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Electrophysiology of human selective attention

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Recordings of event-related brain potentials (ERPs) from human subjects demonstrate several distinctive types of selective attention mechanisms that differ according to stimulus modality. The selection of attended from unattended inputs first makes a significant impact on sensory processing at 50–80 msec after stimulus onset, with larger ERP amplitudes being triggered by attended stimuli. There is little evidence that inhibition or gating of unattended inputs in the peripheral sensory relay nuclei plays a significant role in the rejection of irrelevant stimuli. The timing of successive ERP components indicates that human selective attention has a hierarchical structure, with an early selection of input channel being a prerequisite for the stimulus analysis of detailed features. Separate ERP components demarcate processes of stimulus selection, evaluation, and classification, thus providing a window into the timing of complex mental operations.

The analysis of higher brain functions in humans has been given impetus by the development of techniques that register certain aspects of the spatio-temporal patterning of neuronal population activity through the intact scalp. Advances in neuroimaging techniques using radioactive tracers permit the visualization of metabolically active brain regions that are participating in different attentional, cognitive and linguistic acts^{1–3}. Magnetic resonance imaging may also provide a precise localization of functionally active brain regions⁴. Although these methods allow for reasonably accurate anatomical localization of the actively engaged brain regions, they yield little information about the time course of the neuronal activity. By comparison, high resolution in the time domain can be achieved through scalp recordings of electric and magnetic field fluctuations^{5,6}. Although these recordings generally lack the anatomical

precision of the neurometabolic imaging techniques, they do reveal the temporal patterning of neuronal population activity associated with sensory information processing. The present article describes recent applications of electrophysiological recordings from human subjects to the understanding of certain attentional and perceptual phenomena.

Event-related brain potentials

A sensory stimulus normally triggers a sequence of negative and positive voltage deflections in the scalp-recorded EEG that have characteristic time delays. Since these electrical responses may be synchronized to perceptual, cognitive, or motor events, they have become known as 'event-related potentials', or ERPs. ERPs that are time-locked to external events such as stimulus delivery or the subject's response may be computer-averaged over successive events to

improve their signal/noise ratio.

The waveform of an ERP varies according to the sensory modality and type of stimulus as well as the nature of perceptual and cognitive processes that are engaged. For example, the auditory ERP to a click includes 16 or more distinct components occurring between 1.5 and 1000 msec after the stimulus (Fig. 1). The earliest scalp-recorded waves evoked within the first 10 msec (waves I–VI) arise from synchronous neuronal activity in the auditory pathways and nuclei of the brainstem⁵. In general, the ERP components with latencies shorter than 60–80 msec represent evoked activity in sensory pathways that is relatively independent of the psychological state of the subject. Instead, these early evoked or 'exogenous' components are highly sensitive to both the physical parameters of the eliciting stimuli and the integrity of the mediating neural structures and are useful for the diagnosis of neurological diseases that impinge upon the sensory pathways⁵. In contrast, many of the later, 'endogenous' components do vary according to the state of the subject, the meaning of the stimulus, and the information processing demands of the task. The components depicted in Fig. 1 by dotted and dashed tracings are endogenous waves that accompany, respectively, processes of channel-selective auditory attention (the Nd), the active discrimination of stimulus features

(the N2), and the delivery of task-relevant information (the P3 or P300 wave).

A major research goal of cognitive psychophysicists⁷ is the identification of particular ERP components as markers of distinct perceptual, cognitive and linguistic processes. By imposing a structured task designed to elicit the process of interest, the associated ERPs can clarify the internal structure of the information processing sequences by indicating the timing and order of the sub-stages involved and distinguishing between mechanisms of serial and parallel processing⁸⁻¹⁰. This approach is particularly well suited to the study of mechanisms of selective attention, since the time sequence of ERP components reflects successive levels of sensory transmission.

Levels of selective attention

The human brain can effectively select relevant inputs from the sensory milieu and process them in detail, while ignoring competing stimuli of lesser importance. These selective influences on sensory processing are under discretionary control and allow stimuli in the focus of attention to be discriminated more quickly and accurately and to exert greater control over subsequent behavior than unattended stimuli. Studies of attentional mechanisms by psychologists and neuroscientists alike have attempted to specify at which levels of sensory processing different kinds of information are selected or rejected^{9,10}.

