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Electroencephalographic imaging of higher brain function

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High temporal resolution is necessary to resolve the rapidly changing patterns of brain activity that underlie mental function. Electroencephalography (EEG) provides temporal resolution in the millisecond range. However, traditional EEG technology and practice provide insufficient spatial detail to identify relationships between brain electrical events and structures and functions visualized by magnetic resonance imaging or positron emission tomography. Recent advances help to overcome this problem by recording EEGs from more electrodes, by registering EEG data with anatomical images, and by correcting the distortion caused by volume conduction of EEG signals through the skull and scalp. In addition, statistical measurements of sub-second interdependences between EEG time-series recorded from different locations can help to generate hypotheses about the instantaneous functional networks that form between different cortical regions during perception, thought and action. Example applications are presented from studies of language, attention and working memory. Along with its unique ability to monitor brain function as people perform everyday activities in the real world, these advances make modern EEG an invaluable complement to other functional neuroimaging modalities.

Keywords: electroencephalography; MRI; attention; working memory; language

1. INTRODUCTION

The purpose of functional brain mapping is to measure patterns of neuronal activity associated with sensory, motor and cognitive functions, or with disease processes. To be effective in this, an imaging modality needs both near-millimetre precision in locating regions of activated tissue and sub-second temporal precision for characterizing changes in patterns of activation over time. Increasingly fine anatomical resolution is available from functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) technologies. However, these technologies only provide indirect measures of neuronal electrical activity, and their temporal resolution is too gross to resolve the rapidly shifting patterns of activity that are characteristic of actual neurophysiological processes.

The electroencephalogram (EEG), in contrast, has a temporal resolution as fine as the analogue-to-digital sampling rate used to record it (typically in the range 1–5 ms). For simplicity we use the term EEG in a general sense to refer both to recordings of brain electrical activity and, except where noted, to recordings of brain magnetic activity called magnetoencephalograms or MEGs. The nature of MEG recording technology and the relative strengths and weaknesses of the EEG and MEG approaches have been reviewed elsewhere (Cohen & Cuffin 1991; Leahy *et al*. 1998; Williamson & Kaufman 1987). Here it suffices to say that, from a broad perspective that considers all neuroimaging modalities, the differences between EEG and MEG are slight in comparison with their similarities.

The sensitivity of the EEG to changes in mental activity has been recognized since Berger (1929) reported a decrease in the amplitude of the dominant (alpha) rhythm of the EEG during mental arithmetic. In addition to the type of tonic alterations in brain electrical activity reported by Berger, EEG measurements of phasic, stimulus-related changes in brain activity (such as evoked potentials (EPs)) are well-suited to measuring sub-second component processes of sensory, motor and cognitive processes (Hillyard & Picton 1987; Regan 1989). Measurements of the coherence, correlation or covariance of EEG time-series from different electrode sites help to generate hypotheses about the functional networks that form between different cortical regions during these processes. The temporal resolution and sensitivity of the EEG would seem to make it an ideal complement to fMRI and PET. Unfortunately, the spatial detail provided by conventional EEG recordings has been so coarse that it has only been possible to interpret EEGs meaningfully with respect to underlying functional neuroanatomy at the level of entire cortical lobes, if at all. Although the ability to infer the three-dimensional (3D) distribution of electrical sources in the brain from scalp EEG recordings has fundamental physical limits, the amount of spatial information that can be recovered from the scalp-recorded EEG is frequently underestimated. Indeed, the very low level of spatial resolution obtained from conventional EEGs reflects the fact that activity is measured at only a small number of scalp sites during most routine recordings; moreover, modern spatial signal-enhancing methods have not often been applied. This is rapidly

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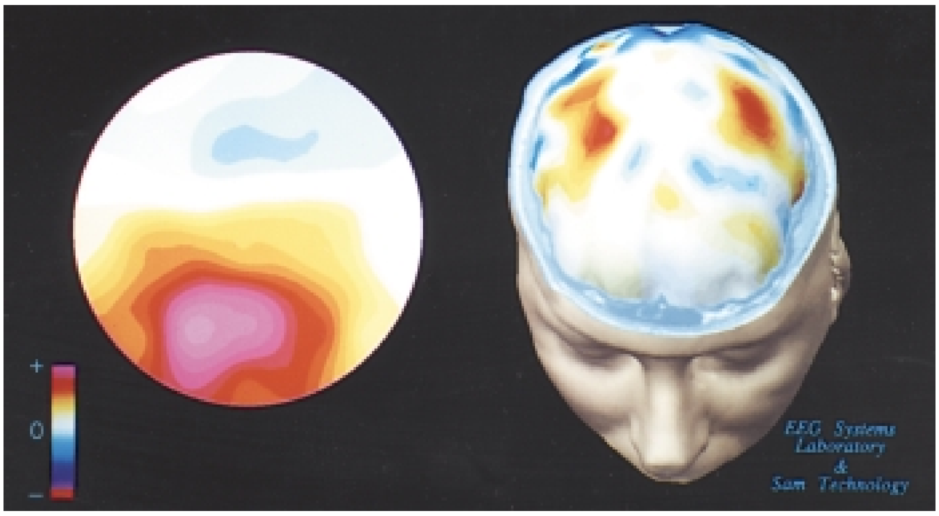

