

Sustained and transient oscillatory responses in the gamma and beta bands in a visual short-term memory task in humans

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Abstract

In a visual delayed matching-to-sample task, compared to a control condition, we had previously identified different components of the human EEG that could reflect the rehearsal of an object representation in short-term memory (Tallon-Baudry et al., 1998). These components were induced oscillatory activities in the gamma (24–60 Hz) and beta (15–20 Hz) bands, peaking during the delay at occipital and frontal electrodes, and two negativities in the evoked potentials. Sustained activities (lasting until the end of the delay) are more likely to reflect the continuous rehearsing process in memory than transient (ending before the end of the delay) activities. Nevertheless, since the delay duration we used in our previous experiment was fixed and rather short, it was difficult to discriminate between sustained and transient components. Here we used the same delayed matching-to-sample task, but with variable delay durations. The same oscillatory components in the gamma and beta bands were observed again during the delay. The only components that showed a sustained time course compatible with a memory rehearsing process were the occipital gamma and frontal beta induced activities. These two activities slowly decreased with increasing delay duration, while the performance of the subjects decreased in parallel. No sustained response could be found in the evoked potentials. These results support the hypothesis that objects representations in visual short-term memory consist of oscillating synchronized cell assemblies.

Keywords: EEG, Delayed matching-to-sample task, 40 Hz, Rhythm, Gamma-band oscillations

Introduction

It is widely agreed that visual tasks involve neural computation in a large number of functionally distinct brain areas. More locally, within each area, several different groups of neurons are activated. How does a unified percept emerge from these distributed activities? Oscillatory synchronization in the gamma band (20–80 Hz) may play a crucial role in linking together the different neurons or functional areas processing different aspects of the same object (Milner, 1974; von der Malsburg, 1985; von der Malsburg & Schneider, 1986; Singer & Gray, 1995).

In support of this hypothesis, epochs of enhanced gamma-band synchronization in response to visually coherent objects have been observed in areas 17 and 18 in anesthetized (Eckhorn et al., 1988; Gray et al., 1989; Engel et al., 1991; Freiwald et al., 1995; Brosch et al., 1997) and awake (Gray & Di Prisco, 1997) cats and in area MT in awake monkeys (Kreiter & Singer, 1992, 1996). These epochs of gamma synchronization are not strictly locked to the

stimulus onset: they are induced by the stimulus, that is, they appear with a jitter in latency from one trial to the next.

In humans, epochs of oscillatory activity in the gamma-band induced by a visual stimulus were observed in intracranial recordings in the occipital lobe (Sem-Jacobsen et al., 1956; Chatrian et al., 1960) and in EEG scalp recordings in different tasks such as visual priming (Jokeit et al., 1994) or multistable perception (Basar-Eroglu et al., 1996; Revonsuo et al., 1997). Induced gamma-band activity in human EEG was shown to increase in response to coherently moving bars (Lutzenberger et al., 1995; Müller et al., 1996, 1997), or to coherent static objects as compared to noncoherent stimuli (Tallon-Baudry et al., 1996). It may thus underlie the feature binding process. More generally, induced oscillatory activity in the gamma band could reflect the activation of an object representation, no matter whether this representation is activated by bottom-up processes as in feature binding or by other mechanisms. Indeed, we have found evidence for increased induced gamma activity when the internal representation of an object is activated by top-down processes (Tallon-Baudry et al., 1997), and when an object representation is held active in visual short-term memory (Tallon-Baudry et al., 1998).

In this latter experiment, gamma activity was observed during the delay period of a delayed matching-to-sample task, and disap-

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peared in a control condition in which no memory process was required: it could therefore reflect the rehearsal of an object in visual short-term memory. Furthermore, it peaked at occipital and bilaterally at frontal sites, which fits with the idea of a synchronized cortical network involved in memory processes centered on ventral visual and prefrontal areas (Fuster, 1997). However, several other components were also found to decrease or to disappear during the delay of the control condition and may therefore also reflect the memory rehearsing process. These components were (1) induced oscillatory activities in the beta (15–20 Hz) range, peaking at occipital and midline frontal electrodes, and (2) in the evoked potentials, a left posterior negativity appearing at the beginning of the delay and a more centro-parietal negativity rising later.

