# Event-related potentials (ERPs) and cognitive processing

*Steven A. Hillyard*

As information is processed within the neural networks of the human brain, the electrical activity arising from millions of participating neurons is summed to form field potentials that can be recorded through the intact scalp. The brain's field potentials include the rhythmic voltage oscillations of the ongoing electroencephalogram (EEG) and the briefer evoked or event-related potentials (ERPs) that are triggered in association with sensory, motor, and cognitive events. While the spontaneous EEG rhythms are sensitive monitors of general states of arousal, consciousness and the sleep-waking cycle, the ERPs reflect more discrete patterns of neural activity that underlie specific perceptual and cognitive processes. These activity patterns are revealed in the scalp-recorded ERP with a high degree of temporal precision (on the order of milliseconds), but the method generally lacks the degree of anatomical localization that is provided by neuroimaging techniques such as positron emission tomography or functional magnetic resonance imaging.

Recent approaches in modeling the neural sources of ERPs, however, have enabled their localization to specific brain structures with improved accuracy. By mapping the scalp topography of an ERP and applying algorithms based on the physics of electrical volume conduction, the positions of the underlying neural generators can be estimated with respect to brain anatomy. In a number of cases, the anatomical regions generating surface ERPs have been verified either by intracranial ERP recordings, by magnetoencephalography or by studies of patients with circumscribed brain lesions. Combined studies of ERP recordings together with neuroimaging methods that reveal patterns of cerebral blood flow and metabolism offer the possibility of defining both the precise time course and the anatomical substrates of information processing in the human brain.

The ERP recording methodology involves the computerized analysis of the voltage-time waveforms recorded from different points on the scalp. The ERPs triggered by sensory signals consist of a sequence of positive and negative voltage deflections (components) that have characteristic time delays and wave shapes. The typical ERP elicited by a brief auditory stimulus, for example, consists of some 16 or more components appearing over the interval 1.5 to 1000 ms after stimulus (Figure 1).

The early ERP components that occur before 50 ms or so represent evoked neural activity in the auditory pathways that is relatively insensitive to changes in the psychological state of the subject. In contrast, many of the later components are highly sensitive to the significance of a stimulus and to the information processing demands of the task. These "endogenous" ERPs have been studied extensively as indices of perceptual and cognitive processes. Several types of endogenous ERPs are depicted by the dotted and dashed tracings in Figure 1: the Nd wave is elicited specifically by auditory signals that are actively attended, while the N2, P3 (P300) and SW (slow wave) components are triggered by signals that are being discriminated and provide task-relevant information.

A major research goal is to identify different endogenous ERP components as markers of specific modes or stages of information processing. This has been achieved in a number of cases through the systematic study of the stimulus, task and behavioral performance variables that influence the component in question. These ERP markers reveal the timing and order of different processing stages and can distinguish among mechanisms of serial and parallel processing. In this way, the ERPs yield information about the neural bases of cognitive processes including selective attention, stimulus recognition, decision-making, memory storage and retrieval and language processing. As objective signs of cognitive operations, abnormal ERP waveforms have diagnostic significance for information-processing disorders associated with developmental, psychiatric and neurological syndromes.

## 1. Selective attention

The brain's attentional systems enable immediately relevant sensory inputs to be processed more effectively than other stimuli and thereby protect higher cognitive centers from sensory overload. Considerable research has been directed at the question of whether stimulus selections occur at an early stage of processing, perhaps by suppressing inputs belonging to particular sensory input channels, or at a later stage of processing after stimuli have been more fully analyzed. Evidence favoring an early selection mechanism has been obtained in a number of ERP experiments in auditory, visual, and somatic sensory modalities, in which discrete stimuli are delivered at rapid rates to two or more sensory channels. For example, if subjects are required to listen to a series of clicks, tones or speech sounds in one ear and ignore a comparable sequence of sounds in the opposite ear, all stimuli in the attended ear will elicit an enlarged, negative ERP (the Nd component) starting at around 70 or 80 ms. Given the short onset latency of this component and its elicitation by all stimuli belonging to the attended channel, it has been hypothesized that this ERP is a sign of an early selection process whereby stimuli are selected or rejected on the basis of whether they possess the elementary sensory feature that defines the channel (e.g., ear of entry). This early selective mechanism also appears to involve an amplitude modulation of evoked ERP components in the auditory cortex at latencies of 20 to 50 ms and 70 to 100 ms, as well as the longer-lasting endogenous Nd wave that appears to be a neural sign of the continued sensory analysis of the attended channel stimuli.

