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Modulation of Spontaneous Brain Activity During Mental Imagery

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ABSTRACT

Magnetic measurements of average power of human alpha activity over the occipital and parietal areas of the scalp reveal spatially selective suppression when abstract figures are briefly presented visually. The duration of suppression increases along with reaction time during a search of visual memory. This implies that the visual system is involved in mental imagery.



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It has long been suspected that blockage of alpha rhythms in the electroencephalogram (EEG) (8-13 Hz) is related to cognition because it occurs during visual attention and accompanies mental imaging (1). Blockage is often described as "desynchronization", which presumes that alpha arises from simultaneously active "generators" that become desynchronized during arousal, causing partial self-cancellation of their fields. This desynchronization is attributed to both non-specific arousal and to sensory-specific thalamic inputs (2). Alpha rhythms are ascribed to oscillating circuits within the cortex as well as to thalamocortical interactions (3). Hence, blockage can result from events at several different levels. Recent magnetoencephalography (MEG) studies suggest that alpha arises from many different sources in occipital and parietal areas (4). Microelectrode studies also suggest that alpha originates in small areas of visual cortex and spreads over relatively short distances (5), and is inconsistent with the notion of its coherence over large cortical regions. These results raise serious questions about the usefulness of the notion of "desynchronization" and suggest that blockage may occur on a local basis.

The distribution and magnitude of alpha suppression depends on the modality stimulated (6). While attention and arousal are still considered as important contributors, the role of other cognitive processes remains to be determined (7).

The accuracy provided by MEG for localizing neuronal activity in sensory cortex (8) may resolve some issues of significance to cognitive psychology. In particular, the conjecture that the machinery of the visual system normally employed in perceiving real objects is also involved in manipulating mental images (9) may now be amenable to a direct test. Alternatively, the visual system may not be involved in mental imagery, and the performance of such tasks could depend, *inter alia*, on the use of propositional knowledge about the objects whose "mental images" are putatively being compared (10). We report that alpha activity is locally suppressed during a task involving matching of mental images, indicating that visual cortex is involved.

We use the term "suppression" rather than "blockage" because we deal simply with a reduction in power of the MEG within the classic band of alpha activity, and not necessarily with the

reduced probability of spindling normally associated with so-called blockage. The method described here is based on one introduced by Kaufman et al. (11) who found that changes in power of several different bands of the EEG accompany visual stimulation, even when the components of the EEG that are time-locked to the stimulus are removed prior to squaring and averaging. The resulting smoothed envelope of EEG power over time remains in step with the visual stimulus, even though the individual oscillations are not time-locked to the stimulus.

This study combined elements of both the Sternberg (12) and Shepard (9) paradigms. A sequence of random polygon shapes was presented for the subject to remember and compare with a subsequently presented "probe" shape. The polygons were presented as white lines against a dark background. The angular subtense of the longest segment of each of these forms did not exceed 3.5 deg. Three forms were presented sequentially below and to the right of fixation (about 0.5 deg obliquely downward from the center of a fixation cross) for one second each and separated by 0.3 sec. One second after the last of the polygons, the color of the fixation cross changed from white to red, warning the subject to maintain fixation. Two seconds later the "probe" was presented in the same place for only 100 msec.

Subjects followed one of two different sets of instructions. One instruction (the Simple Reaction Time, SRT) required pressing a button as soon as possible after seeing the probe, whether or not the probe had been a member of the memory set. The second instruction (the Choice Reaction Time, CRT) required pressing a button if the probe matched one of the members of the original "memory set" or a different button if it did not match. After a response deadline of 4 sec, a tone of either high or low pitch indicated whether the probe matched or did not match. Three seconds later the entire process was repeated, using a set of forms drawn at random from a total population of 12 such forms.

A 5-channel SQUID-based Neuromagnetometer (13) detected the magnetic field at many places normal to the posterior portion of the head covering occipital and parietal areas. The time course of the average alpha power was determined by bandpassing the MEG from 8-12 Hz and

computing the variance around the average response in that band. This variance about the mean response in the **alpha** band is equivalent to the power (mean square field). Fluctuations in power over the duration of the averaging epoch cannot be attributed to changes in coherence of the activity, but are due exclusively to changes in its amplitude, even though this activity is not time-locked to the stimulus (14).

