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Generators of the late cognitive potentials in auditory and visual oddball tasks

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Abstract

Recordings directly within the brain can establish local evoked potential generation without the ambiguities always associated with extracranial electromagnetic measures. Depth recordings have found that sensory stimuli activate primary cortex and then material-specific encoders. Sensory-specific areas remain active for long periods, but by about 200 ms are joined by activation in widespread brain systems. One system is related to the orientation of attention. It is centered in paralimbic and attentional frontoparietocingular cortex, and associated with the P3a. A second system associated with P3b envelopes cognitive contextual integration. It engages the ventral temporofrontal event-encoding cortices (inferotemporal, perirhinal, and ventrolateral prefrontal), association cortices (superior temporal sulcal and posterior parietal), and the hippocampus. Thus, even in simple tasks, activation is widespread but concentrated in particular multilobar systems. With this information, the late cognitive potentials can be used to monitor the probable location, timing and intensity of brain activation during cognitive tasks. © 1998 Elsevier Science Ireland Ltd.

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1. Introduction

1.1. Methodological alternatives for localizing the spatiotemporal pattern of cognitive activity in the human brain

1.1.1. Electroencephalogram (EEG) and evoked potentials (EPs)

These have the advantages of great temporal resolution and a direct relation to neuronal information-processing. Information is carried between neurons, and is integrated within neurons via current flowing across active brain synapses. In some circumstances, the resulting net extracellular current flow can be recorded on the scalp as the EEG. That is, the EEG is the result of the passive instantaneous electrical propagation from active brain synapses to the scalp recording electrode. When the EEG is averaged with respect to a repeated behavioral event, random background EEG will cancel and only that part of the EEG (termed the EP) related to the behavioral event will remain. Careful examination of EPs across many tasks and subjects has demonstrated that they are composed of a series of components, each defined by its latency, polarity, scalp topography, and behavioral correlates (Halgren, 1990). Successive EP components are related to successive stages in information-processing, from the strictly sensory to the highest integrative levels, termed ‘endogenous’. Since these EP components are generated by synaptic current flows, they could provide a critical link between cognitive and neural processes. That is, if the intracranial generators of scalp EP components could be identified, then the intensity, onset and duration of activation of specific brain systems could be monitored, without risk or expensive equipment, in normal subjects during cognitive tasks, and functional models for the role of these synapses in generating behavior could be tested. In addition, these functional probes would be of great utility in the basic understanding and clinical evaluation of neurological and psychiatric disorders.

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Unfortunately, one cannot unambiguously infer the location of the synapses that generate an EP component (i.e. the 'propagating generator') from its scalp topography. This process of estimating cerebral generators from an observed scalp EP topography is known as 'solving the inverse problem'. In theory, an infinite number of different generator configurations in the brain could result in the same EP topography at the scalp. Laplacian transforms and spatial deconvolutions can estimate the voltage distribution at the exterior cortical surface with a 2 cm accuracy (see Gevins, 1998, and Koles, 1998). However, only about 30% of the cortex can be monitored in this fashion, and even the locally recorded EPs from electrodes on the cortical surface may be generated in deeper sites.

In the simplest and still most common solution of the inverse problem, the scalp EP distribution is assumed to arise from a single dipole. First, initial values of that dipole's location, orientation and strength are approximated. The propagation of electrical potentials from that dipole to the recording electrodes at the scalp is then calculated analytically by modeling the head as concentric spheres (brain, cerebrospinal fluid, skull and scalp) of differing conductances. The error between the calculated and the measured electrical field patterns is then used to modify the dipole's parameters, and the resulting field is re-calculated. This process is repeated in an iterative manner until the dipole's position, orientation and strength no longer change significantly between iterations.