In accordance with the early selection hypothesis, stimuli in unattended channels, which lack the Nd wave, are not processed as fully as are attended-channel stimuli. Thus, in experiments where the attended channel is defined in terms of two features such as pitch and localization, stimuli that are rejected early on the basis of one feature do not show ERP signs of being processed for the other feature. These data and comparable findings in visual attention experiments support hierarchical, interactive models of attention. It appears that elementary stimulus features such as location and pitch are selected first, while more complex combinations of attributes are registered and selected at subsequent stages. The timing of different ERP components indicates that some feature analyses are performed serially while others occur in parallel.

In the visual modality, the earliest ERP changes occur during spatial selective attention, as, for example, when subjects attend to a flashing light in one visual field while ignoring concurrent flashes in the opposite field. Flashes in the attended field elicit an entire sequence of enhanced components over the occipital scalp, including P1, N1, P2 and N2 waves between 100 and 300 ms after stimulus (Figure 2). These ERP components that are modulated by visual-spatial attention appear to be generated in multiple extrastriate visual cortical areas rather than in the primary visual (striate) cortex itself. Both ERP and neuroimaging studies suggest that visual-spatial attention operates by modulating the flow of information from striate cortex to multiple extrastriate areas under the influence of an attentional control network in the frontal and parietal lobes.

The P100 and N170 components of the visual ERP show similar patterns of amplitude modulation in other spatial attention tasks including cued orienting to a location in the visual field and searching a visual display for a target. This ERP pattern appears to reflect an early selection mechanism that facilitates the processing of stimuli that are located within the "spotlight" of spatially focused attention. In contrast, selective attention to other visual features such as color, spatial frequency, and shape is manifested in longer latency (150 to 300 ms) ERP configurations. Since these later attention-sensitive components differ from one another in scalp distribution as well as in wave shape, they can be used to chart the time course of separate feature analyses in different visual-cortical areas.

## 2. Stimulus discrimination and classification

The late positive P300 component is readily elicited in tasks where subjects detect and respond to targets that occur randomly in a sequence of non-targets. The P300 that is triggered on detecting such relevant signals appears to be more closely tied to the moment of decision when the subject classifies the stimulus than with the organization and production of the response. The P300 latency thus gives a measure of how rapidly stimuli can be recognized and classified as relevant to the assigned task.

The triggering of P300 depends critically on memory processes, since incoming stimuli have to be matched against memory traces to recognize the relevant events. The P300 also depends on the subject's ability to judge the likelihood of upcoming events, since its amplitude is highly sensitive to stimulus probability. The P300 also provides an indication of the subject's discriminative capabilities, and, for that reason, has been useful for investigating cognitive development in children. To determine whether a child can discriminate between two classes of stimuli, for example, a random sequence of those stimuli can be presented with one being less probable than the other. If the child displays a P300 (or other late endogenous component) that is selectively triggered by the infrequent events, this would constitute unequivocal evidence that the child has made the discrimination. Thus the presence of a P300 reveals the integrity of a number of cognitive systems, making this ERP useful in the assessment of different kinds of cognitive deficits. For example, a significant prolongation of P3 latency has been observed in cases of Alzheimer's disease and other dementias, presumably reflecting the slowing of memory comparison and recognition processes.

The timing of endogenous ERP components such as the P300 can also be used to study the time course and sequencing of the information processing stages that intervene between stimulus and response. While the N2 (N200) and P300 waves primarily reflect perceptual discrimination and classification processes, the preparation for motor response is indexed by a "lateralized readiness potential" (LRP) that is generated in the motor cortex contralateral to the responding musculature. Studies of these ERPs have demonstrated that stimulus information is passed along from one stage to the next in a continuous "cascade" such that motor processes may be activated before perceptual processing is completed.

## 3. Memory processes

Several ERPs have been identified that bear a close relationship to specific forms of memory and retrieval processes. In the auditory modality, short-term sensory memory is reflected in a "mismatch negativity" (MMN) component that is triggered by deviant stimuli within a repetitive sequence of sounds. The MMN is elicited (at 150 to 250 ms) by stimuli that deviate in pitch, intensity, timing, localization, or even in more complex acoustic features, and its occurrence signals a mismatch between the incoming stimulus and the sensory memory trace of the immediately preceding stimulus. Because the MMN can be elicited by deviant sounds that are ignored by the subject, this ERP provides evidence that multiple features of auditory inputs are automatically analyzed and stored in short-term memory whether they are actively attended or not.

