PROPHESIES COME TRUE
What's·new in event-related brain potential (ERP) research since 1984

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INTRODUCTION

The past five years have been an especially exciting time to watch the event-related brain potential (ERP) technique being applied to the study of human cognition. It was a period of transition from a time when the discovery, identification, and categorization of endogenous ERP components dominated to one in which ERPs were used successfully to address issues central to normal and abnormal cognition.[1,2] Significant progress also came in the form of new analytical tools for the localization of ERP component generators (e.g., dipole source modelling) although the practical utility of these tools still needs to be evaluated. It was the beginning of an era when fewer cognitive ERP studies were designed to ask "I wonder what will happen if I manipulate variable X?" and relatively more investigations were aimed at testing specific hypotheses about the nature and time course of various mental operations. Suffice it to say, one review chapter can no longer do justice to the abundance of findings in the field of cognitive electrophysiology. Unlike in the past, issues rather than components now determine the literatures within which contemporary ERP observations are bandied about. Accordingly, what follows is a parochial sampler of current issues within cognitive ERPs limited in scope by time and space. In each case a question is posed and an example of how ERP data have been brought to bear upon its answer is provided.

Does attention modulate the flow of sensory information at an early level of processing or does it bias higher recognition and decision systems to favour specific inputs?

Electrophysiological (e.g., ERP) studies with human subjects are playing an increasingly important role in the analysis of the timing of the stimulus selection processes involved in attention.[3-5] A plethora of studies attest to the sensitivity of several ERP components to subjects' attentional deployments. In short, the results of these studies indicate that information about sundry stimulus attributes becomes available to attentional mechanisms at different rates, depending not only upon the characteristics and modality of the eliciting stimuli but also on the nature of the task demands. Moreover, these electrophysiological responses have proven so exquisitely sensitive and reliable as indices of stimulus selection processes that we may be at the threshold of using the late components of the ERP to assess dysfunctional attentional systems in much the same way that the audiologist uses brainstem evoked responses to assess the integrity of the auditory system.

Visuospatial selective attention

The prototypical selective attention experiment using ERPs requires that stimuli from two or more input channels be delivered in a randomized order relatively quickly as subjects attend first to events in one channel, then to events in the other and so on. Attention-related effects are inferred from the differences in the average ERPs elicited by the same physical stimuli as a function of attentional condition, that is, when the stimuli are in the focus of attention versus when they are outside it (i.e., actively ignored). Variants of this experimental design
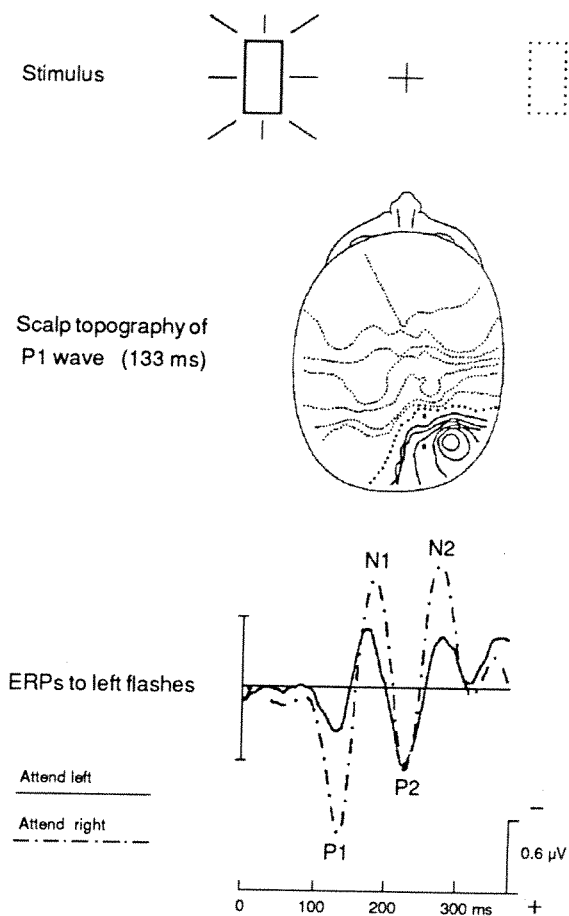
Stimulus

Scalp topography of
P1 wave (133 ms)

ERPs to left flashes

N1   N2

P2

Attend left

Attend right

P1

0.6 µV

0   100   200   300 ms   +

Fig.1. Visual ERP changes in a typical spatial attention task. Stimuli (top) were bars flashed on a video screen in random order to locations 5 degrees to the left and right of the fixation point (+). Interstimulus intervals (ISIs) were randomized between 250 and 500 ms. The subjects' task was to attend to and discriminate the height of the bars at one location (ignoring the other) and to press a button on detection of a slightly shorter bar (target) that occurred 10% of the time. Attention is sustained at one location for the duration of a 1-to 2 minute run. The predominant response to a left flash begins as a voltage shift (P1 wave) over the contralateral occipital scalp beginning around 90-100 ms (topographic voltage map, middle). Overlaid (bottom) are ERPs to left flashes when attended (dot-dash) and ignored (attend right; solid). From ref. 6.

have been conducted within the auditory (e.g., tones, speech), somatosensory (e.g., shocks to fingers, wrist) and visual (e.g., bars of light, letters, numbers, words) modalities. Within this experimental paradigm "early selection" models* of visuospatial attention have received strong support. Focusing attention on a particular location in space at the expense of all others is indexed reliably by amplitude modulations in a specific series of components, principally the P1-N1-P2-N2. The most consistently observed pattern of ERP components elicited by stimuli in the attended channel includes increased amplitudes of the P1 and N1 components with no significant changes in either their shapes (morphology) or amplitudes across various scalp locations (topography) (Fig. 1).

This pattern of results (namely, an increase or decrease in the amplitude of a component without an accompanying change in its waveshape) is most consistent with an attentional mechanism of early sensory gating that is mediated by descending neural influences upon the afferent sensory pathways.

Recently, Mangun and Hillyard[6] mapped both the voltage gradient of the P1 component (using multiple electrodes and a spherical spline function* to interpolate among electrode locations) as well as the second spatial derivative of the voltage gradients across the scalp (CSD - current source density, see ref. 8). CSD analysis provides a reference-free estimate of the instantaneous electrical currents that are flowing from the brain perpendicularly to the scalp at each location,[9] thereby supporting some inferences about the generators of cortical ERP components. On the basis of these analyses, Mangun and Hillyard concluded that the P1 emanated from a locus in the extrastriate visual cortical areas 18 and 19; the location of this source in response to a given stimulus remained the same whether it was attended or unattended (Fig. 2).

♥   Early selection theories propose a rapid rejection of irrelevant stimuli after minimal analysis of their rapidly analyzable attributes (typically, simple physical characteristics such as location). Models of late selection, on the other hand, propose relatively full analyses of all stimulus attributes prior to any selections taking place.

♦   A surface spline is the surface obtained by minimizing the bending energy of an infinite plane constrained to pass through known points. The surface spline allows interpolation of data recorded from irregularly spaced electrodes, gives a continuous surface and provides better estimates of the locations of the extrema.[7]
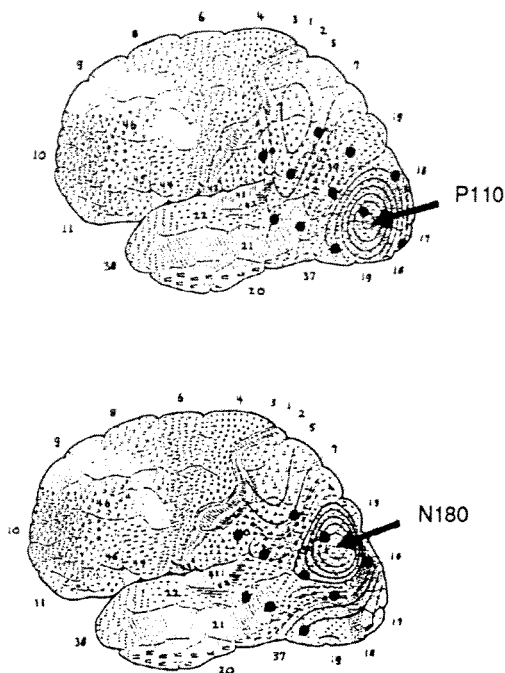
Fig. 2. Superimposition of grand average CSD contours for P1 (P110) and N1 (N180) attention effects to upper right stimuli upon a "classic" cytoarchitectonic map of the left hemisphere. The maximum CSD sink for the N1 effect is situated dorsally in relation to the CSD source of the P1 effect. This correspondence between the surface CSD and the underlying cortical areas must be considered approximate at present, since group-averaged ERP data were used and the relationship of electrode sites to Brodmann's areas was based on the averaged radiographic data of Homan et al.[67] From ref. 68.

