in younger than in older children: the same maturational profile that has previously been reported for the negative component Nc (Courchesne, 1983). This negative component has been suggested to be a sign of enhanced auditory and visual attention (see also later, among the ERP components in visual paradigms), since it was elicited in response to surprising, interesting, or important stimuli (Courchesne 1978, 1990).

A similar negativity was also found when participants had to reorient their attention back to a task after distraction by 'novel' sounds (Escera et al., 2001) or in response to unexpected frequency changes in auditory stimuli (Schröger et al., 1998, 2000). This negativity was called the reorienting negativity (RON) by Schröger et al. (1998). Being of comparable latency and scalp topography, the Nc and RON might, in fact, reflect the same neural process. Interestingly, as noted by Courchesne (1990), the maturational time course of the Nc (amplitude increase across infancy and early childhood followed by a gradual decline through preadolescence) is parallel to the synaptic density changes in the frontal cortex reported by Huttenlocher et al. (1979), and to the metabolic activity changes as reported by Chugani et al. (1987). Thus, the Nc might reflect the development of the higher-order cognitive functions associated with the frontal cortex.

An Nc-like, frontally maximal negativity was found not only in response to surprising or 'novel' stimuli, but also to non-novel speech-syllable contrasts in newborns and very young infants (Dehaene-Lambertz and Dehaene, 1994; Kurtzberg et al., 1984; Friederici et al., 2002a). This might indicate that for a newborn infant any stimulus change might be 'novel' or surprising, whereas with increasing age a capacity to respond only to the most

attention-getting stimuli matures (Courchesne, 1990).

In infants, negative and positive slow waves (NSW and PSW) were observed to follow the Nc under certain circumstances. Deregnier et al. (2000) obtained NSW in response to a stranger's voice compared with the maternal voice in sleeping newborns. In Courchesne's early work (1978), a long-latency positive slow wave (PSW) was also observed to infrequently presented stimuli. Nelson and colleagues have speculated that these waves are typically invoked by stimuli that infant has only partially encoded and indicate detection of novel stimuli against a background of familiar stimuli (de Haan and Nelson 1997, Nelson 1994; see Nelson & Monk, 2001 for discussion).

Components related to lexical and syntactic processing. Further auditory ERP paradigms are related to linguistic processing of acoustic stimuli. In these paradigms, words, nonsense words or sentences are presented to participants that are either appropriate in the semantic or syntactic context or violate some linguistic aspects (for a recent review see Friederici, 2002, 2005). Mills and colleagues (2004) have shown that 14- and 20-month-old infants responded with a larger amplitude of N200-N400 to known words than to nonsense words. In addition, Friedrich and Friederici (2005) have shown an N400-like semantic incongruity effect in 19-month-old infants. The N400 is usually elicited by sentences that end with semantically inappropriate words (Kutas and Hillyard, 1983). In the study of Friedrich and Friederici (2005), object words were presented either matching the concurrent visual stimulus or not. In response to semantic incongruity a slow negative wave was observed starting from about 400 ms and reaching significance between 800 to 1400 ms. In addition, the congruous words elicited more negative responses than the incongruous words in the shorter latency range, matching Mills et al.'s (2004) finding that known words elicited more negative response than unknown or nonsense words. Korpilahti et al. (2001) also reported that the second negativity (denominated as Late Mismatch Negativity) was significantly

larger in 4 to 7-year-old children for words than for pseudowords, which led the authors to propose that this Late MMN might reflect the detection of semantic anomaly.

The ERP studies of sentence structure processing in adults have shown that syntactic (grammatical) violations are associated with two ERP components: an early left anterior negativity (ELAN) and a late, centro-parietal positivity (P600) (Friederici, 2002). Recently, Oberecker and Friederici (2005) have shown that children below three years of age also responded with an early left negativity and late positivity to syntactic violations. These deflections, however, peak later and persist longer in children than in adults.

### **ERPs to Visual Stimuli**

ERPs have proven to be a very useful tool in studying the development of visual processing. The goal of this section is to give an overview of the primary ERP components that have been used to study the development of visual processes in human infants. It is beyond the scope of this chapter to provide an exhaustive review of the development of all components previously reported in visual event-related potential studies (DeBoer, Scott, & Nelson, 2004; de Haan, Johnson, and Halit, 2003; Nelson, 1994; Nelson & Monk, 2001; Taylor, Batty, and Itier, 2004). We will therefore mainly focus on the well-studied components observed during face processing which will be discussed in the order of their temporal occurrence in the waveform.