Figure 1. High-resolution EEG mapping of somatosensory cortex activation. The image on the right is a 122-channel, computer-enhanced topographic map of the potentials evoked by repetitive electrical stimulation of the left middle and right index fingers. The scalp-recorded EEG data have been mathematically deblurred and projected down to the external surface of the subject's brain, which was reconstructed from his MRI. It is clear that localized areas of the left and right cerebral cortex have been activated, corresponding to the stimulation of the fingers on the right and left hands. The image on the left shows a conventional, 18-channel topographic EEG map (viewed from above the head, with the nose at the top) evoked by the same stimuli; there is an obvious lack of useful spatial information.

changing: an increasing number of laboratories have been recording EEGs (and MEGs), from more than 100 locations, post-processing data to increase spatial detail, and in some cases registering these data with other images of brain structure and function.

2. ENHANCING THE SPATIAL RESOLUTION OF THE EEG

Better spatial sampling is the first requirement for extracting more detailed information about higher brain function from scalp-recorded EEGs. The 19-channel '10/20' montage of electrode placement (Jasper 1958) commonly used in clinical and research EEG recordings has an inter-electrode distance of *ca.* 6 cm on a typical adult head. This spacing might be dense enough for detecting signs of gross pathology or of differentiating the gross topography of EP components, but it is insufficient for resolving the finer topographical differences that are important in studying higher brain functions. By increasing the number of electrodes to over 100, average inter-electrode distances of *ca.* 2.5 cm can be obtained on

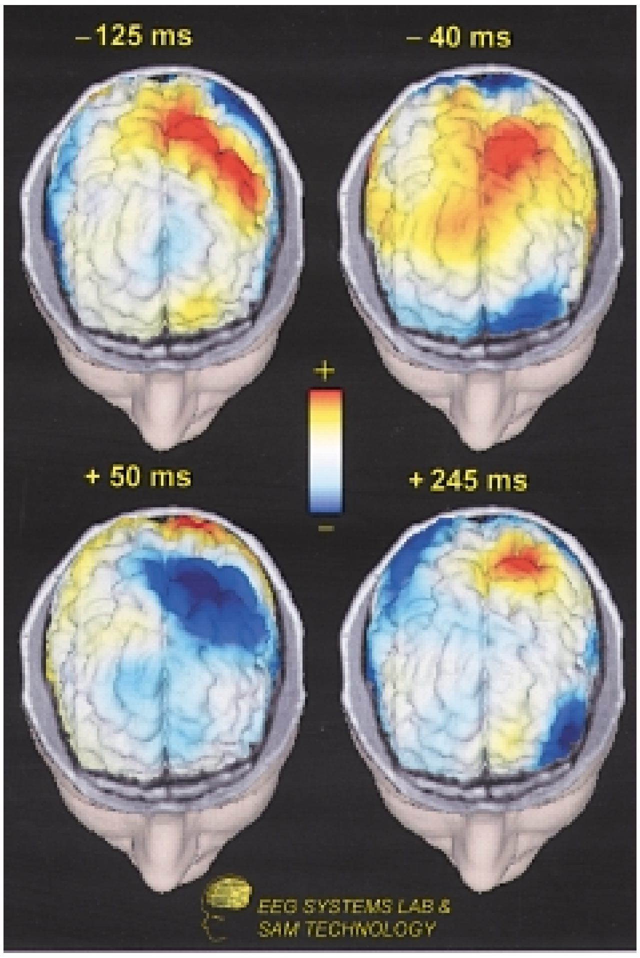

Figure 2. Deblurred movement-related potentials. EPs, time locked to the onset of a button press response made with the right middle finger, were recorded from a high-density (128 channel) electrode montage attached to the scalp. The

Figure 2. (*Cont.*) blurring effect of the scalp and skull were mathematically removed by using the deblurring method; the resulting spatially sharpened data were projected on to the cortical surface, which was constructed from the subject's MRI. Activity at two instants before the button press (top) and two instants after the button press (bottom) are plotted. Activation both before and after the response is strongly lateralized to the left hemisphere (the hemisphere contralateral to the hand used to make the response). This figure shows lateralized activation of the precentral gyrus before and immediately after a button press response is made; *ca.* 250 ms after the response, the focus of activation moves to the postcentral gyrus.