Perhaps the best-known physiological theory of attention postulates that unattended sensory inputs are inhibited or gated at peripheral levels of the sensory pathways¹¹. This could occur either by means of centrifugal projections to the receptors or initial relay nuclei or, by reticular modulation of transmission through the sensory relay nuclei of the thalamus¹². A number of experiments using animal subjects have found evidence for the selective modulation of sensory input to the cortex as a function of stimulus relevance⁹.

The possibility that subcortical gating acts as an attentional mechanism in humans has been investigated through scalp-recordings of the auditory brainstem components (Waves I-VI) to click and tonal stimuli. To date, the bulk of evidence indicates that early transmission through the brain-stem is modified little (if at all) by the

AUDITORY EVENT-RELATED POTENTIALS

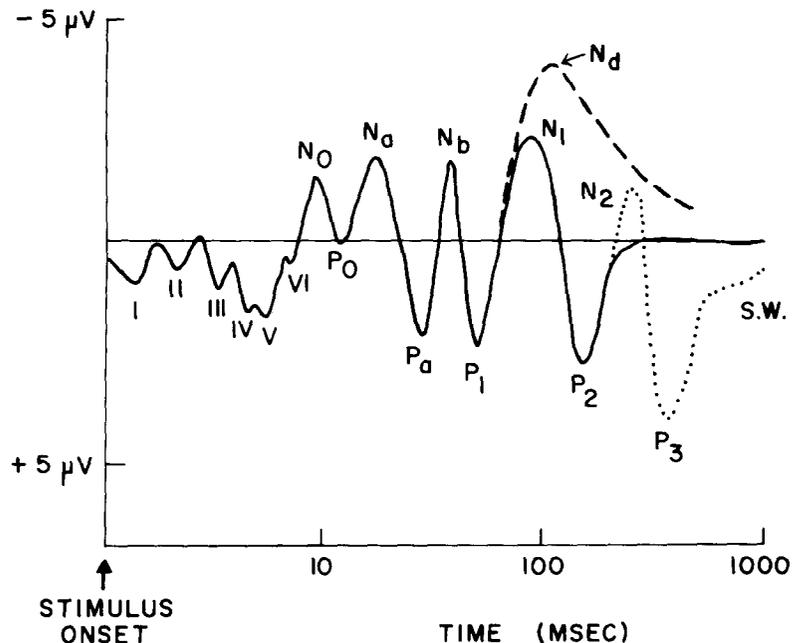


Fig. 1. Idealized waveform of the human auditory event-related potential, showing brainstem (Waves I-VI), mid-latency, and long-latency components observable in most subjects. The solid tracing represents the 'exogenous' or evoked components, while the dashed and dotted lines show endogenous components associated with different modes of processing. Recording is from a central scalp electrode referred to the mastoid process, with scalp negativity represented by an upward deflection²⁶.

shifting of attention towards and away from trains of auditory stimuli¹³. Similarly, impulses arising from peripheral nerve stimulation can be visualized in the somatosensory ERPs at the levels of the dorsal column pathways in the spinal cord, the medial lemniscus, thalamo-cortical projections and primary receiving cortex². Despite the existence of major descending projections to the lower relay levels of the somatosensory pathways, a number of studies have found that transmission up to and including the primary cortex remains invariant when attention is directed towards and away from the evoking peripheral nerve shocks^{14,15}. Thus, the ERP evidence indicates that peripheral gating does not play a substantial role in either human auditory or somatosensory attention. The situation regarding pre-cortical gating is less clear in the visual system, because of uncertainty as to the origins of the earliest detectable scalp-recorded components (see below).