P1. Visual stimuli reliably elicit a positive-going component between 90 and 150 ms, called P1, in individuals of all ages (de Haan, Johnson, and Halit, 2003). It has been shown that from 4 years of age, P1 latency is shorter to upright than inverted faces and similarly, the P1 is shorter to faces than to objects (Taylor, Batty, and Itier, 2004). There is also evidence to suggest global effects of facial expressions of emotion on the P1 (Batty and Taylor, 2006). However, some of the effects observed could not be replicated (Roisson et al., 1999) and it



has been argued that low-level physical differences, which were not controlled for in these studies, or more general attentional top-down processes might influence the properties of this early visual ERP component (for a discussion see de Haan, Johnson, and Halit, 2003).

N170/N290 and P400. In adults human faces elicit an N170 response, which is most prominent over posterior temporal sites and is larger in amplitude and longer in latency to inverted than to upright faces (Bentin et al., 1996; de Haan, Pascalis, and Johnson, 2002). Other kinds of objects evoke a similar response around this latency in adults (generally called N1). This component is not modulated by the inversion of monkey faces (de Haan, Pascalis, and Johnson, 2002), nor when upright objects are compared to inverted objects (Bentin et al., 1996). This selective effect has been taken as evidence for a special face-processing mechanism generating the N170.

From studies examining the influence of stimulus inversion on infants' ERP responses to faces, it has been suggested that the infant N290 is a precursor to the adult N170. As the N170, the infant N290 is a negative-going deflection observed over posterior electrodes. Its peak latency decreases from 350 ms at 3 months to 290 ms at 12 months of age (Halit, de Haan, and Johnson, 2003). In the studies that measured ERPs to upright and inverted human and monkey faces (de Haan, Pascalis, and Johnson, 2002; Halit, de Haan, and Johnson, 2003) the amplitude of the infant N290 at 12 months of age, like the adult N170, enhanced to inverted human but not to inverted monkey faces when compared to upright faces. However, the amplitude of the N290 was not affected by stimulus inversion at an earlier age (3 and 6 months). These younger infants showed an inversion effect on the amplitude of the P400 that follows the N290.

The P400 that follows the N290 is a positive deflection most prominent over lateral posterior electrodes, and its peak latency decreases from 450 to 390 ms between 3 and 12 months of age (Halit, de Haan, and Johnson, 2003). This component is similar to the adult

N170 in two ways: first, like the adult N170, the P400 is more prominent at lateral electrodes (de Haan, Pascalis, and Johnson, 2002; Halit, de Haan, and Johnson, 2003), and secondly, like the adult N170, the peak latency of the P400 is shorter to faces than to objects (de Haan and Nelson, 1999). However, unlike the adult N170, the modulation of the amplitude of the P400 at 3 and 6 months is not specific to inverted human faces, since it was also observed in response to inverted monkey faces (de Haan, Pascalis, and Johnson, 2002; Halit, de Haan, and Johnson, 2003). By 12 months of age, infants' P400, like the adult N170, appears to be longer in latency to inverted human faces, but does not differ between upright and inverted monkey faces. This suggests that, like the N290, the P400 becomes more finely tuned to human faces towards the end of the first year. However, it is important to note that similar amplitude enhancement for faces when compared to matched visual noise was observed in the infant N290 and adult N170, whereas the elicited P400 only showed a latency effect (Figure 2), which makes it unlikely that the P400 is the main precursor of the adult N170 (Halit et al., 2004).

The development of the brain processes reflected in the N170/N290 continues well beyond infancy (for a review see Taylor, Batty, and Itier, 2004). While the latency of the adult N170 is delayed by inversion, no such effect has been observed for the latency of the infant N290 at any age (de Haan, Pascalis, and Johnson, 2002; Halit, de Haan, and Johnson, 2003). There is evidence that suggests that this latency effect is not apparent until 8 to 11 years (Taylor, Batty, and Itier, 2004). Another important developmental finding is that while the amplitude of the adult N170 is larger to the monkey faces, infants' N290 shows the opposite pattern. An adult-like modulation of the amplitude of the N170 has not been reported until 13 to 14 years (Taylor, Batty, and Itier, 2004).