Are these components really sustained; that is, do they really last until the end of the delay? This is an important issue because sustained activities are more likely to reflect the continuous rehearsing of the sensory trace of the memorized object than transient activities (e.g. not lasting until the end of the delay). However, it was not possible to distinguish sustained from transient components in this first experiment: since the delay duration was fixed and rather short, the time course of these different components may have been influenced by this strict timing. For instance, the occipital gamma activity tended to decrease before the end of the delay, which may be interpreted as an active anticipation of S2 onset. On the other hand, it may also indicate that this component was in fact a transient response and could not reflect a continuous rehearsing process in visual short-term memory. Another example is the centro-parietal negativity in the evoked potentials: since it was rising until the end of the delay, it could be either implied in a sustained memory process, or in an expectancy process.

To further elucidate the functional role of each of these components, we investigated their time courses. In the present experiment, we used the same delayed matching-to-sample paradigm, but with different delay durations (Fig. 1), one of them (d1 condition) being the one used in our previous experiment for comparison purpose. Our aim was to disclose sustained components (lasting until S2 onset) from transient components (ending before the end of the delay). Transient components may reflect the initial start-up of the memory process, while sustained components are more likely to reflect a continuous rehearsing process in memory.

Material and methods

Subjects

Thirteen right-handed subjects (4 females, mean age 27 years) with normal or corrected-to-normal vision gave their written informed consent to participate in the experiment.

Protocol

Subjects performed a delayed matching-to-sample task (Fig. 1). Stimuli were smoothly deformed rings (see below) without any sharp angle, presented in black on a light gray background on a video monitor (refresh rate 68 Hz). The viewing distance was 1.5 m.

Each subject performed six blocks of 90 trials. Each trial began with the appearance of a red fixation cross (0.07 deg) for 800 ms, followed by the first stimulus S1 for 400 ms. The duration of the delay could be either 800 ms (d1 condition), 1200 ms (d2 condition), or 1600 ms (d3 condition). These three conditions were randomly intermixed. At the end of the delay, the second shape S2 appeared for 400 ms. It either matched S1 (go trials, $P = 0.2$) or differed from S1 (no-go trials, $P = 0.8$). Go and no-go trials were randomly presented, with no more than two consecutive go trials. The difficulty of the task (difference between S1 and S2) was constantly adapted to the subject's performance (see below). Subjects were instructed to press a mousekey with the right hand on go trials, and that accuracy was more important than response speed. They were also instructed to blink only during intertrials intervals. The intertrial interval was randomized between 2 and 3 s.

Stimuli construction (S1)

Stimuli were strictly parametrized by 12 anchor points of polar coordinates (r_i, θ_i) , with $\theta_i = (2\pi/12)(i - 1)$, $i \in [1 \dots 12]$ and r_i being randomly chosen at each trial between r_{\min} and r_{\max} , corresponding to visual angles of 0.88 deg and 1.23 deg, respectively. The interpolation function between four successive anchor points $(r_1, \theta_1) \dots (r_4, \theta_4)$ is given by Lagrange's polynomial