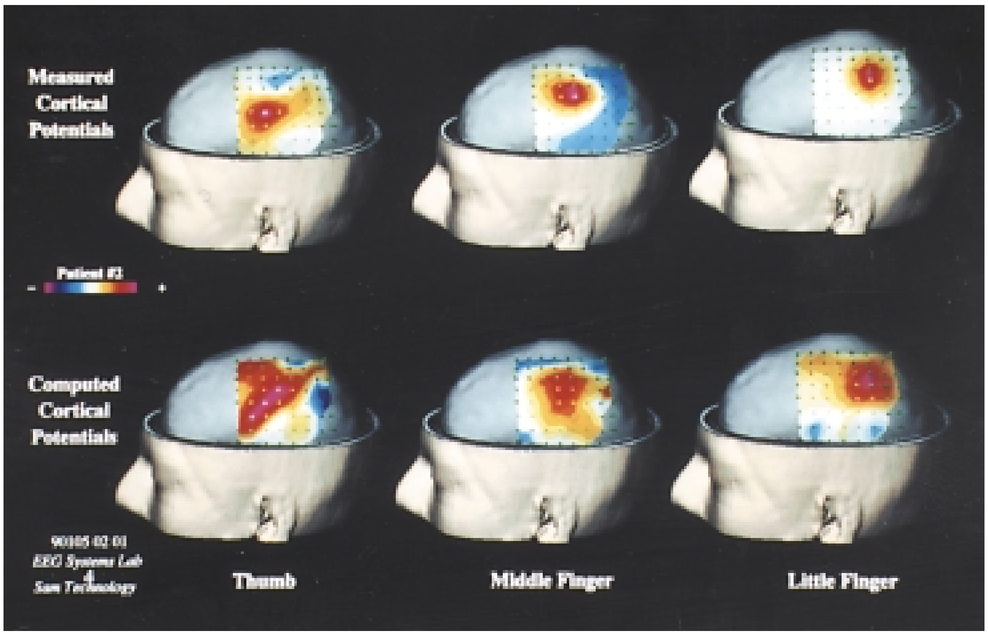

Figure 3. Validation of the EEG deblurring method by comparison with data recorded directly from the cortical surface. A 64-channel grid was implanted in this epilepsy patient as part of clinical care; the thumb, middle finger and little finger of the right hand were stimulated separately. Average evoked cortical potentials recorded with the intracerebral grid are shown at the top; the computed cortical potentials produced by the deblurring method are at the bottom. The main maxima and minima are similarly located. Improvements to deblurring are being made to reduce the noise amplification evident at the edge of the recording array.

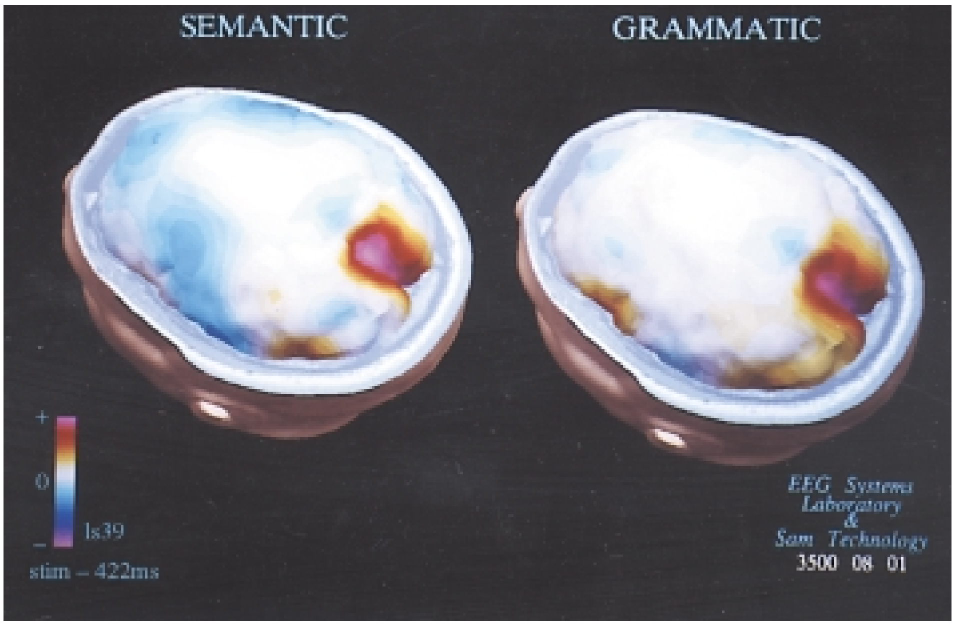

Figure 4. Deblurred EPs during reading. The processing of syntactic (grammatical) words differs from the processing of content (semantic) words. The image on the right shows the result of deblurring an EP that reached peak amplitude *ca*. 445 ms after the presentation of pronouns that were the subject of a short sentence. It had a focus of activity over the left lateral frontal operculum, and a duration of *ca*. 200 ms. The image on the left illustrates the deblurred EP elicited by presentation of content words at the same point in time. Both classes of words show common activation over the left parietal region and over the calcarine cortex during this interval. Unlike PET or fMRI, with EEG it is usually unnecessary either to combine data from several subjects or to subtract an experimental condition from a presumed control so as to measure the neuronal patterns of mental processes.

an average adult head. This is within the range of the typical cortex-to-scalp point spread function (i.e. the size of the scalp representation of a small, discrete cortical source) (Gevins *et al*. 1990).

For electrical (but not magnetic) recordings, the usefulness of such increased spatial sampling remains limited by the distortion of neuronal potentials as they are passively conducted through the highly resistive skull (Gevins *et al*. 1991; Van den Broek *et al*. 1998). This distortion amounts to a spatial low-pass filtering, which causes a blurring of the potential distribution at the scalp. In recent years a number of spatial enhancement methods have been developed for reducing this distortion.