Furthermore, while the amplitude of the adult N170 is not affected by direction of gaze (Grice, Halit, Farroni, Baron-Cohen, and Johnson, 2005; Taylor, Itier, Allison, and

Edmonds, 2001), it has been shown that the amplitude of the N290 in 4-month-old infants is modulated by eye gaze (Farroni, 2002, 2004). In these studies, faces with direct gaze compared to faces with averted gaze elicited an enhanced N290 in infants' ERPs, which might indicate that a face with direct gaze is the perceptually more 'prototypical' for 4-month-olds than a face with averted gaze. This suggests that face and eye gaze share common patterns of cortical activation early in ontogeny, which later partially dissociate and become more specialized.

It is important to note that the development of face processing is not only associated with progressive specialization of cortical populations but also with a broadening of certain representations. Using an adaptation paradigm (Grill-Spector and Malach, 2001), Gliga and Dehaene-Lambertz (in press) showed that view-specific (front-view and profile) and view-invariant face representation are accessed in adults at the level of the N170. On the contrary, only view-dependent representations are employed by 4 months old infants, as reflected by an N290 response suppression when front-view faces are repeated but not when faces with different orientations are repeated.

Negative component (Nc). The Nc is one of the most studied components in infant ERP research. This component is a negative deflection that occurs between 400 and 800 ms after stimulus onset, and is most prominent over frontal and central electrode sites. The Nc has been thought of as an obligatory attentional response sensitive to stimulus familiarity (Courchesne, Ganz, and Norcia, 1981; Quinn, Westerlund, and Nelson, 2006; Snyder, Webb, and Nelson, 2002) that is not only observed in response to visual stimuli but also to stimuli in other modalities (see above in the section on auditory ERPs and also Grossmann, Striano, and Friederici, 2005, 2006; Purhonen et al., 2004). Dipole modelling has revealed that the cortical sources of the Nc can be localized in the anterior cingulate and other prefrontal regions (Reynolds and Richards, 2005). The Nc has been observed in a series of studies using a

visual oddball paradigm (Ackles and Cook, 1998; Courchesne, Ganz, and Norcia, 1981; Karrer and Ackles, 1987; Karrer and Monti, 1995). The infant Nc has consistently been found to be greater in its amplitude to the infrequent stimulus event when compared to the frequent stimulus. In this context, the Nc has been interpreted as reflecting either infants' allocation of attention, with the greater negativity to the infrequently presented stimulus indexing orientation towards the novel or more unexpected event (Courchesne, Ganz, and Norcia, 1981; Nelson, 1994), or as a more generalized arousal elicited by novel or infrequent stimuli (Richards, 2002).

However, the Nc is also thought to reflect recognition processes, as the Nc is greater in its amplitude to the mother's than to a stranger's face (de Haan and Nelson, 1997), and it is also greater to familiar than to novel toys (de Haan and Nelson, 1999) when faces and objects are presented with equal probability. A recent longitudinal investigation of infants' visual ERPs to novel and familiar faces and objects revealed that the exact response properties of the Nc and other ERP components undergo complex development throughout the first year of life (Webb, Long, and Nelson, 2005). In this study, the Nc was found to decrease in its latency and increase in its amplitude towards the end of the first year, which reflects the general developmental pattern observed during infancy.

Alternatively, the Nc may reflect processing of semantic and/or emotional information, as its amplitude has also been found to be modulated by the emotional content of a face (Nelson and de Haan, 1996). Furthermore, the direction of the difference in the amplitude between mother's and stranger's face changes with age. Namely, children younger than 24 months show a larger Nc to mother's face, but children older than 45 months show a larger Nc to stranger's compared to mother's face (Carver, Dawson, Panagiotides, Meltzoff, McPartland, Gray, and Munson, 2003). Carver et al. (2003) interpreted this finding as indicating that the caregiver's face is particularly salient during the first two years of life, as

children are forming their relationship and bond with the caregiver, but that these are well-enough established by 4 years that these children can begin to allocate more resources to processing strangers' faces. This supports the view that the Nc is related to the relative 'emotional/semantic' salience of a stimulus (Nelson and de Haan, 1996; Carver et al., 2003). All in all, the available evidence seems to suggest that the Nc reflects attentional processes that are affected by the familiarity, recognition and emotional content of the stimulus.

