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C.M. Michel, L. Kaufman, and S.J. Williamson

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Magnetic and electric recordings of average power within the restricted alpha band (10-12 Hz) were made over the parietal and occipital areas of the human scalp while subjects were engaged in the mental imagery task of comparing an object with one previously seen but rotated and perhaps also mirror reflected. Alpha power was found to be suppressed while the subjects were engaged in the comparison, and the duration of suppression increased with the minimum rotation angle to achieve a match. This is additional evidence that visual cortex is engaged in the process of mental imagery. Moreover, for large rotation angles, where the task is markedly more difficult, a shift in the spatial pattern of suppression indicates that the left parietal area of the cortex becomes involved.

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ABSTRACT

Electric and magnetic recordings of average power within the high alpha band (10-12 Hz) were made over the parietal and occipital areas of the scalp while subjects were engaged in the mental imagery task of Cooper and Shepard. The subject had to determine whether an abstract probe figure was identical to a memory figure presented earlier at a different orientation, or whether it was the mirror image of the memory figure. Alpha power was found to be suppressed while the subjects were engaged in the comparison, and the duration of suppression increased with the minimum rotation angle to achieve a match. This is additional evidence that visual cortex is engaged in the process of mental imagery. Moreover, for large angles, where the task is markedly more difficult, a shift in the spatial pattern of suppression indicates that the left parietal area becomes involved.

INTRODUCTION

The question of whether the visual system is involved in mental imagery has long been debated (Golla et al., 1943; Shepard & Meltzer, 1971; Shepard & Cooper, 1982; Kosslyn, 1983; Farah, 1984; Anderson, 1985; Farah, 1988; Farah et al., 1988). Shepard and his colleagues (Shepard & Metzler, 1971; Cooper & Shepard, 1973; Finke & Shepard, 1986) concluded from extensive behavioral experiments based on mental rotation tasks that mental imagery involves the same neural circuits as those employed in processing real visual images. For instance, the interstimulus interval needed to produce optimum stroboscopic rotation of a form increases at the same rate with increasing increment of angle as does the time to mentally rotate the same form to achieve a match.

This correspondence suggests that the machinery of the visual system is involved in imagery tasks. However, alternative theories (e.g., Pylyshyn, 1981) argue that the same increase in time required for mental rotation with greater angles could be accounted for if more time is required to test hypotheses in working memory about abstract features of these same visual objects. One way toward resolving such issues is to establish directly whether the visual areas of the brain are actually active when subjects mentally rotate imagined objects. In this paper we test the hypothesis that the electrophysiological activity of visual areas of the brain is altered during mental rotation, and that behavioral indices of mental rotation time coincide with these changes in cortical activity.

There is some precedent for this. For example, Farah and her colleagues employed the event-related potential (ERP) to determine whether visual areas are differentially affected by the formation of mental images. Farah (1988) and Farah et al. (1988) recorded the ERPs to visual stimuli that were or were not preceded by an acoustic cue. They demonstrated that mentally imaging a stimulus before it was presented increased detection accuracy and enhanced the amplitude of the first negative ERP component (with 170 ms latency) over temporo-occipital recording sites. This effect on early modality-specific stages of information processing led Farah et al. (1988) to conclude that mental imagery is accompanied by changes in the visual system, and these are correlated with the content of the image.

While these results suggest that visual cortex becomes differentially active if a person forms mental images of objects about to be seen, similar enhancements of the same components of the ERP accompany selectively attending to objects in visual space (Mangun & Hillyard, 1988). Recently, Peronnet and Farah (1989) recorded enhancement in the amplitudes of broad, late components (400-1700 ms) of the ERP during a mental rotation task. These changes were detected with midline electrodes and were proportional to the angle of mental rotation needed to achieve a match. However, these results fail to separate more generalized attentional effects from processes that are specific to mental imagery. The drain on attentional resources may also affect measures of brain activity. Thus, tasks requiring more effort may produce greater changes in response amplitude or more enduring changes in level of brain activity than do easier tasks. In a recently described experiment by Ruchkin et al. (1991) event related slow wave potentials were studied for visual stimuli with easy and with difficult rotation angles. They found that slow wave negativity at centro- parietal sites increased with increasing rotation difficulty, which might suggest the involvement of visual cortical areas in mental rotation. However, even here the durations (latencies) of these slow waves do not correspond to the times required for mental rotation, although enhanced amplitude with increased rotation difficulty was observed. As in Farah's experiments, these differences in amplitude of slow waves do not constitute direct evidence that the time course of activity in visual or non-visual areas of cortex is related to mental imagery, as reflected in the mental rotation task. No hypotheses are presented to link time required to perform mental rotation to a change in amplitude of an ERP component.

Roland & Friburg (1985) observed an increase in regional cerebral blood flow (rCBF) in the occipital regions when subjects imagined walking in their own neighborhoods. Different changes in blood flow were noted when the same subjects performed a mental arithmetic task. Single photon emission (SPECT) studies of blood flow during other kinds of imagery tasks revealed changes in blood flow in occipital areas, but also in parietal and frontal areas (Goldenberg et al., 1989). Analysis of the mean model dipole generator sources of the Delta-Theta and Alpha EEG frequency bands revealed more posterior locations of the dipoles that were associated with spontaneous thoughts of "visual imagery" type than those that were associated with thoughts of "abstract" type (Lehmann et al., 1991). Although these results indicate spatially selective brain activity associated with mental imagery, they cannot be related to the actual time required to perform the imagery task. Similarly, in virtually all other studies demonstrating relations between changes in brain activity and other mental imagery tasks, none have shown a connection between time to perform the task and the duration of change in level of brain activity.

There is increasing evidence that the amplitude of spontaneous cortical rhythms are modulated over specific anatomical areas of the scalp when a subject is engaged in sensory, motor and cognitive tasks. For instance, activity in the alpha frequency range (8-12 Hz) is suppressed over posterior areas after visual stimulation (Berger, 1930; Kaufman & Locker, 1970; Pfurtscheller, 1986) and before and after eye movements (Lehmann, 1971). Beta rhythm (18-30 Hz) is suppressed in central regions in association with hand movements (Jasper & Andrews, 1938; Pfurtscheller, 1981), and central mu rhythm (7-13 Hz) is bilateral symmetrically suppressed during planning and execution of unilateral movements (Pfurtscheller & Aranibar, 1979). Extensive studies carried out by Pfurtscheller and collaborators revealed reduction in alpha band power ("desynchronization" in their terminology) whose strength and spatial distribution was related to specific sensory-motor (Pfurtscheller & Aranibar, 1979) and cognitive tasks (Pfurtscheller & Klimesch, 1991).

Kaufman et al. (1989; 1990) measured the change in level of alpha-band activity in the magnetoencephalogram (MEG) over different scalp regions during performance of imagery and of verbal tasks. The durations of these changes over the visual areas were commensurate with behavioral indices of task completion. Similar changes were noted for verbal tasks, but not over the visual areas.