Non-spatial visual selective attention

While scanning and focusing in space are clearly important, objects have many attributes besides their location in space that may attract, hold and guide one's attention. These include: colour, spatial frequency, orientation, shape or various conjunctions of these features. Selective focusing of attention based on such non-spatial features of visual stimuli is not reflected in enlarged N1 and P2 components but rather in a distinct pattern of ERP changes (Fig. 3). The most prominent of these is the enhancement of a broad negative component (called the "selection negativity") beginning at 150-200 ms and extending for several hundred milliseconds.[10,11] The onset latency of this selection negativity is a function of the complexity and discriminability of the attention-directing cues; for example, the earlier Nd starts the more easily discriminable the directing cue is.
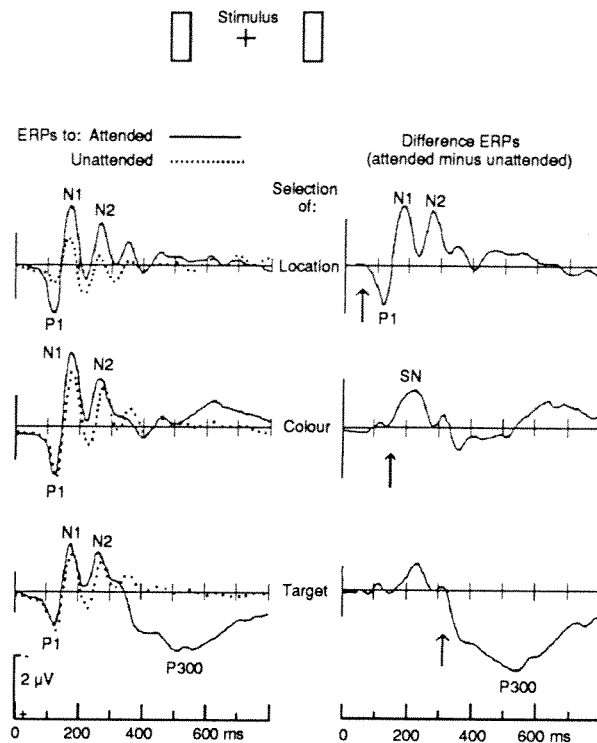

Fig. 3. Event-related potentials associated with selection of location, colour, and shape (target). Stimuli consisted of red and blue bars flashed in random order to the left and right visual fields. Subjects attended to bars of a particular colour at one location and responded to slightly shorter target bars that occurred infrequently at the attended location. Grand average ERPs recorded from occipital scalp to all stimuli (red and blue) occurring at a particular location are shown in the top tracing. When that location was attended, there was an enhancement of the P1, N1, and N2 components of the ERPs to stimuli occurring there as compared to trials in which the opposite side was attended. The ERPs averaged separately for attended versus unattended colours (collapsed over red and blue bars) showed a different pattern of ERP change (middle tracing), consisting principally of a slow negative component beginning at 150 ms and lasting until about 300 ms. Finally, when the correct combination of location, colour, and bar height (i.e., a target) is detected, a P300 component is elicited by the target (bottom tracing). From ref. 6.

In principle, the different patterns and sequences of ERP effects associated with spatial and nonspatial selection can be used to track the time course of cue selections for a multidimensional stimulus (i.e., a stimulus with multiple features). Indeed, several investigators have put this logic to the test and concluded that the selection for non-spatial visual features (as reflected in the selection negativity) is hierarchically contingent upon the prior selection for location (as reflected in enlarged N1-P2

components). For example, Hillyard and Munte[12] had subjects respond to slightly smaller target bars having both a specified colour (red or blue) and a specified location (left or right). They found that all the stimuli at the attended location elicited equally enlarged Pl and Nl components regardless of their colour but that the amplitude of the selection negativity for colour was influenced by whether the stimulus occurred in the attended or unattended location; the Nd was much larger in amplitude for stimuli in the attended location. Thus, once stimuli were rejected because they were not in the attended spatial location, they were not analyzed further, even if they shared other features (such as colour or duration) with the target stimuli. Like the nontarget stimuli, target stimuli in the attended location elicited an enhanced Nl and a selection negativity; in addition, they elicited a subsequent P3 component. By contrast, the ERPs to targets in the unattended channel did not exhibit a P3 component.

Are some simple visual features detected automatically and preattentively? And, how are such pop-out effects influenced by spatial selective attention?

Pop-outs in a full-field presentation

Some objects seem to "pop-out" from a visual display by virtue of having a simple feature (such as their colour) that distinguishes them from the rest. Indeed, several authors have suggested that this automatic feature detection may underlie texture segregation. Recently, Luck and Hillyard[13] used ERPs to examine the proposed automaticity of pop-out detection. In one of their studies, the stimuli consisted of arrays of 8 items each, of which one (i.e., the pop-out) differed from the others on half the trials. The background array items were small, blue, vertically-oriented rectangles; the pop-out stimuli differed from these background stimuli either in colour (i.e., green), orientation (i.e., horizontal), or size (i.e., larger). For each block of trials, one of the pop-out stimulus types was designated as a target (and required a button press with one hand) while the other two pop-out stimulus types were designated nontargets and called for the same response as the other background stimuli (a button press with the other hand).

As anticipated, the ERPs to the target stimuli were distinct from those to the background stimuli; target

ERPs were characterized by a large N2 over anterior recording sites, an N2 component over posterior sites, and a P3 component maximal over posterior sites. Of note for present purposes, however, is the fact that the ERPs to arrays containing nontarget, pop-out stimuli also differed from those to arrays containing only background stimuli. While these nontarget, pop-out arrays did not elicit a P3 component or a posterior N2 component, they did elicit a large N2 over anterior recording sites (Fig. 4). The presence of this frontal N2 was taken as evidence that a "pop-out" is registered automatically even when its discrimination is not necessary for successful task performance.
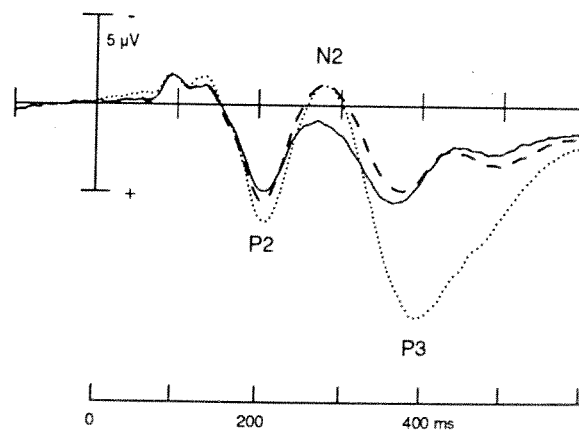

Fig. 4. Grand average ERPs (N=12 subjects) elicited by no pop-out (solid), non-target pop-out (dashed), and target pop-out (dotted) stimulus arrays in the experiment of Luck and Hillyard.[13] These ERPs were averaged over left and right frontal electrode sites. From ref. 5.

