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Application of EEG, ERP and intracranial recordings to the investigation of cognitive functions in children

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Abstract

Neurophysiological measures can provide important information about the substrate of cognitive function in children, and most importantly, can give precise temporal information about 'on-line' brain function. These measures can be readily used in infants and children, and we present some examples of their application to understanding cognitive development. The most widely used of these techniques for developmental research is the method of event-related potentials (ERPs). In addition, the electroencephalogram (EEG) and the more rarely used invasive, intracranial investigations are also important to furthering our knowledge of how the brain–behaviour relations develop. The paper summarizes practical issues and presents some selected examples of experimental and clinical research.

Introduction

In this paper we review some of the basic issues in the application of neurophysiological measures to development, and highlight a few areas of research in this field. We start with EEG, the oldest of the techniques, and end with intracranial studies which are not frequently used in children, but can provide powerful insights into brain function. The greater portion of the paper is on ERPs, due to the large number of studies with this technique. The paper is not and could not be exhaustive. Although there is much less neurophysiological research in children compared to adults, there is still a vast literature and we have sampled only portions thereof. The reader is strongly encouraged to pursue areas that have caught his/her attention, starting hopefully with some appropriate references cited in the paper, as much of the work in this field has data that are critical for better understanding cognitive processes in adults as well as complementing psychological studies in children.

EEG

The electroencephalogram (EEG) measures ongoing electrical activity of the brain, recorded from electrodes placed on the scalp. It is widely used in clinical settings, as it is the first and most important investigation for the diagnosis and management of epilepsy, which is the most common reason for referral to neurology in childhood. EEG is also a critical tool in evaluating patients' status in intensive care settings, both paediatric and neonatal (e.g. Murdoch-Eaton, Darowski & Livingston, 2001; Saliba, Marret, Chavet-Queru, Degiovanni & Laugier, 1998). The analyses for clinical settings differ from those used for research in the developmental neurosciences, as they are concerned largely with the identification and localization of abnormalities in the EEG (e.g. Ochi, Otsubo, Chitoku, Hunjan, Sharma, Rutka, Chuang, Kamijo, Yamazaki & Snead, 2001; Otsubo, Shirasawa, Chitoku, Rutka, Wilson & Snead, 2001), and the utilization of this information for neurosurgical interventions in the most severe cases (Snead, 2001; Duchowny, Jayakar & Koh, 2000).

However, as there are dramatic EEG changes with age that reflect cortical development, an obvious prerequisite for cognitive development, EEG can be used to assess cognitive functions and improve our understanding of the relation between brain maturation and behavioural development. The EEG rhythms are conventionally classified into different frequency bands (delta (<4 Hz), theta (4–7 Hz), alpha (8–12 Hz), beta (13–30 Hz)) and gamma-band oscillations (30–70 Hz, centred at 40 Hz) which have different developmental patterns. In the neonatal period the waking EEG contains largely slow frequencies (delta and theta), with the higher frequencies (alpha and beta) increasing in relative power with age (Gasser, Verleger, Bacher & Sroka, 1988; Harmony,

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Marosi, Diaz de Leon, Becker & Fernandez, 1990). The decreases in the lower frequency bands occur in the first years of life, whereas the increases in alpha typically continue until early adolescence, while beta continues to mature until adulthood. These changes also proceed at different rates in different cortical areas (Wada, Ogawa, Sonoda & Sato, 1996), allowing estimation of cortical maturity of the various brain regions (Anokhin, Lutzenberger & Birbaumer, 1999; Takano & Ogawa, 1998). The rate of maturation posteriorly is almost twice that seen at central sites (Benninger, Matthis & Scheffner, 1984) and is slowest at anterior sites (Gasser, Jennen-Steinmetz, Sroka, Verleger & Mocks, 1988), continuing until late adolescence. EEG measures are typically the relative or absolute power in spectral analyses, calculated through fast Fourier transform, although analyses more sensitive to age-related spectral changes have been developed (Alvarez-Amador, Valdes Sosa, Pascual, Marqui, Galan Garcia, Biscay Lirio & Bosch Bayard, 1989). For these analyses artefact-free epochs of EEG are selected and submitted to spectral analysis. The EEG power spectrum is preferably calculated from many EEG derivations as the frequency bands are topographically localized, e.g. the alpha rhythm is most typically seen over the occipital scalp. The relative power reflects the percentage of the total EEG signal contained in each frequency band. The relative power of alpha and beta tend to increase with age while the lower frequency bands decrease. As the overall amplitude of EEG signal decreases across childhood, perhaps due to neuroanatomical (white and grey matter maturation) and physical (skull) development, so does the absolute power in most frequency bands. Thus, the measures of relative power and absolute power show different age-related profiles (Gasser, Verleger, Bacher & Sroka, 1988; Somsen, van't Klooster, van der Molen, van Leeuwen & Licht, 1997).

The resting EEG spectral measures have been used in comparisons of children with normal cognitive development, and children with learning disabilities (Harmony, Marosi, Becker, Rodriguez, Reyes, Fernandez, Silva & Bernal, 1995), dyslexia (Klimesch, Doppelmayr, Wimmer, Gruber, Rohm, Schwaiger & Hutzler, 2001) and attention deficit disorders (e.g. Bresnahan, Anderson & Barry, 1999). Generally, decreased power in the higher frequency bands is seen in the clinical groups (Fein, Galin, Yingling, Johnstone, Davenport & Herron, 1986), suggesting maturational lag, although the EEG measures also can monitor maturational spurts in these children (Harmony *et al.*, 1995). Children at risk for various reasons also can show EEG abnormalities (Harmony *et al.*, 1990), which can aid in the selection of children for remedial interventions.

In addition to the above analysis of the spontaneous or resting EEG, spectral changes that occur in response to a cognitive event or stimulus can also be extracted from the ongoing EEG. This method is call Event-related Synchronization (ERS) or Desynchronization (ERD). The frequency bands have been linked with differing cognitive processes (e.g. Ray & Cole, 1985; Fernandez, Harmony, Silva, Galan, Diaz-Comas, Bosch, Rodriguez, Fernandez-Bouzas, Yanez, Otero & Marosi, 1998; Klimesch, 1999). For example, the post-stimulus theta is related to working memory access (Klimesh *et al.*, 2001), and the gamma band to perceptual binding (Tallon-Baudry, Bertrand, Delpuech & Pernier, 1996). EEG spectral analyses, conducted on EEG epochs obtained during cognitive tasks, investigate localized task-specific increases (or decreases) in power (Basar, Basar-Eroglu, Karakas & Schurmann, 1999), and are readily applied to children (Roberts & Bell, 2000; Galin, Raz, Fein, Johnstone, Herron & Yingling, 1992; Klimesch, 1999). Fernandez *et al.* (1998) investigated performance on three different tasks (colour discrimination, verbal working memory and word classification tasks) in children, and analysed EEG segments prior to the stimuli as predictors of task performance. The EEG data were submitted to source analysis and they reported changes in EEG power that varied in both the maximal frequency of response and its localization as a function of task. Harmony *et al.* (2001) found localized changes in power spectra at lower frequencies for a word task, and in higher frequencies for a figure task, and the location of these changes (also submitted to source analysis) differed between tasks (temporo-occipital regions for words, and prefrontal and anterior temporal regions for the figures), suggestive of the underlying brain areas being preferentially involved in these tasks. Thus, with the careful application of source analysis programs it may be possible to obtain more accurate spatial localization of the EEG activity and hence deduce the brain areas involved in specific cognitive processes.