Using intracranial microstimulation (Cohen et al., 1990; Cuffin et al., 1991; Gharib et al., 1995), or comparison with electrocorticography (Nakasato et al., 1994), the accuracy of such models in localizing an assumed single intracranial generating dipole from extracranial EEG is fairly high, but cognitive EPs do not satisfy this assumption: as will be shown below, cognitive EPs are generated by extended surfaces in multiple brain areas, rather than by a single dipole. Dipole localization methods that take into account the temporal as well as the spatial evolution of the EPs provide an additional constraint, but are still ill-posed (Sherg and Von-Cramon, 1985).

1.1.2. Magnetoencephalogram (MEG)

Synaptic activation not only results in the extracellular current flows that generate the EEG, it also results in intracellular current flows that are the main generators of the MEG. Compared to the EEG, the MEG is very little affected by the type and location of tissue surrounding the generator, and especially that of tissue lying between the generator and the sensor (Hari and Lounasmaa, 1989). However, it is still not possible to unambiguously infer from the topography of the extracranial magnetic field the location of the synapses that generate it. Like the EEG, the MEG will cancel unless there is adequate spatiotemporal synaptic synchrony, and furthermore, radially oriented current flows cannot be detected using MEG. Nonetheless, the MEG is sensitive to different generators than the EEG, and thus it is useful to have both sources of information in order to distinguish between possible generator configurations (e.g. Wood et al., 1985).

1.1.3. Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI)

These can be used to survey the entire brain for localized changes in glucose metabolism or blood flow that follow neural activity in cognitive tasks. However, the fMRI signal to a single stimulus has a delay of about 2 s and a gradual rise of 3–5 s, and the temporal resolution of PET is at best 45 s. Consequently, the temporal resolutions of PET and fMRI are insufficient to resolve individual cognitive stages.

A linear approach to the inverse problem has been developed that constrains the solution to lie within the cortex and perpendicular to its surface, and then uses a posteriori variance estimates for sources based on sensor spatial covariance (Dale and Sereno, 1993). In addition, the solution can be biased toward areas that were shown to be activated in the same task by fMRI (Nenov et al., 1991; Dale et al., 1995). Modeling studies have suggested, that within limits, this method of integrating fMRI with MEG and EEG data is very promising for arriving at reasonable hypotheses for the spatiotemporal activation pattern of local cortical regions during cognitive tasks. However, it must be emphasized that the result of these calculations is still a hypothesis that needs to be confirmed by direct methods.

1.1.4. Scalp EP recordings after brain lesions

Scalp EP recordings after brain lesions in humans have provided important information regarding possible brain generators of scalp EPs (Knight, 1990). Clearly, destruction of a propagating generator would usually be expected to diminish the corresponding scalp EP component. However, it is difficult to evaluate the possible influences of remaining generators (which could show a compensatory increase in strength), of the removal of 'canceling' generators (which could actually result in a post-lesional increase in amplitude), and of any skull defect (which alters the distribution of current and thus the scalp EP amplitude). Furthermore, unless synaptic current flows are somewhat synchronous and spatially aligned, they will cancel and remain 'occult' to a remote electrode. Finally, the activated synapses within the EP generating structures may project from neurons in another 'trigger structure' that in turn relies upon calculations performed elsewhere in some 'antecedent structure' (for a more complete discussion of these interpretative issues see Halgren et al., 1986). In order to identify the brain stages of information-processing, occult as well as propagating generators, and trigger as well as antecedent structures must be located. It would be expected that the lesion of a trigger would produce an EP deficit topographically more extensive than the lesion site would suggest, and lesion of an antecedent structure would produce a task-specific EP reduction.

This article focuses on the results from our laboratory

using direct intracranial recordings in humans to localize the generators of cognitive EPs.

2. Methods

The most direct indication that a given structure is a generator of a particular EP component is when recordings from that structure locate large focal polarity-inverting potentials with similar timing and task correlates as that component. Such recordings are possible using electrodes implanted inside the brains of epileptic subjects for the purpose of localizing their epileptic focus prior to its surgical removal (Chauvel et al., 1996). During the time that the patients are waiting for the arrival of a spontaneous seizure, they may consent to perform cognitive tasks while their relatively normal brain regions are recorded.