Besides spatially selective alpha suppression, Kaufman et al. (1989, 1990) demonstrated with magnetoencephalographic recordings that the duration of alpha suppression increases in a systematic way that is closely related to some cognitive functions. In a task where subjects were engaged in comparing the image of an abstract figure with a memory set of three figures previously seen, the duration of parieto-occipital alpha suppression was comparable to the reaction time indicating whether there was a match or not. Moreover, the suppression of alpha power was enhanced over areas along the midline of the occipital scalp. This corresponds to neuronal sources lying within the visual cortex. Suppression was also observed in the same time window for what may be a particularly strong source of alpha rhythm - the parieto-occipital sulcus (Williamson & Kaufman, 1989; Williamson et al., 1989), the posterior bank of which is a visual area. Together with the temporal window within which suppression is observed, this provides strong evidence that the visual cortex participates in the process of mental imagery. However, the case would be more compelling if the duration of a cognitive task were manipulated by increasing the task difficulty, and as a result a strong positive covariation were found between reaction time to task completion and the alpha suppression duration.

This was the case for scanning short-term memory for a previously heard musical tone (Kaufman et al., 1992). A Sternberg task was carried out in which subjects determined whether a tone matched one just heard in a memory set. There was a significant positive correlation between the duration of alpha suppression measured over the right temporal area and the number of tones in the memory set. Moreover, the spatial pattern of suppression over the scalp correlated with the pattern for the magnetic N100 response of primary auditory cortex. This indicates that the source of the suppressed rhythm includes the primary auditory cortex. Direct evidence for spontaneous rhythmic activity at about 10 Hz in auditory cortex was recently reported by Tiihonen et al. (1991) from magnetic source images. Thus there is converging evidence that spontaneous rhythms are produced by many cortical areas, and when a particular area becomes involved in a sensory or cognitive process the corresponding rhythm is suppressed. This provides opportunities for a broad range of studies of cognitive functions, with the advantage that the signal being monitored is considerably stronger than that of event-related fields or potentials.

Behavioral studies show that the rate of increase in time to complete mental rotation is clearly and strongly related to the angle through which the form must be rotated to obtain a match (Cooper & Shepard, 1973). In view of the earlier findings that the duration of alpha suppression is commensurate with performance of other imagery tasks, and that these effects are specific to particular cortical regions, motivates this study. The present study was carried out to test a central issue that was unanswered by previous studies: whether the temporal duration of alpha suppression over the visual cortex correlates with the behavioral measure of reaction time as the time required to complete a mental rotation task is made to vary. To accomplish this, we recorded multichannel magnetic (MEG) and electric (EEG) signals over the posterior scalp while subjects performed the mental rotation paradigm introduced by Cooper and Shepard (1973). In this task subjects are asked to discriminate normal from mirror reflected versions of alphanumeric characters when they are tilted at different angles with respect to the upright position. This well controlled and replicated task is known to produce clear correlations between the angle of tilt and reaction time, suggesting different durations of the neuronal processing time that presumably corresponds to the time required to perform the mental rotation task.

RESULTS

Reaction Time and Suppression Duration

The visual inspection of all single traces indicated that alpha rhythm was suppressed after the memory as well as after the target figure in all 9 EEG channels and all 30 MEG channels in all subjects. The interval between the memory and target figure was long enough to reestablish alpha activity before the onset of the target stimulus. The computed suppression duration had to be corrected on the basis of the inspection of the individual traces in 19.5% of all cases. In these cases, the automatic duration computation failed mainly because of low alpha amplitude at the time of stimulus onset and thus there was a corresponding small decrease of alpha after the stimulus. There was no significant difference across the different MEG or EEG sensors. Statistical comparison of the suppression duration of the different sensors by repeated measure ANOVA's failed to show any significant differences. For further analysis the suppression duration values were averaged over all sensors, separately for each subject, each angle and each condition.

Fig. 1a (MEG) and Fig. 1b (EEG) show representative alpha amplitude traces of one subject, separately for non-rotated (mean of 0 and 360 deg) and for markedly rotated angles (mean of 150 and 210 deg). The traces are means over all 30 MEG and all 9 EEG sensors respectively. They illustrate that both EEG and MEG show stronger and prolonged suppression of alpha amplitude during the time a subject was identifying the target figure (S2) as compared to the time after the presentation of the memory figure (S1). Moreover there is evidence for longer suppression when subjects match markedly rotated forms to non-rotated targets.

Fig. 2 shows the individual traces of reaction time, EEG-, and MEG-suppression duration as a function of the angle of the target figure, separately for the correct and for the mirror reflected targets. Although individual differences were observed, the general trend for inverted U-shaped curves was evident, i.e. reaction time as well as suppression duration increased with increasing rotation angle. In all traces, non-rotated target stimuli (0 and 360 deg) produced faster reaction times and shorter suppression durations than markedly rotated stimuli. There was no consistent difference between reaction time and the duration of EEG- or MEG alpha suppression. The mean reaction and suppression times were different between the subjects but it did not affect the differences between the rotation angles.

Fig. 3 shows the mean and standard error of the reaction time and the suppression durations over the six subjects as a function of the rotation angle. These data were statistically tested for consistency over subjects by repeated measure ANOVA's with the factors "condition" (2 levels: correct and mirror) and "angles" (8 levels). It resulted in highly significant main effects of the factor "angle" [reaction time: F(7,35) = 22.0, p < .001; MEG suppression duration: F(7,35) = 15.2, p < .001; EEG suppression duration: F(7,35) = 20.43, p<.001]. The main effect for the factor "condition" was significant for the reaction time only [F(1,5) = 11.1, p = .02] while no differences between correct and mirror reflected targets were found for the EEG and MEG suppression duration [MEG: F(1,5) = 0.9, EEG: F(1,5) = 0.6]. Clear statistical proof for the inverted U-shaped profiles were revealed by polynomial contrast analysis, where the quadratic trend was highly significant for all three variables [Reaction time: F(1,5) = 29.8, p = .003; MEG suppression duration: F(1,5) = 51.3, p < .001; EEG suppression duration: F(1,5) = 63.5, p < .001].

Spatial Features

Fig. 4 illustrates on EEG and MEG maps of one subject how the analyzed field descriptor (center of gravity or centroid) is related to the field pattern. It also illustrates the main topographical distribution of alpha activity over the parieto-occipital area: Power is maximal over medial occipital sites for the EEG and over left and right lateral sites for the MEG. Across subjects, the average locations of the centroids of the EEG and the MEG alpha amplitudes did not differ significantly between the eight different rotation angles. That is, unlike the reaction time or suppression duration data, there were no significant ANOVA or polynomial contrast effects for field amplitudes. However, significant differences were found in the comparison of the centroid locations between the non-rotated (mean of 0 and 360 deg) and large rotation angles (mean of 150 and 210 deg). The centroid locations of these two rotation conditions are shown in Fig.5.

The analysis of the early suppression period after the target (T2, between 0 and 500 ms as defined in Fig. 6) showed a more occipitally located centroid than after the memory figure. This shift was independent of the rotation angle of the target figure and was evident in the EEG and in the MEG pattern. The shifts were small but they were in the same direction in all 6 subjects for the MEG centroid (Wilcoxon test: Z = 2.2, p = .028 for both angles) and in 5 of the 6 subjects for the EEG centroid (Z = 1.99, p = .046 for both angles).