Pop-outs and selective attention

An interesting twist came in a subsequent experiment[14] wherein pop-out stimuli of a similar type were incorporated in a visuospatial selective attention ERP paradigm. Standard and pop-out stimuli were flashed to both the left and right visual fields while subjects attended to targets in one visual field and ignored those in the other. As expected, the pattern of ERP results for pop-out stimuli in the attended channel were the same as those following full-field presentation: namely, an anterior and posterior N2 and posterior P3 to target pop-out stimuli, and an anterior N2 component to non-target pop-out stimuli. More surprising, however, were the results for the

op-out stimuli in the unattended channel: "relevant" op-out stimuli (i.e., those with the same characteristics as the stimuli designated as targets in the attended channel) and "irrelevant" pop-out stimuli had distinct response profiles (Fig. 5).
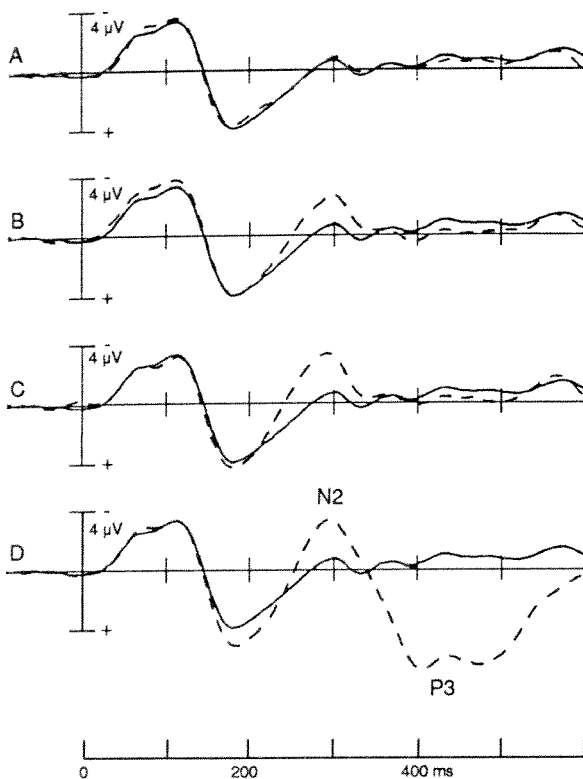

Fig. 5. Comparison of grand average ERPs elicited by no pop-out stimuli (solid) and four types of pop-out stimuli (dashed). A: Irrelevant pop-out on the unattended side. B: Irrelevant pop-out on the attended side. C: Relevant pop-out on the unattended side. D: Relevant pop-out on the attended side. These ERPs were averaged over left and right frontal electrode sites and collapsed across target pop-out type and direction of attention. From ref. 5.

Specifically, ERPs to unattended "relevant" pop-out stimuli exhibited the anterior N2 component and were thus indistinguishable from the ERPs elicited by "irrelevant" pop-out stimuli in the attended channel. By contrast, ERPs to "irrelevant" pop-out stimuli in the unattended channel were indistinguishable from those elicited by background stimuli in either channel. That is, there was no distinctive electrophysiological marker of pop-out status when an irrelevant pop-out stimulus

appeared in a spatial location that was being actively ignored. Certainly, the hierarchical relation implied by these ERPs results differs from that in the previous experiment, calling either the automaticity of the pop-out phenomenon or the validity of using the anterior N2 as a measure of it into question. In either case, these results challenge the ingenuity of future researchers of this issue.

What types of attentional deficits do schizophrenics exhibit?

ERP indices of auditory selective attention

A hierarchical processing sequence also appears to be the norm for the selection and analysis of auditory signals (e.g., ref. 3). The principal effect of attending to one channel of sounds (e.g., those in one ear) while actively ignoring another (e.g., the other ear) is seen in an enlargement of a negative ERP elicited by stimuli in the attended channel around 100 ms or so (typically the region of the Nl component). Several studies have demonstrated that this attention-related negativity can be dissociated from the Nl component per se, often extending for several hundreds of milliseconds beyond the Nl peak (e.g., ref.15). Accordingly, this negativity is best visualized in the difference wave formed by subtracting the ERPs to stimuli in an unattended channel from the ERPs to those same stimuli when they are in the focus of attention; this difference is referred to interchangeably as either the processing negativity (PN) or the negative difference (Nd) wave.

As long as the task discrimination is difficult or stimuli are presented rapidly (such as with interstimulus intervals (ISI) of 200-400 ms), pitch, location, and intensity can each serve as a cue to elicit an Nd. The onset latency of the Nd is, in part, a function of the rate of stimulation, being delayed at slower rates. Many investigators view the Nd as a reflection of the continued processing of stimuli in an attended auditory channel subsequent to early selection based on analyses of their simple sensory features (such as pitch, location, intensity, etc.). The more prolonged late portion of the Nd is taken as a sign of the short-term maintenance of the stimulus features that define the attended channel.

Several research groups have noted that adult schizophrenics have reduced selective attention effects

(e.g., N1 and Nd); interpretation of these findings is confounded, however, because many of these studies were conducted with patients taking neuroleptic medication. For example, Baribeau-Braun et al[16] found that schizophrenics were able to focus attention effectively on tones in one ear while ignoring those in the other ear when the stimuli were presented at a fairly fast rate. However, the schizophrenics' performance suffered both when the stimuli were presented at slower rates or when attention had to be divided equally among several input channels. Thus, these authors proposed that although schizophrenics have no problems using simple sensory cues to direct their attention, they nonetheless experience difficulties in such tasks because they cannot choose, organize and maintain an effective strategy for optimal processing of the task-relevant information.

Michie et al[17] drew similar conclusions from their results in a study of unmedicated schizophrenics performing a variant of the multidimensional attention task first reported by Hansen and Hillyard.[18] The primary purpose of the Hansen and Hillyard study was to test between the hypotheses (1) that the dimensions of location and pitch are processed independently and exhaustively and (2) that the processing of one dimension is contingent on the processing of the other. The stimuli to be attended were distinguishable from those in the unattended channel by their pitch and by their location; in addition, target stimuli differed from the standard stimuli in their durations. An important aspect of the experimental design is that the difficulty of discriminating the two nontarget dimensions was manipulated so that one dimension (for example, location - left versus right ear) was significantly easier than the other (pitch, 900 versus 960 Hz). In both the Hansen and Michie studies, when the location discrimination was easy and the pitch discrimination was difficult, the following pattern of results obtained: in the attended location, high and low pitch tones alike elicited ERPs containing an early negativity (the location Nd) beginning around 100 ms relative to tones in the unattended location. Only stimuli of the appropriate pitch elicited a later selection negativity around 200 ms (the pitch Nd) followed by a large long-lasting negativity. The ERPs to tones of the appropriate pitch occurring at the unattended location did *not* show a second separation due to pitch. This ERP pattern was thus taken to reflect a hierarchy of selection in which processing of the

difficult pitch dimension was subsequent to, and contingent upon, selection of the easy location dimension.

In this paradigm, Michie et al[17] found several attention-related ERP abnormalities in the schizophrenics. Among them was a lack of this second separation, namely, the Nd associated with the selection of pitch at the attended location. Specifically, the ERPs of these unmedicated schizophrenics, although smaller than that of the controls, showed an early effect of attention to location around the Nl latency; they did not, however, show either a later separation reflecting the selection of the pitch dimension or the subsequent long duration, late frontal component of the processing negativity (Fig. 6).
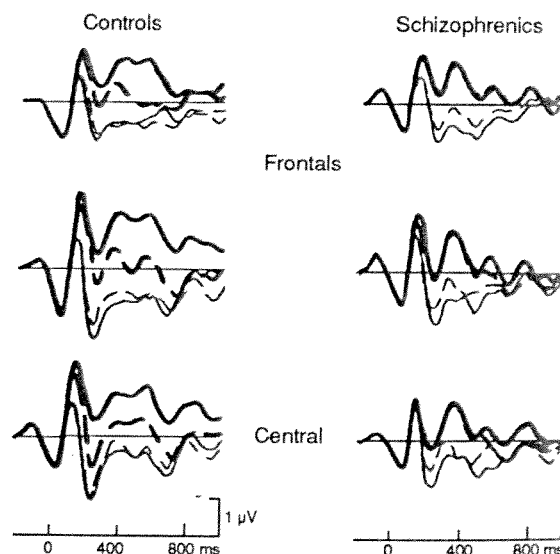

Fig. 6. Grand average ERPs to standard, short duration (D-) stimuli for healthy controls (left column) and unmedicated schizophrenics (right column). ERPs to four types of standards are superimposed: standards matching the attended target on location and pitch (L+P+D-; thick solid line), location only (L+P-D-; thick dashes), pitch only (L-P+D-; thin dashes), and neither pitch nor location (L-P-D-; thin solid line). From ref. 17.