Another analysis procedure for EEG is coherence, which depends on the power and phase dynamics between two signals (two electrode sites); the covariation reflects the strength of their relationship. Measures of EEG coherence, within frequency bands at electrode sites overlying different brain areas under certain conditions can be taken as evidence of functional coupling among brain regions. High values of coherence have been interpreted as evidence for coactive neuronal populations, information exchange or coordination between or among the brain regions (Knyazeva & Innocenti, 2001), or common input from a third region. Coherence measures are made in ongoing EEG during rest periods and/or during different types of tasks (e.g. mental calculation, mental rotation). Systematic changes with age, such as patterns of regularly spaced growth spurts in coherence and increasing long-distance coherence (Thatcher, 1992) are thought to reflect brain maturational processes and have been applied to the understanding of the development of brain function (Case, 1992). Coherence measures need to be carefully interpreted, however, if studies with different methodologies are to be compared, as a coherence pattern may be more dependent on the coherence method than state (Florian, Andrew & Pfurtscheller, 1998; Nunez, Silberstein, Shi, Carpenter, Srinivasan, Tucker, Doran, Cadusch & Wijesinghe, 1999; Nunez, Srinivasan, Westdorp, Wijesinghe, Tucker, Silberstein & Cadusch, 1997). With this caveat in mind, there are still many interesting findings of coherence changes with age (Srinivasan, 1999; Anokhin *et al.*, 1999), including studies in young infants (Bell & Fox, 1992). Coherence measures have also been applied to the study of cognitive developmental disorders (e.g. Marosi, Harmony, Sanchez, Becker, Bernal, Reyes, Diaz de Leon, Rodriguez & Fernandez, 1992) where fewer age-related changes in coherence are noted in the clinical groups.

EEG analyses are particularly valuable in infants when there are fewer other options for investigating brain–behaviour relations. In an impressive series of studies Bell and Fox have demonstrated that increases in spectral power (in the 6–9 Hz range) are related to brain development (Bell & Fox, 1992) and coherence measures can reflect achievement of motor milestones (Bell & Fox, 1996). When EEG was assessed during object permanence tasks, frontal EEG findings distinguished the group of infants able to perform the most difficult task (with a long delay) (Bell & Fox, 1992), while occipital EEG power correlated individually with task performance (Bell & Fox, 1997). Recently, measures of gamma oscillations, related to binding of features in adults (Herrmann, Mecklinger & Pfeifer, 1999; Tallon-Baudry *et al.*, 1996), have shown a similar pattern of results in infants. When infants were presented with an illusory object, increased gamma oscillations were seen, but only at the age at which behaviourally infants appear to see objects as units (Csibra, Davis, Spratling & Johnson, 2000).

Thus there are considerable age-related changes in the EEG, which given appropriate analyses, can aid in the understanding of basic as well as task-specific cortical development.

Event-related potentials (ERPs)

When ongoing EEG is averaged, time-locked to stimulus or response events, the resultant waveforms are referred to as ERPs. The ERPs reflect discharges from large populations of neurons, linked to specific aspects of sensory and cognitive processing. They provide from millisecond to second analyses of the stages of information processing during a wide range of cognitive tasks (for reviews see Picton & Hillyard, 1988; Kutas, 1991; Mecklinger, 2000). ERPs are easily employed with children (Friedman, 1991; Taylor, 1995) and are valuable in studying a range of cognitive processes in children of all ages, as they can be recorded for task-relevant or irrelevant stimuli, in passive or active tasks.

ERP waveforms are typically designated by their polarity (N = negative; P = positive) and either order of occurrence (e.g. P1, N1, P2, N2, P3 etc.) or mean latency in milliseconds after stimulus presentation (e.g. N170, P360, P550 etc.). The various ERP components are usually quantified in terms of the peak latency and maximum amplitude from a pre-stimulus baseline, but an area measure under a broad peak is also used, particularly in infants. ERP waveforms differ depending upon the modality and cognitive processes utilized. For example, the vertex N1 in auditory tasks is related to early processing and attention (Näätänen & Picton, 1987; Oades, Dittmann-Balcar, Schepker, Eggers & Zerbin, 1996) whereas in the visual modality, the N1 is recorded over posterior occipito-temporal brain areas and can index attention to a location (Handy & Mangun, 2000; Novak, Solanto & Abikoff, 1995) or processing visual stimulus features (Han, Liu, Yund & Woods, 2000; Taylor & Khan, 2000). Some components have also been linked to specific cognitive operations, such as N170 with encoding faces (Bentin, Allison, Puce, Perez & McCarthy, 1996) and N400 with indexing semantic incongruities (Kutas & Hillyard, 1980).

Methodological details

As in adults, ERPs are best recorded from electrodes set in electrode-caps or electrode nets (Johnson, de Haan, Hatzakis, Oliver, Smith, Tucker & Csibra, 2001) (sized according to the children's head sizes), such that the inter-electrode distances are not variable. Also, as children will not sit quietly and calmly for long periods of time, the expediency of placing many electrodes quickly as well as accurately with caps or nets is a huge advantage. For recording the ERPs, the recently published guidelines (Picton, Bentin, Berg, Donchin, Hillyard, Johnson, Miller, Ritter, Ruchkin, Rugg & Taylor, 2000) should be followed. In developmental studies, group ERP averages should be made over no more than one or two years in childhood, 2–3 years in adolescence, and only groups with a range of 1–2 months in infant studies. This is due to the considerable decreases in latency