A significant shift in the centroid in the parietal direction was found for the late target period T3 (between 500 and 1000 ms) when the target was largely rotated. This shift resulted in significant differences in the comparison between the late and the early period (period T3 vs period T2) for the EEG (Z = 1.99, p = .046, 5 of 6 subjects) and for the MEG (Z = 2.2, p = .28, 6 of 6 subjects). Direct differences between non-rotated and markedly rotated targets within period T3 was significant for the parietal shift of the EEG centroid (Z = 2.2, p = .028, 6 of 6 subjects). In addition, the centroid of the alpha pattern during this late suppression period was located more to the right for the large rotation angles as compared with the non-rotated angles. However, this difference was significant for the MEG measurement only (Z = 1.99, p = .46, 5 of 6 subjects).

DISCUSSION

The reaction time results in this study clearly replicated the findings described by Cooper & Shepard (1973). Reaction time increased with increasing rotation of the target figure from the normal orientation. Therefore the mental rotation task clearly fulfilled our requirements to produce different response latencies for different levels of task difficulty. As proposed by Finke & Shepard (1986) the present reaction time results are consistent with the notion that subjects mentally carry out a rotation of the figure to the normal position before making an identification. Our data are consistent with a linear variation, implying that the time to re-orient the figure is proportional to the rotation angle. Since there was no difference in the reaction and suppression times between the corresponding angles from 0 to 150 deg and from 210 to 360 deg, the figures seemed to be re-oriented either in the clockwise or counter-clockwise direction, depending on the smallest angle of rotation needed to produce the upright position. The responses to the mirror reflected letters appeared to be about 50 ms longer than those to the letters with correct orientation, indicating that additional processes were required when the stimuli were mirror reflected. However, this additional amount of time was essentially independent of the rotation angle.

Both the MEG and the EEG measures showed suppression of the alpha activity after the presentation of the stimuli. Suppression was observed after presentation of the memory figure as well as the target figure. All recorded MEG and EEG channels showed this suppression of the alpha amplitude. This finding is in agreement with early EEG-reports about parieto-occipital alpha blocking after visual stimulation (Morrell, 1966).

The present study has now established a clear relationship between the increase in duration of suppression of parieto-occipital alpha band neuronal activity and reaction time as task difficulty is increased in a mental rotation paradigm. Both increased by about 200 ms for largest angles of rotation in a consistent fashion for each subject. This trend was independent of the different individual's reaction times for the non-rotated targets (0 and 360 deg). Interestingly, while the reaction time was generally longer for mirror reflected than correctly oriented target stimuli, this was not revealed by the duration of the alpha suppression. The RT data imply that decisions regarding reflected letters are more difficult to make than those regarding non-reflected letters. Since this does not appear in our parieto-occipital data, it suggests that the effects are not due to task difficulty alone. However, since the difference in the reaction time was relatively small, the absence of such an effect could have been due to the uncertainty in establishing suppression onset and offset times. Alternatively, the decision as to whether the letter was reflected as well as rotated may have engaged cortical areas outside the parieto-occipital region.

The accuracy in determining these physiological measures was dependent on the strength of the alpha rhythm at stimulus onset. Because cortical excitations (alphons) that produce the parade of spindles comprising the alpha rhythm have many different spectral and temporal configurations (Williamson et al., 1989), there may be none in the relevant cortical areas at the moment of interest and therefore suppression may not have been clearly observed. However, these cases were rare and alpha suppression occurred in the majority of the cases. The fact that this suppression was stronger and markedly longer when the subject was engaged in the figure identification task, and its duration was longer when this task was made more difficult (large rotated targets) indicates that the region of the brain supporting this rhythm was involved in the mental rotation task. As noted earlier in a study of mental imagery in a figure matching task, sources in the visual cortex (Kaufman et al., 1990) and parieto-occipital sulcus (Williamson et al., 1989) contribute to these fields. Although the number of sensors employed to measure the EEG and MEG activity was rather small, changes of the spatial pattern during the period of alpha suppression were observed. The analysis of the locations of the centroids of electric and magnetic field power registered by the sensors revealed small but statistically significant shifts depending on the task requirements of the stimuli (memory vs. target figure) and depending on level of difficulty for the rotation task (non-rotated vs. large rotated targets). The spatial patterns of MEG and EEG alpha signals often consist of only two extremas with opposite polarity (Lehmann et al., 1987; Williamson & Kaufman, 1987, 1989; Michel et al., 1992).

Neuronal current sources within the parieto-occipital sulcus are oriented perpendicular to the sulcus, so their magnetic field (and field-power) extrema are over the left and right ends of the sulcus and their electric field extrema are over occipital and parietal areas. These extrema dominate the spatial pattern of alpha power. They are supplemented by activity within the parietal areas as well. Assuming anatomical symmetry, sources in visual cortex within the longitudinal fissure and calcarine sulcus would produce weaker alpha field power over occipital and parietal regions. For such dipolar field patterns the center of gravity of the maps (where the two extremas are squared) approximates the 2-dimensional location on the scalp of the underlying equivalent generator. A shift of this point within the measured array indicates changes in the average spatial activity pattern of the different neural populations exhibiting the spontaneous activity (Lehmann, 1987; Michel et al., 1992).

In the first 500 ms after the memory and target figures, the centroid locations of both the EEG and the MEG shifted towards more occipital regions after the target figure as compared to the same period after the memory figure, independent of the time needed to identify the stimulus. This means that early suppression was stronger in the parietal region when an analysis task was required with the visual stimulus. Alpha pattern differences between the non-rotated and large rotated targets were found in the later period (500 - 1000 ms) after the target stimuli, where the centroids shifted towards the right (significant for the MEG) and parietal areas (significant for the EEG) when processing the targets with the large rotated angles. This effect suggests additional suppression of neuronal activity in the left occipital area. Our study was not designed primarily to study hemispheric differences, and in view of the confusing literature (Erlichman & Barrett, 1983; Kosslyn, 1987; Papanicolaou et al., 1987; Corballis & Sergent, 1989a, 1989b; Servos & Peters, 1990) further studies that also include recordings of the brain's electrical activity over the temporal, central and frontal areas are needed to define a clear left hemispheric involvement in mental imagery. However, the spatial changes described in this paper give the first evidence for local changes of alpha activity that depend on the task demands. Clearly, it could be of considerable interest to supplement these result in future experiments by recordings with larger arrays of field sensors. Together with the newly developed Minimum-Norm Least-Squares procedures for obtaining inverse solutions ("MNLS inverse") for measurements of the distribution of average magnetic field power (Wang et al., 1992), it will be possible to map in detail the evolution of the activity pattern associated with alpha suppression. The high temporal correlation between behavioral measures and alpha suppression make this physiological measure a clear candidate for studies of brain processes that serve cognitive functions.