This result, together with the fact that Nds were delayed in latency and P3s to target tones were reduced in amplitude, was taken to suggest an overall deficit in the planning and execution of selective listening strategies (i.e., in the control functions responsible for allocating processing resources) by schizophrenic individuals. Further elegant studies such as this with other patient populations will help determine which, if any, of these abnormalities are specific to schizophrenics.

What are the neurophysiological processes that underlie the directing of spatial attention from the central to the peripheral visual field? And, are these different in adults versus children or as a function of gender?

While the multichannel selective attention paradigm has been most heavily investigated, recently several laboratories have adapted either Posner's cueing paradigm or other types of cueing paradigms to ERP analysis.[6,19] For example, Harter and his colleagues[10,19] asked their subjects to respond to a target stimulus in the left or right visual field cued by a prior signal. In contrast to earlier work using this paradigm that focused on the response to the target, these investigators examined the ERPs following the arrow cue and preceding the actual presentation of the targets in an attempt to delineate the neural processes that prepare and direct the visual system to respond selectively to relevant stimuli. Effects of directing attention to the right versus left visual field were evident as early as 200 ms after the onset of the cue arrow. Both children and adults showed an increased negativity over the contralateral scalp sites between 200-500 ms after the cue; this potential was bigger over the right hemisphere in children and less asymmetric and sometimes showed a slight reversal in adults. Children and adults also exhibited differences in the anterior-posterior distribution of the potentials over the scalp: centro-parietal in children versus parieto-occipital in adults. In both children and adults, the early effect was followed by a later effect between 400 and 800 ms.

The early negativity was taken as an index of right hemisphere control of the attentional orienting mechanism. The later negativity was viewed as a sensory-specific potential reflecting the increased excitability of specific sensory cortices: if the target is presented to the precued visual field, a larger P1 and N1 are produced. Although there were no differences between boys and girls in the lateralization measures, both the behavioural and CNV data indicated that boys were generally more vigilant.

These data are tantalizing. First, they show that one can measure slow brain potentials that appear to index the executive processes of directing attention in visual space. Second, they suggest developmental and gender differences in these processes. And third, these data are an instance of the rebirth of empirical interest in the very slow potentials (lasting from seconds to minutes and often requiring DC recordings) of the brain (see refs. 20-24).

What types of attentional deficits characterize autistic individuals?

Recently Courchesne and his colleagues[25-27] reported that adult autistics have grossly abnormal attention-related ERP effects (e.g., Nd, N270, Nc); moreover, they found the deficits to be more pronounced for auditory stimuli. In one of their studies, ERPs were recorded to a random mixture of sounds and flashes while subjects attended selectively to one modality (that is, responding to an infrequent visual target in one condition or an infrequent auditory target in the other). Under these conditions, when undergraduate controls detected target stimuli in the attended modality, the ERPs to all the stimuli in that modality were characterized by an enhanced negative ERP over the front of the head (auditory Nd and Nc, visual N270 and Nc) and an enhanced positivity over the back of the head (P3b and visual P400). In contrast, the autistic subjects did not show the enhanced negativities and had significantly reduced positivities.

In a subsequent experiment, subjects were required not only to respond to each target but also to use that target stimulus as a cue to shift the focus of their attention and search for target stimuli in the other modality. In this situation, wherein subjects had to shift their attention back and forth between auditory and visual streams of stimuli fairly quickly, the autistics were again severely impaired. Behaviourally, the autistic subjects took more than five times longer on the average than normal controls to shift their attention; their ERPs likewise indicated that they processed the cue to shift attention very differently from the way the control subjects did. The P700 response to the cue, indicating that attentional focus must be switched to the other modality, was significantly smaller in the autistics (Fig. 7).

The diminution or absence of these various ERP effects was interpreted as reflecting the malfunctioning of the neural mechanisms underlying capturing, maintaining, and shifting of attention. On the basis of magnetic resonance image (MRI) measurements, Courchesne[28] has

suggested that these attentional deficits in autistic individuals may be the consequence of abnormal development of the cerebellum, possibly with an abnormal contribution from the parietal lobe as well.
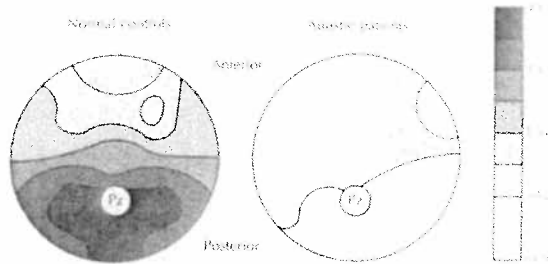

Fig. 7. Shifting attention brain responses. Topographic maps showing the distribution of the ERP response to an auditory stimulus signalling a shift in attention. Anterior indicates frontal scalp sites; posterior indicates parieto-occipital scalp sites. Control subjects showed a parietally maximal positive ERP response that peaked approximately 700 milliseconds (P700) following onset of the auditory cue to shift. Autistic patients failed to show this response. Pz-scalp site over parietal lobes. From ref. 30.

What are the processes that prepare the motor system for action and what are the consequences of such preparatory operations? Is information transmission continuous or discrete? More specifically, to what degree is partial information about a stimulus used to prime a response before the information is fully processed?

A central issue in contemporary research on human information processing concerns whether information is processed and transmitted in discrete stages, with each stage receiving output from a prior stage only after it has completed its bit-crunching chores, or whether information flows more continuously, being transmitted as soon as it becomes available regardless of the eventual accuracy or utility of such partially digested information. No doubt the truth lies somewhere in between these two alternatives (perhaps in a hybrid such as the asynchronous discrete coding model outlined by Miller[29]). Indeed, Miller has argued that rather than choosing between these extremes, research efforts should be aimed at determining the size and number of information chunks transmitted in any given situation; i.e. in defining the

critical aspects of situations in which information transmission seems more discrete than continuous and vice versa.

For present purposes it is best to view information processing as grossly comprising two stages: a stimulus evaluation stage and a response selection stage. From this perspective, the real question is whether or not response selection processes (activity in the motor side of the system) can be influenced by stimulus evaluation processes (identification of stimulus information) before the evaluation is completed (i.e. before sufficient information has been extracted from the stimulus to enable the correct response to be produced) or not. In order to answer this question it is essential to have an index of subthreshold response activation.

In the past five years, it has been demonstrated that the lateralized negative potentials (a.k.a. readiness potentials) that precede left and right hand overt responses can provide such a measure because they mirror fluctuations in differential activations of the two hands in situations where different responses have been assigned to them.[29-33] The procedure is based on the demonstration that the lateralized part of the readiness potential reflects the differential involvement of the left and right cortices in preparing to execute a unimanual motor act, being relatively invariant over a range of movement parameters other than side of movement. However, because this lateralized motor-related activity can overlap other non-motor-related potentials that are lateralized, the measure used in such studies is the difference in total lateralization for left hand and right hand responses (Fig. 8). This difference yields the lateralized readiness potential (LRP) - an index that reflects exclusively differential central response activation processes.