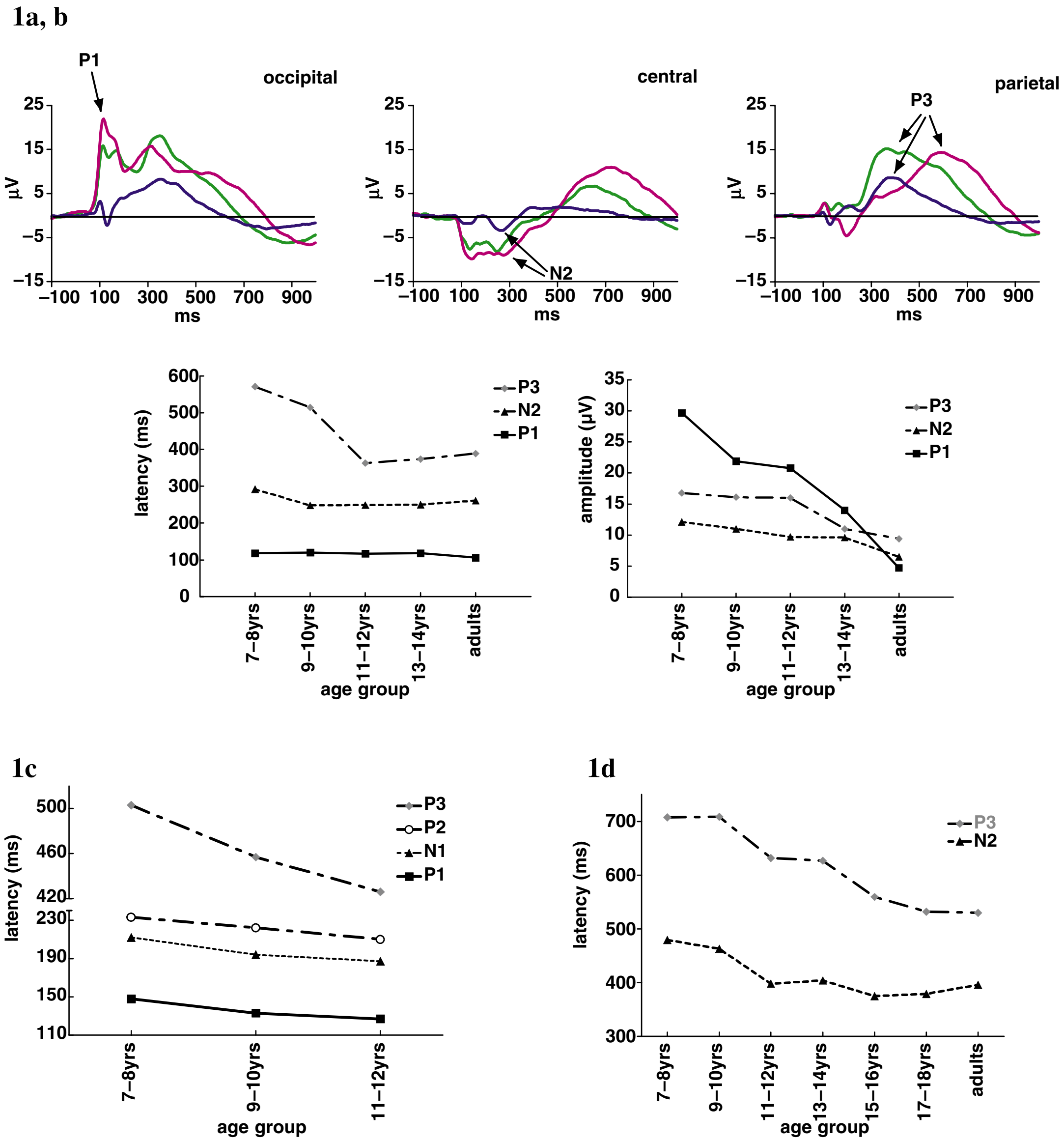

Figure 1 *(a) Grand average ERPs in a visual categorization task (animal/non-animal) from three groups of subjects, 7–8-year-olds (pink line), 11–12-year-olds (green line) and adults (blue line), showing age-related changes in three components measured occipitally (P1), centrally (N2) and parietally (P3). In (b), the mean latencies (left) and amplitudes (right) for these data across five age groups are shown. Note the different patterns as a function of the component. For example, P1 does not change in latency for this task, but shows tremendous decreases in amplitude. In contrast the N2 and P3 show early latency changes (completed by 9–10 years for N2, and 11–12 years for P3), but amplitude changes that start later (particularly for the P3) and continue until adulthood (adapted from Batty & Taylor, 2002). NB. N2 amplitudes are plotted as absolute values for better comparison with the positive components. (c) Mean ERP latencies from four components in a serial visual search task, showing small but significant decreases in the early components across the three age groups, and larger age-related changes for the P3 (from Taylor, Malone & Khan, 1999 and Taylor & Khan, 2000). (d) Mean latencies of the N2 and P3 components in a reading categorization task (animal/non-animal) showing decrease in the N2 until 11–12 years of age, and in the P3 until 17–18 years of age (from Taylor & Eals, 1996). Although this was essentially the same task used for the data in Figure 1a, b, the fact that in this task the children had to read the words rather than looking at briefly presented coloured pictures, made the task harder, added stages of processing related to reading and thus the P3 reached adult levels only in late teens rather than pre-teens.*

and either decreases or increases in amplitude with age, which is greater the younger the child. If averaging occurs across a wide age range, these developmental changes would be obscured and the variability would be increased. It is recommended that peaks be measured only over the areas where the peak is maximal (Picton *et al.*, 2000). This is particularly important to consider in developmental studies as the distribution of peaks changes with age, and the maxima cannot necessarily be decided upon until after the data are collected and examined. Hence, the number of electrodes should be reasonable (>15 active electrodes) and evenly spread over the scalp, for both a better definition of waveforms and of their age-related changes, as larger age effects are often seen in lateral and anterior sites. Also, if source analyses are to be undertaken (which to date have unfortunately been rarely used with developmental data sets), then adequate sampling must include areas overlying the inferior regions of the brain. In order to deduce localization of ERP sources, the application of specialized, complex programs such as BESA or VARETA are recommended (Picton, Alain, Woods, John, Scherg, Valdes-Sosa, Bosch-Bayard & Trujillo, 1997; Scherg & Berg, 1996), but they require considerable knowledge and expertise to use. The available software for source analyses is modelled on adult heads, and care must be taken in interpreting these solutions particularly in young children, when some of the head, skull and size assumptions in these programs may not apply, or may need to be modified.

The latencies and amplitudes of all the ERP components change with age, as ERPs reflect cognitive processing, which changes tremendously over childhood. Some of the earlier components reach adult latencies (but not usually amplitudes) in early childhood, while others continue to change until adulthood (see Figure 1), depending upon the complexity of the cognitive processing they reflect.