Three male subjects were studied in detail, with ages of 37, 41 and 61 (a left-hander). The time-course of average spontaneous alpha power throughout the epoch was also studied for 6 other subjects, both male and female. These additional results were essentially the same as those described here, except that the field patterns were not so carefully mapped.

Alpha power for CRT and SRT trials (Fig. 1) is sharply suppressed after presentation of each probe and quickly recovers for the SRT trials. However, suppression is prolonged following the probe for the CRT trials. Similarly, choice RTs for the probes were significantly longer than simple RTs. Average simple and choice RTs obtained during the trials are shown as arrows superimposed on the alpha power plots. Similar results were obtained with all nine subjects, although the level of alpha power and the degree of its suppression varied among individuals and with location across the scalp. In the SRT trials the average RT nearly coincides with the time at which alpha power reaches its minimum. However, the choice RTs tended to occur well into the recovery phase of the alpha power, indicating that subjects were comparing the previously seen probe stimulus to the memory set throughout the period of suppression in alpha power.

A conventional averaged visually evoked field (VEF) is also shown in Fig. 1. It represents an average of responses at several different positions over the scalp, as more than 30 trials were needed to obtain a relatively noise-free version of the evoked response. The duration of the VEF is much shorter than either the variation in power or the RT. There is a consistent difference in amplitudes of VEFs obtained under CRT and SRT conditions, with the former having a larger amplitude and somewhat longer duration (~100 msec) than the latter. The difference in duration is far smaller than the difference in RT. This is similar to Farah's results (15), where the

amplitude of the 173 msec component of the average evoked potential (VEP) was larger when an image of a stimulus was formed prior to its presentation, and smaller when no image was formed. Her effect is widely distributed over parietal and occipital electrodes but the limited number of electrodes make it impossible to determine the degree to which the evoked response of interest arises from a particular region of the brain.

To test for the existence of local suppression of brain activity in the alpha band while processing a mental *image*, the magnitude of average alpha power within a 2 sec interval 200 msec prior to presentation of the probe was plotted as a function of position over the posterior scalp, as projected onto a plane (Fig. 2a). The magnitude of this *baseline alpha* differs among subjects (Fig. 2b). Subject LK exhibits very strong alpha over his left hemisphere, and significantly weaker activity over the right hemisphere. Subject BS has somewhat higher levels over the right hemisphere, and subject CS has even less than that exhibited by BS. Such individual differences in the strength and distribution of alpha cannot be attributed to differences in skull thickness (16) as the thickness of the skull has a negligible effect on magnetic fields. Differences and asymmetries in underlying brain anatomy and functional neural states must be the main causes of the observed differences.

Despite these individual differences, the two regions of greatest baseline alpha on either side of the midline for LK and BS (Fig. 2c) overlap the positions of field extrema associated with the VEF. As the center of a line connecting these field extrema determines the position of an underlying equivalent current dipole source, neuronal activity lies near the longitudinal fissure with the current predominantly parallel to the fissure. However, because of the asymmetry in the pattern, it is likely that several different sources of varying orientation contribute to the observed field. The distribution of baseline alpha obtained from subject CS is far more complicated than for the other two subjects, suggesting contributions from a complex array of sources in the longitudinal and calcarine fissures.

During the period of suppression (Fig. 2d), the *residual alpha* clearly exhibits an approximately dipolar pattern for subjects LK and BS. During maximum suppression the locations of the extrema of LK are about 6 cm above the inion and 3 or 4 cm to either side of the midline, which places the source of the residual neuronal alpha activity in visual cortex near the longitudinal fissure. The peak alpha activity over BS's right hemisphere is about 5 cm above inion and 5 cm to the right of the midline. There are several peaks over the left hemisphere about 4 cm to the left of the midline and as high as 7 cm above the inion. The depth of equivalent current dipole source that accounts for most of LK's pattern is approximately 2.5 cm beneath the scalp. A large shallow sheet of dipolar sources at this depth would be associated with a much wider separation between the field extrema. The relatively shallow depth is consistent with activity of a confined region of visual cortex. Assuming a separation of about 9 cm between the extrema for subject BS, the depth of the source would be about 3 cm. Fig. 2d shows the distribution of the ratio of residual to baseline alpha power. This *relative alpha suppression* is most pronounced about the midline about 6 cm above the inion for subjects LK and BS. Therefore, the greatest relative suppression for both subjects is located approximately over the visual cortex. The distribution of the change is not so clear for subject CS, perhaps because the overall level of baseline alpha was extremely low.