Like scalp EEG, intracranial (iEEG) has a very high temporal resolution ($<$1 ms) and a direct relation to synaptic communication. Unlike scalp EEG, iEEG also has very high spatial resolution (effectively limited only by electrode size and spacing), and can unambiguously identify EP generators. For example, if the locally recorded EP component is much larger than in adjacent structures, and changes amplitude and polarity over short distances, then that component is without question generated locally. Thus, iEEG provides the only unambiguous method, or 'gold standard,' for determining if a structure generates a given EP component.

Intracranial recordings may either be made with surface strips or grids of electrodes or with stereotactically placed depth electrodes. We have used the latter in these studies. Depth iEEG has three limitations. First, depth electrodes are only implanted for strictly clinical purposes in patients with long-standing epilepsy, and thus may record abnormal responses. In most cases, epileptogenic pathology attenuates the local cognitive potentials (Squires et al., 1983; McCarthy et al., 1987; Wood et al., 1988; Meador et al., 1989; Puce et al., 1989; Halgren et al., 1991a). However, occasionally, epileptiform hyper-responsiveness can also be observed (Altafullah and Halgren, 1988; Clarke et al., 1995). Nonetheless, it is possible to select for study patients who perform cognitive tasks in the normal range, and who produce normal scalp cognitive EPs. Furthermore, epileptiform activity is localized in time and space, and so it is possible to select patients, sites and epochs for analyses that are electrographically normal.

A second limitation of depth recordings is that they provide unambiguous localizing information only in a small region surrounding the electrode contact, and, in a given patient, electrodes are only implanted into a limited region. To achieve 3.5 mm resolution (the inter-electrode spacing used in our studies), about 10 000 recording sites would be needed. However, we only record from about 80–120 contacts (arrayed in 5–9 electrodes) in a given patient. This limitation can be partially overcome by comparing results across a large number of patients with electrodes in different regions. In the data to be discussed here, about 4000 sites were sampled during the 'oddball' paradigms. However, certain brain regions remain undersampled because they are seldom involved in epileptogenesis and/or they are difficult to approach surgically. Poorly sampled regions include the insular/opercular cortices, and the most dorsal parietal, posterior occipital, and anterior frontal cortices. Conversely, due to their common involvement in epileptogenesis and the existence of a safe surgical approach, the hippocampus and amygdala have been recorded from more than any other brain area.

A third limitation of iEEG is that evaluating the possible contribution of a demonstrated local EP generator to the extracerebral EEG/MEG field is complicated, requiring an accurate computational model that incorporates knowledge of: (1) the detailed spatial configuration of dipoles within the generating structure; (2) the strength of each dipole; and (3) the 3D distribution of tissues with different impedances in the head. Since such an ideal model has never been realized, the exact relationships of the generators of cognitive EPs in the brain to scalp recordings, remains unclear. The fact that the dorsal convexity of the cortex has been poorly sampled with intracranial recordings only compounds this serious challenge.

3. Results

3.1. Intracerebral potentials to rare target and distractor auditory and visual stimuli

Subjects received an auditory discrimination task with target and non-target rare stimuli ('standard oddball paradigm'). In some cases, the target, distracting and frequent tones were completely balanced across blocks for pitch and volume. Variants included an analogous visual discrimination task, or auditory tasks where the rare target event was the omission of a tone, or the repetition of a tone within a series of alternating tones. In some subjects, the same auditory stimuli were delivered but the patient ignored them while reading. Three general response patterns could be distinguished on the basis of their waveforms, latencies and task-correlates (Fig. 1; Baudena et al., 1995; Halgren et al., 1995a,b).