ERP studies have contributed to our knowledge of the development of cognitive processes including attention (Courchesne, Akshoomoff & Ciesielski, 1990; Jonkman, Kemner, Verbaten, Van Engeland, Camfferman, Buitelaar & Koelega, 2000), memory (Cycowicz, Friedman & Snodgrass, 2001; Hepworth, Rovet & Taylor, 2001; Nelson, 1992), face perception (Taylor, McCarthy, Saliba & Degiovanni, 1999), language (Byrne, Connolly, MacLean, Dooley, Gordon & Beattie, 1999; Holcomb, Coffey & Neville, 1992; Mills & Neville, 1997) and reading (Licht, Bakker, Kok & Bouma, 1992; Taylor, 1993). ERPs can also be a valuable method for studying abnormal cognitive development in patient populations such as dyslexia, attention deficit disorders or autism. In this section we will briefly review the use of ERPs in some of these areas, starting with normative studies, followed by examples of clinical applications.

Visual attention studies

Attention is critical at all stages of cognitive processing, and developmental changes in attention are well documented in the behavioural literature. Although many studies have measured N2 (around 200 ms post-stimulus) and P3 (also referred to as P300, as in adults in simple tasks, it occurs at 300 ms post-stimulus) in attention tasks (Friedman, 1991; Johnson, 1989; Taylor, Malone & Khan, 1999), recent reports have shown very early stages of information processing to be sensitive to visual attention (Mangun, Hillyard & Luck, 1992; Mouchetant-Rostaing, Giard, Delpuech, Echallier & Pernier, 2000), even in young children (Taylor & Khan, 2000). This suggests that measuring earlier stages of processing may be important for elucidating details of specific attentional changes with development.

A debate in the adult literature has focused on the attentional demands for feature and conjunction processing; whether attention is required for processing all visual information or whether there are pre-attentive or parallel channels for simple features (Treisman, 1988; Wolfe, Cave & Franzel, 1989). A related issue, dealing primarily with the encoding of conjunction of features, is referred to as the 'binding problem'; how are individual features (such as colour and shape) bound together and associated with the appropriate object among many in the visual field? (For a review of recent issues and research on binding, the reader is referred to the issue of *Neuron*, vol. 24, 1999, pp. 5–115.) Using single-feature pop-out tasks to assess parallel processing, and a conjunction of features task to study serial processing, Taylor and Khan (2000) found decreases in ERP latencies with age (7–12-year-olds), but also P1, N1 and P2 latency effects that varied with task. P1 to arrays containing a colour pop-out were larger and earlier when those arrays were targets than non-targets, demonstrating top-down modulation of processing, consistent with the guided search model of visual processing (Wolfe *et al.*, 1989). Serial processing, seen most clearly in the non-target trials (as searching continues longer when no target is found (Chun & Wolfe, 1996)), was reflected in anterior P2 amplitude modulations that also varied with task and age. Thus, feature-specific top-down processing was found in children, starting with P1 which was sensitive to attention to colour, the processing of form yielded effects only starting with N1, while more controlled search was reflected in later anterior components.

These tasks used stimulus arrays, however, thus confounding binding or conjunction of stimulus features with visual search of the array (Woods, Alain & Ogawa, 1998). In subsequent tasks, items were presented singly, in a rapid visual search paradigm (Cortese, Bernstein & Alain, 1999) to investigate attention to single features of colour or form, or their conjunction (Theunissen, Alain, Chevalier & Taylor, 2001). Compared with adults, children had longer N1 and P2 latencies, and larger P1 and P2 amplitudes. For both P1 and P2, hemispheric asymmetries seen in adults (RH>LH for P1 and LH>RH for P2) were present only for the colour task in children. This suggests that the more difficult processing related to form and conjunction continues to mature between 12 years and adulthood. For both groups, however, there were no ERP latency effects as a function of single feature task versus conjunction task, suggesting that the binding of features can proceed in parallel with the processing of single features, consistent with recent models of perceptual processing (Bartels & Zeki, 1998; Wolfe *et al.*, 1989). These examples demonstrate that developmental studies are valuable in and of themselves for the understanding of cognitive processes in childhood, but can also be critical in confirming models of cognitive processing based on adult data (Enns, 1993).

Developmental studies of face processing

Faces are the most important visual stimuli to us for our social interactions, yet the understanding of our proficiency in recognizing large numbers of faces remains limited despite extensive study in the last decade. Specialized neural networks for processing faces have been proposed (Allison, Puce & McCarthy, 2000; Haxby, Hoffman & Gobbini, 2000), largely involving posterior and inferior temporal regions of the brain. Scalp recorded ERPs show a face-sensitive component (referred to as N170 (Bentin *et al.*, 1996; George, Evans, Fiori, Davidoff & Renault, 1996)), largest at posterior temporal leads. Numerous adults' ERP studies have demonstrated the sensitivity of N170 to various types of facial stimuli.

The impressive aptitude for face processing in adults, referred to as expertise, is in contrast to much poorer skills in children (Baenninger, 1994; Chung & Thomson, 1995; Ellis, 1992; Flin, 1985). It is not clear from the behavioural literature whether face processing undergoes qualitative or quantitative change with age, and the role of configural versus featural processing in this development. ERPs allow the assessment of developmental changes that occur in the neural substrates underlying face processing. Taylor *et al.* (1999) first demonstrated that, as in adults, N170 was sensitive to faces in children (from 4 years of age), and found gradual latency and distributional changes with age. A larger study investigated the role of configural processing in this development; stimuli included faces, inverted faces, eyes-only and control stimuli, and adults and children (4–15 yrs) were tested (Taylor, Edmonds, McCarthy & Allison, 2001). P1 was shorter in latency to faces than all other stimuli, across all age groups, suggesting that some early encoding of faces occurs at this latency. N170 latency decreased with age, but the greatest developmental changes were seen with upright faces, and the least with eyes-only stimuli (see Figure 2). Protracted but differing developmental curves for upright and inverted faces argued that both require configural processing, and that development in face processing is due primarily to improvement in this aspect of face encoding. Regardless of age, eyes evoked the largest N170, and only eyes had a consistently right-sided distribution. These results suggested that the underlying neural structures associated with processing faces and eyes are different, and the presence of an eye detector, which has a rapid maturational course.