A late positive ERP (300 to 600 ms) has been found to be a reliable predictor of conscious (explicit) memory storage and retrieval. For example, if a subject is attempting to memorize a list of words for subsequent recall, the words that will later be recalled (or recognized) correctly will elicit a larger positivity than words that are later forgotten. This positive ERP has been interpreted as either a sign of the initial encoding of the stimulus in memory or of the updating of the memory trace due to its distinctiveness. Other long-latency ERPs are elicited when previously learned material is retrieved from memory. Memory-related ERPs corresponding to these surface-recorded components have been recorded from medial temporal lobe structures including the hippocampus in neurological patients studied with implanted electrodes. These ERPs thus provide a window into the timing of memory storage and retrieval operations in the human temporal lobe.

## 4. Language processing

ERPs are being increasingly studied as online, non-intrusive measures of linguistic processing in the brain. Different classes of ERPs have been identified as indices of lexical, syntactic and semantic aspects of language and of the hemispheric specialization for language functions. ERPs also reflect the division of the lexicon into open class (content) words such as nouns, verbs and adjectives and closed class (function) words including prepositions, conjugations and auxiliaries.

Specific ERP components have been associated with the development of semantic expectancy during reading. The ERPs to semantically anomalous words in otherwise meaningful sentences are marked by an enhanced negativity between 300 and 600 ms after stimulus (the N400). In general, the amplitude of N400 is inversely proportional to the predictability or expectancy of a word presented in a semantic context. Thus the N400 wave seems to provide a graded index of semantic expectancies and may reflect the amount of prior semantic priming for particular words. The fact that N400 is triggered immediately by each unexpected word provides strong support for linguistic models that postulate immediate, online sentence comprehension rather than the storage of words in a buffer for delayed analysis.

## 5. See also

Arousal: the activation of behavior
Cognition
Evoked potentials, auditory, human
Evoked potentials, clinical
Neglect (selective inattention)
Cognitive disabilities, diagnosis

## 6. Further reading

Giard MH, Fort A, Mouchetant-Rostaing Y, Pernier J (2000): Neurophysiological mechanisms of auditory selective attention in humans. *Frontiers in Bioscience* 5:84-94 [MEDLINE]

Hillyard SA, Kutas M (2002): Event-related potentials and magnetic fields in the human brain. In: Davis KL, Charney D, Coyle JT, Nemeroff C, eds. *Neuropsychopharmacology: The Fifth Generation of Progress.* Philadelphia: Williams & Wilkins, pp. 427-439

Hillyard SA, Mangun GR, Woldorff MG, Luck SJ (1995): Neural systems mediating selective attention. In: Gazzaniga MS, ed. *The Cognitive Neurosciences*. Boston: MIT Press, pp. 665-681

Hillyard SA, Picton TW (1987): Electrophysiology of cognition. In: Plum F, ed. *Handbook of Physiology*, Section 1: *The Nervous System*, vol. V: Higher Functions of the Brain, Part 2. Bethesda, MD: American Physiological Society, pp. 519-584

Kutas M, Dale A (1997): Electrical and magnetic readings of mental functions. In: Rugg MD, ed. *Cognitive Neuroscience*. Cambridge, MA: MIT Press, pp. 197-242

Kutas M, Federmeier K, Coulson S, King JW, et al. (2000): Language. In: Cacioppo J, Tassinary L, Bernston G, eds. *Handbook of Psychophysiology*. Cambridge: Cambridge University Press, pp. 576-601

Luck SJ, Woodman GF, Vogel EK (2000): Event-related potential studies of attention. *Trends in Cognitive Science* 4:432-440 [MEDLINE]

Martinez A, Di Russo F, Anllo-Vento L, Sereno MI, et al. (2001): Putting spatial attention on the map: timing and localization of stimulus selection processes in striate and extrastriate visual areas. *Vision Research* 41:1437-1457 [MEDLINE]

Naatanen R (1992): *Attention and Brain Function.* Hillsdale, NJ: Lawrence Erlbaum Associates Rugg MD, Coles MGH, eds. (1995): Electrophysiology of Mind. Oxford: Oxford University Pres

## 7. References

Hillyard SA, Kutas M (1983): Electrophysiology of cognitive processing. *Annu Rev Psychol* 34:33-61 [MEDLINE]

Hillyard SA (1993): Electrical and magnetic brain recordings: contributions to cognitive neuroscience. *Curr Opin Neurobiol* 3:217-224 [MEDLINE]

Di Russo F, Martinez A, Hillyard SA (2003): Source Analysis of Event-related Cortical Activity during Visuo-spatial Attention. *Cerebral Cortex* 13:486-499 [MEDLINE]