The psychological concept of 'early' selective attention does not necessarily imply gating at the sensory periphery. Instead, it refers to a mechanism whereby stimuli belonging to an irrel-

evant input channel (e.g., sounds in an unattended ear or flashes at an unattended location) are rejected or attenuated prior to the completion of perceptual processing^{10,16}. Such early selection is assumed to reject irrelevant inputs rapidly, thereby reducing the build-up of perceptual data from unattended sources and protecting higher analysers from sensory overload. The question of early versus late selection (the latter implying no selection prior to a full perceptual analysis) has been hotly debated over the years, but ERP evidence is steadily accumulating that favors the existence of distinct forms of early selection in the different modalities.

Early auditory selection

The design of attention experiments employing ERPs necessitates the presentation of stimuli belonging to two or more input channels in randomized order, while subjects attend in turn to events in one channel at a time¹⁰. In the auditory modality, for example, subjects can be instructed to listen to a rapid sequence of clicks, tones, or speech sounds presented to one ear while ignoring a comparable sequence

of stimuli in the opposite ear. The assigned task is to listen for occasional 'target' stimuli in the attended channel, which are difficult to discriminate from the more frequent 'standard' stimuli. Under these conditions, all stimuli within the attended channel (targets and non-targets alike) elicit a broad negative component (the Nd or 'negative difference' wave) that onsets at 60–80 msec post-stimulus (Figs 1 and 2).

An early Nd wave can be produced when attended and unattended channels are distinguished by rapidly discriminable cues such as tonal frequency (pitch), intensity, or phonetic pattern¹⁷, as well as by ear of delivery. The latency of onset of the Nd is primarily determined by the speed with which attended and unattended channel cues can be discriminated, while its amplitude depends upon how much attention is being allocated to the channel in question. Thus, Nd amplitudes are greater when attention is focused on one channel of input rather than divided between two or more channels¹⁸. This latter finding, together with the positive correlations observed between Nd amplitude and target detection accuracy, suggests that at least part of the Nd negativity is a neural sign of the detailed processing of attended-channel events following the early stimulus selection^{16,19}.

Supporting the hypothesis that the Nd reflects an early stage of sensory selection are findings that stimuli in unattended channels, which lack the Nd wave, are not processed as fully as are attended-channel stimuli. This is evident in the ERPs to the infrequent target stimuli. Targets in the attended channel elicit a large P3 or P300 component (a positive wave peaking at around 300 msec, see Fig. 1) indicative of correct target detection, whereas the P300 is absent or greatly reduced to targets in the unattended channel. In addition, the normal, inverse relationship of P300 amplitude to stimulus probability is eliminated in the unattended channel¹⁶. These ERP findings imply a hierarchical stimulus selection mechanism, whereby inputs are first selected according to their distinct and conspicuous physical properties (i.e., which channel they belong to), and only those stimuli surviving this initial stage of selection (reflected in the early Nd) are examined further for their more refined features (reflected in either a later phase of the Nd or a P300 wave)²⁰.

Little is known at present about the neural systems that give rise to the Nd attention effect. Patients with lesions of the frontal lobes show reduced Nd amplitudes, but the Nd does not appear to be generated in the frontal lobes themselves²¹. There are strong similarities in latency and waveform between the human Nd effect and patterns of single unit activity recorded from the auditory cortex of monkeys performing in analogous attention tasks²². Although such cross-species comparisons are only suggestive at present, these findings are consistent with studies of cerebral blood flow in humans, which indicate that channel-selective auditory attention involves the processing of attended inputs in the auditory cortical fields and adjacent association cortex under the executive control of the frontal lobes³.

Pharmacological studies have suggested a role for the endogenous opiates in the regulation of the Nd attention effect²³. In a selective listening task, the opiate antagonist naloxone produced an enhancement of the Nd attention effect at frontal electrode sites, indicative of an improved selectivity of auditory attention. Arnsten *et al.*²³ suggested that naloxone's effect on attention may be mediated via

those areas of the frontal cortex that are particularly rich in opiate binding sites.