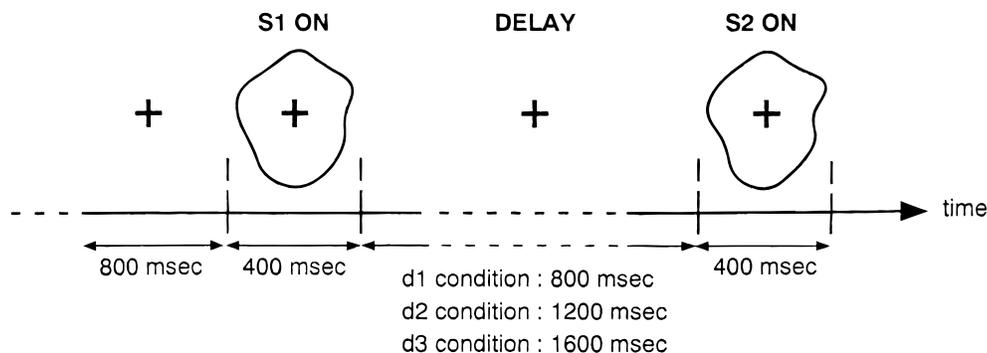


Fig. 1. Delayed matching-to-sample task. Two shapes were presented separated by a blank screen where only the central fixation cross remained. The delay between the two stimuli S1 and S2 was randomly chosen at each trial among three values: 800 ms (d1 condition), 1200 ms (d2 condition), or 1600 ms (d3 condition). Subjects were required to press a button when the two shapes were identical (20% of the trials). Stimuli were smooth shapes, without any sharp angle, to avoid as much as possible any explicit verbal description. The difficulty of the task (difference between S1 and S2) was constantly adapted to keep the subject's performance between 80 and 90% correct.

$$r(\theta) = \sum_i r_i \frac{\prod_{j \neq i} (\theta - \theta_j)}{\prod_{j \neq i} (\theta_i - \theta_j)},$$

where i and j vary between 1 and 4. Only the inner segment, between (r_2, θ_2) and (r_3, θ_3) , was drawn. The same procedure was applied until the 12 segments of the curve were drawn.

Stimulus S2 and adjustment of the difficulty of the task to the subjects' performance

In no-match trials, S2 was derived from S1 by modulating the radii of the 12 anchor points: $r_i(S2) = r_i(S1) * (1 \pm x * coeff)$, where x varies randomly between 0.5 and 1. The sign of the modulation (increase or decrease r_i) was chosen randomly and independently for each anchor point. The value of *coeff* (coefficient of difficulty) was set to 12% at the beginning of a block of recording and then