METHODS

Subjects

Six healthy, paid volunteers (2 males and 4 females) participated in this study after giving their informed consent. Their ages ranged from 19 to 31 years. All of them were right handed and had normal, uncorrected vision. Before the actual recording sessions each subject performed at least 2 training runs of the task without recordings being made. Subjects were informed to respond as quickly as possible while trying to maintain high accuracy.

Visual Presentation

The time sequence of a single epoch is illustrated in Fig. 6. It begins with the presentation of a fixation point on a viewing screen positioned in front of the subject. This is produced from outside our magnetically shielded room by an Elektrohome video projector controlled by an Amiga 2000 computer. The memory figure in the upright position was presented under the fixation point 700 ms later. After 200 ms it was turned off while the fixation point persisted for 1.2 s on the screen. Then the target figure was presented for 200 ms duration. Subsequently the screen was darkened for 3.2 s until the fixation point for the next epoch was presented. Eight different figures were generated (letters C, E, F, G, L, P, S) with a font that distinguishes between upright and inverted presentation of the letters C, E, and S. The target figure was always the same as the memory figure but was tilted clockwise by a randomly selected angle from the set 0, 50, 100, 150, 210, 260, and 310 deg. In addition, each target figure was randomly chosen to be presented either normal or mirror reflected. The subject's task was to press one of two buttons with the right hand to indicate whether the target figure was normal or mirror reflected.

Recording Methods

The electric signals (EEG) were recorded from 9 electrodes positioned over the posterior area of the scalp as shown in Fig. 7 (C3, Cz, C4, P3,Pz, P4, O1, Oz, O2 according to the 10-20 system). The electrode at Cz was used as the recording reference, and the data were recomputed to express signals relative to the average reference (Lehmann & Skrandies, 1980). EEG data were bandpassed between 0.1-30 Hz.

Magnetic data (MEG) were recorded with a 5-channel neuromagnetometer (Williamson et al., 1984) located within a magnetically shielded room. The probe, consisting of detection coils and SQUID sensors to which they were attached, was immersed in liquid helium within a fiberglas cryogenic vessel. The detection coils were second-order gradiometers with 1.5 cm diameter and 4 cm baseline, arranged with four sensors equally spaced on a 2 cm circle and the fifth in the center. Bandpass filters for the MEG channels were set for 0.1-50 Hz. MEG signals were recorded from 6 different probe locations, each obtained in an individual session. The sequence of positions was varied across subjects. The approximate positions for magnetic recordings in comparison with the 9 EEG positions are illustrated in Fig. 7.

Procedure

Both EEG and MEG signals were recorded for 5 s of each epoch, starting with the presentation of the fixation point at the -2 s time point in Fig. 6. A separate trigger channel and two separate response channels as well as information about the presented stimulus (letter, angle, and type) were simultaneously recorded. The data were digitized with a sampling rate of 128 Hz and stored on computer disk for off-line analysis. Each subject participated in 6 sessions on 3 different days within less than 2 weeks. On each day, 2 experimental sessions were performed with different probe positions, separated by a rest break of 20 min. Each session consisted of 6 runs of 40 epoches each. One run lasted 3.6 min and was followed by a pause of 1 min. Each session began with electrodes being attached to the scalp, and then the subject was comfortably positioned on a kneeling chair inside the magnetically shielded room. Torso and head were tilted forward so that they were supported by firm cushions and vacuum casts. A system of mirrors was adjusted so that the target (3 cm height) was presented in the lower visual field at a distance of 36 cm from the subject (viewing size of the figure was 4.8 deg arc).

The recording positions of the neuromagnetometer probe relative to three cardinal landmarks on the head (left and right periauricular points and nasion) of each subject was determined by standard procedures (Yamamoto et al., 1988) using the Probe Position Indicator system (Williamson & Kaufman, 1989). Two receivers were stuck to a Velcro headband, and their positions were recorded relative to the three landmarks on the head to establish the head-based coordinate system. The location and orientation of the probe relative to this head-based coordinate system was determined automatically before and after each recording (PPI system, Biomagnetic Technologies Inc., San Diego, CA).

Data analysis

Pilot studies suggested that the clearest suppression was observed within the higher alpha bandwidth of 10-12 Hz. Consequently each 5 s record of EEG and MEG recordings was bandpassed in the range 10-12 Hz (-3 db points) using a digital FIR filter with a rolloff of 48 db/octave. The filtered signals were squared and then low-pass filtered with a cutoff of 6 Hz, to provide a slowly varying envelope of the alpha rhythm's power. These power traces were averaged over the 6 runs of each session, separately for the 8 angles and the 2 conditions (correct or mirror reflected target). Only correct responses were included in the average, which left about 20 epoches to be averaged together for each run, depending on the random generator and number of correct responses. The square root of averaged power values were then taken, providing the "alpha amplitude" for each average.

The durations of alpha suppression after the memory figure, and after the target figure were computed separately. To determine the onset of suppression the program searched for the time when the average amplitude fell below 50% of the amplitude span between the preceding maximum and the following minimum. The offset of suppression was defined similarly as when the amplitude rose above 50% of the span between the minimum and the following maximum. These time marks were accepted when the amplitude exceeded the 50% threshold for at least 100 ms. The search was carried out within the time period between -1.7 s and 0 s for the memory figure and between 0 s and 2.8 s for the target figure. Traces were then randomly displayed, without identification, on a computer monitor together with the time marks for onset and offset, and corrections were made where there were obvious miss-identifications by the computer algorithm.

While the present experiment was not designed to characterize the spatial evolution of magnetic or electric field power, it was possible to obtain some preliminary information about changes in the distribution under the sensor arrays. As a practical measure we focussed on a one-point descriptor for the spatial pattern of the alpha at each moment in time: the location of the center of gravity or centroid (Lehmann, 1987; Michel et al., 1992). In contrast to potential maps where two centroids describe the positive and the negative half of the fields, there is only one controid for power maps. It is assumed that a shift of the centroid location means a shift of the dominant alpha activity across the scalp. The spatial extent of the sensor array was sufficiently broad over parietal and occipital regions to indicate if the centroid shifts away from the region where alpha suppression had been dominant. The mean locations of the centroids, described by their anterior-posterior and their left-right locations were compared between different time periods by averaging the centroids over three different 500 ms time intervals: after the onset of memory figure, after the onset of the target figure, and between 500-1000 ms after the target figure. The latter two periods reflecting early and late parts of the target-induced alpha suppression.

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Reprint requests should be sent to Christoph M. Michel, EEG-EP Mapping Laboratory, Neurology Department, University Hospital, CH-8091 Zurich, Switzerland.

REFERENCES

Anderson, J.R. (1985). *Cognitive psychology and its implications.* 2nd edition, New York: W.H. Freeman & Company.

Berger, H. (1930). Ueber das Elektrenkephalogram des Menschen II. *Journal of Psychology and Neurology, 40,* 160-179.

Cooper, L.A., & Shepard, R.N. (1973). The time required to prepare for a rotated stimulus. *Memory and Cognition, 1,* 246-250.

Corballis, M.C., & Sergent, J. (1989a). Hemispheric specialization for mental rotation. *Cortex, 25,* 15-25.