The simplest and most widely accessible of these methods is the spatial laplacian operator, usually referred to as the laplacian derivation (LD). It is computed as the second derivative in space of the potential field at each electrode. The LD is thought to be proportional to the current entering and exiting from the scalp at each electrode site (Nunez 1981; Nunez & Pilgreen 1991), and is independent of the location of the reference electrode used for recording. It is relatively insensitive to signals that are common to the local group of electrodes used in the computation, and is thus more sensitive to high spatial frequency local cortical potentials. A simple method of computing the LD assumes that electrodes are equidistant and at right angles to each other, an approximation that is only reasonable at a few scalp locations such as the vertex. A more accurate approach is based on measuring the actual 3D position of the electrodes and using 3D spline functions to compute the LD over the actual shape of a subject's head (Le *et al*. 1994). The main shortcoming of the LD is that it unrealistically assumes that the skull has the same thickness and conductivity everywhere, which limits the improvement in spatial detail that the method can achieve.

This shortcoming of the LD can be ameliorated by using a realistic model of each subject's head to correct the EEG potential field locally for distortion resulting from conduction to the scalp. One such method is called finite element deblurring. It provides a computational estimate of the electrical potential field near the cortical surface by using a realistic mathematical model of volume conduction through the skull and scalp to project scalp-recorded signals downwards (Gevins *et al*. 1991, 1994*b*; Le & Gevins 1993). Each subject's magnetic resonance image (MRI) is used to construct a realistic model of his or her head in the form of many small tetrahedral elements representing the tissues of scalp, skull and brain. By assigning each tissue a conductivity value, it is possible to calculate the potential at all finite element vertices by using Poisson's equation. Given that the actual conductivity value of each of these finite elements is unknown, a constant value is used for the ratio of scalp to skull conductivity; the conductivity of each finite element is set by multiplying this constant by the local tissue thickness as determined from the MRI. Thus, even though true local conductivity is unknown, the procedure is well-behaved with respect to this source of uncertainty, because it accounts successfully for relative conductivity variation due to regional differences in scalp and skull thicknesses.

In initial applications, the deblurring method has been shown to be reliable and more accurate than the LD (Gevins *et al*. 1991, 1994*b*). This improvement occurs at the expense of obtaining and processing each subject's structural MRI. Although deblurring can substantially improve the spatial detail provided by scalp recorded EEGs, it does not provide conclusive information about the location of generating sources. Nevertheless, the improved spatial detail facilitates the formation of more specific hypotheses about the distribution of active cortical areas during perceptual, cognitive and motor tasks.

The issue of blurring of brain signals by the skull can be largely avoided by recording the magnetic rather than the electrical fields of the brain, because the skull has no effect on magnetic field topography. However, this transparency does not eliminate the need for using a high density of sensors to make an accurate map of the spatial topography of brain magnetic fields. Furthermore, the problems of locating generator sources are as severe for MEG as they are for EEG (see below). Further, the cost of MEG technology is at least an order of magnitude greater than that required for EEG studies, and the associated infrastructure required to perform MEG studies is more complex and inflexible. Thus, for most laboratories, and for some applications (particularly those in which a subject's head cannot be immobilized, such as long-term monitoring or ambulatory recordings), MEG does not provide a viable alternative to EEG recordings.

3. VERIFICATION AND APPLICATION OF HIGH-RESOLUTION EEG IN EXPERIMENTAL STUDIES

Exploratory studies of deblurring and other high-resolution EEG techniques focused on the spatial enhancement of sensory EPs, in which a great deal of *a priori* knowledge exists concerning their underlying neural generators (Gevins *et al*. 1994*b*). For example, figure 1 contrasts the spatial detail obtained for the somatosensory stimulation of fingers on each hand by using conventional 18-electrode EEG mapping methods with that obtained using 124 electrodes and deblurring. The deblurred somatosensory responses clearly isolate activity to the region of the central sulcus in each hemisphere. Similar localization has been obtained with movement-related potentials. Figure 2 illustrates the results of deblurring potentials locked in time to a button-press response made with the right hand. The major foci of activity occur in the contralateral (left hemisphere) in the somatomotor region of the pre-central and post-central gyri. Demonstrations such as these serve to verify the reasonableness of the approach, but a better validation is obtained by a comparison of the deblurred potentials with subdural grid recordings in epileptic patients undergoing evaluation for ablative surgery. So far these validation studies have produced a reasonable degree of agreement between the deblurred potentials and those measured directly at the cortical surface (figure 3).

Recent developments suggest that high-resolution EEG methods are useful tools in the experimental analysis of higher-order brain functions. For example, spatial enhancement of EEGs related to component processes in reading has yielded results that are highly consistent with current knowledge of the functional neuroanatomy thought to be involved with visual pattern recognition and language functions (Gevins *et al*. 1995*a*). In one study, EPs were elicited during a simple cued matching task requiring one of four types of matching judgement: graphic (visual identity of unfamiliar non-letter character strings), phonemic (homophonic pseudo-words), semantic (antonymy) and grammatical (noun–verb agreement). Each trial of the task began with a cue that indicated which of the four conditions to expect. After 1 s this cue was followed by the first stimulus, which in turn was followed 1 s later with the comparison stimulus. Several striking between-condition differences were evident in highly localized EP patterns. For example, larger amplitude EP waves occurred in the grammatical condition (relative to the other language tasks) at 445 ms after the first stimulus; the duration of the wave was only *ca*. 200 ms. These potentials were largest at scalp locations near the presumed region of Broca's language area in the frontal cortex of the left hemisphere (figure 4), and their task correlates are consistent with the postulated functional neuroanatomy of this region. Thus, the functional localization of cognitive processes inferred from spatially enhanced and anatomically registered electrophysiological measurements can be compared with the results of lesion studies and other neuroimaging approaches. As a complement to these approaches, the fine-grained temporal resolution of EP measurements, in combination with improved topographic detail, adds valuable insights gained by characterizing both the regionalization of functions and the sub-second dynamics of their engagement.