The development of face processing in infants has been investigated with ERPs also, as behavioural studies have found that neonates respond preferentially to faces or face-like patterns, which suggests that face-specific regions identified in adults may be functioning from birth (Maurer, 1985; de Schonen, Deruelle, Mancinci & Pascalis, 1993). De Haan *et al.* (2001) compared ERPs to human and non-human primate faces, both upright and inverted, in 6-month-old infants. The adults' N170 showed sensitivity to upright human faces that was not observable at any point in the infants' ERPs. An 'infant N170' did, however, show sensitivity to the species of the face. These findings suggest a process of gradual specialization of cortical face processing systems during postnatal development. In other studies 7-month-old infants' ERPs were recorded while they viewed neutral, happy and fearful faces, and responses at about 400 ms differentiated emotional from neutral and happy from fearful faces (Nelson & de Haan, 1996). Infants tested in an identity recognition task showed differentiation of novel from familiar faces at a similar time-point, but with a different topography (de Haan & Nelson, 1997). These results show that infants' ERP responses to facial expressions are different from those to facial identity and thus do not reflect only the relative familiarity of the expressions.

Longer latency components have also been investigated with face tasks in infants and have shown that 6-month-olds could recognize their mothers' pictures. ERPs differed for mother versus stranger regardless of similarity, but for mother versus dissimilar stranger the Nc (frontal-central component, between 250–700 ms) was affected whereas for mother versus similar stranger a longer-latency slow wave was affected. The ERPs were more

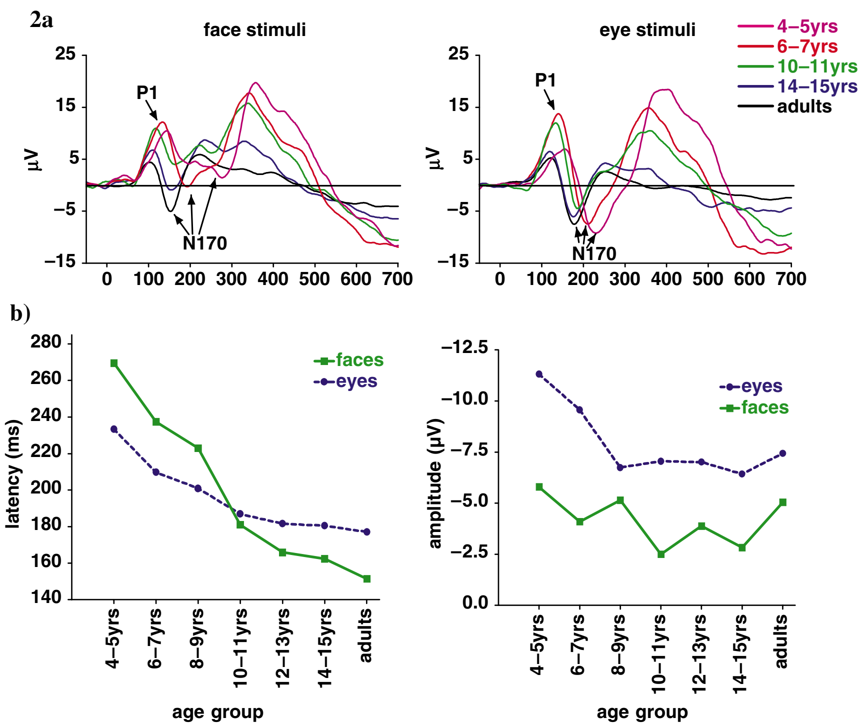

Figure 2 *(a) Grand average ERPs in a faces task recorded from right posterior temporal site (P8), from upright faces stimuli (left) and eye stimuli (right) for five age groups; (b) presents the changes across all age groups in average N170 latencies (right) and amplitudes (left) for the face and eye stimuli. N170 latency to eyes matures more rapidly, and although the amplitude decreases over the three younger age groups, it remains larger than N170 to faces across all age groups (adapted from Taylor* et al.*, 2001).*

sensitive in assessing facial recognition in infants than the traditional behavioural measure of looking time (de Haan & Nelson, 1997). Three components were shown to be differentially sensitive to aspects of object versus face processing: faces versus objects at an occipital P400, recognition of familiarity (Nc) and encoding of novelty (frontal slow wave) (de Haan & Nelson, 1999). All of these studies demonstrate that ERPs can provide invaluable information on category knowledge in infants, and when and how various aspects of visual processing and recognition develop. The studies in childhood demonstrate the prolonged maturational course of acquiring expertise, and underline the importance of developmental studies for assessing this expertise.

Early auditory ERPs

This section thus far has demonstrated developmental changes in children to visual stimuli; comparable age-related development occurs in the auditory modality. The most studied early auditory component in adults is the N1 (Näätänen & Picton, 1987). It consists of a vertex component, N100 or N1b, generated in the supratemporal planes of the auditory cortices, but which has a fronto-central distribution due to the sources being oriented anteriorly, and two components recorded over temporal sites, N1a and N1c at 75 ms and 130 ms, respectively, which appear to originate on the lateral surface on the superior temporal gyri. Thus, there are three separate measures of early auditory processing, which are valuable in determining which part(s) of the temporal lobes are implicated in auditory cognition.

Several studies using tone stimuli have shown larger temporal responses (N1a and N1c) in young children, with larger vertex N1s (N1b) in older children and adults (deCrévoisier, Peronnet, Girod, Challet & Revol, 1975; Bruneau, Roux, Guerin, Barthelemy & Lelord, 1997). Although some other studies have found less consistent results (Tonnquist-Uhlén, Borg & Spens, 1995; Oades, Dittmann-Balcar & Zerbin, 1997) these differences could be due to paradigm differences. Pang and Taylor (2000) confirmed the earlier findings that showed a maximal N1 at the temporal electrodes in children, and a maximal N1 at the vertex in adults, and demonstrated asynchronous age-related changes for the three N1 components. The vertex N1b showed a parietal distribution that shifted anteriorly with age. The N1c measured over the left hemisphere matured earlier than the N1c over the right hemisphere and matured earlier to speech stimuli than to tones. These data suggest more precocious development of the left hemisphere and of the generators underlying speech processing. With click stimuli, Ponton, Eggermont, Kwong and Don (2000) also found substantial and asynchronous changes in all of the early auditory ERP components, extending into adolescence. They argued that these changes paralleled maturational changes in auditory cortex, such as synaptic density, and helped explain the prolonged maturational time-course for certain auditory processing skills, such as those related to speech recognition. The above two studies also caution against generalizing across studies when different electrodes arrays are used, as the components are differentially visible and can appear to have different maturational curves, depending on where the responses are recorded.