The prototypical experimental paradigm in which the lateralized readiness potential can be used to answer questions about partial preparation is one which engenders conflict. The important design features of such paradigms are (1) that two aspects of the same physical stimulus or stimulus display prime different responses, one priming the right hand and the other the left hand, and (2) that these two aspects are manipulated such that they are analyzed with different time courses (i.e., one before the other). In this way, responses associated with preliminary and complete stimulus evaluation are put into
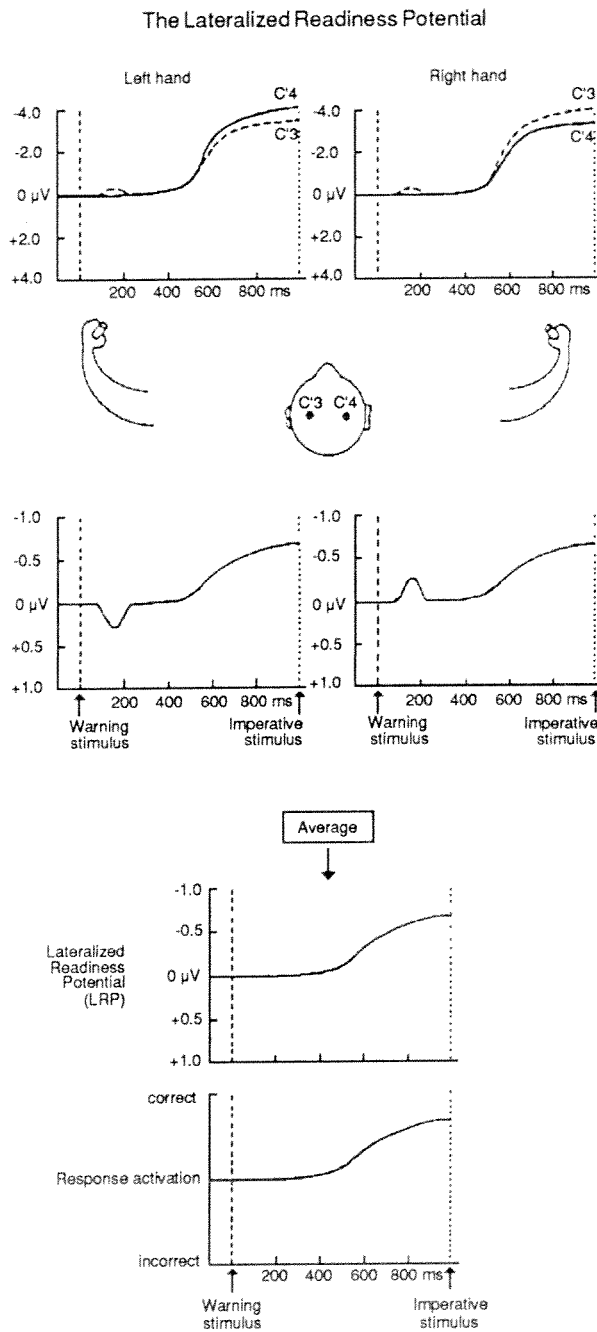
The Lateralized Readiness Potential

Fig. 8. Derivation of the lateralized readiness potential. Separately for each hand, the potential ipsilateral to the responding hand is subtracted from the potential contralateral to the responding hand. The lateralized readiness potential is the average of the values for left- and right hand movements. Asymmetrical activity that is common to both left- and right hand movements is eliminated by the averaging. From ref. 47.

conflict: preliminary evaluation leads to preparation of one response whereas complete evaluation leads to preparation of the other. Given that the two responses are assigned to the different hands, a reversal in laterality of the lateralized readiness potential reflects a shift in priming of the incorrect response to priming of the correct one.

In short, ERP experiments based on the lateralized readiness potential measures have provided evidence in favour of early communication, showing that the activity of the motor system can be influenced by preliminary phases of stimulus evaluation. Such experiments have also indicated that, whereas early communication is possible in some cases, it does not always occur. Current investigations are thus aimed at delineating the stimulus, response, and strategic factors which determine whether or not (and if so, when) the response system can or does take advantage of information from only partial stimulus evaluation.

Is there a point of no return beyond which response processes cannot be interrupted and the response is invariably executed?

Now and then we must abruptly stop some act that we are performing or were about to begin. But can we, in fact, stop at any point, and if not, what are the critical factors determining when we can and when we cannot? Within the literature on motor control this is a question of whether or not there is a "point of no return", i.e., a point during response preparation or execution beyond which movements can no longer be interrupted or inhibited and must therefore proceed to completion. In a typical paradigm designed to address this question, subjects performing a reaction time task are presented unpredictably with a stop signal that instructs them to inhibit the response they were about to make; on different trials, the stop signal is presented at varying, unpredictable delays following the stimulus.[34,35] Inferences are based on subjects' success at withholding their responses following the stop signal.

De Jong et al[34] employed such a paradigm while recording overt movements, muscle activity and event-related brain potentials. They concluded that central response activation processes as indexed by the lateralized readiness potential *can* be interrupted. In fact, they found that

even the overt response could be interrupted up to the very moment at which it reached criterion. Thus, the ERP data indicated that a response can be inhibited at any time during its activation and execution, and argued against the existence of a "point of no return" in response processing. The lateralized readiness potential data also showed that the mechanism of response inhibition was not strictly due to inhibition of central response activation processes. For example, on trials with a partial response, the interruption of the LRP occurred too late to be directly responsible for the interruption of the overt response. Likewise, on trials when responses were withheld without any muscle activity or overt movement, there was nonetheless an LRP that under normal conditions would have supported movement initiation. Taken together, these results suggest that in addition to the inhibition of central response activation mechanisms, a more peripheral inhibitory mechanism operates to interrupt a response. Clearly, these paradigms can fruitfully be applied to patients with hypothesized deficits in motor planning and execution (e.g. Parkinson's patients, Huntington's patients, and patients with frontal lobe damage, etc.).

Is the visual system organised differently following auditory deprivation since birth? Are the visual systems that subserve the processing of foveal and peripheral visual information differentially affected by such auditory deprivation, and what are the consequences for behaviour? To what extent do the characteristics of the first language of an individual determine the nature of the hemispheric specializations for non-language materials?

We spend so much time trying to understand how the average brain subserves our everyday perceptions, memories and behaviours that we tend to forget that there probably is no "average" brain. If we believe that the brain is the substrate for behaviour, should we be surprised to find anatomical or physiological differences between the brain of a concert pianist and that of a grocery store clerk or a college professor of mathematics? I wouldn't, but at the moment there is little direct evidence for such differences. Examination of post-mortem material from human visual cortex indicates substantial variability in the size of the area as well as the location of major sulci and gyri. What is the source of this variability ? Will it account for the difference between a major league player with a .300 batting average and one sent back to the minors? Perhaps. Another question that immediately arises is whether such differences are innate, and, if so, whether they are modifiable.

One of the clearest results from years of research in the neurosciences has been the demonstration that the developing brain is sensitive to differential experiences. Most of the evidence for neuronal plasticity has come from within the domain of nonhuman research - kittens or cats exposed to an environment with only one type of visual input or none at all (e.g.ref. 36), rats raised in impoverished environments without objects or playmates (e.g., ref. 37), and birds deafened to their own songs or robbed of their natural hormonal fluctuations[38] are but a few examples. The results of these experiments have attested to the profound effect of such manipulations on a variety of brain measures, including the fine structure of the nervous system, and the physiology and electrophysiology of the cortex (e.g. ref.39).

Although most of these studies have focussed on the effects of early experience on brain areas directly associated with the altered sensory modality (for example, decreases in the number of binocular cells in the visual cortex after monocular deprivation), there is also evidence that after unimodal sensory deprivation, there is *compensatory neural reorganization* in the neural systems that would have subserved the deprived modality for processing information in the intact modality. For example, many years ago Bonaventure and Karli[40] compared the cortical distribution of the auditory EP in normal mice versus mice with hereditary retinal degeneration. Normally, auditory EPs cannot be recorded over the visual cortex, but in these blinded mice the visual cortex was not silent to auditory stimulation, as evidenced in reasonable AEPs. Thus, a visual area which normally has little to do with processing these auditory stimuli reorganized itself to take on some of this function.

Similar compensatory changes have been observed in the auditory cortex to visual stimulation following auditory deprivation. Typically, it is not possible to record VEPs over the auditory or somatosensory cortices of hearing mice; however, a different picture emerges after

auditory deprivation. Rebillard and his colleagues[41,42] examined the distribution of flash VEPs in the cortex of congenitally deaf white cats and observed very large VEPs not only over the visual but also over the auditory areas. Such data are consistent with the hypothesis that a neural system which develops to subserve one modality may process information from other modalities if deprived of its original input. In sum, for nonhuman animals there is some evoked potential evidence that areas deprived of their normal input can and do take up other functions; there is also the possibility, although no direct evidence, that the intact cortical areas may become even better at what they do in compensation for a missing modality.