Modern EEG methods have also been used to study sub-second and multi-second distributed neural processes associated with working memory, the cognitive function of creating a temporary internal representation of information during focused thought (Gevins *et al*. 1996; McEvoy *et al*. 1998). In task conditions that placed a high load on working memory functions, subjects were asked to decide whether the stimulus on each trial matched either the verbal identity or the spatial location of a stimulus occurring three trials previously (*ca*. 13.5 s ago). This required subjects to concentrate on maintaining a sequence of three letter names or three spatial locations concurrently; they had to update that sequence on each trial by remembering the most recent stimulus and could drop the stimulus from four trials back. In two corresponding control conditions, only the verbal identity or spatial location of the first stimulus had to be remembered. Both spatial and verbal working memory tasks produced highly localized momentary modulation of EPs over prefrontal cortical areas relative to control conditions, with deblurred voltage maxima approximately over Brodmann's areas 9, 45 and 46 (figure 5). These brief (*ca*. 50 ms and 200 ms) events occurred in parallel with a sustained EP wave and were maximal over the superior parietal lobe and the supramarginal gyrus, with a slight right-hemisphere predominance. It began *ca*. 200 ms after stimulus onset, returned to near the baseline by *ca*. 600 ms after stimulus in control conditions, and was sustained up to *ca*. 1 s or longer in the working memory conditions. The sub-second EP effects occurred in conjunction with multi-second changes in the ongoing EEG, of which the theta-band power focused over the midline frontal cortex is shown in figure 5 (Gevins *et al*. 1997; Smith *et al*. 1999). These EEG findings might provide the first direct evidence in a single experiment to support the idea that the various types of attention are associated with neural processes with distinct time-courses in distinct neuronal populations. The increased theta-band power might be a marker of the continuous focused attention required to perform the task, and might reflect the engagement of the anterior cingulate gyrus, a conjecture supported by dipole modelling (Gevins *et al*. 1997). In contrast, the momentary attention required for scanning and updating the representations of working memory might be reflected in increased EP peaks over lateralized regions of dorsolateral prefrontal cortex, whereas the maintenance of a representation of the stimuli being remembered might be reflected in the parietally maximal EP wave and other concomitant changes in the EEG (Gevins *et al*. 1996, 1997).

4. IDENTIFYING THE SOURCES OF EEG PHENOMENA

Neither the LD, nor more-advanced EEG spatial enhancement algorithms such as deblurring, nor MEG recordings, provide any conclusive 3D information about where the source of a scalp-recorded signal lies in the brain. In some cases, such as when healthy subjects perform difficult cognitive tasks and strong signals are recorded over areas of association cortex (i.e. dorsolateral prefrontal, superior and inferior parietal, inferotemporal and lateral temporal), the hypothesis that EEG potentials are generated in these areas is the most plausible. However, counter-examples can always be presented. In addition to a visual examination of the potential field distribution, another procedure for generating hypotheses about the neuroanatomical loci responsible for generating neuroelectric events measured at the scalp is called dipole modelling (Fender 1987; Scherg & Von Cramon 1985). Dipole modelling uses iterative numerical methods to fit a mathematical representation of a focal, dipolar current source, or collection of such sources, to an observed scalp-recorded EEG or MEG field.

Source modelling does not, in general, provide a unique and physically correct answer about where in the brain activity recorded at the scalp is generated, because solving for the source of an EEG or MEG distribution recorded at the scalp is a mathematically ill-conditioned 'inverse problem' that has no unique solution; additional information and/or assumptions are required to permit choice between candidate source models. Although some of this *a priori* information is obvious and harmless (i.e. that the potentials must arise from the space occupied by the brain), other assumptions border on presupposing unknown information (i.e. that the potentials arise only from the cortex, or that the number of active cortical areas is known).

One simple, convenient, and potentially clinically useful approach for potentials elicited by simple sensory stimulation is to assume that the scalp potential pattern arises from a single point dipole source, as shown in figure 6. Although not anatomically or physiologically realistic, such simple models can sometimes be useful for locating the centre of mass of primary sensory cortex and hence major functional landmarks such as the central sulcus. When justified by simple voltage topography (figure 7), models of this sort can also be useful for generating initial hypotheses about the possible sources underlying other phenomena.