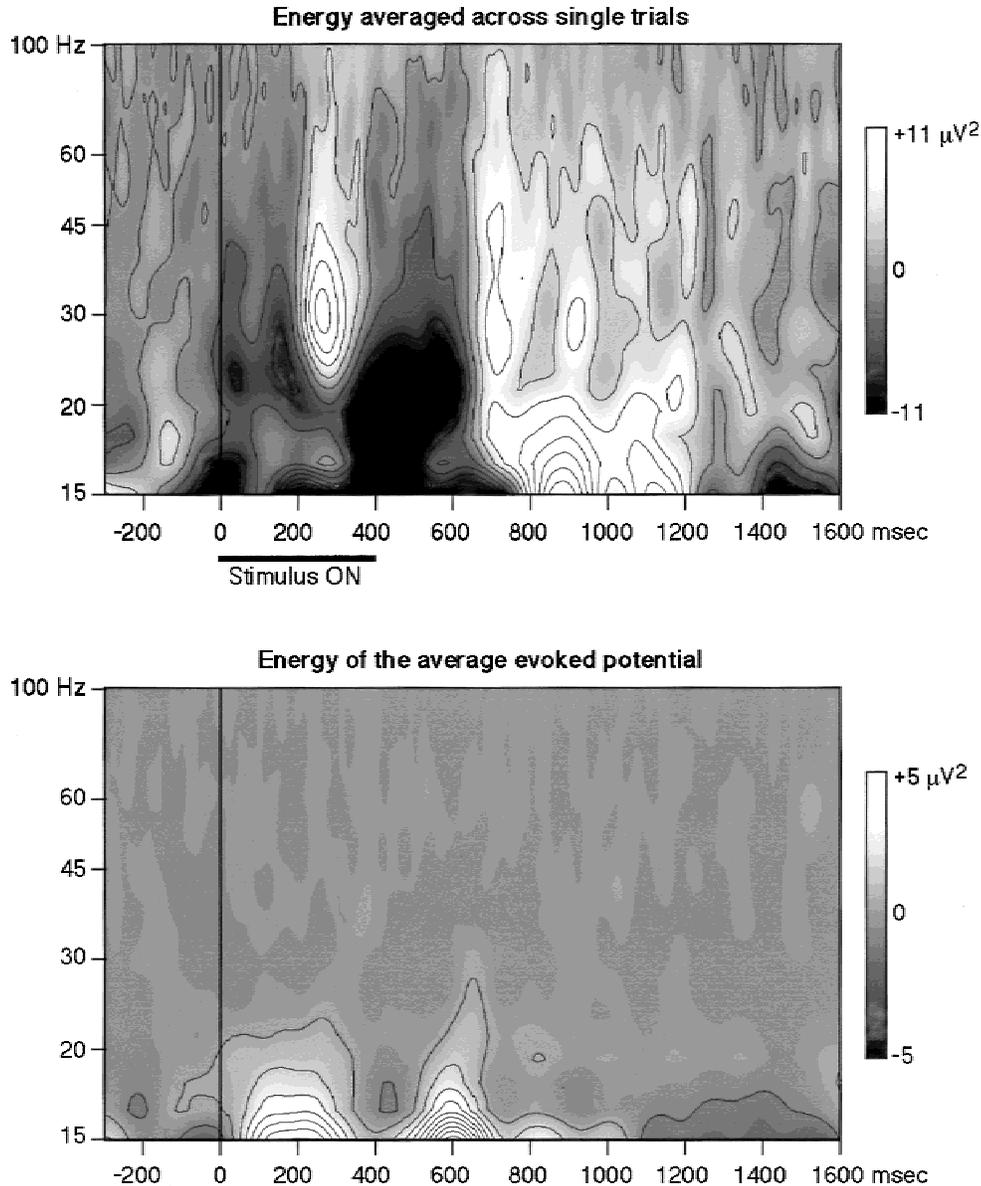


Fig. 2. Time-frequency distribution of the energy averaged across single trials (top) and of the energy of the average evoked potential (bottom), at electrode POz in the d2 condition, grand average across the 13 subjects. Time is presented on the x axis, frequency on a logarithmic scale on the y axis. The level of energy is coded on a gray scale. It can be positive or negative, depending on whether it increases or decreases with respect to a baseline level taken in the prestimulus interval. Gamma (24–60 Hz) activity is observed in response to stimulus onset around 280 ms. Activities in the gamma and beta (15–20 Hz) ranges occur during the delay. All these activities disappear in the energy of the average evoked potential: they are *induced* by the stimulus (or in other terms not phase-locked to the stimulus).

modified at each trial according to the subject's performance computed on the last 20 trials (or on the last available trials at the beginning of a block), irrespective of the delay duration. If this moving average performance fell below 80%, *coeff* was increased by 1%, and the task became easier. On the contrary, if the performance was above 90%, *coeff* was decreased by 1%, and the task became more difficult. The upper and lower limit values of *coeff* were set at 20% and 4%, respectively.

Recordings

EEG was continuously recorded at a sampling rate of 500 Hz (0.1–120 Hz analog bandwidth) from 13 silver electrodes referenced to the nose. Electrode impedances were kept below 10 k Ω at 15 Hz. Since the different components we observed in the previous experiment tended to be lateralized on the left side, electrodes were placed over the left hemisphere and midline. According to the 10–20 system, their locations were Iz, T5, O1, POz, P3, Pz, T3, C3, Cz, FT3, F3, and Fz. An additional electrode OM1 was placed at 30% of theinion-left tragus distance. The EOG was also recorded from the medial upper and lateral orbital rim of the left eye. Epochs contaminated with eye blinks or eye movement artifacts were off-line rejected.

Time-varying energy in the 24–60 Hz and 15–20 Hz band

So-called *induced* (or not stimulus-locked) oscillatory activities appear with a jitter in latency from one trial to the next. They thus tend to cancel out completely in the averaged evoked potential. The method used here (described in detail in Tallon-Baudry et al., 1996) is a wavelet-based time-frequency decomposition of the signal between 15 and 100 Hz, and provides the time-varying energy of the signal in each frequency band. Averaging the energy across single trials allows for the analysis of induced oscillatory activities. When this method is applied to the average evoked potential, only activities phase-locked to stimulus onset show up.