When ERPs to standard and rare deviant auditory stimuli in passive paradigms are subtracted, the difference potentials show a mismatch negativity (MMN). The MMN is generally reported to reflect automatic detection of auditory change (in frequency, pitch, location, duration, etc.) (Näätänen, 1995) and is being increasingly applied to developmental questions. Although originally reported with very simple recordings to be stable across childhood (Kraus, McGee, Micco, Sharma, Carrell & Nicol, 1993), recent studies have shown significant amplitude and latency changes with age (Gomot, Giard, Roux, Barthelemy & Bruneau, 2000; Oades *et al.*, 1997; Cheour, Leppanen & Kraus, 2000; Shafer, 2000). With the inclusion of larger electrode arrays the developmental studies also provide important insight into the neural sources of the MMN (Gomot *et al.*, 2000). As the MMN readily differentiates speech and non-speech stimuli (Korpilahti, Krause, Holopainen & Lang, 2001; Näätänen, 1995) many applications of MMN have been to assess language function in dyslexic or learning disabled populations (Baldeweg, Richardson, Watkins, Foale & Gruzelier, 1999; Leppanen & Lyytinen, 1997) or speech perception in children with cochlear implants (Eggermont, Ponton, Don, Waring & Kwong, 1997; Ponton, Eggermont, Don, Waring, Kwong, Cunningham & Trautwein, 2000). Despite significant differences being found between clinical and control groups, the application of MMN to developmental disorders on an individual basis is still in its infancy (Csepe & Molnar, 1997; Picton, Alain, Otten, Ritter & Achim, 2000).

Dyslexia

Reading is a complex skill, integrating speech sounds with visual symbols, that does not proceed smoothly in 8–10% of otherwise normal children. This is an enormous educational as well as socio-economic problem, as poor reading skills can interfere with adult job search, professional success and self-esteem. Although some studies have investigated neural correlates of reading development in normal children at the letter and word level (e.g. Licht *et al.*, 1992; Taylor, 1988, 1993) as well as at the semantic level (Holcomb *et al.*, 1992; Taylor & Eals, 1996), most studies with reading or reading-related tasks have been used with dyslexic populations in attempts to identify the cognitive dysfunction(s) that produce the reading disability. Early reports looked at simple ERP paradigms and the P3 (Holcomb, Ackerman & Dykman, 1985, 1986; Stelmack & Miles, 1990), and found deficits in dyslexic children, but these studies did not allow precise specification of cognitive processing dysfunction. As dyslexics often present with phonological deficits, many studies have recorded the auditory MMN and found abnormalities that correlated with the degree of phonological impairment, such as spectral processing deficits or specific deficits in speech sound processing (Baldeweg, Richardson *et al.*, 1999; Kraus, McGee, Carrell, Zecker, Nicol & Koch, 1996). These results point to a deficit of pre-attentive mechanisms for sound and speech processing as a possible source of the difficulties in learning to read. Other investigations have included long latency ERPs to reading tasks (Brandeis, Vitacco & Steinhausen, 1994; Taylor & Keenan, 1990), rhyming tasks (Ackerman, Dykman & Oglesby, 1994) and orthographic and phonological tasks (McPherson, Ackerman, Holcomb & Dykman, 1998; Taylor & Keenan, 1999) and also found deficits at these later cognitive stages of processing. These various data emphasize the importance of examining both earlier and later components, as dyslexic children may show impairments at different levels of processing. It is also recommended that several complementary tasks be used within a study to better define cognitive processing abilities as well as disabilities.

A number of studies have reported differences in ERP scalp distributions between control children and dyslexics (Brandeis *et al.*, 1994) or subgroups of dyslexics (Taylor & Keenan, 1990, 1999) suggesting that rather than a maturational lag, there are underlying differences in cortical utilization during reading. Yet only a few studies have found that lateralization differed between dyslexics and controls (Khan, Frisk & Taylor, 1999; McPherson *et al.*, 1998).

A concern with many of the studies completed in this field is that although subtypes of dyslexia with different processing disabilities have been identified (Castles, Datta, Gayan & Olson, 1999) many ERP studies have not grouped or selected subjects accordingly. The behavioural deficit needs to be correctly defined (e.g. with phonological measures such as non-word repetition for the phonological subtype, for instance) at the time of the ERP studies. Dyslexic children with visual impairment and those with primarily auditory impairment would likely have different patterns of ERPs on tasks in the two modalities. For studies of dyslexia both auditory and visual tasks that vary in difficulty are suggested, and in particular tasks that manipulate or challenge temporal processing as well as reading tasks *per se*, should be included.

Attention deficit hyperactivity disorder (ADHD)

ADHD is the most common psychiatric disorder in childhood, affecting 9% of boys and 3% of girls (Szatmari, Offord & Boyle, 1989). It is heterogeneous, with several subtypes and frequently co-morbid with learning or conduct disorders; these need to be documented for any studies with this population (E. Taylor, 1998). ADHD also has serious ramifications at a socio-economic level due to children with ADHD being at much higher risk for school failure and delinquency, the effects of which extend into adulthood. Numerous studies have investigated ERP correlates of ADHD, to understand ADHD itself, and as a model of attention to better understand the neural processing and localization of attentional functions (see Oades, 1998, for a review). Early studies measured only the late P3 component while recent studies have shown that early peaks better reflect stages of processing dysfunction (Brandeis, van Leeuwen, Rubia, Vitacco, Steger, Pascual-Marqui & Steinhausen, 1998; Pliszka, Liotti & Woldorff, 2000). Based on ERP findings, some reports have suggested that ADHD is a result of processing strategy differences such as resource or capacity-allocation (Jonkman *et al.*, 2000; Yong-Liang, Robaey, Karayanidis, Bourassa, Pelletier & Geoffroy, 2000), while others have argued for problems in inhibitory control, based on poor performance in ADHD children in stop-task paradigms (e.g. Rubia, Oosterlaan, Sergeant, Brandeis & Leeuwen, 1998).

Methylphenidate is the most common treatment for ADHD, as it tends to improve attention and behaviour. However, as the precise nature of methylphenidate on attention is not clear, many investigations of ADHD have included drug response conditions. Methylphenidate has been shown to normalize P3 in ADHD children, who are often reported to have smaller and/or longer latency P3s (Klorman, Brumaghim, Fitzpatrick, Borgstedt & Strauss, 1994; Taylor, Voros, Logan & Malone, 1993). Sunohara, Malone, Rovet, Humphries, Roberts and Taylor (1999) also found drug effects on early components, as methylphenidate increased N2 and P2 latencies to normal range, suggesting slower and more careful encoding, less attentional impulsivity on medication. In contrast, P3 shortened in latency with methylphenidate suggesting greater speed in closure or post-decisional processes. Hence, the attention deficit produced dysfunction at different stages of processing, which were differentially affected by the medication. Jonkman *et al.* (2000) found that performance was enhanced with methylphenidate, but not the allocation of attentional capacity. This was in contrast to an earlier study, where no drug effects were seen (Jonkman, Kemner, Verbaten, Van Engeland, Kenemans, Camfferman, Buitelaar & Koelega, 1999) on ERPs on attentional measures of interference, although accuracy increased. Thus, the effects of methylphenidate on ERPs are not general across studies, but are sensitive to the cognitive demands of the tasks used and stages of processing assessed. ERPs can facilitate the understanding of the stages of processing that are impaired in ADHD children, and the effects of medication therapy on these processes.