Corballis, M.C., & Sergent, J. (1989b). Mental rotation in a commissurotomized subject. *Neuropsychologia, 27,* 585-597.

Erlichman, H., & Barrett, J. (1983). Right hemisphere specialization for mental imagery: a review of the evidence. *Brain and Cognition, 2,* 55-76.

Farah, M.J. (1984). The neurological basis of mental imagery: a componential analysis. *Cognition, 18,* 245-272.

Farah, M.J. (1988). Is visual imagery really visual? overlooked evidence from neuropsychology. *Psychological Review, 95,* 307- 317.

Farah, M.J., Peronnet, F., Weisberg, L.L., & Perrin, F. (1988). Electrophysiological evidence for shared representational medium for visual images and visual percepts. *Journal of Experimental Psychology, 117,* 248-257.

Finke, R.A., & Shepard, R.N. (1986). Visual functions of mental imagery. In K.R. Boff, L. Kaufman, & J.P. Thomas, (Eds), *Handbook of Perception and Human Performance: Vol. II, Cognitive Processes and Performance* (pp. 1-55). New York: John Wiley and Sons.

Goldenberg, G., Podreka, I., Steiner, M., Willmes, K., Suess E., & Deecke, L. (1989). Regional cerebral blood flow patterns in visual imagery. *Neuropsychologia, 27,* 641-664.

Golla, F.,Hutton, E.L., & Walter, W.G. (1943). The objective study of mental imagery. I. Physiological concomitants. *Journal of Mental Sciences, 75,* 216-223.

Jasper, H.H., & Andrews, H.L. (1938). Electro-encephalography. III. Normal differentiations of occipital and precentral regions in man. *Archives of Neurology and Psychiatry, 39,* 96- 115.

Kaufman, L., & Locker Y. (1970). Sensory modulation of the EEG. *Proceedings of the Americal Psychological Association, 75th Meeting,* 179-180.

Kaufman, L., Glanzer, M., Cycowicz, Y.M., & Williamson, S.J. (1989). Visualizing and rhyming cause differences in alpha suppression. In S.J. Williamson, M. Hoke, G. Stroink, & M. Kotani (Eds.), *Advances in Biomagnetism* (pp. 241-244). New York: Plenum Press.

Kaufman, L., Schwartz, B., Salustri, C., & Williamson, S.J. (1990) Modulation of spontaneous brain activity during mental imagery. *Journal of Cognitive Neuroscience, 2,* 124-132.

Kaufman, L., Curtis, S., Wang, J.-Z., & Williamson, S.J. (1992). Changes in cortical activity when subjects scan memory for tones. *Electroencephalography and Clinical Neurophysiology, 82,* 266-284.

Kosslyn, S.N. (1983). *Ghosts in the Mind's Machine.* New York: Norton Press.

Kosslyn, S.N. (1987). Seeing and imagining in the cerebral hemispheres: a computational approach. *Psychological Review, 94,* 148-175.

Lehmann, D. (1971). EEG, evoked potentials, and eye movements. In P. Bach-y-Rita & C.C. Collins (Eds.), *The control of eye movements* (pp. 141-173). New York, London: Academic Press Inc.

Lehmann D. (1987). Principles of spatial analysis. In A.S. Gevins & A. Remond, (Eds.), *Handbook of Electroencephalography and Clinical Neurophysiology, Vol.1: Methods of Analysis of Brain Electrical and Magnetic Signals* (pp.309-354). Amsterdam: Elsevier.

Lehmann, D., & Skrandies, W. (1980). Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalography and Clinical Neurophysiology, 48,* 609-621.

Lehmann, D., Ozaki, & Pal, I. (1987). EEG alpha map series: brain micro-states by space-oriented adaptive segmentation. *Electroencephalography and Clinical Neurophysiology, 67,* 271-288.

Lehmann, D., Michel, C.M., Henggeler, B., & Brandeis, D. (1991). Source localisation of spontaneous EEG using the FFT Dipole Approximation: Different frequency bands, and differences with classes of thoughts. In I. Dvorak & A.V. Holden (Eds.), *Mathematical approaches to brain functioning diagnostics.* (pp. 159-169). Manchester, New York: Manchester University Press.

Mangun, G.R., & Hillyard, S.A. (1988). Spatial gradients of visual attention - behavioral and electrophysiological evidence. *Electroencephalography and Clinical Neurophysiology, 70,* 417-428.

Michel, C.M., Lehmann, D., Henggeler, B., & Brandeis, D. (1992). Localization of the sources of EEG delta, theta, alpha and beta bands using the FFT Dipole Approximation. *Electroencephalography and Clinical Neurophysiology, 82,* 38-44.

Morrell, L.K. (1966). Some characteristics of stimulus-provoked alpha-activity. *Electroencephalography and Clinical Neurophysiology, 21,* 552--561.

Papanicolaou, A., Deutsch, T., Bourbon, G., Will, K., Loring, D., & Eisenberg, H. (1987). Convergent evoked potential and cerebral blood flow evidence of task-specific hemispheric differences. *Electroencephalography and Clinical Neurophysiology, 66,* 515-520.

Peronnet, F., & Farah, M.J. (1989). Mental rotation - an event- related potential study with a validated mental rotation task. *Brain and Cognition, 9*: 279-288.

Pfurtscheller, G. (1981). Central beta rhythm during sensory motor activities in man. *Electroencephalography and Clinical Neurophysiology, 51,* 253-264.

Pfurtscheller, G. (1986). Event-related desynchronization mapping: visualization of cortical activation patterns. In: F.H. Duffy (Ed.), *Topographic Mapping of Brain Electrical Activity* (pp.99-111). Stoneham: Butterworth.

Pfurtscheller, G., & Aranibar, A.(1979). Evaluation of event- related desynchronization (ERD) preceding and following voluntary self-paced movement. *Electroencephalography and Clinical Neurophysiology, 46,* 138-146.

Pfurtscheller G., & Klimesch W. (1991). Event-related desynchronization during motor behavior and visual information processing. In C.H.M. Brunia, G. Mulder, & M. Verbaten (Eds.), *Event-Related Brain Research, Electroencephalography and Clinical Neurophysiology* (pp.58-65). Amsterdam: Elsevier.

Pylyshyn Z.W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychologigical Review , 88,* 16-45.

Roland, P.E. & Friburg, L. (1985). Localization of cortical areas activated by thinking. *Journal of Neurophysiology., 53,* 1219-1243.

Ruchkin D.S., Johnson, R., Canoune, H., & Ritter, W. (1991). Event-related potentials during arithmetic and mental rotation. *Electroencephalography and Clinical Neurophysiology, 79,* 473-487.

Servos, P., & Peters, M. (1990). A clear left hemisphere advantage for visuo-spatially based verbal categorization. *Neuropsychologia, 28,* 1251-1260.

Shepard R.N., & Meltzer J.(1971). Mental rotation of three-dimensional objects. *Science, 171,* 632-634.

Shepard R.N., & Cooper, L.A. (1982). *Mental Images and their Transformations.* Cambridge: MIT Press.