To quantify the time-varying energy of the signal around a frequency f_0 , the signal was convoluted with complex Morlet's wavelets $w(t, f_0)$ (Kronland-Martinet et al., 1987) having a Gaussian shape both in the time (standard deviation σ_t) and in the frequency domain (standard deviation σ_f) around its central frequency f_0 : $w(t, f_0) = (\sigma_t \sqrt{\pi})^{-1/2} \cdot \exp(-t^2/2\sigma_t^2) \cdot \exp(2i\pi f_0 t)$, with $\sigma_f = 1/2\pi\sigma_t$ and $f_0/\sigma_f = 7$. The time-varying energy $E(t, f_0)$ of the signal in a frequency band around f_0 is the squared norm of

the result of the convolution of the complex wavelet $w(t, f_0)$ with the signal $s(t)$: $E(t, f_0) = |w(t, f_0) * s(t)|^2$.

This method was applied on each single trials with f_0 ranging from 15 to 100 Hz in 1-Hz steps, and the results were averaged across single trials to quantify induced activities. We then considered, as in our previous study, the energy averaged in the two frequency bands 24–60 Hz and 15–20 Hz. The mean energy of the prestimulus (between –300 and –50 ms) was considered as a baseline level and subtracted from the prestimulus and poststimulus energy, separately in these two frequency bands. The same method was applied to the average evoked potentials.

Data analysis

On average, 128.5 correct trials per subject in the d1 condition, 129.0 in the d2 condition, and 121.8 in the d3 condition were included in the analysis after artifact rejection. Because we were interested in the analysis of activities during the delay, and not in the responses to S2, go and no-go trials were pooled together to increase the signal-to-noise ratio. Since subjects' performance was kept between 80 and 90% correct, there were not enough incorrect trials to analyze them.

The nonparametric Wilcoxon test for matched pairs and the nonparametric Quade test for related samples and Conover procedures as *post hoc* tests of significance were used (Conover, 1980). The Quade test is an extension of the Wilcoxon signed-rank test to the case of several related samples. It is performed by ranking data paired by subjects and provides an F value indicating whether or not there is a significant effect of the factor tested. If this effect is significant, Conover procedures indicate in which pairs of experimental conditions significant differences occur.

Results

Behavioral results

Each subject performed 180 trials in each condition. There were on average 30.1 ± 1.3 errors in d1 condition (delay = 800 ms), 28.4 ± 1.8 in d2 condition (delay = 1200 ms), and 34.0 ± 1.3 in d3 condition (delay = 1600 ms). The effect of delay duration on the number of errors was significant ($P < 0.01$, Quade test), and corresponded to a significant increase of the number of errors in the d3 condition (Conover procedures: d1–d3 conditions $P = 0.018$; d2–d3 conditions $P = 0.004$; d1–d2 conditions $P = 0.51$). There

Fig. 3. A: Time course of the induced energy in the 24–60 Hz band, at electrode POz and F3 in the three conditions. Following the OFF response, a slowly decreasing activity can be observed at POz. At F3 a more transient component appears at the beginning of the delay. B: Probability (Wilcoxon test for matched pairs) that the 24–60 Hz energy averaged in moving 200-ms time-windows significantly differs from baseline level (inverted logarithmic scale) in the d3 condition at posterior electrode POz (square) and at electrode frontal F3 (circle). The 24–60 Hz energy remains higher than baseline level for a longer duration at POz than at F3. No significant variation of the 24–60 Hz energy can be observed in the EOG (cross, thin lines). C: *Left.* Time course of the 24–60 Hz energy in the d1 condition (thick line) and in our previous experiment in the memory (thin line) and control (thin dashed line) conditions at electrodes POz and F3. At electrode POz, the 24–60 Hz energy falls down before the end of delay when the delay duration is fixed (thin line), whereas it remains sustained (arrow) when the end of the delay cannot be predicted (thick lines). At electrode F3, no such effect can be observed—rather, the activity seems more transient in the d1 condition than in our previous experiment. *Right.* Probability (Wilcoxon test) that the 24–60 Hz energy averaged in moving 200-ms time-windows significantly differs from baseline level (inverted logarithmic scale) in the d1 condition (square, thick line) and in the memory condition of our previous experiment (circle, thin line). At POz (top diagram), the level of gamma energy remains significantly higher than baseline until the end of the delay when its duration cannot be predicted. On the contrary at electrode F3 (bottom), it tends to be more transient when the delay duration cannot be predicted.