Early visual selection

In the visual modality, the earliest ERP changes are produced during spatial-selective attention when, for example, attention is focused on a flashing light in one visual half-field while comparable flashes in the contralateral hemi-field are ignored^{24–26}. In this case, flashes in the attended field elicit an enhanced sequence of ERP components over the posterior scalp (Fig. 3). Although the latencies vary with stimulus location and brightness, this attention effect typically includes positive peaks at about 130 and 230 msec (P130 and P230) and negative peaks at about 190 and 280 msec (N190 and N280). Since this same pattern of components is elicited by both attended and unattended flashes (the latter at reduced amplitude), it appears that visual-spatial attention acts by modulating or gating a series of exogenous components of the visual ERP rather than by initiating endogenous neural activity in the manner of the auditory Nd wave²⁷. The fact that the earliest discernible evoked component (the P130 onset at 80–100 msec) is modulated by

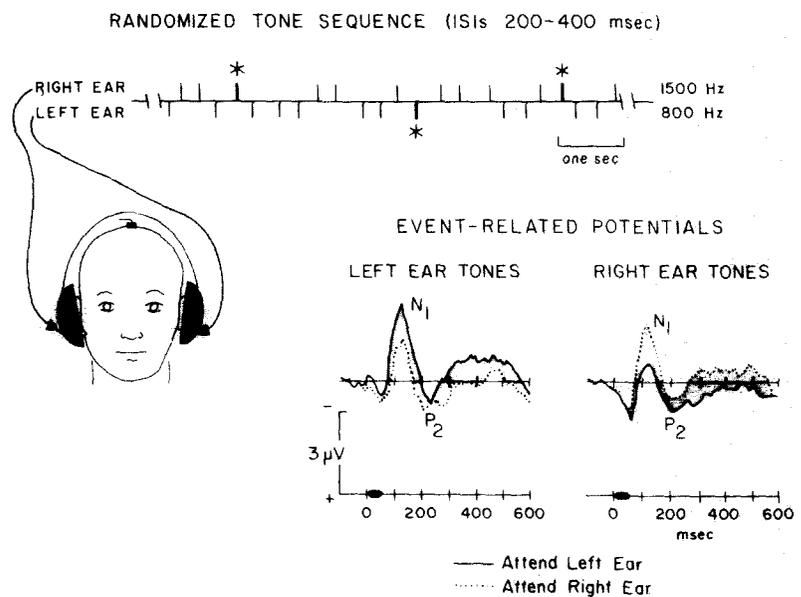
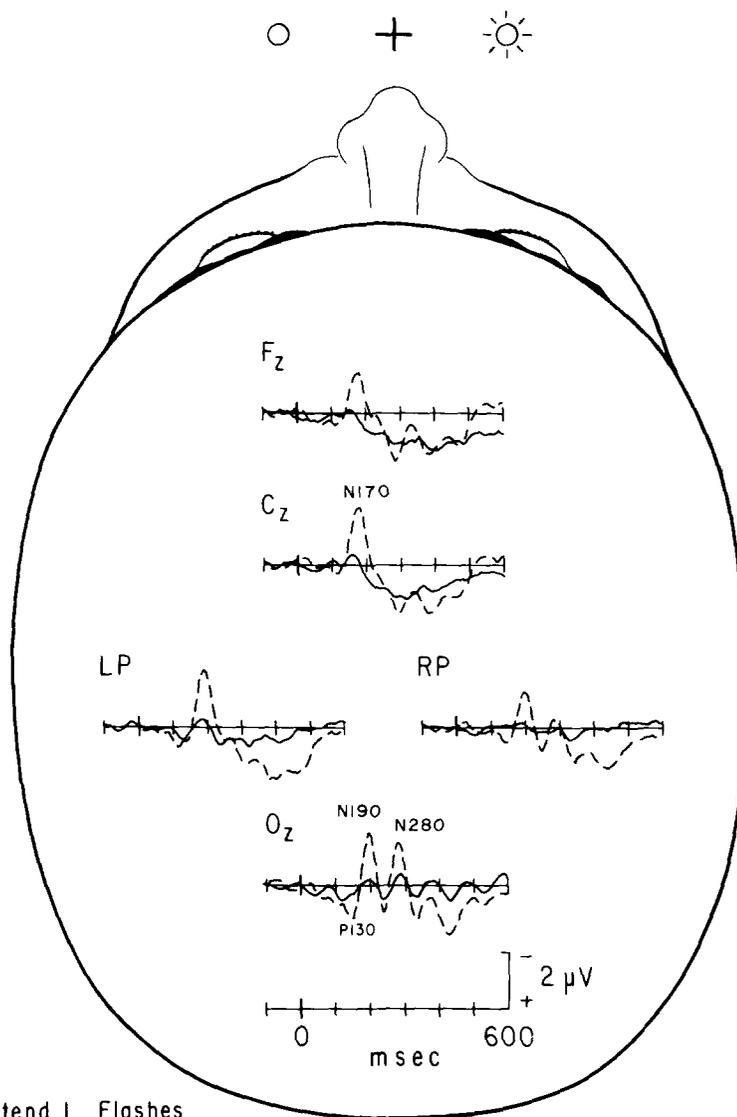