Tiihonen, J., Hari, R., Kajola, M., Karhu, J., Ahlfors, S., & Tissari S. (1991). Magnetoencephalographic 10-Hz rhythm from the human auditory cortex. *Neuroscience Letters, 129,* 303- 305.

Wang , J.Z., Williamson, S.J., & Kaufman, L. (1992). Magnetic source images determined by a lead-field analysis: the unique minimum-norm least-squares estimation. *IEEE Transactions on Biomedical Engineering, 39,* 665-675.

Williamson, S.J., & Kaufman, L. (1987). Analysis of neuromagnetic signals. In A.S. Gevins, & A. Remond, (Eds.), *Handbook of Electroencephalography and Clinical Neurophysiology, Vol.1: Methods of Analysis of Brain Electrical and Magnetic Signals* (pp. 405-488). Amsterdam: Elsevier.

Williamson, S.J. & Kaufman, L. (1989). Advances in neuromagnetic instrumentation and studies of spontaneous brain activity. *Brain Topography, 2,* 129-139.

Williamson, S.J., Pelizzone, Y., Okada, D., Kaufman, L., Crum, B., & Marsden, J.R. (1984). Magnetoencephalography with an array of SQUID sensors. In H. Collan, P. Berglund, & M. Krusius, (Eds.), *ICEC10: Proceedings of the Tenth International Cryogenic Engineering Conference,* Guildford, England (pp. 339-348). Stoneham: Butterworth.

Williamson, S.J., Wang, J.-Z. & Ilmoniemi, R.J. (1989). Method for locating sources of human alpha activity. In S.J. Williamson, M. Hoke, G. Stroink, & M. Kotani (Eds.), *Advances in Biomagnetism* (pp. 257-260). New York: Plenum Press.

Yamamoto, T, Williamson, S.J., Kaufman, L.; Nicholson, C. & Llinas, R. (1988). Magnetic localization of neuronal activity in the human brain. *Proceedings of the National Academy of Sciences USA*, 85, 8732-8736.

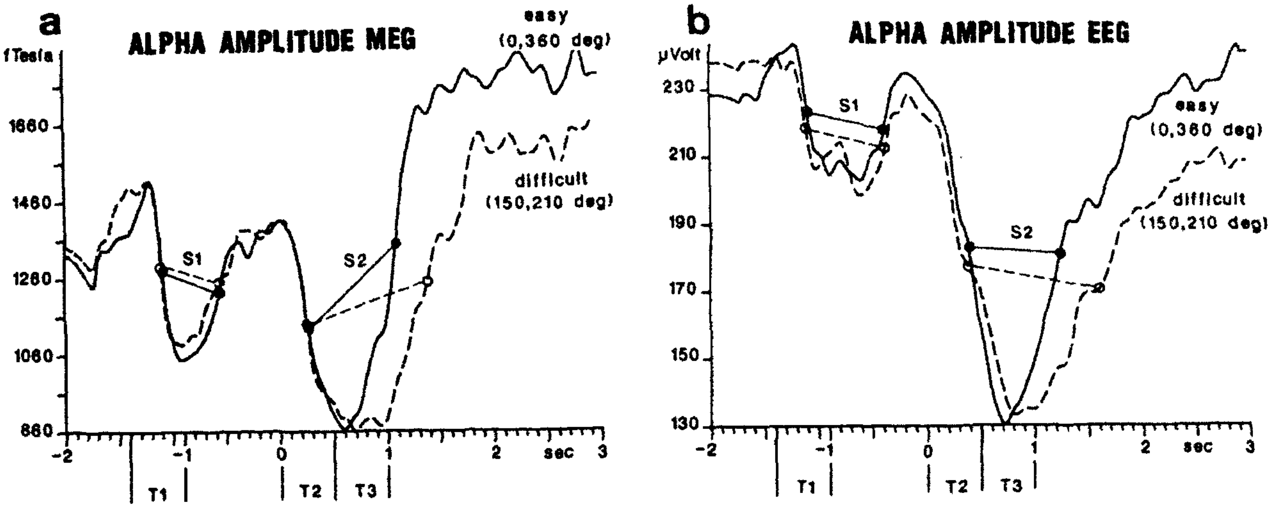

Figure 1: Five-second alpha amplitude traces of one subject as the mean over all MEG and EEG channels respectively. The time origin indicates the onset of the target figure. Separate traces are shown for the non-rotated angles (mean for 0 and 360 deg) and for the large rotated angles (mean for 150 and 210 deg). The computed suppression duration after the memory and after the target figure for this case are indicated (S1 and S2). The time periods (T1, T2, T3) marked along the x-axis designate the epochs that were selected for averaging the centroid locations (see Fig. 5). (a) MEG alpha amplitude, averaged over all 30 sensor positions. (b) EEG alpha amplitude, averaged over all 9 electrode positions and the 6 sessions.