Plots similar to those of the baseline alpha (Fig. 2b) were constructed for alpha power averaged over the interval 2500 - 2700 msec after presentation of the probe. The spatial variation of this *recovered alpha* is highly correlated with the plots of baseline alpha. The coefficients of correlation are 0.98 for LK, 0.81 for BS, and 0.80 for CS, which are significant with $p < .001$. Thus, the initial and final distributions of alpha power in a trial are similar.

It is widely believed that blocked alpha is replaced by beta activity (16 - 24 Hz). This predicts a rise in the usually weaker beta power during alpha suppression. We did not detect any such increase in beta during suppression. In fact, there is a correlated decrease in power during alpha suppression. Also, the distribution of power across the scalp is not the same as that of the

alpha band, as only a small percentage of the variance in the beta distributions could be accounted for by the alpha distributions of Fig. 2b (29% for LK, 1% for BS, and 60% for CS, whose beta activity nearly equalled the level of his alpha activity). Partly independent neuronal populations must be responsible for spontaneous activity in these two bandwidths, although both populations exhibit suppression when subjects search visual memory.

These data support the notion that power within the alpha and beta bands is systematically reduced during the performance of a mental task involving the matching of memories of visual images. The source of this reduction appears to be in the visual cortex, a finding that is consistent with local cerebral blood flow studies (17). This effect depends upon the mental load presented by the task, as indicated by its correspondence with the RT. It cannot be attributed solely to visual attention, since visual attention is paid to the display throughout the entire time-course of both the SRT and CRT tasks. Yet alpha power grows after presentation of the memory set and once again after presentation of the probe while the subject awaits presentation of the next memory set. We conclude that areas of visual cortex are involved in this process of matching mental images.

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14. The subject was given 30 trials involving the SRT task, and then 30 trials involving the CRT task. This was repeated in sequence with the sensors moved to new locations until the field had been measured at 45 - 65 different positions over the posterior portion of the scalp. The voltage provided by each sensor is bandpassed (0.1 - 50 Hz) by analog filters and recorded in a computer. The average visually evoked field time-locked to the stimulus onset was determined for each 30 trial run, within a bandwidth of 1 to 20 Hz. A similar average evoked response was obtained within the bandwidth 8-12 Hz, and the variance about this average was computed for each 30 epoch trial and smoothed by a low-pass filter at 8 Hz to determine how the average spontaneous alpha power varied with time across the epoch. A similar procedure was carried out for signals in the bandwidth 16 - 24 Hz to provide average spontaneous beta power.
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FIGURE CAPTIONS

Fig. 1. Dashed trace (Simple RT) and solid trace (Choice RT) represent variances (power) about the average magnetic response within the 8-12 Hz band recorded at one place external to the scalp of subject LK. Field is expressed in femtotesla (fT). The mean RTs associated with each of these traces are indicated by arrows with error bars representing 1 SD. An average evoked field (1-20 Hz) is above the power plots.

Fig. 2. (a) Distribution of average alpha power across the posterior scalp is portrayed by an azimuthal equal distance projection, in which equal distances across the surface of a spherical representation of the head from the center of projection are mapped onto equal distances across a flat surface. The *x*-axis of this plane corresponds to a horizontal line normal to the midline, while the *y*-axis is the vertical parallel to the midline. (b) Distribution for three subjects of average *baseline alpha*, defined as the average alpha power observed within a 200 msec interval 100 msec prior to presentation of the visual probe in the CRT condition. (c) Distribution of alpha power averaged over a 100 msec interval centered on the moment of maximum suppression, illustrated in Fig. 1, defined as the *residual alpha*. The locations of the midlines are indicated by the short lines in these graphs. (d) Distribution of the ratio of residual to baseline alpha, which defines the *relative alpha suppression*.