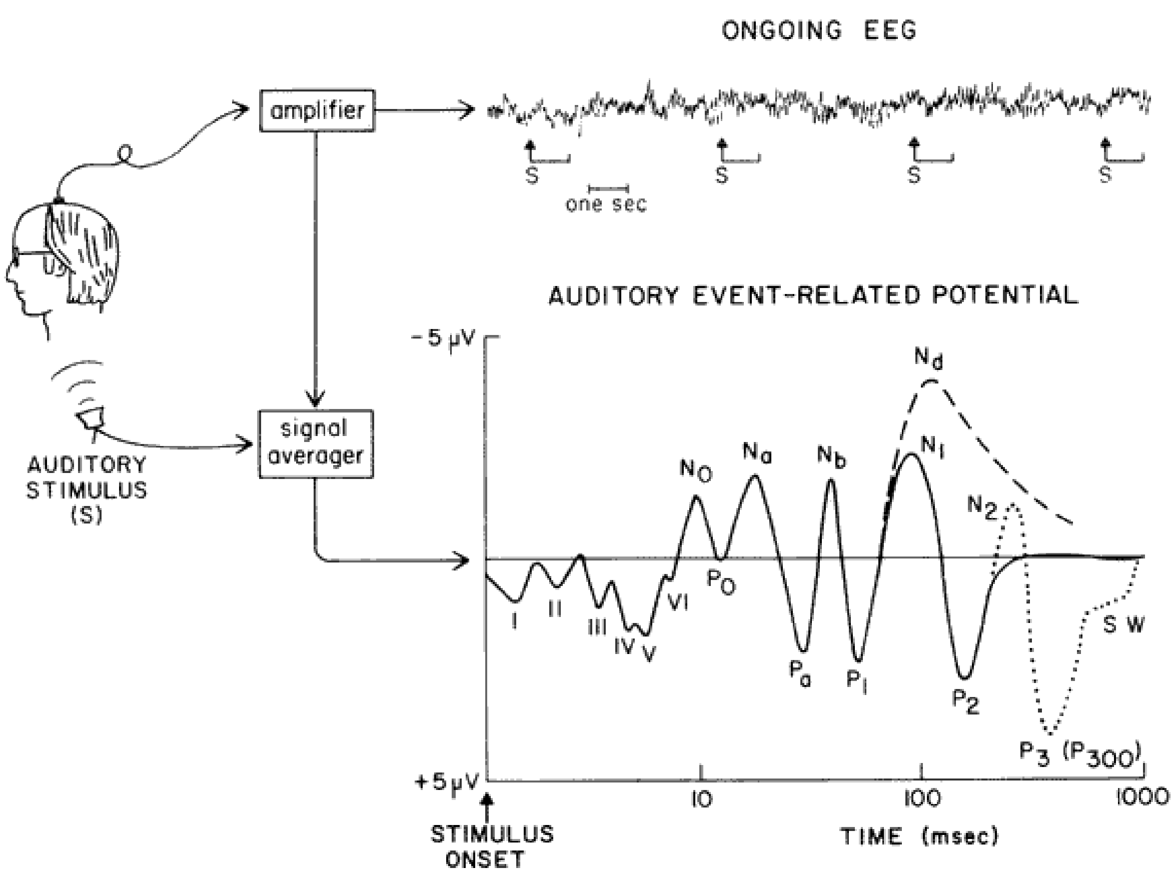

**Figure 1.** Waveform of the computer-averaged auditory event-related potential (ERP) to a brief sound. The ERP is generally too small to be detected in the ongoing EEG (top) and requires computer averaging over many stimulus presentations to achieve an adequate signal-to-noise ratio. The logarithmic time display allows visualization of the early brain stem responses (waves I-VI), intermediate evoked components, and long-latency endogenous components (Nd, N2, P300 and SW, or slow wave). ERP components are labeled according to their polarity, P (positive) or N (negative), followed either by a small number or letter (P3, Pa, etc.) that specifies the ordinal position of the wave in a particular sequence or by a larger number (P300, etc.) that refers to the latency of the wave in milliseconds. (From Hillyard and Kutas, 1983.)