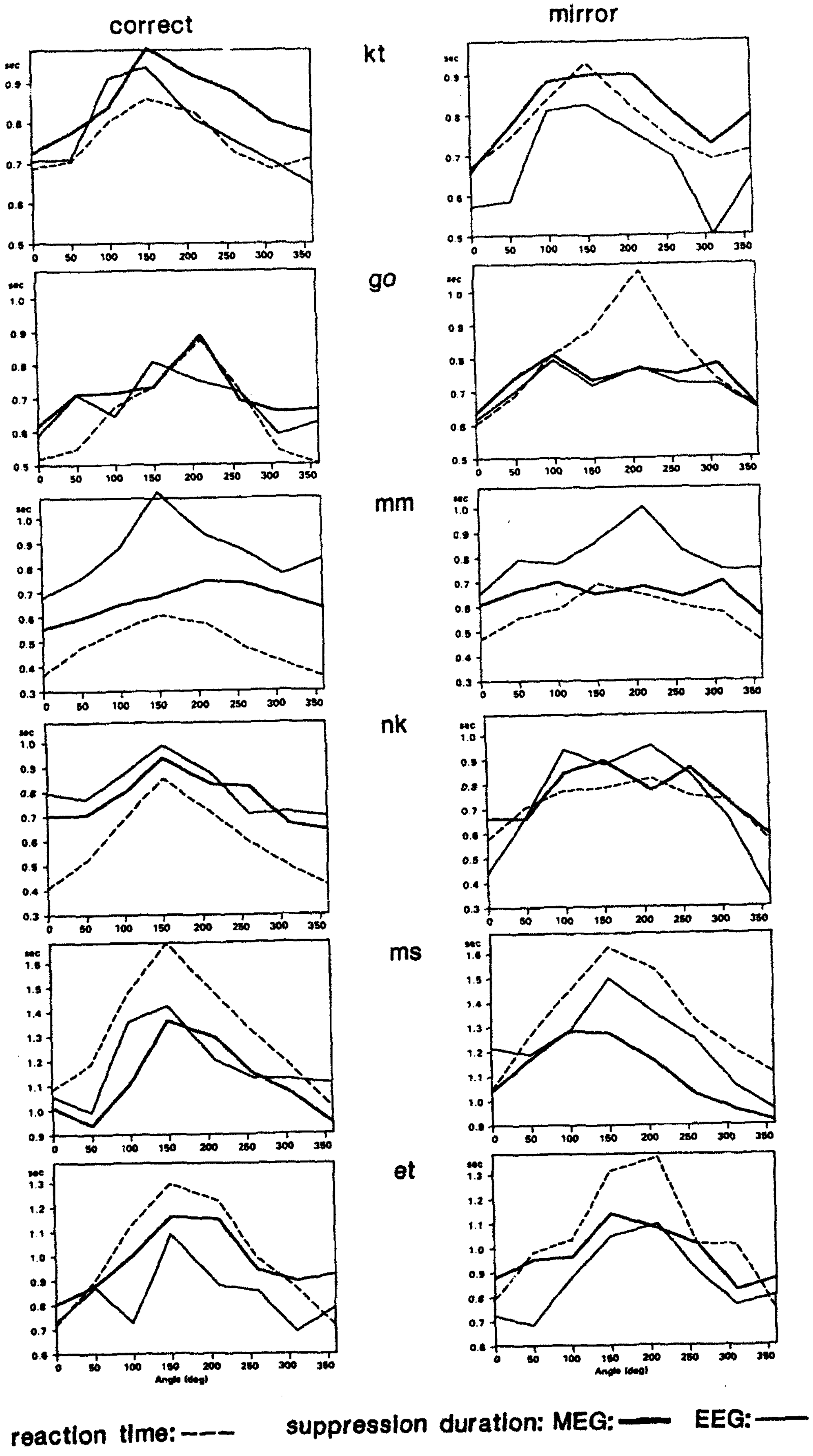

Figure 2: Individual's mean reaction time compared with MEG- and EEG suppression duration for different rotation angles of the target figures for each of 6 subjects. Separate traces are drawn for the correctly oriented (left) and for the mirror reflected (right) target figures.

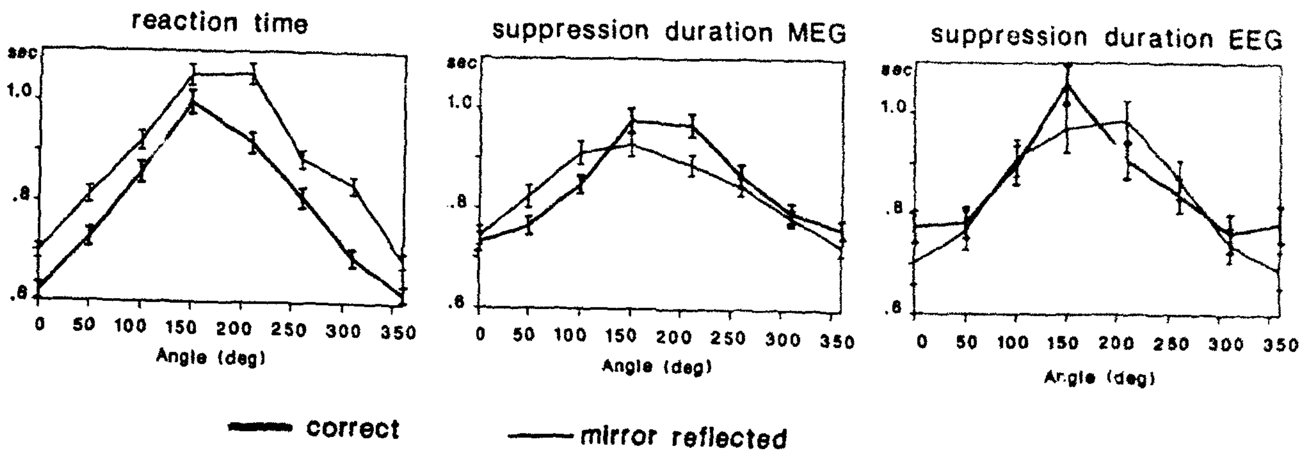

Figure 3: Mean and standard error (N = 6) of the reaction time together with MEG- and EEG suppression durations for the different rotation angles of the target figures. Separate traces are drawn for the correctly oriented and for the mirror reflected figures.

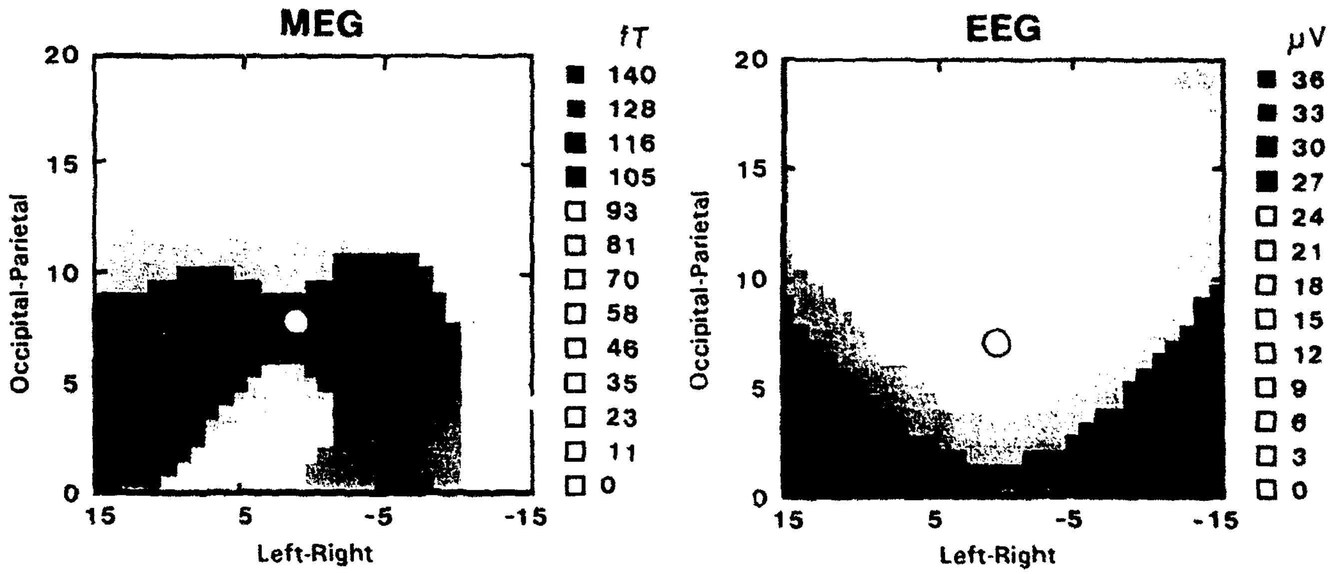

Figure 4: EEG and MEG alpha amplitude maps for one subject. The maps are means over 500 ms intervals when the target figure was rotated by 150 deg. Note the MEG patterns are oriented approximately perpendicular to the EEG patterns. The locations of the respective amplitude centroids are marked by white dots. The values on the axis are in centimeters, with the inion at the origin for the occipital-parietal axis and the midline at the origin for the left-right axis, with negative to the right.