Most complex scalp-recorded electrophysiological phenomena are poorly approximated by a single dipole source model, and obtaining estimates of the strength and 3D locations of the underlying neuronal generators when there are multiple, time-overlapped active sources has widely recognized practical and theoretical difficulties (Miltner *et al*. 1994; Mosher *et al*. 1992). Intense effort is being allocated to the development of improved methods for source analysis for electrical phenomenon that are likely to arise from multiple and/or distributed sources (Gorodnitsky *et al*. 1995; Grave de Peralta-Menendez & Gonzalez-Andino 1998; Koles 1998; Mosher *et al*. 1992; Tesche *et al*. 1995; Wang *et al*. 1993). Even so, regardless of which method is used to formulate them, such source generator hypotheses must ultimately be verified

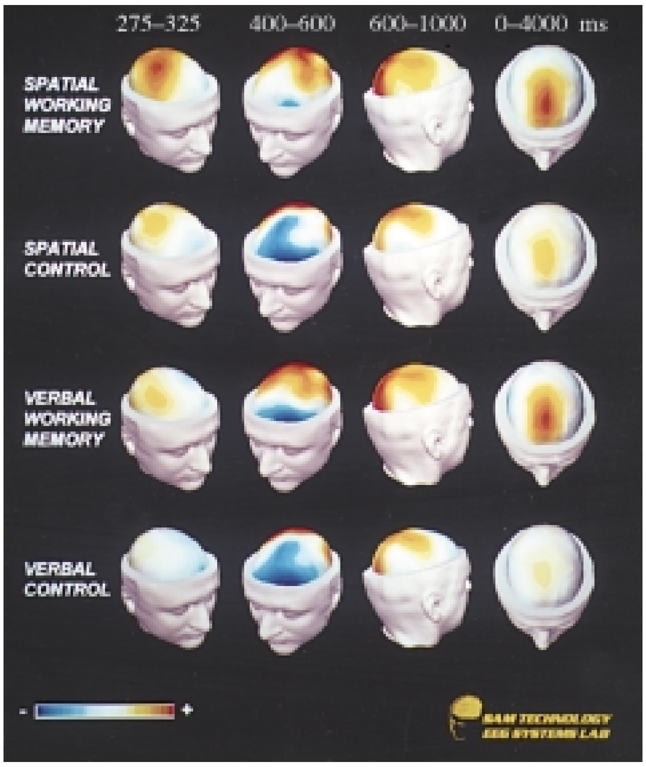

Figure 5. Deblurred EPs and ongoing EEG related to sustained focused attention. High-resolution EEG methods have made it possible to measure both sub-second phasic and multi-second tonic regional brain activity simultaneously during the performance of cognitive tasks. In this experiment a sequence of increased sub-second EP peaks and waves was observed over frontal (first and second columns) and parietal (third column) cortices during a difficult working memory task, in comparison with control conditions with lower working memory requirements. These sub-second changes in the working memory tasks were accompanied by longer-lasting (4 s) increases in ongoing EEG theta-band power (fourth column). These EEG findings suggest that various types of attention are associated with neural processes that have distinct time-courses in distinct neuronal populations. The amplitude scale is constant across experimental conditions within each column; the EP scale is voltage, the EEG scale is *z*-scored spectral power.

independently. In rare cases this might be done in patient populations in the context of invasive recordings performed for clinical diagnostic purposes. More commonly, another type of imaging modality, such as PET or fMRI, has to be employed. Indeed, one promising approach to this issue is to use information about the cortical regions activated by a task as mapped by 3D functional neuroimaging methods such as fMRI or PET to constrain source models, and to derive information about the spatio-temporal dynamics of those sources from EP measurements (George *et al*. 1995; Heinze *et al*. 1994; Mangun *et al*. 1998; Sereno 1998; Simpson *et al*. 1995).

5. DISTRIBUTED FUNCTIONAL NETWORKS OF SIMPLE COGNITIVE TASKS

Independently of whether definitive knowledge of source configurations exists, changes in the spatial distribution of EEG phenomena can be used to characterize the neural dynamics of thought processes. Even the simplest cognitive tasks require the functional coordination of a large number of widely distributed specialized brain systems. A simple response to a sensory stimulus involves the coordination of sensory, association and other areas that prepare for, register and analyse the stimulus, the motor systems that prepare for and execute the response, and other distributed neuronal networks. These distributed networks serve to allocate and direct attentional resources to the stimulus, to relate the stimulus to internal representations of self and environment to decide what action to take, to initiate or inhibit the behavioural response, and to update internal representations after receiving feedback about the result of the action. In the ongoing EEG, hypotheses about functional interactions between cortical regions are sometimes drawn from measurements of statistical interrelationships between time-series recorded at different sites. These can be quantified by various measures of spectral, wave shape or information-theory similarity, including spectral coherence (Walter 1963), correlation (Brazier & Casby 1952; Gevins *et al*. 1981, 1983; Livanov 1977), covariance (Gevins *et al*. 1987, 1989*a*,*b*), information measures (Callaway & Harris 1974; Mars & Lopes da Silva 1987), nonlinear regression (Lopes da Silva *et al*. 1989) and multichannel time-varying autoregressive modelling (Gersch 1987).