Intracranial recording of ERPs in adults and children

Surgical implantation of EEG electrodes (multi-contact sub-dural arrays or depth electrodes, usually spaced 1 cm apart) is an increasingly common procedure in patients with refractory focal epilepsy. This permits extra-operative localization of the seizure onset zone and of its relation to functionally eloquent cortex. Intracranial ERPs (iERPs) are extracted from the electrocorticogram (ECoG) in much the same way as from scalp-EEG, except that their voltage is much larger (up to 150 μV) and they have a high spatial resolution, in contrast to scalp ERPs, which are distorted due to the spatially integrating properties of cerebrospinal fluid, skull and skin. iERP components are often visible in very few adjacent electrode contacts, spanning a few square cm, with steep amplitude gradients, suggesting close proximity to the cortical generators. This feature is the main reason why iERPs are now a firmly established method of modern cognitive neuroscience, combining the temporal resolution of scalp ERPs with a spatial resolution that is comparable to that of fMRI. It is important to bear in mind that there are obvious limitations to this method, because electrodes are inserted for clinical reasons only to restricted areas of the brain. The great majority of iERP studies reported so far have been performed in adult patients, and only very occasionally in children and adolescents. We have grouped those studies into sections with different emphasis on language, perception, attention and memory, respectively.

Language ERPs were recorded from the exposed frontal and temporal cortex during neurosurgery while patients were awake (Fried, Ojemann & Fetz, 1981; Ojemann, Ojemann, Lettich & Berger, 1989) using paradigms such as silent naming. Areas were identified that were active for language but not for spatial processing of the same stimuli. In addition to the slow cortical ERPs in response to speech perception and production recorded with ECoG, this group was also able to record single neuron responses to speech stimuli using microelectrodes inserted into the lateral and superior temporal cortices (Creutzfeldt, Ojemann & Lettich, 1989).

Early category-specific ERPs were identified in ventral and lateral temporal cortex in response to face stimuli, pictures of objects, letters, numbers and colours (Allison, Puce, Spencer & McCarthy, 1999), recording in 98 patients with electrodes on the cortical surface. These data supported the existence of functionally specialized visual processing modules, and particularly contributed to our understanding of processing faces (Allison, McCarthy, Nobre, Puce & Belger, 1994; McCarthy, Puce, Belger & Allison, 1999; Puce, Allison & McCarthy, 1999). A word recognition pathway was also discovered in the fusiform gyrus of the inferior temporal lobe (Nobre, Allison & McCarthy, 1994).

The neural generators of attention-dependent ERPs commonly recorded in oddball tasks were identified by systematic iERP sampling of different brain areas in 39 patients (Halgren, Baudena, Clarke, Heit, Marinkovic, Devaux, Vignal & Biraben, 1995). Endogenous ERPs with a widespread scalp distribution (such as P3 and N4) were found to have multiple, concurrently active intracerebral generators (reviewed in Halgren, Marinkovic & Chauvel, 1998; Rugg, 1995). P3a components to novel stimuli were recorded in paralimbic, frontal and temporo-parietal cortices implicated in directing attention.

The exploration of human medial temporal lobe function with iERPs began with the detection of long latency P3b-like potentials to target stimuli in the hippocampal formation and amygdala (Halgren, Squires, Wilson, Rohrbaugh, Babb & Crandall, 1980). Scalp P3b potentials were reported to have intracranial homologues in a neocortical network including the ventral frontal and superior temporal cortices, implicated in event encoding and contextual integration (Halgren *et al.*, 1998). Field potentials related to semantic processing (N400-like) were localized to the anterior medial temporal lobe (McCarthy, Nobre, Bentin & Spencer, 1995). The distributed neocortical and hippocampal network supporting subcomponents of long-term memory (semantic, episodic) was also studied with iERPs (Guillem, Rougier & Claverie, 1999). Clinical applications of memory iERPs were aimed at providing diagnostic markers of the functional integrity of the hippocampal formation before temporal lobe surgery (Elger, Grunwald, Lehnertz, Kutas, Helmstaedter, Brockhaus, Van Roost & Heinze, 1997). Depth electrodes implanted bilaterally along the length of the hippocampal formation provided a unique insight into the operation of the hippocampal formation in novelty detection (Grunwald, Lehnertz, Helmstaedter, Kutas, Pezer, Kurthen, Van Roost & Elger, 1998) as well as into the sequence of activation of the rhinal cortex and hippocampus during the formation of verbal memory traces (Fernandez, Effern, Grunwald, Pezer, Lehnertz, Dumpelmann, Van Roost & Elger, 1999).

More recently, iERP research has also begun to identify the cortical generators of fast cortical oscillations (Crone, Boatman, Gordon & Hao, 2001; Lachaux, Rodriguez, Martinerie, Adam, Hasboun & Varela, 2000). This is a rapidly growing area due to the assumed role of gamma (or 40 Hz) oscillations in perceptual binding (reviewed in Tallon-Baudry & Bertrand, 1999) as well as in the genesis of pathological seizure activity (Traub, Whittington, Buhl, LeBeau, Bibbig, Boyd, Cross & Baldeweg, 2001).

As mentioned above, the application of iERPs to paediatric patients and to developmental studies is still in a very early stage. A major obstacle is the often-limited cooperation of children. Liasis, Towel and Boyd were the first to use attention-independent auditory stimulation with tones and speech sounds in children to identify cerebral generators of mismatch negativity (MMN) potentials in the superior temporal lobe (Liasis, Towell, Alho & Boyd, 2001). Previous source localization studies with EEG and MEG in adults implicated bilateral MMN dipole sources deep in the primary auditory cortex to account for the scalp MMN. However, the studies by Liasis *et al.* identified additional generators of MMN in the lateral superior temporal and dorsolateral frontal cortex (see Figure 3; Liasis, Towell & Boyd, 1999, 2000). The existence of multiple MMN generators had been suspected on the basis of scalp recordings (Giard, Perrin, Pernier & Bouchet, 1990; Baldeweg, Klugman, Gruzelier & Hirsch, 2002) but had remained inconclusive without such direct evidence.