3.1.1. Modality-specific responses to rarity

The earliest potentials apparently related to rarity were recorded in the auditory association cortex of the posterior superior temporal plane (Halgren et al., 1995a). One major problem in interpreting recordings from this area is that typical auditory oddball tasks confound specific dishabituation with rarity per se. We dealt with this confound by using a paradigm with alternating tone sequences, with the oddball being the tone that is the same as the preceding tone. In this paradigm, the rare tones are *more* habituated than the frequent. A second problem interpreting such recordings is

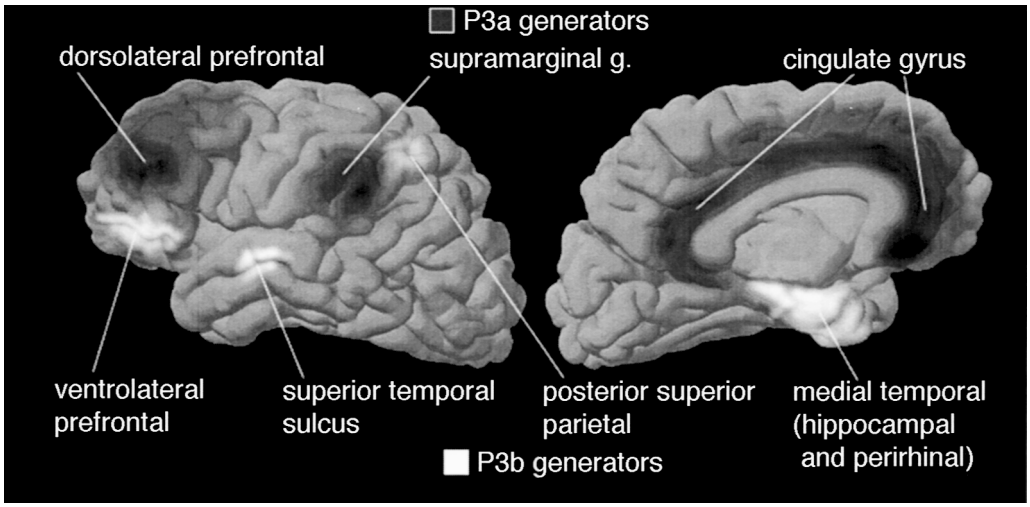

Fig. 1. Summary of brain areas where P3s were found to be generated by simple rare stimuli in signal detection tasks. The P3a is evoked by rare stimuli, regardless of whether they are targets or non-targets, overtly attended or unattended, auditory or visual. It is generated in a frontoparietocingulate system that has been associated with the orientation of attention (areas shaded dark in the figure). It is associated with an electrodermal response and represents the cortical component of the orienting response. The P3b (lighter areas) is evoked by attended visual or auditory stimuli that must be definitively processed. Its principle generators are in the hippocampus, superior temporal sulcus, ventrolateral prefrontal cortex, and (probably) intraparietal sulcus. The P3aud (not indicated) is generated in the superior temporal plane to auditory stimuli only, and is insensitive to attention. Lateral (left) and medial (right) views are shown. Diagram based on recordings from about 4000 intracranial sites (Halgren et al., 1980, 1995a,b; Stapleton and Halgren, 1987; Smith et al., 1990; Baudena et al., 1995).

that typical auditory oddball tasks confound rarity with differences in sensory characteristics. We alternated the tone pitch that was rare, frequent or distractor across blocks, so that the sensory characteristic of each was, on average, identical when averaged across blocks. Using these manipulations it was possible to demonstrate a series of potentials that were related to rarity per se (as opposed to sensory differences or to habituation). These were generated in the superior temporal plane. The earliest potential was a large positivity superimposed on early components and peaking at 150 ms. Subsequent components could be large, focal and/or inverting in polarity, and usually included a positivity at 230 ms and a negativity at 330 ms. All components in this area were specific to the auditory modality. They were insensitive to instructions to ignore the stimuli, and generally inverted across the Sylvian fissure. Thus, the positivity at 150 ms may correspond to the mismatch negativity, as was suggested independently by Kropotov et al. (1995). Similarly, the negativity at 330 ms is termed P3aud (Fig. 1). Although the propagation to the scalp of the P3aud remains to be established, one may note that other potentials generated in the superior temporal plane propagate strongly to the vertex, and that post-lobectomy studies suggest that the generation of the P3 is partly modality-specific (Johnson, 1989).