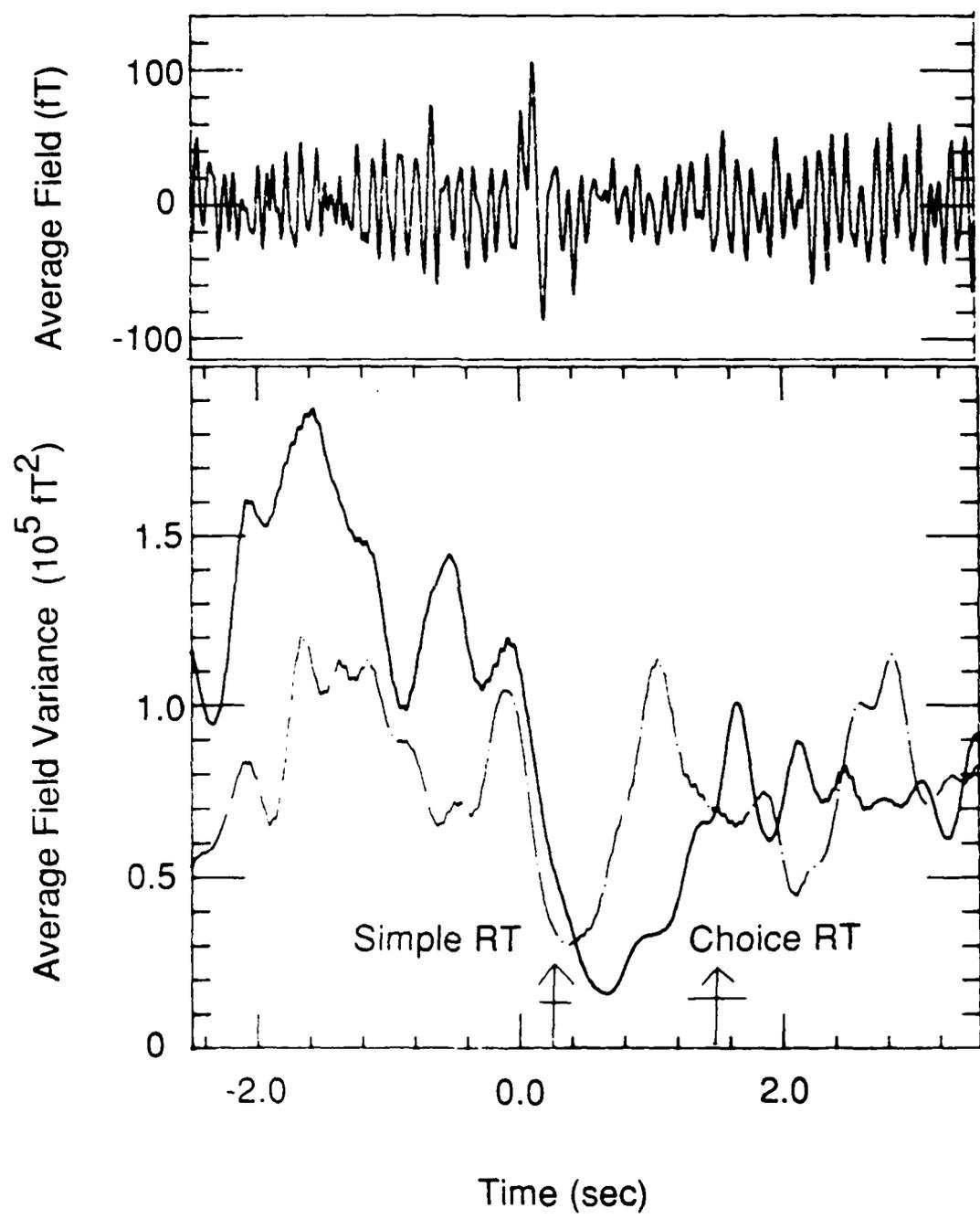


Figure 1