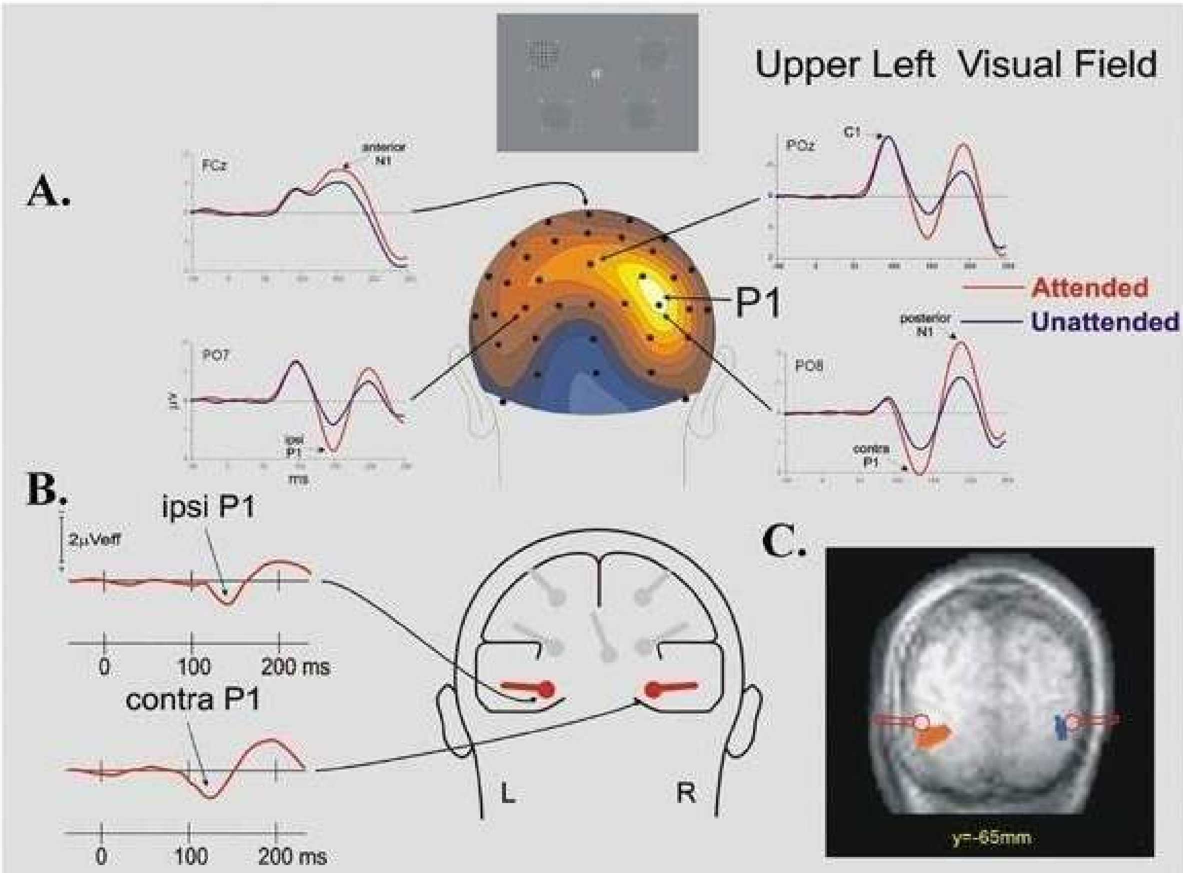




**Figure 2.** (A) Amplitude enhancement of visual ERP components during visual spatial attention. Circular checkerboard stimuli were flashed in random order to the 4 quadrants of the visual field (top) while subjects focused their attention on stimuli in only one quadrant at a time. The eyes remained fixed on a central cross. ERPs were recorded from 62 scalp sites and were averaged separately for stimuli in each quadrant under each attention condition. Waveforms shown are grand average ERPs from four scalp locations in response to the upper left field stimuli under conditions when they were attended (red tracings) and when unattended (blue tracings, while attention was directed to the upper right stimulus). Note the attention-related enhancements of ERP components including the contralateral P1 (130 ms), ipsilateral P1 (150 ms), posterior N1 (190 ms) and anterior N1 (150 ms) waves. In contrast, the earlier C1 component (90 ms), which is proposed to originate from the primary visual (striate) cortex, was not affected by attention. The head map shows the scalp voltage distribution of the late phase of the P1 component (100-130 ms) that was enhanced by attention over contralateral occipital areas. (B) Dipole model of the neural generators of the late P1 attention effect. Head model shows that dipoles accounting for the P1 attention effect are located in ventral occipital cortex. Waveforms at left represent the time course of activity in each model dipole corresponding to the enhanced neural activity in contralateral and ipsilateral occipital lobes. (C) These dipole positions correspond closely to focal regions of neural activity revealed by functional magnetic resonance imaging (fMRI) obtained in the same experiment but in a separate session. Red and blue regions represent cortical zones showing increased neural activity during attend-right and attend-left conditions, respectively. These findings indicate that spatial attention modulates the flow of visual information along the ventral-occipital pathway in the time range 100-130 ms after stimulus onset. (Data from F. Di Russo, A. Martinez, and S. Hillyard, 2003.)