Some of the above methods can be used to characterize the spatio-temporal relationships between sub-second EP components. Because the EP waveform delineates the time-course of event-related mass neural activity of a neuronal population, the coordination of two or more populations during task performance should be signalled by a consistent relationship between the morphology of the EP waveforms emitted by these populations, with consistent time-delay (Gevins & Bressler 1988). If the relationships are linear, as they often seem to be, this coordinated activity might be measured by the lagged correlation or covariance between the EPs, or segments of EPs, from different regions (Gevins *et al*. 1987, 1989*a*,*b*). One such measure of this type of process is referred to as an EP covariance (EPC). (Of course, a significant covariance of this type is only a measure of statistical association and does not map the actual neuronal pathways of interaction between functionally related populations.) Studies of the neurogenesis of EPCs are still in their infancy (Bressler *et al*. 1993; Gevins *et al*. 1994*a*), and any interpretations of EPCs in terms of the underlying neural processes that generate them must therefore be made very cautiously. (It is noted, however, that EPC results have so far been highly consistent with the known large-scale functional neuroanatomy of frontal, parietal and temporal association cortices.) Meanwhile, EPCs have provided fascinating glimpses of the complex, rapidly shifting, distributed neuronal processes that underlie simple cognitive tasks.

The EPC technique has yielded its most interesting results as a tool for studying preparatory attentional networks, the changes in brain activity associated with readiness for an impending event or action. For example, subjects in one experiment (Gevins *et al*. 1987, 1989*a*,*b*) performed a task that required graded finger-pressure responses with either the right hand or the left hand

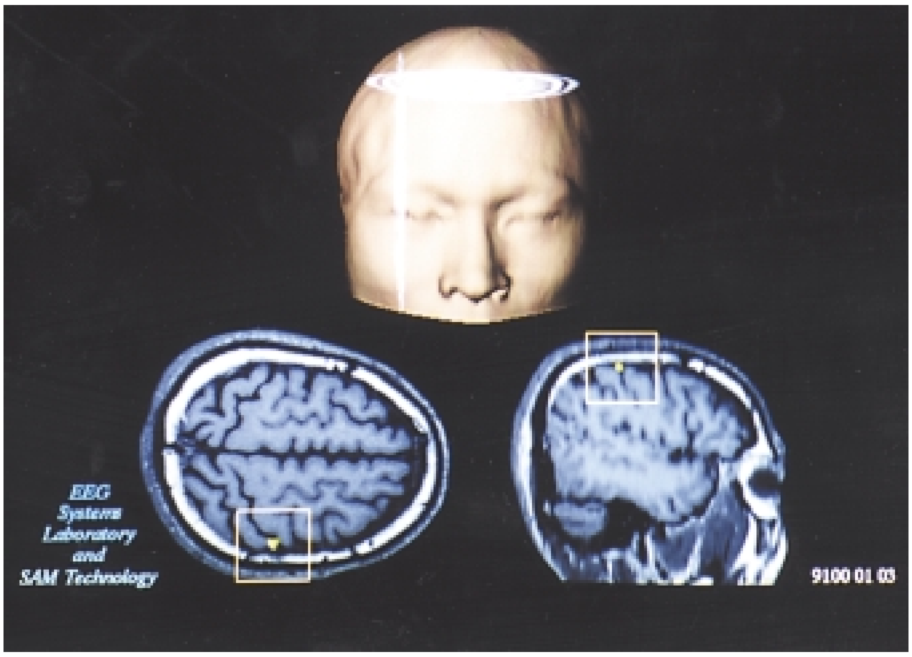

Figure 6. Localization of an EEG dipole model in the somatosensory cortex of the right hemisphere from scalp-recorded data evoked in response to transient electrical stimulation of the left index finger. This popular type of source generator localization modelling produces anatomically plausible results in the case of simple sensory stimulation.

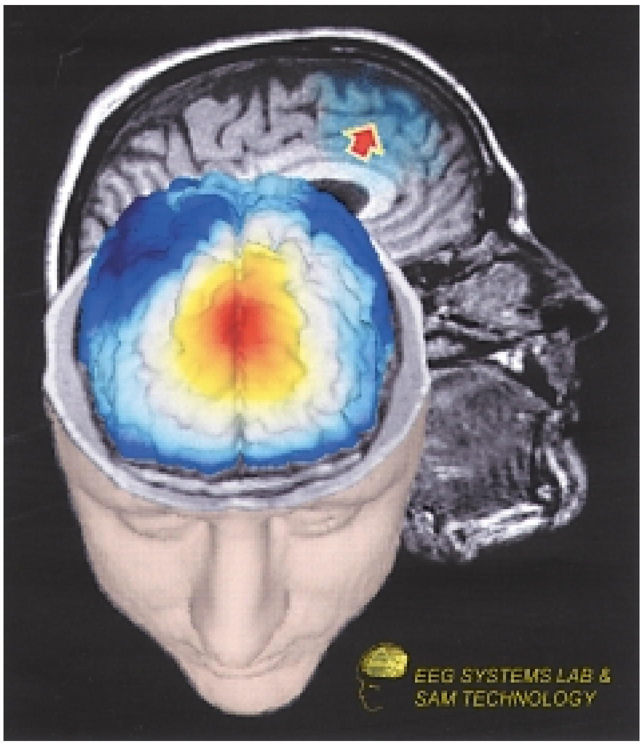

Figure 7. Deblurred frontal midline theta EEG activity and localization of the corresponding source model in the region of the anterior cingulate cortex. Topographic data correspond to the difficult working memory task condition depicted in figure 5 (Gevins *et al*. 1997). The data were processed with the deblurring method, and the spatially sharpened results were projected on to the cortical surface, which was constructed from the subject's MRI. The upwards-orientated arrow superimposed on the midline sagittal image depicts the localization of a point dipole source model for these data.