3.1.2. The P3a system for the orientation of attention; inferior parietal, cingulate, and dorsolateral prefrontal cortex

The most widespread intracranial response to rare stimuli is a triphasic waveform with sharp negative, positive and

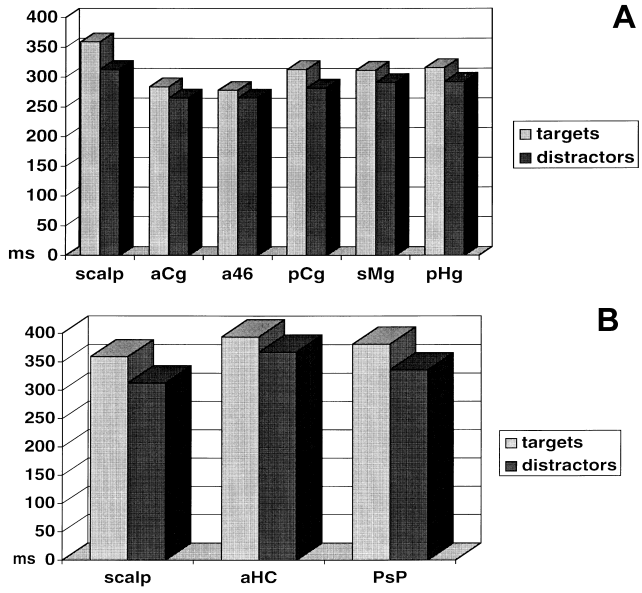

Fig. 2. Latencies of P3a (A) and P3b (B) in different brain areas. (A) The P3a has a significantly shorter latency in frontal sites (including anterior cingulate gyrus, aCg, and Brodman's area 46 in the dorsolateral prefrontal cortex, a46), than in parietal sites (including posterior cingulate gyrus, pCg, and supramarginal gyrus, sMg), or temporal sites (including parahippocampal gyrus, pHg). At all sites, the depth P3a is earlier than the scalp P3. (B) The depth P3b is later in the anterior hippocampus (aHC) and the posterior parietal cortex (PsP) than at the scalp. For all sites and components, the response is earlier to distractor than to target stimuli. However, this difference is small and insignificant for many depth sites, especially for the P3a. Data from Halgren et al. (1995a,b) and Baudena et al. (1995).

Table 1
Behavioral dissociations between intracranial P3 components

Component	Evoking stimuli		
	Task-relevant auditory	Task-relevant visual	Task-irrelevant auditory
P3aud	Yes	No	Yes
P3a	Yes	Yes, if attention is 'grabbed'	Yes
P3b	Yes	Yes	No

Note that simply subtracting the potentials evoked by attended rare tones from those evoked by ignored rare tones would decrease the number of intracranial generating structures from >9 to about 3.

negative peaks at about 210–220, 280–320 and 390–420 ms, respectively (Fig. 1; Wood and McCarthy, 1985; Alain et al., 1989; Smith et al., 1990; Halgren et al., 1995a,b; Baudena et al., 1995). This waveform is evoked by rare target and distracter stimuli, regardless of whether they are overtly attended to. It is not modality-specific, but is more easily evoked by the auditory than the visual modality. It is only weakly evoked in cognitive tasks with words or faces (Halgren et al., 1994a). The positive peak has a significantly shorter latency than the scalp P3 (Fig. 2A). In its task correlates and latency, this peak is similar to what has been termed 'P3a' at the scalp (Squires et al., 1975; Courchesne et al., 1975; Snyder and Hillyard, 1976), and the same terminology has been adopted for the depth, with the entire waveform being termed 'N2a/P3a/SW.'