Fig. 2. Paradigm for demonstrating early ERP changes with channel-selective attention. Randomized sequences of tones are delivered to the left (800 Hz) and right ears (1500 Hz) at intervals shown on upper axis. Asterisks indicate 'target' tones (of slightly longer duration) that subjects attempt to detect in one ear at a time. Grand average ERPs to standard (non-target) tones in each ear are shown as a function of attend-left and attend-right ear conditions. The shaded area represents the difference waveform between the ERPs to attended and unattended tones and is called the Nd (negative difference) component²⁵.

ERPs to Right Flashes



Attend L. Flashes

Attend R. Flashes

Fig. 3. Grand average ERPs over 12 subjects in response to standard (non-target) flashes in the right visual field. The subject's task was to report occurrences of the slightly brighter targets in the sequence of flashes in one visual field at a time. Dashed tracings show ERPs elicited by the right flashes during the attend-right condition, and the solid tracings were recorded during the attend-left condition. ERPs are shown for different scalp sites located over frontal (Fz), central (Cz), occipital (Oz), and left (LP) and right (RP) parietal areas. The ERPs to left field flashes (not shown) have a mirror-image pattern of enhanced N170 amplitude over the RP recording site. Based on Ref. 26.

attention suggests a gating of inputs at a relatively early stage of visual processing, but the anatomical locus of these effects remains uncertain. It is possible that this attentional selectivity could be imposed as early as the level of the lateral geniculate relay^{12,24}.

Visual-spatial attention also produces enhancement of a sharp nega-

tive component (N170) over the contralateral parietal and anterior scalp. The waveform of this lateralized ERP closely resembles attention-related modulations of neuronal discharge patterns recorded from the parietal lobes of monkeys in similar attentional tasks²⁸. This suggests that the scalp-recorded ERP reflects the average population response of parietal lobe

areas that play homologous roles in attention in different primate species.

When visual stimuli are selected from one another on the basis of features other than spatial location (e.g., by their color, orientation, or size), different ERP patterns are produced. With these cues, attended stimuli elicit a slow, endogenous negativity over the posterior scalp in the latency range 150–350 msec^{25,27}. The onset latency of this ERP depends on the complexity and discriminability of the attention-directing cues. This N150–350 wave resembles the auditory Nd component, but is localized over the visual cortex in contrast to the frontal-central distribution of the Nd. Possibly, these broad negativities reflect the detailed processing of attended inputs in modality specific cortex.

When sets of multi-featured stimuli are presented, and subjects must select them on the basis of two or more sensory attributes, the latencies of the associated ERPs give indications of the timing and structure of the underlying attentional process. In one type of experiment, stimuli were varied in both their color and spatial location (e.g., red or blue flashes were presented at right or left locations), and subjects attended to one color-location combination at a time while ignoring the other three combinations^{25,27}. In this situation, the selection for stimulus color (indexed by the N150–350 wave) was found to be subordinate to the selection for the more discriminable cue of spatial location (indexed by a posterior P130/N170/N270 sequence). Only stimuli at the attended location that elicited the enhanced posterior sequence were further processed for their color attributes. These different levels of attentional selection were hierarchically ordered and each had a distinct time course and ERP signature. In addition, the ERPs indicated that attention operates first by selecting the individual features of a stimulus and then by identifying the 'conjunction' of features that define the relevant object²⁹.