Negative and positive slow waves (Nsw and Psw). Just like auditory stimuli, visual stimuli have also been found to elicit slow wave activity in infants' ERPs following the Nc. The amplitude of these slow waves vary as a function of stimulus familiarity and presentation probability. For example, in a visual oddball paradigm (Nelson and Collins, 1991), 6-month-old infants were familiarized to two faces and were then presented with one of the familiar faces frequently (60 %), the second familiar face infrequently (20 %), and a group of novel faces frequently (20 %). In this study, only the brain activation following the Nc differed between conditions. The infrequently presented novel face elicited a long-latency negative slow wave (Nsw), which was interpreted as reflecting processes related to novelty detection. The infrequently presented familiar face elicited a long-latency positive slow wave (Psw), which, according to the authors, reflected processes related to updating a decaying memory. ERPs to the frequently presented familiar stimulus returned to baseline, indicating the recognition of a well-encoded face for which memory updating was no longer necessary. The view that the Psw reflects how much a visual stimulus is encoded is further supported by the finding that its amplitude decreases with stimulus repetition throughout an experimental session (Snyder, Webb, and Nelson, 2002). Based on these and other findings (see Nelson, 1994) it has been argued that infants' Psw might be a precursor to adults' P300, which is thought to be involved in context updating (Donchin and Coles, 1988; Friedman, 1991; Nelson and Collins, 1990), whereas the Nsw might be specific to infants since it has not been

observed beyond infancy.

### **ERPs to multimodal stimuli**

Most developmental ERP studies have concentrated on examining the neural correlates of processing stimuli presented only in a single modality. However, it is of great interest to understand how the human brain that develops in a multimodal world uses and integrates information from different senses. Only a few attempts have been made to assess brain processing in multimodal designs which have revealed insights into the neural underpinnings of infants' cross-modal integration abilities from the haptic to the visual modality (Nelson, Henschel, and Collins, 1993) and from the visual to the auditory modality (Grossmann, Striano, and Friederici, 2006; Friedrich and Friederici, 2005). For example, 7-month-old infants' processing of emotionally congruent and incongruent face-voice pairs was investigated using ERP measures (Grossmann, Striano, and Friederici, 2006). Infants watched facial expressions (happy or angry) and heard a word spoken with either an emotionally congruent or incongruent tone of voice. The ERP data revealed that the amplitude of a negative component (Nc) and a subsequent positive component (Pc) in infants' ERPs varied as a function of crossmodal emotional congruity (Figure 3). Emotionally incongruent face-voice pairs elicited a larger Nc in infants' ERPs than emotionally congruent pairs. Conversely, the amplitude of infants' Pc was found to be larger to emotionally congruent words than to incongruent words. Based on previous work that has shown that an attenuation of the negative component and an enhancement of the later positive component in infants' ERPs reflects the recognition of an item (Nelson, Thomas, de Haan, and Wewerka, 1998), it was suggested that 7-month-olds integrate emotional information across modalities and recognize common affect in the face and voice. Interestingly, presenting multimodal stimuli allowed the use of an unusually high number of trials for analysis, suggesting an

advantage of multimodal over unimodal stimuli in capturing infants' attention (Grossmann, Striano, and Friederici, 2006). This is of special interest considering the generally low signal-to-noise ratio (SNR) of infant ERP studies. Moreover, a recent study employed a novel interactive paradigm to assess the neural correlates of joint attention in 9-month-old infants, and found that neural processing in infants is enhanced when learning takes place in the context of a joint attention interaction (Striano, Reid, and Hoehle, in press). The amplitude of the elicited ERP component was substantially larger in this study than that seen in previous literature, which may be due to the new paradigm employing live interaction. The usage of multimodal stimuli and interactive paradigms has the advantage of an increased social significance for the child and of a higher ecological validity when compared with those ERP paradigms utilized in the past. It is experimentally challenging but worthwhile to continue to improve the paradigm on ERP studies by modifying the tasks so that they are in accordance with the child's world.

### **Saccade-related ERPs**

The electrical brain activity can also be analyzed in relation to events that are not externally but internally generated by the participants. In particular, response-related ERPs are calculated by time-locking the EEG to the manual responses (e.g., key presses) performed during the task. Of course, infants do not usually participate in tasks that require manual responses, but they are quite proficient in performing another type of action: eye movements.