In lateral-to-medial penetrations by depth electrodes with multiple recording points, N2a/P3a/SW amplitudes often change only slowly with distance. This pattern could result from very diffuse cortical generation (Klee and Rall, 1977). Occasionally, large (120 μV) P3as with steep voltage gradients are observed laterally, especially near the inferior frontal sulcus and in the supramarginal gyrus. Clear inversions of the P3a occur in anterior cingulate cortex and its inferior extension, the gyrus rectus (Halgren and Marinkovic, 1995; Baudena et al., 1995). The dorsolateral prefrontal, inferior parietal, and cingulate cortices are highly interconnected anatomically, and lesions in these sites are associated with neglect and other attentional deficits (Heilman and Watson, 1977; Selemon and Goldman-Rakic, 1988; Mesulam, 1990). Amongst these areas, the prefrontal cortex may play a leading role, inasmuch as the scalp P3a can be eliminated by prefrontal lesions (Knight, 1984; Wood et al, 1985b). Furthermore, the latency of the depth-P3a is significantly shorter in frontal than in posterior sites (Fig. 2A).

The N2a/P3a/SW thus is evoked by stimuli that demand processing because of their potential biological significance. It prominently engages areas that can localize the evoking stimuli, as well as those that can help prepare the organism to make a rapid response. The additional less prominent diffuse activation observed during the N2a/P3a/SW may represent the polling of virtually all cortical areas to arrive at a rapid if schematic evaluation of the stimulus. Biologically prepotent stimuli also evoke the orienting response: autonomic phenomena that prepare the organism to respond, most typically measured as an increase in electrodermal conductance (Sokolov, 1990). In normal subjects, the scalp P3a is only evoked by rare distracting sounds if those sounds also evoke an electrodermal response, strongly suggesting that the depth P3a may embody the cortical component of the orienting response (Halgren and Marinkovic, 1995).

3.1.3. The P3b event-encoding system: hippocampus, superior temporal sulcus, lateral orbitofrontal cortex, intraparietal sulcus

Depth electrodes often record a different pattern of activity to rare stimuli. In striking contrast to the N2a/P3a/SW, this response is abolished if the subject is instructed to ignore the stimuli, and its latency is about 380 ms, significantly later than the scalp P3 (Fig. 2B). In these respects, this response is similar to what has been termed the P3b at the scalp, and it is termed the depth P3b (Fig. 1). The depth P3b is characterized by a broad waveform with frequent polarity inversions. It is largest in the hippocampus (Halgren et al., 1980; Halgren et al., 1995b; Stapleton and Halgren, 1987; McCarthy et al., 1989), but local generation is also well-established in a limited region of the superior temporal sulcus, and the ventrolateral prefrontal cortex. Local generation is likely in the intraparietal sulcus and (by inference) in the anterobasal temporal lobe (possibly rhinal cortex) (Halgren et al., 1995a,b; Baudena et al., 1995). These areas generally subserve high-level supramodal associations derived from declarative, semantic and primary memories. The depth P3b is modality non-specific, and is associated with a modality non-specific N2b possibly generated in rhinal cortex. It is also evoked (but at a much longer latency) in more complex cognitive tasks, for example by repeated words or faces (Halgren et al., 1994a,b).