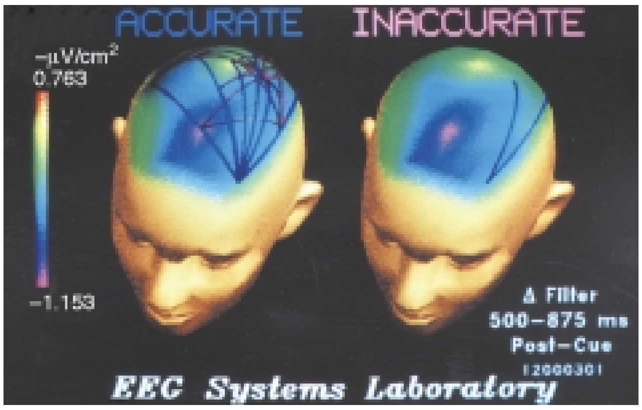

Figure 8. Preparatory EPC patterns preceding accurate and inaccurate responses. EPCs involving left frontal, midline precentral and left central and parietal electrode sites are prominent in patterns preceding accurate responses (by 0.5–1 s) (left). The number and magnitude of EPCs that precede inaccurate responses are smaller (right).

proportional to visual numeric stimuli from one to nine. The hand to be used was cued 1 s before the stimulus. A 375 ms EPC analysis window spanned the interval preceding the stimulus number so as to measure how EP patterns differed according to the hand that subjects expected to use. Figure 8 shows right-hand preparatory EPCs for seven subjects for those trials for which the response (*ca*. 0.5–1 s later) was subsequently either accurate or inaccurate. The set of subsequently accurate trials are characterized by covariances of the left prefrontal electrode with electrodes overlying the same motor, somatosensory and parietal areas that were involved in actual response execution. (Simultaneous measurement of flexor digitori muscle activity showed that the finger that would subsequently respond was not active during the preparatory interval.) The preparatory patterns preceding inaccurate responses differed markedly from those preceding accurate responses, with fewer EPCs between the left frontal site and other electrodes. Such results suggest that one important role of frontal lobe integrative mechanisms is the anticipatory scheduling and coordination of the activation of those specialized brain regions that will participate in a future cognitive event.

With respect to measuring spatial interrelationships between measurements of the ongoing human EEG, there is currently a renewed interest in coherent brain activity in the 40 Hz range or in a broader high-frequency 'gamma' band (*ca.* 35–100 Hz). This interest derives largely from studies of neuronal activity in animal preparations that suggest that 40 Hz or gamma-band oscillations might represent the action of an integrative mechanism for binding the distributed neural populations activated by a sensory experience into an integrated percept (Freeman 1975; Freeman & Skarda 1985; Gray *et al*. 1989). It has been suggested that such coherent activity is measurable over distributed regions of the human scalp with EEG (Sheer 1989) or MEG (Llinás & Ribary 1993). However, in studies of brain electrical activity recorded directly from the cortical surface in human neurosurgical patients while they performed somatosensory discrimination tasks, no spatial modulation of gamma-band activity was found to be related to stimulus type in a simple somatosensory discrimination task (Menon *et al*. 1995), although such evidence was abundant in the lower-frequency EPs (Gevins *et al*. 1994*a*; Menon *et al*. 1995).

6. CONCLUSIONS

The neurophysiology of mentation involves the rapid coordination of processes in widely distributed cortical and subcortical areas. The electrical signals that accompany higher cognitive functions are subtle, spatially complex, and change both in a tonic multi-second fashion and phasically in sub-second intervals in response to environmental demands and internal representations of environment and self. No one brain-imaging technology is currently capable of providing both near-millimetre precision in localizing regions of activated tissue and sub-second temporal precision for characterizing changes in patterns of activation over time. However, by combining several technologies it seems possible to achieve this degree of fine spatio-temporal resolution. Modern high-resolution EEG is especially well-suited for monitoring rapidly changing regional patterns of neuronal activation accompanying purposive behaviours, whereas fMRI seems ideal for precisely determining their 3D localization and distribution. It is a topic of current research to determine how to combine EEG and fMRI data from the same subjects doing the same tasks.

Finally, an obvious but often unconsidered feature of EEG technology is worth mentioning: its extreme compactness and simplicity. This fact has important practical considerations that are frequently not considered in scientific discussions of brain-mapping technology. For example, EEG has the potential to serve as a sensitive, low-cost, portable monitor for clinical assessment and other applications (Gevins *et al*. 1998; A. Gevins and M. E. Smith, unpublished data). The compactness of EEG technology also means that, unlike all other functional neuroimaging modalities (which require massive machinery, large teams of technicians and complete immobilization of the subject), EEGs can be collected from an ambulatory subject who is literally wearing the entire recording apparatus. This feature of EEGs will facilitate research into the still uncharted territory of how brains think when performing everyday activities in the real world (Gevins *et al*. 1995*b*).

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