Saccade-related potentials are usually time-locked to the initiation of eye-movements, though one can also calculate ERPs to the termination of the saccades (i.e., the fixation) as well. These time points can be identified from the horizontal and vertical electrooculograms (EOG) that are usually co-registered with the EEG. Saccades are usually preceded by characteristic pre-saccadic components, like the sharp spike potential (SP), the pre-saccadic

positivity (PSP), both maximal over parietal areas, and the pre-saccadic negativity (PSN) measured over the anterior cortex (Balaban and Weinstein, 1985; Csibra, Johnson, and Tucker, 1997). The spike potential is absent in young infants' saccade-related potentials, and its development is discussed in another chapter of this handbook (Johnson, Mareschal, and Csibra, XXXX) in the context of the early development of the visual pathways (see also Csibra, Tucker, and Johnson, 1998; Csibra, Tucker, Volein, and Johnson, 2000).

The other pre-saccadic potentials also differ between infants and adults. Richards (2000) identified a pre-saccadic positivity over anterior areas in infants that preceded the start of the eye movement by about 50 ms. This component occurred only when infants made a saccade towards a pre-cued target, and it did not emerge before 20 weeks of age. A similar pre-saccadic positivity in a later study was localized to the superior frontal gyrus (Richards, 2005).

While the pre-saccadic potentials differ markedly between infants and adults, the post-saccadic lambda wave behaves functionally the same way in infants as in later ages. The lambda wave is a sharp potential appearing over visual cortical areas that is generated when a peripheral target stimulus is foveated (Kurtzberg and Vaughan, 1977). This wave is essentially a visual ERP to the newly fixated stimulus, and it can be detected in both 6- and 12-month-olds (Csibra et al., 1998, 2000).

### **Event-Related Oscillations**

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 analyse 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 brain waves were recorded (e.g., Tallon-Baudry and Bertrand, 1999). Oscillatory neural activities are usually restricted both in 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. There are two types of EROs: *evoked* EROs are oscillations which are phase-locked to the corresponding event and can be recovered from averaged, non-filtered ERP waveforms; *induced* EROs are not phase-locked and are obtained from raw EEG before averaging. Evoked oscillations are usually short-latency responses while induced oscillations can occur both close to and farther away from the corresponding events (Csibra, Davis, Spratling, and Johnson, 2000; Herrmann and Mecklinger, 2000). For detailed guidance as to the calculation of these oscillations see Herrmann, Grigutsch, and Busch, 2005; and Csibra and Johnson, in press).

We illustrate the use of gamma-band oscillations by recent studies that explored neural correlates of one of the most debated phenomenon of infant cognition: the representation of hidden objects. Sustained responses in neural circuits have been identified as a mechanism for maintaining representations of objects during a period of occlusion (Rainer and 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 measured infants' electrophysiological responses to occlusion events at the age where reaching behaviour does not yet show evidence of understanding "object permanence" (Kaufman, Csibra, and Johnson, 2003). Six-month-old infants were 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. We hypothesised that gamma-band oscillatory activity may be present in the infant brain during object occlusion. The results are illustrated in Figure 4. Statistical analyses on the average gamma-band (20-60 Hz) EROs revealed higher activity in the Unexpected than in the Expected Disappearance condition both before and after the 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. These ERO changes were largely restricted to the right 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. 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. Indeed, we found no significant increase in gamma activity over right-temporal channels time-locked to the Unexpected Appearance event.

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, and 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 young infants' competence with moving objects from perceptual routines that track objects through space and time (Scholl and Leslie, 1999). Whatever the exact neural basis of these effects, the finding that increased gamma-band activity is associated with the representation of hidden objects will inform fundamental issues about how infants process their visual world.

## Future Directions

Ten years ago only a handful of pioneering laboratories recorded and analyzed infant EEG and ERPs to study the neural bases of cognitive development. Today many researchers use these methods and we expect that the number of infant electrophysiological laboratories will increase further in the future. However, we also expect that, beyond this horizontal extension, the techniques that applied to these recordings will also improve significantly. Here we discuss just one example of such developments, which has already proven to be a successful tool for understanding the neural bases of cognitive development in infancy.