Studies of the cognitive correlates of the scalp N2b/P3b have led to the hypothesis that they reflect the controlled or conscious processing of an event, with the P3b representing the closure or completion of that processing (Posner, 1975; Desmedt, 1981; Donchin et al., 1983; Näätänen and Picton, 1986; Hillyard and Picton, 1988; Hoffman, 1990). For example, the P3b is present if, and only if, independent behavioral data show that the stimulus has captured the subject's attention and reached his or her awareness. P3b onset occurs at about the same latency as the specification of the subject's response, suggesting that the P3b begins when the stimulus has been sufficiently processed to be accurately perceived (Kutas et al., 1977; Desmedt, 1981; McCarthy and Donchin, 1981). The finding that the depth P3b is generated in multiple limbic and multimodal association cortex areas is also consistent with this hypothesis. In summary, the task correlates, latency, topography and generators of the depth-P3b suggest that it embodies the closure of the cognitive event-encoding cycle.

In summary, the scalp P3 to attended rare auditory stimuli reflects contributions from 3 separate generating systems. Two of these systems, P3a and P3b, simultaneously engage multiple structures in frontal, parietal and temporal lobes. Thus, the P3 represents a widespread corticolimbic modulation of the systems responsible for orienting attention toward a possibly significant stimulus, as well as for the subsequent encoding of that stimulus into a cognitive event. Our data suggest that, in order to distinguish between the different P3s, it is necessary and sufficient to record the responses to rare attended stimuli in at least two modalities, with an ignore condition in one modality.

3.2. Intracerebral potentials to novel and repeated words and faces

Additional EPs are evoked by more complex cognitive tasks that involve stimuli that are meaningful within a large semantic system, such as words, faces and objects. The earliest of these have peak latencies of 150 to 220 ms, and respond specifically to a particular class of items, such as words or faces (Halgren et al., 1991b, Halgren et al., 1994a,b; Allison et al., 1994). An N310-N430-P630 sequence to words and faces is recorded by depth electrodes during a task requiring recent declarative memory for words and faces (Smith et al., 1986; Halgren et al., 1994a,b). These components are largest and polarity inverted in the hippocampal formation and amygdala, but are also prominent in the ventrolateral prefrontal cortex, and are probably locally generated in many sites including the lingual gyrus, lateral occipitotemporal cortex, middle and superior temporal gyrus, temporal pole, supramarginal gyrus, posterior cingulate gyrus, and parts of the prefrontal cortex.

3.3. Other late cognitive potentials

At least two other brain systems associated with late cognitive EPs have been described, but are beyond the scope of this chapter (Halgren, 1990; Halgren and Marinkovic, 1996). The first is the contingent negative variation (CNV), a widespread sustained negativity observed between two stimuli (S1 and S2), when the identity of S1 must be maintained in primary (working) memory in order to respond appropriately to S2. With iEEG, large CNVs have been recorded in central, parietal and especially prefrontal cortices (Groll-Knapp et al., 1980). The second is the RP (readiness or Bereitschafts potential), a late negativity occurring at about 650–900 ms latency in the word tasks described above, or for a more extended period preceding spontaneous movements (see also Gevins, 1998). Intracranial recordings suggest that the RP is generated in precentral and premotor cortices (Ikeda et al., 1992; Rektor et al., 1994; Halgren et al., 1994b), although contributions from other areas may also be present (Arezzo et al., 1987; Halgren, 1991).

4. General discussion

4.1. Organizing principles of late cognitive EPs

Although limited, intracranial recording studies of cognitive EPs permit one to propose some general organizing principles characterizing the human brain's temporospatial pattern of activation during cognitive tasks (Halgren and Marinkovic, 1996). The most striking conclusion is that most areas are activated by a task even if they are not necessary for its performance.