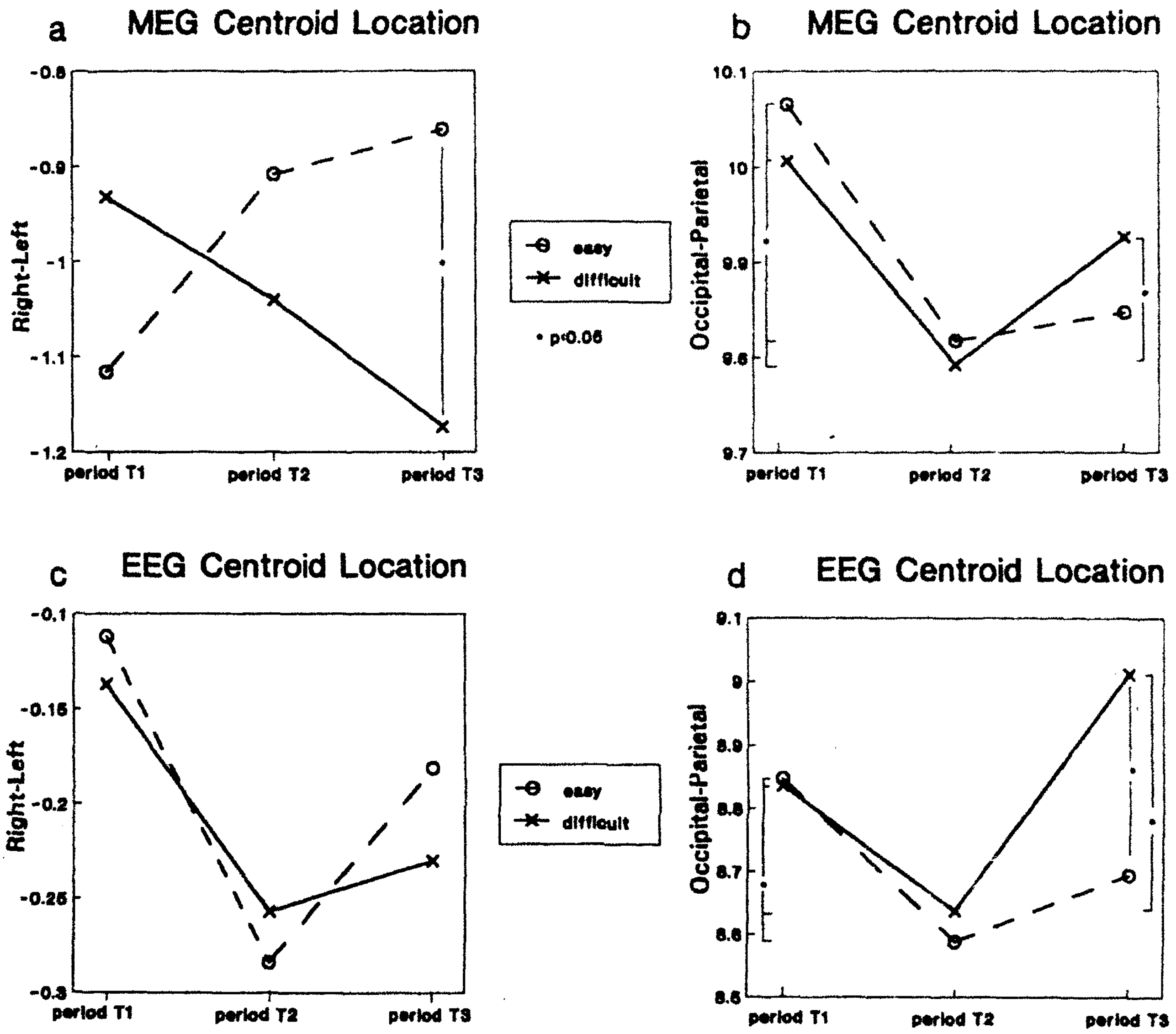

Figure 5: Location of the centroids of the MEG and the EEG field patterns, averaged over 3 different time periods: T1: 0-500 ms after onset of the memory figure; T2: 0-500 ms after onset of the target figure; and T3: 500-1000 ms after onset of the target figure. Separate traces are shown for the non-rotated (0, 360 deg) and large rotated (150, 210 deg) target figures. All points are the medians over six subjects. Statistically significant differences (Wilcoxon-tests) are marked by an asterisk and vertical lines. Coordinate axes are as in the preceding figure. (a) Right-Left location of the cenrtroid of the MEG field (negative is in right hemisphere). (b) Occipital-Parietal location of the centroid of the MEG field. (c) Right-Left location of the centroid of the EEG field. (d) Occipital-Parietal location of the centroid of the EEG field.

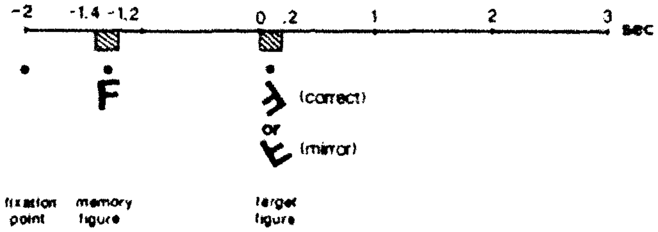

Figure 6: Representation of the time sequence of events for a single 5-s epoch. The time origin indicates the onset of the target figure. The memory figure appears between - 1.4 s and -1.2 s, and the rotated target figure (same letter) appears between 0 and 0.2 s. A fixation point on top of the figures is continuously presented throughout the period between - 2 s and 0.2 s. This example shows a 150 deg rotated target figure. The target figure was randomly presented either in correct orientation, or as the mirror reflected image.

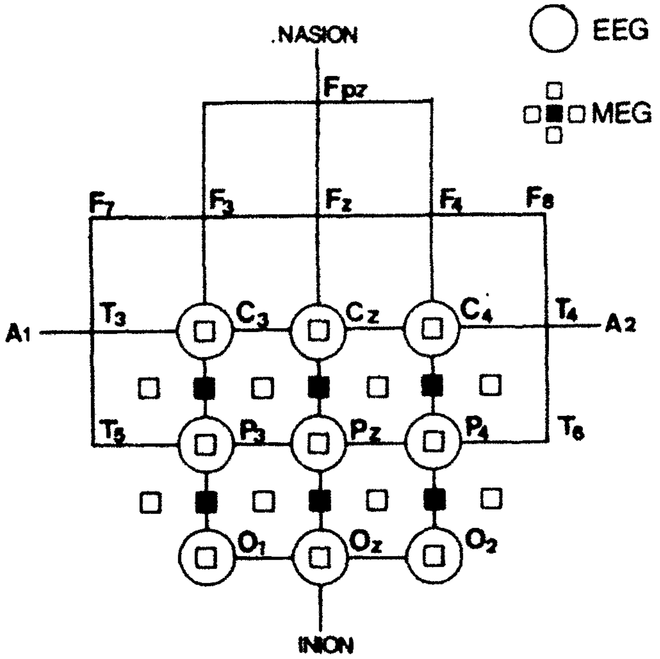

Figure 7: Positions of the 9 EEG electrodes (circles) and 30 MEG sensors (squares) with respect to the 10-20 system. Solid squares indicate the middle sensor for each placement of the 5-channel MEG probe.