Several attempts have been made to localize ERP components and ERO signals to specific anatomical structures in adults. However, so far there is no generally agreed solution for such an *inverse problem*. Applying the techniques developed for source localization of adult ERPs to recordings from infants is hampered by two factors. First, these techniques require clean data, which are free from 'noise' (brain activity unrelated to the eliciting event), and preferably reflect the activation of a single neural source or very few sources. It is very difficult to obtain such clean recordings from human infants, primarily because of the low number of averageable trials in infant studies. Second, source localization techniques depend on assumptions about anatomical structures like the skull, the cerebrospinal fluid, and the cortical convolutions. The physical parameters, and the maturation, of these anatomical details are not well known for young infants, and applying the parameters used in adult research could lead to mislocalization in infants.

A potential way to overcome these difficulties is to apply some kind of statistical method to separate underlying sources behind ERPs in the statistical, rather than in the physical, space. Such techniques may allow us to explore and compare the activity of functionally independent neural sources without committing ourselves to their exact anatomical location. However, if such a source separation procedure successfully isolates the

activation of a neural source, it will be more likely to reflect the functioning of a single structure than are ERP components, and it will be more easily localizable in the brain itself as well.

One such technique, which has been applied to infant ERPs, is called Independent Component Analysis (ICA, Bell and Sejnowski, 1995). ICA attempts to decompose the raw EEG signal into the sum of independently generated signals by making assumptions about the statistical distribution of the neural activation of the sources. This kind of decomposition has been shown to successfully isolate neural activity related to face and gaze processing (Johnson et al., 2001, 2005) and allocation of spatial attention (Richards, 2005) in infant ERPs. For example, Johnson et al. (2005) found that ICA components reflecting face processing in the occipital and temporal cortices were larger in amplitude when the eyes of the face displayed direct, rather than averted, gaze. This is consistent with earlier ERP reports by Farroni et al. (2002, 2004). However, the ICA analysis also identified further sources that were sensitive to gaze direction, and a subsequent localization attempt estimated that these sources originated from the prefrontal (possibly orbito-frontal) cortex. Such an effect was not uncovered in traditional ERP analyses, and this illustrates the possible power of statistical source separation methods.

Other neuroimaging methods could help further to clarify the interpretation of ERP and ERO results. Although source localization of infant electrophysiological findings is difficult, mapping these activations onto brain images collected by structural MRI (see chapter XXX) in infants (preferably the same ones who provided the electrophysiological data) reduces the degrees of freedom considerably. Alternatively, magnetoencephalography (MEG), a technique that is much more expensive and technically more challenging than EEG can also be used with infants (e.g., Imada et al., 2006). MEG recording is less affected by the blurring effect of the several layers of tissues between the cerebral cortex and the sensors and

hence provides a better signal for localization. Another possibility is combining electrophysiological measures with neuroimaging techniques that target functional hemodynamic changes in the brain. Especially promising is the combination of EEG and fNIRS (see chapter XXX) methods, because this latter optical imaging technique is non-invasive and requires less cooperation from young infants than does fMRI. Such co-registration is possible (e.g., Koch, Steinbrink, Villringer, & Obrig, 2006) and offers a unique opportunity to uncover the functioning of cortical mechanisms of human infants.

Although electrophysiological techniques do not offer accurate high-resolution images of their brain, they are valuable tools in assessing the neural underpinnings of the tremendous cognitive development that humans go through during the first years of life. This is why ERPs and related measurements have become ineliminable methods in the cognitive neuroscience of human infants.

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## Figure Legends

Figure 1. Auditory event-related potentials as a function of age, stimulus probability and duration. The left panel (A) represents ERP responses to harmonic tones of three different frequencies presented randomly mixed with probability of .33 each (see Kushnerenko et al., 2002a). The right panel (B) shows the ERPs to the harmonic tones presented with the same ISI but with probability of .85. Negativity is plotted upwards.

Figure 2. Event-related potentials to faces and matched visual noise stimuli in 3-month-old infants. Note that positivity is plotted upwards. (Adapted from Halit, Csibra, Volein, and Johnson, 2004.)

Figure 3. Seven-month-old infants' ERP responses to emotionally congruent (solid) and incongruent (dotted) face-voice pairs. Negativity is plotted upwards. (Adapted from Grossmann, Striano, Friederici, 2006.)

Figure 4. Gamma-band EROs time-locked to a tunnel-lifting event in 6-month-old infants. In the "Unexpected Dispppearance" condition the infants had just seen a train entering the tunnel. The difference map represent the scalp distribution of the oscillatory activity. (Adapted from Kaufman, Csibra, and Johnson, 2003.)