This latter example serves to highlight the potential value of combining developmental scalp ERP studies with a systematic sampling of iERPs in the developing brain. Our group is currently using speech iERPs to identify eloquent cortex in children. This invasive approach might also help to consolidate our knowledge of cortical generators of the ERPs in children and may thus contribute to the understanding of the functional and anatomical maturation of the human brain. Importantly, it may also shed light on how early brain pathology disrupts brain development and how the developing brain responds to injury.

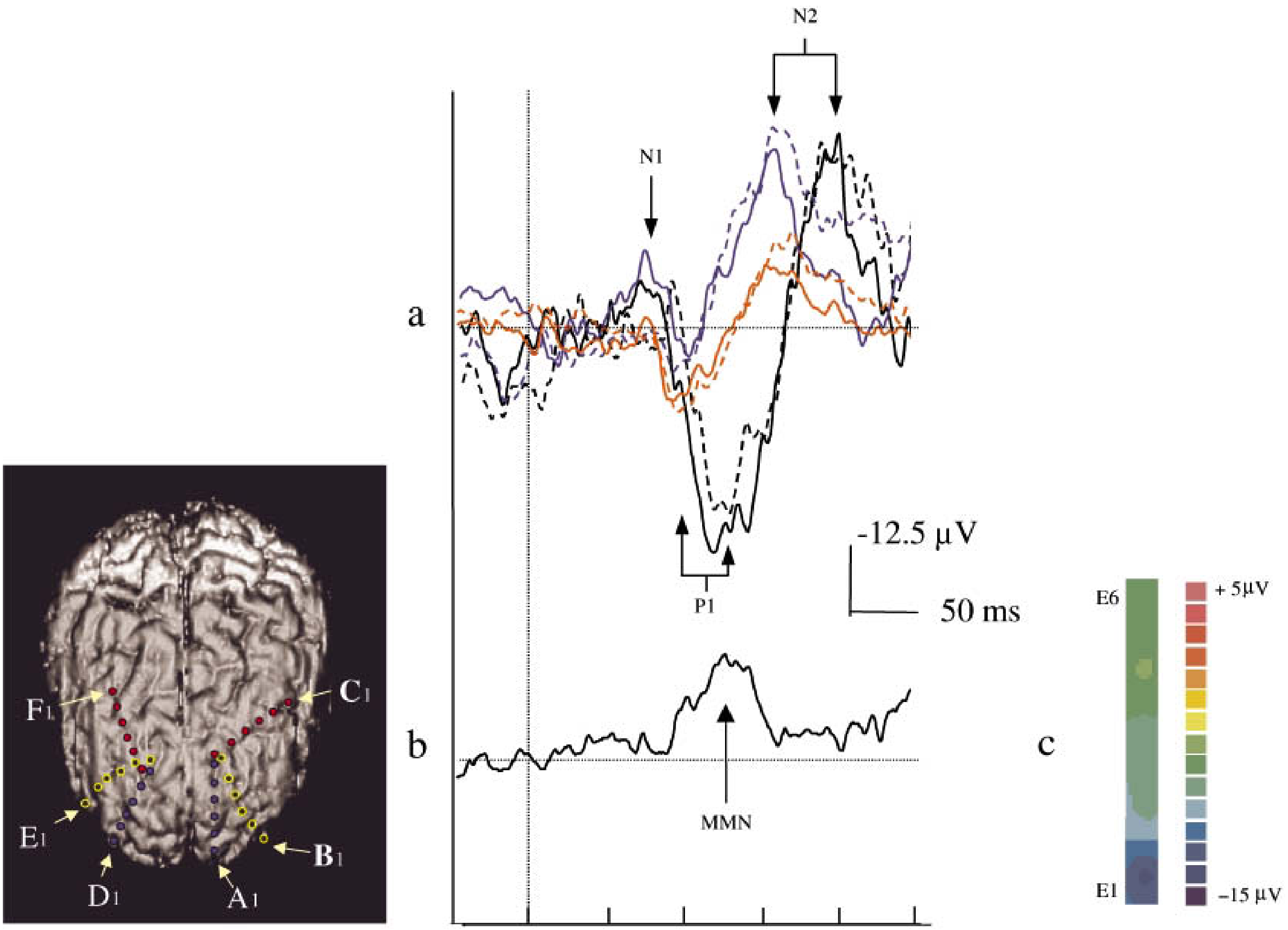

Figure 3 *Intracranial recording of mismatch negativity (MMN) potentials from the right lateral prefrontal cortex in a 6-year-old child. Left: 3-D MRI rendering of patient's brain with six co-registered contact subdural strips (A–F), extracted from post-implantation CT. Note all ERPs were recorded maximally at contact E1. (a) ERP waveforms recorded to standard tone (700 Hz, 75 ms; red line), deviant tone (700 Hz, 25 ms; blue line) and 'telephone buzz' (1.3, 1.6, 3.4 and 4.5 kHz power bands, 75 ms; black line) stimuli over contact E1 of the right lateral prefrontal cortex. Solid lines represent ERPs recorded from first block of stimuli while dashed lines represent ERPs recorded from the second block of stimuli. Note the increased amplitude and shift in component latency 'telephone buzz' waveform. The vertical dashed line represents stimulus onset. (b) ERP subtraction waveform of deviant-standard revealing MMN component whose peak latency is shown by vertical arrow. (c) Voltage distributions of sub-dural electrode strip 'E' at latency corresponding to peak amplitude of MMN shown in (b). Note strong local gradient of responses recorded at E1. (Reprinted from Liasis, Towell & Boyd,* Cognitive Brain Research, ***11*** *(2), 227–233. Copyright (2001) With permission of Elsevier Science.)*

Conclusions

The paradigms presented in this paper demonstrate the value of neurophysiological measures in examining the development of cognitive processes, with greater emphasis on the value in detailed investigations of the early stages of information processing. Although we have presented only some examples, cognition is readily investigated using a wide range of procedures, in both normal and clinical developmental populations.

The future of these techniques seems assured, as they are more readily applied in children than other neuroimaging techniques, and most importantly they provide information on the timing of cortical function that is largely missing from fMRI studies. Although the application of source analysis is not yet widely used for these data, this seems a logical next step, as then finer spatial localization can be obtained, in conjunction with the temporal information. The combination of EEG and ERP measures with iERPs and fMRI would maximize knowledge gained from all of these techniques.

Through systematic analysis of EEG or averaged EEG waveforms especially in task-specific conditions, one can follow cognitive processing from the early stages of stimulus encoding through the series of subsequent stages of cognitive processing and response execution. Developmental studies are critical to cognitive neurosciences as they contribute to our understanding of models of cognitive processing and to our knowledge of the brain regions implicated in specific cognitive processes.

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