Visual ERP experiments have also been aimed at defining the properties of 'attentional channels'. The concept of a channel in sensory processing usually refers to a particular class of receptors, a particular sensory feature, or a set of neurons that is tuned to some specific feature. An attentional channel, in contrast, can be defined as the set of stimuli that is processed more effectively as a result of paying

attention⁹. This definition is not circular, but rather describes how narrowly attention is focused along a particular sensory dimension. Rather than having invariant tuning properties, an attentional channel may be adjusted rapidly in accordance with momentary shifts in stimulus relevance. The 'bandwidth' of such a channel refers to the size of the attended zone along the pertinent sensory dimension (i.e., the width of the attentional 'spotlight').

The bandwidth of the attentional channel for visual-spatial frequency has been studied in a task where subjects attended to checkerboard stimuli having a particular check size that were presented among others of different check-sizes³⁰. A broad N150–350 component was maximal in response to checks of the attended size, and its amplitude declined progressively following checks of larger or smaller sizes, thereby defining the tuning curve for this attentional process. The bandwidth of this ERP-defined attentional channel corresponded closely to the bandwidth of the passive, size-specific channel defined by interocular interference experiments¹¹. Accordingly, it was proposed that attention to spatial frequency operates by modulating the transmission in feature-specific input channels. Analogous ERP studies with auditory and somatosensory stimuli have defined the properties of attentional channels along other sensory dimensions^{15,17}.

Somatosensory attention

Focusing attention upon stimuli applied to one part of the body (e.g., to one hand) while ignoring similar contralateral stimuli is also associated with an event-related negativity in the 75–150 msec range (termed the N140). Desmedt and Robertson¹⁵ delivered a random sequence of electric shocks to the index and middle fingers of both hands, with subjects instructed to respond selectively to stimulation of only one finger at a time. A hierarchical selection process was manifest in the ERPs, with the N140 indexing an early selection of all inputs to the attended hand, and a P300 wave (labelled P400 in Fig. 4) associated with the subsequent selection of the target finger. Unlike the auditory Nd, the somatosensory N140 has a lateralized scalp distribution, being largest over the somatosensory cortical region contralateral to the attended part of the body. Based on their scalp distri-

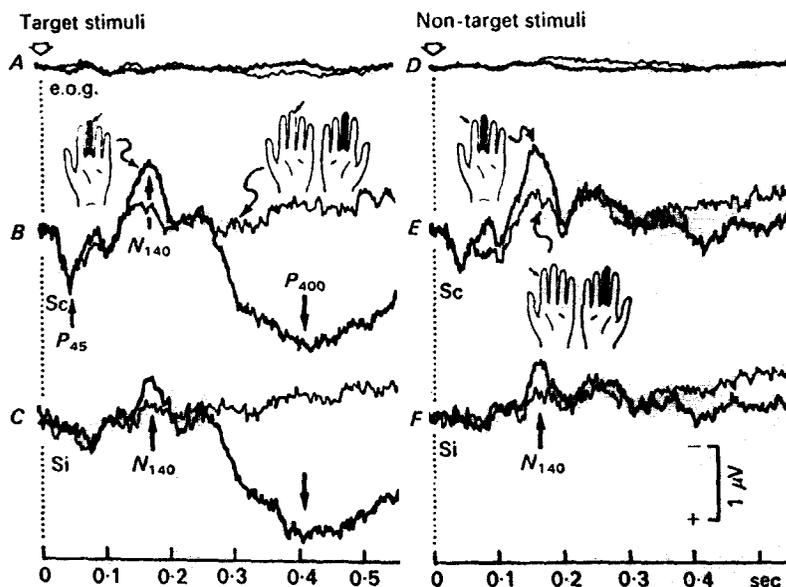


Fig. 4. ERPs during somatosensory selective attention to random sequences of shock stimuli applied to four fingers. The subjects counted the target stimuli to the third finger of either the left (thicker traces) or the right hand (thinner traces). In the hand figurines, the attended finger is represented in black and the small arrow points to the stimulated finger that evoked the ERP in question. Tracings A and D are vertical eye movement controls. Tracings B and E are somatosensory ERPs recorded from the contralateral parietal scalp (Sc) and elicited by stimuli applied to the third (B) or second (E) fingers of the left hand. Tracings C and F are corresponding ERPs recorded simultaneously from the ipsilateral (Si) parietal electrode. The N140 is larger contralaterally for both target and non-target stimuli to the left hand; the P300 (P400) wave is symmetrical and only occurs following target stimuli. The early P45 component only appears contralaterally in B and E and is not affected by the task¹⁵.