For example, as shown above, simple 'oddball' tasks engage widespread neocortical and limbic areas. Given that simple sensory discriminations can be performed in the absence of a neocortex (Bitterman, 1975; Tuber et al., 1980), it is clear that none of the telencephalic areas 'activated' in this task are essential for basic task performance. Even within the telencephalon, lesions of the areas with the most prominent EPs during the auditory oddball task would not be expected to affect performance. For example, the largest depth EPs during this task are recorded in the hippocampus, but bilateral lesions of the hippocampal formation producing severe amnesia do not impair performance on this task (Polich and Squire, 1993). A similar observation was made in a visual 'oddball' task where the subjects were presented with simple stimuli in the left or right hemifield and needed to respond with either the left or right hand. Again, even when both stimulus and response needed to involve only one and the same hemisphere, depth recordings indicated that outside of the specific sensory and motor areas both hemispheres were about equally involved (Clarke et al., 1992). Similar findings are observed in more complicated tasks, as described above, where activation is prominent in both hemispheres to both words and to faces, despite the well-known laterality of essential processing areas implied by lesion studies. Thus, the brain seems to adopt the strategy of engaging all potentially useful areas, even though the probability may be very low that they will contribute to immediate task performance.

While widespread divergent associations (typical of 'conscious' processing) are intentionally rendered superfluous in many psychological tasks, they could be essential in the natural environment where adaptation often and unexpectedly requires the creative interpretation of events and the formulation of novel strategies for survival and reproduction. Specifically, this strategy permits incidental learning, self-monitoring for behavioral accuracy and consequences, and the widespread integration of processed stimulus information with the contents of short-term, recent and remote, semantic and working memories, as well as with the current cognitive context. In comparison to these benefits, the cost of habitual widespread activation would seem to be minimal, given that in homeotherms all brain areas must be provided with continuous metabolic support, regardless of whether they are engaged by the task or not.

Although intracranial cognitive EP recordings suggest

that cognitive activation is widespread, it is also is highly organized in functional systems. The functional systems are extensive, including areas that are close to the primary sensory and motor cortices. For example, in the auditory oddball task, the cortex adjacent to primary auditory area in the posterior superior temporal plane is active for more than one second after a rare tone (Halgren et al., 1995a). Conversely, even precentral gyrus shows very early potentials, beginning at about 120 ms to either tones or complex stimuli (words or faces; Halgren et al., 1994b; Baudena et al., 1995; Clarke et al., 1995). Some components (for example the P3a) may even have shorter latencies in prefrontal as compared to posterior sites.

4.2. Implications for source modeling

These data have clear implications for the dipole source modeling methods described in the Introduction. Each late EP component is produced by the superimposition of multiple generating structures, each of which is an extended convoluted surface. Thus, source modeling of scalp-recorded late EPs requires correspondingly complicated models. Clearly, source localization of late cognitive EPs based on a single 'equivalent dipole' is unrealistic: the scalp P3 in the usual auditory oddball task could receive contributions from: (1) the superior temporal plane (P3aud); (2) supramarginal gyrus (P3a); (3) dorsolateral prefrontal cortex (P3a); (4) cingulate gyrus (P3a); (5) gyrus rectus (P3a); (6) hippocampus (P3b); (7) superior temporal sulcus (P3b); (8) posterior parietal lobe (P3b); and (9) ventrolateral prefrontal cortex (P3b). Multiple simultaneous dipole modeling potentially provides a more accurate model but must be approached with great caution. Such modeling usually involves several subjective decisions regarding the number of dipoles, as well as the latencies and sensor channels to use for modeling. These choices can have profound effects on the results, and are difficult to make a priori without rendering the results of modeling at least partially circular. Finally, using single dipoles to model entire generating surfaces not only are intrinsically unrealistic, but also can introduce significant error in anatomical localization: the equivalent current dipole may be significantly displaced from the center of the generating surface (Hari et al., 1988). It may be wise to use task manipulations in order to isolate the P3b from the P3a and the P3aud before source modeling in order to reduce the number of structures contributing to the measured field pattern (Table 1).

5. Conclusion

Large distributed cortical systems are activated during the late cognitive evoked potentials N2, P3 and SW. These systems are concerned with the orientation of attention and the contextual integration of cognitive events. While it is difficult to measure activity in individual brain areas using cognitive EPs, they provide an excellent means for monitoring on-line the activation level in these core cortical systems for cognition.

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