Striking as these results are, there are almost no data showing that this apparent reorganization has functional consequences; for this it is necessary to assess behaviour as well as anatomy and physiology. This combined approach has been adopted by Neville and colleagues in comparing the scalp recorded visual evoked potentials of three groups of subjects: normally hearing adults, congenitally deaf adults (i.e. individuals who have been deprived of auditory input since birth) and normally hearing adults whose first language was American Sign Language by virtue of being born to deaf parents. Comparing the visual ERPs of individuals from these three groups makes it possible to distinguish consequences of early auditory deprivation from those due to a different mode of language acquisition.

In the first of these studies, VEPs were recorded over multiple scalp locations to small white rectangles of light flashed either at fixation or approximately 8 degrees to the right or left of fixation at randomly intermixed interstimulus intervals of 0.5, 1 or 3 seconds.[43] There were striking differences between hearing and deaf subjects in the amplitudes of each of the major components of the VEP, namely the N150 and the P230 components, especially in responses to peripheral stimuli.

Thus, we have some electrophysiological evidence for neural reorganization in the human brain following auditory deprivation. The relative enhancement of the N150 over frontal and temporal regions in the deaf is consistent with the idea that auditory areas deprived of their normal input have been reassigned to the processing of visual information. The specificity of this enhancement to peripheral but not foveal stimuli might reflect either less plasticity in foveal systems or a special compensation for peripheral sensory processing in the deaf, who rely on vision for localizing events in the periphery much more than the hearing. The increased amplitude of the P230 component in the deaf over occipital regions of the scalp is consistent with structural changes observed in cortical areas associated with the intact modality and might reflect increased visual sensitivity.

Neville and Lawson[44-46] tested the generality of some of these findings in three similar groups of subjects by comparing their ERPs and behaviour in a task requiring focused attention in order to detect target motion in different regions of visual space. In this experiment, subjects kept their eyes fixated on the centre, and depending upon the task instructions, they directed their attention but not their eyes to either the left, right or centre. Whenever they detected motion (which could be in one of eight directions) in the attended location, they pressed a button indicating the direction of motion; these so-called target events occurred very infrequently. As previously mentioned, examination of the ERP effects of selective attention in such tasks typically requires comparing the ERPs elicited by the same physical stimuli in a specific location when they are in the focus of attention and when they are not (yielding the difference wave reflecting differential selective attention). Comparison of this difference wave for nontarget stimuli for the hearing and deaf individuals revealed three main differences: (1) Overall the deaf generated much larger attention effects than did the hearing on the N1 component and a subsequent later positivity (called PD); (2) More specifically, for both the N1 and PD components the enhanced attention effects were most evident at the occipital sites; the deaf showed large attention effects at the occiput whereas the hearing showed almost none at all over that region; and (3) deaf subjects had much larger N1 effects over the left hemisphere than did the hearing regardless of the visual field of presentation.

These results support the proposal that the neural systems that mediate attention to visual space and perception of motion are different in normal hearing and congenitally deaf individuals. Although there are ERP differences between attention to the centre and to the periphery which are consistent with the view
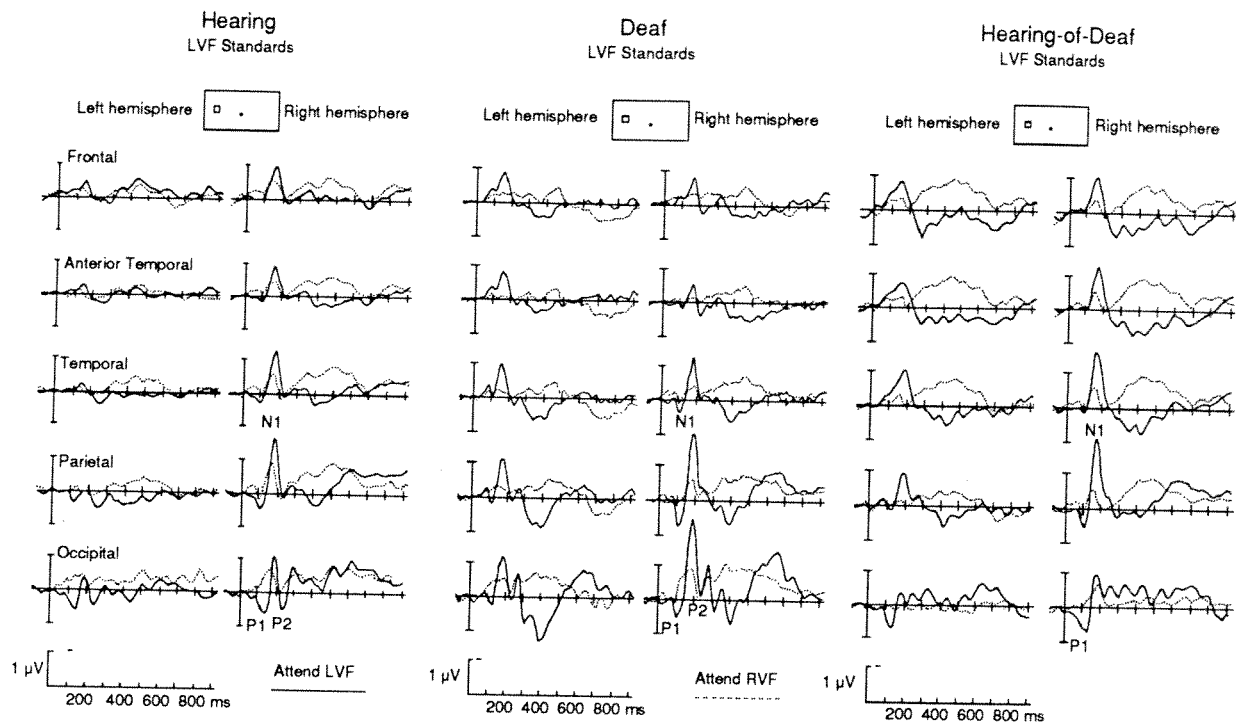
Fig. 9. ERPs averaged across 12 Hearing subjects (left panel), 12 Deaf Ss (centre panel) and 12 Hearing-of-deaf Ss (right panel) to standard stimuli presented to the left visual field (lvf) when attended (Attend LVF) and when unattended (Attend RVF). Recordings from left and right frontal, anterior temporal, temporal, parietal and occipital cortex. From ref. 47.

that stimuli in these regions are processed by somewhat separate and parallel visual systems, the differences are the same for the deaf and the hearing. The major group differences occur in the systems that mediate perception and attention to peripheral but not central visual space. For the peripheral stimuli, the ERP data indicate a greater involvement of the right and left occipital regions as well as a greater role for the left hemisphere for the deaf.

These differences are best interpreted in light of the ERPs of the hearing individuals with deaf parents. By examining their ERPs in this paradigm we can determine the extent to which each of these group differences in attention is attributable to sensory deprivation versus the acquisition of a visuospatial sign language. Again, relative to the normally hearing and congenitally deaf individuals, these hearing-of-deaf adults show very similar waveform morphologies; differences occur primarily in the size and scalp distribution of the attention effects. In the occipital regions, it is clear that the hearing-of-deaf

look more like the hearing than the deaf subjects; that is, they did not show the large N1 or PD effects. In contrast, in terms of the lateral distribution of the attention effects, the hearing-of-deaf are more similar to the deaf in that they show substantial effects over the left hemisphere in response to left visual field stimuli.