butions, these attention-related negativities (auditory Nd, visual N150–350 and somatosensory N140) appear to represent modality-specific processing that leads to stimulus identification¹⁴.

Discrimination and decision processes

Stages of stimulus discrimination and classification that follow the initial selection of input channel are reflected in longer-latency ERP components. When a stimulus has task-relevance and delivers information that the subject is searching for, it elicits a prominent P300 wave, usually preceded by a N2 (or N200) component and followed by a longer lasting 'slow wave'. The amplitude of the P300 increases as a function of the prior uncertainty (improbability) of the relevant event, the confidence with which the signal is detected, and the degree to which the stimulus information is utilized^{8,9,16,31}. Thus, the P300 is a sensitive index of the effective information content of a stimulus.

The P300 has a similar parieto-central scalp distribution for stimuli in all modalities, while the preceding N200 wave has a modality-specific distribution, being larger over pre-occipital areas for visual stimuli and

over the vertex for auditory stimuli³². The latencies of both the N200 and P300 are increased as the informative cues are made less discriminable. Accordingly, it has been proposed that the N200 wave is a sign of modality-specific stimulus evaluation and classification processes that lead up to a decision regarding the task-relevance of the stimulus³²; the P300 then reflects the post-decision processing of the effective stimulus information. The nature of this post-decision processing is still unclear, but there is evidence suggesting that the P300 may be associated with an updating of memory to incorporate the new information^{8,33} and the accessing of information to conscious levels of processing³⁴. The proposed link between P300 and memory is intriguing in light of evidence provided by depth recordings from epileptic patients having implanted electrodes, which suggests that a portion of the P300 activity arises in or near the hippocampus, a structure essential for certain forms of memory storage³⁵.

In experiments where rapid, discriminative motor responses are required to different types of stimuli, it has been shown that the latencies of

both N200 and P300 are determined more by stimulus evaluation processes than by the timing of the ultimate response³⁶. That is, the onset of P300 demarcates the time by which the relevant stimulus alternatives have been evaluated and categorized according to their informational value. This property of the P300 has been exploited to dissociate separate stages of sensory evaluation and response mobilization in several types of cognitive tasks, including the Sternberg memory-matching paradigm and the Stroop color-word task⁹. In this way, the P300 and associated components have enabled tests of competing theoretical models of perceptual decision-making.

Conclusion

Although the field of cognitive ERP research is at an early stage of development, some solid links have been established between ERP components and distinct forms of selective attention, discrimination, and perceptual decision making. In order to utilize these relationships to explore the neural bases of higher brain functions, further work is needed on both psychological and physiological levels. On the one hand, ERPs can be used to refine psychological models by providing a window on the timing of intermediate stages of information processing that may not be discernible from the final motor output. On the other hand, by demarcating the occurrence of endogenous brain activity spatially and temporally, ERP studies can guide investigations of the neurophysiology (single and multiple unit activity) and neuropharmacology (the participating neurotransmitter systems) that underly cognitive activity. While the psychological experiments are best carried out in human subjects, neurophysiological and neuropharmacological investigations use invasive techniques that are normally restricted to animal studies. Accordingly, it would be of great value to identify animal models or homologs of the principal types of endogenous human ERPs²⁸. The existence of cross-species

ERP homologies would be strong evidence that comparable psychophysiological processes were going on in the brains of human and animal species and would allow cognitive events studied in humans to be related more closely with animal neurophysiology. In this way, ERPs recorded from the scalp and from implanted depth electrodes³⁵, together with evidence from neurometabolic imaging³, neuromagnetic recording⁶, can serve as a bridge between the psychological and microphysiological levels of brain function.

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