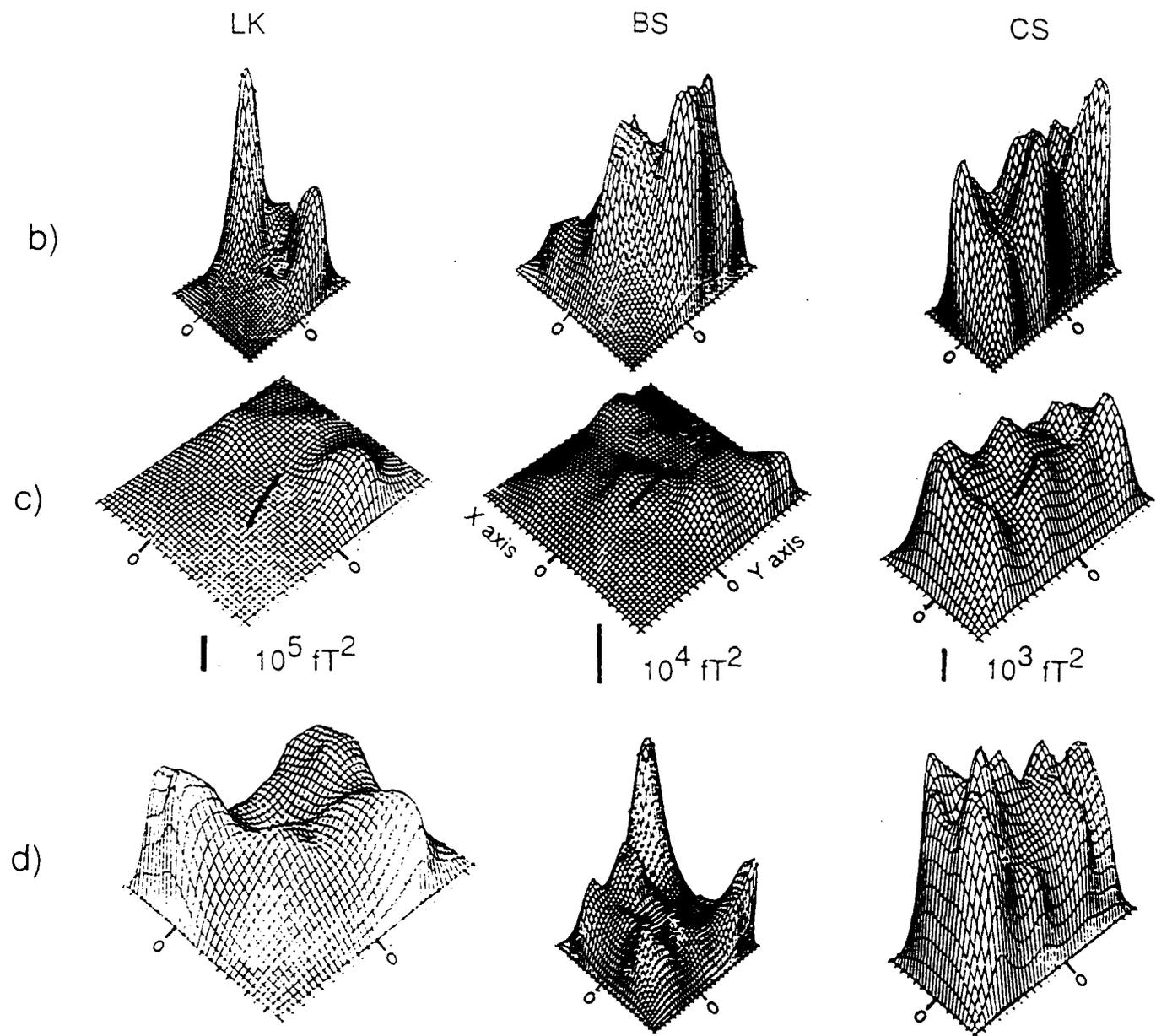
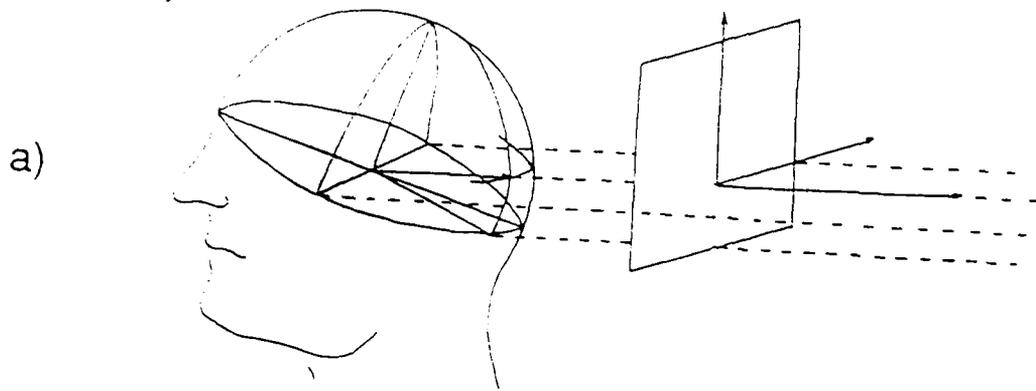


Figure 2