As the significantly enhanced N1 and PD effects over the occipital region are specific to deaf individuals, they are most likely a consequence of auditory deprivation since birth. In contrast, the apparently greater involvement of the left hemisphere for attention related to movement detection for both the deaf and the hearing-of-deaf suggests that this effect is probably a consequence of the early acquisition of sign language. The behavioural data also show that in terms of motion detection, the hearing-of-deaf are more like the deaf than the hearing subjects; that is, the hearing subjects showed a left visual field (right hemisphere) advantage whereas both the deaf and the hearing-of-deaf subjects showed a right visual field (left hemisphere) advantage.
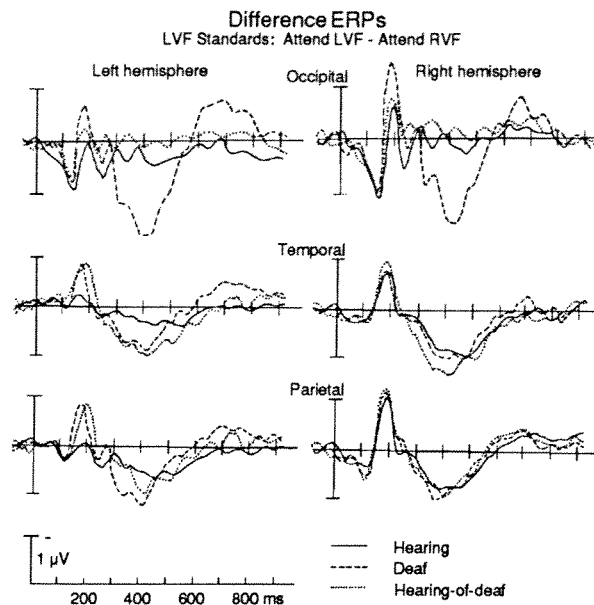
Difference ERPs
LVF Standards: Attend LVF - Attend RVF

Left hemisphere   Occipital   Right hemisphere

Temporal

Parietal

1 μV

―――― Hearing
------ Deaf
········· Hearing-of-deaf

200 400 600 800 ms

Fig. 10. Difference ERPs, formed by subtracting ERPs to unattended LVF stimuli from ERPs to the same stimuli when attended, from hearing, deaf and hearing-of-deaf subjects. Recordings from left and right temporal , parietal and occipital regions. From ref. 45.

Thus both the ERP and behavioural data are consistent with the hypothesis that the hemisphere which predominantly serves language carries at least some (if not all) of the functions that are most needed for efficient first language processing. In the case of ASL but not spoken English, one of these functions includes the detection of motion in the periphery.
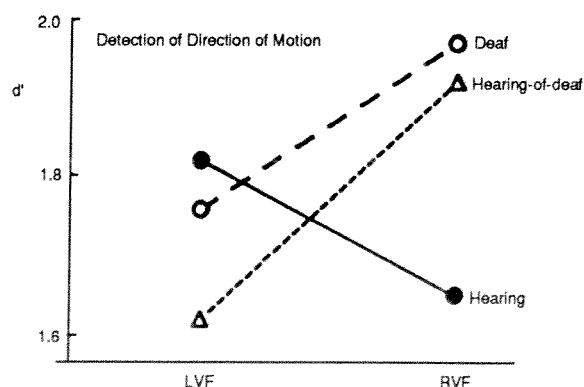
2.0

Detection of Direction of Motion   ○ Deaf

d'   △ Hearing-of-deaf

1.8

○

1.6 △   ● Hearing

LVF   RVF

Fig. 11. Detection (d') of moving targets in the left and right visual fields (LVF and RVF) for hearing (solid), deaf (dashed), and hearing-of-deaf (dotted) subjects. From ref. 45.

Using the same logic, Neville and her colleagues compared the ERPs of hearing, congenitally deaf, and hearing-of-deaf adults elicited by semantic anomalies, open class (nouns, verbs, adjectives, and adverbs) and closed class (conjunctions, prepositions, articles, auxiliaries) words during the processing of written English and signed ASL sentences to arrive at the conclusion that it is competence in grammatical recoding that is both necessary and sufficient to stabilize a genetic bias for left hemisphere mediation of language functions, regardless of the modality through which language is acquired.[47-49]

Does a sentence context facilitate the processing of the individual words within it, and, if so, how might this occur? For example, to what extent are the time courses of activation of an ambiguous or poly semous word's semantic representation(s) altered by the sentential context?

The majority of studies on lexically ambiguous words (e.g. *watch, bank, bug*) have suggested that all meanings of ambiguous words are simultaneously activated upon presentation, with the contextually inappropriate meaning being discarded at some later time (see ref.50). For example, in a text about sailors on the high seas, the word *deck* has been found to activate not only text-related concepts such as *ship,* but also text-inappropriate concepts related to casinos and gambling such as *cards.* It is argued that in properly designed studies, a biasing context cannot influence the activation of all the possible meanings of an ambiguous word because the mental lexicon (i.e. the representation of individual words within our minds) is viewed as an impenetrable module.

Van Petten and Kutas[51] questioned this conclusion and suggested that the finding of multiple access may be an artifact of the experimental paradigm designed to measure it. In a typical experiment examining this issue, subjects are presented with a sentence (biasing one sense of the ambiguous word) that ends in an ambiguous word (i.e. a homograph). Shortly thereafter (at various lags), subjects are presented with a target word which they are required to name or to make a lexical decision about; this target word is related either to one or the other of the meanings of the ambiguous word or unrelated to both.

Homograph sentence	Contextually appropriate target	Contextually inappropriate target	Unrelated target
The gambler pulled an ace from the bottom of the deck.	cards	ship	parent
It is not legal for an employer to consider a person's religion or race.	colour	run	art
The logger cut down the tree with a chain saw.	axe	look	proof
The bicycle mechanic fixed the flat tyre and repaired the broken spoke.	wheel	talked	pill

Filler sentence	Related target	Unrelated target
He bought a quart of milk and a dozen eggs.	bacon	buckle
The sweater was knitted from blue and grey wool.	lamb	cigar

The box above shows sample stimuli as used by Kutas et al[62] in a typical homograph probe experiment.
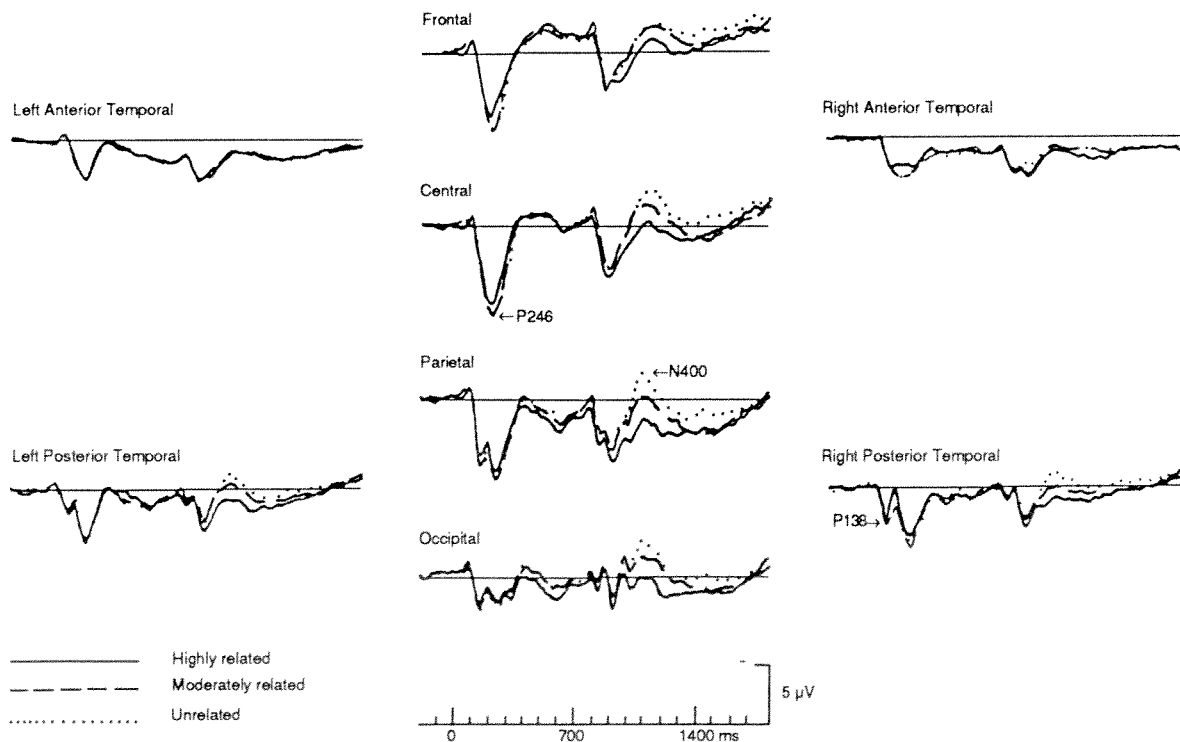

Fig. 12. Grand average ERPs (n=11) elicited by word pairs during the delayed letter search task. The three waveforms superimposed represent ERPs in response to highly related, moderately related and unrelated word pairs, with the degree of relation based on a combination of published and experimentally gathered production norms. From ref. 52.

In general, only a very short interval between the ambiguous word and the onset of the target word yields priming for targets related to either meaning; a longer interval yields priming only for targets related to the contextually appropriate sense. Thus we felt it possible that the target word, rather than serving as a neutral probe for determining how the preceding ambiguous word was processed, may itself have served as a source of context in the interpretation of the ambiguity. If this were the case, then although the sentence context may have constrained access to a single meaning of the ambiguous word initially, the subsequent presentation of the probe (related to the alternate meaning) could have activated the previously inappropriate or irrelevant meaning.

We examined this possibility by comparing the ERPs elicited by probe words following the final words of sentences (with contexts biasing the less dominant of the meanings of the ambiguous word when it occurs in isolation) at either a short or a long lag. Our use of the ERP for this purpose was based on previous results from several laboratories showing the amplitude of the N400 component to be sensitive to the degree to which two words in a pair are semantically related (e.g.ref 52). We knew that the amplitude of the N400 elicited by the word *cat* would be smaller if it followed the word *dog* than if it followed the word *table* (Fig. 12, opposite).

Essentially similar results are observed whether subjects are required to categorize the target word,[53-57] to decide whether or not it is a real word in the subject's primary language,[58,59] to remember the word for a subsequent recognition test,[60] or to read it so that a subsequent decision could be made as to whether or not it contained a target letter.[52,61]

We adopted the lexical ambiguity probe word technique but used the ERP to provide a more detailed picture of the time course of the processing of the ambiguous word and the following probe word. We presented sentences which biased one reading of an ambiguous word, followed by a probe word that was either (1) related to the sententially appropriate sense, (2) related to the inappropriate sense, or (3) unrelated to either. With a 700 ms interval (onset to onset) between the ambiguous word and the probe, the contextually relevant probe elicited a smaller N400 than did the unrelated one; this difference was apparent at around 300 ms after the onset of the probe word.

In contrast, the contextually irrelevant probe word elicited an N400 that was indistinguishable from that to the unrelated probe. However, with a short stimulus onset asynchrony (SOA) between the ambiguous word and the probe (200 ms onset-to-onset), both the relevant and irrelevant probe ERPs showed a priming effect, paralleling our reaction time (naming latency) data for these conditions. Moreover, the priming effect observed for irrelevant probes in the short SOA condition was substantially delayed (by about 200 ms) relative to that for the relevant probes.
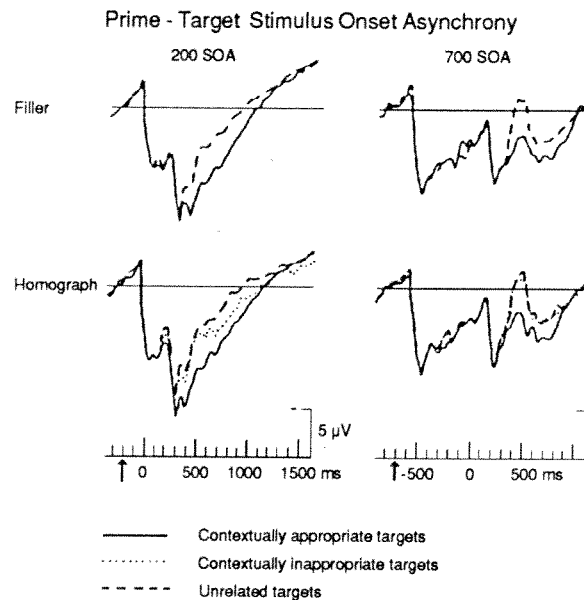

Fig.13. ERPs elicited by sentence-terminal words and subsequent probe words at a central midline scalp site (vertex or Cz). "Filler" sentences ended with unambiguous words. The sentences were presented at time indicated by the arrow and probe words at time 0. From ref. 51.

Thus these data did not support the view that both meanings of the ambiguous word were simultaneously activated. Rather, they were more in line with our suggestion that the irrelevant probe itself took on a double role, not only as a probe but also as context for the alternative interpretation of the ambiguous word; in other circumstances, this phenomenon has been referred to as backward priming. While our interpretation of the priming for the irrelevant probe as backward priming may turn out to be incorrect, our N400 data make an important contribution in that they must be accounted for by any theory of how and when the meanings of

ambiguous words are processed. Substantial ERP data have also become available to address other questions at the core of modern psycholinguistic research (see refs. 62-64).

RELATED THOUGHTS, SUMMARY, AND CONCLUSIONS

To date, cognitive ERP data have been most useful in providing evidence in favour of or against hypotheses about the relative timing of various mental operations and about changes in the functional organization of the brain following brain damage or different early experiences. Early versus late selection theories of selective attention, the extent to which stimulus evaluation and response selection and execution processors exchange information before all of it is fully analyzed, and whether one or both meanings of an ambiguous word are accessed simultaneously regardless of context all concern questions of the time course of processing. Each is a question on which ERP evidence has successfully been brought to bear. The available data argue for (1) a primacy of spatial over non-spatial features for control of the attentional focus in the visual domain, (2) the possibility of continuous flow of stimulus information to response mechanisms, and (3) against simultaneous activation of both meanings of a homograph. In addition, these ERP findings have afforded new ways of theorizing about how our brains might process information. The picture of psychological and physiological mechanisms provided by a continuous measure such as the ERP has led to a view of mental operations and their interactions that differs substantially from previous ones based primarily on reaction time data. On the whole, punctate measures such as the RT fostered discrete stage models. Continuous measures have allowed researchers to stop searching for the "magic" moments of cognition and to focus instead on delineating the time course of cognition, presuming it to be as fluid as our sense of consciousness. A similar revolution is taking place in the domain of computer modelling of cognition as the von Neumann architecture metaphor is replaced by more neurally inspired models.*

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*   Specifically, metaphors based on the serial, digital computer versus the parallel, distributed computer wherein knowledge is inherent in patterns and strengths of connections.

Besides this change in the theoretical frameworks within which ERP experiments are designed and results are interpreted, certain facts that cut across cognitive ERP studies have emerged. As our studies become more complex and we require more in-depth processing by our subjects, individual variability becomes more evident. This includes variability due to subject options/strategies as well as that resulting from different brain organizations. For instance, several experiments on recall performance have revealed not only very different patterns of performance but also very different relations between behaviour and modulation of P3 component amplitudes as a function of subjects' memorization strategies.[64,65] Moreover, several ERP studies of reading have revealed differences between right-handed subjects with only right-handed family members and right-handed subjects who have left-handers in their immediate family: ERPs elicited by content or open-class words (e.g. nouns, verbs, adjectives and adverbs) are more lateralized in the former group than than the latter (e.g,.ref. 62). On occasion, there have been reports of different ERP patterns for males and females as well. The fact that there are changes with age is too obvious to need more than passing mention, although it may be less obvious that the specific effects of aging may be quite different for different ERP components. These tidbits are of note because they impact the choice of control populations against which patients are compared as well as the interpretation of "abnormal" patterns in various clinical groups.

Finally, a few words on how cognitive ERPs may be applied to the investigation of clinical populations. For the moment, there are no simple "cognitive" paradigms that can be given to a patient in a short session with the results read off unequivocally by a technician. Without donning a doomsayer's cap, I doubt that such ERP tests of cognitive function will be appearing any time in the near future. Cognition is a complicated and tricky business and this is no less true when an individual has brain damage. A solid experimental design is as important for addressing a question in a clinical sample as it is in a group of undergraduates. There seems little point in adapting a cognitive paradigm to the clinic without having at least some prediction about the way the ERPs should differ from a normal control group and why!

On the whole, studies aimed at addressing a specific issue or answering a specific question have a greater chance of making a contribution than those aimed merely at seeing what happens to a component in particular abnormal populations.

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