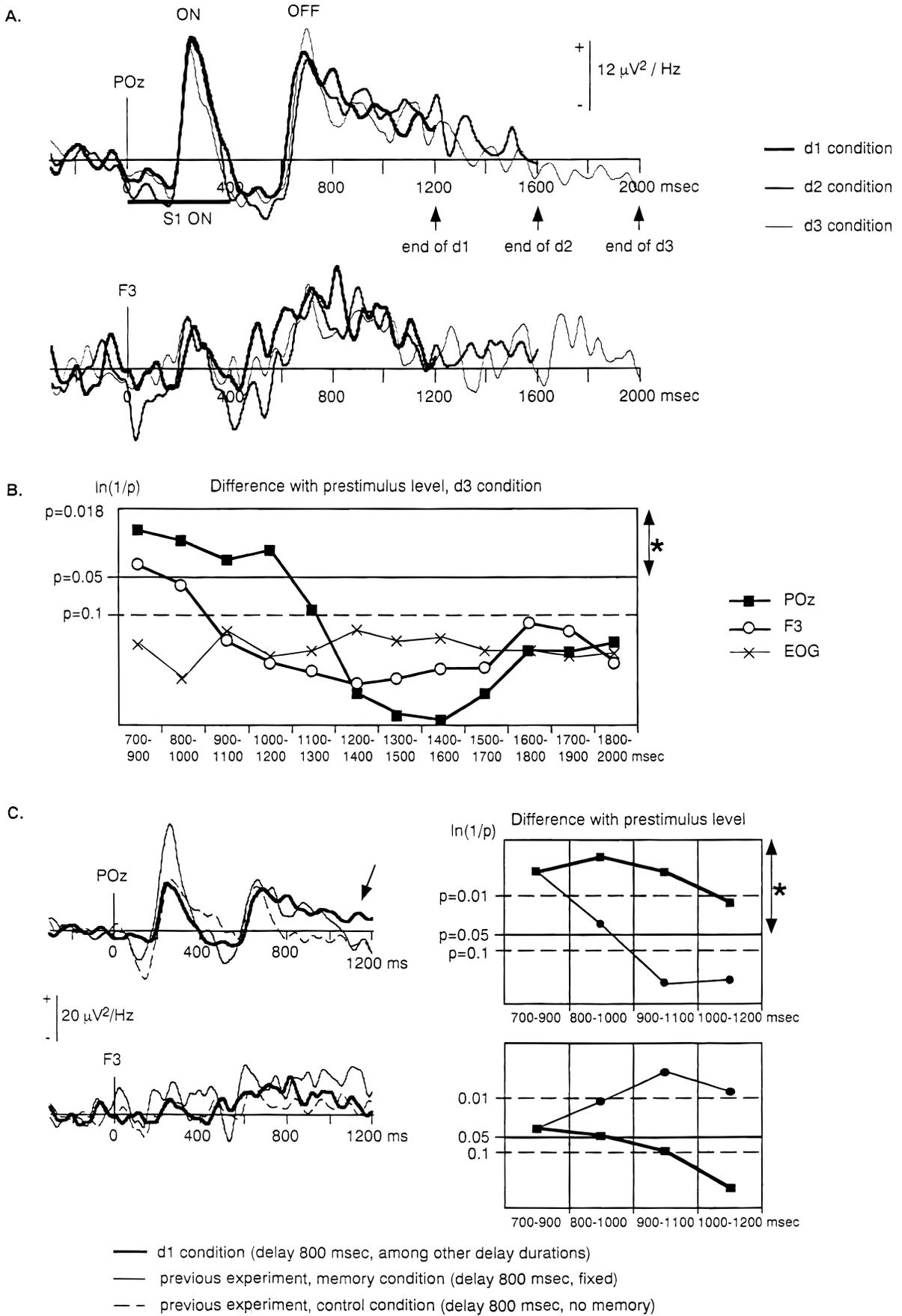


FIGURE 3

was no difference between the coefficients of difficulty in the three conditions (mean 11.8%, Quade test, $P > 0.2$).

Reaction times measured from S2 onset were on average 788.6 ± 32 ms in the d1 condition, 806.5 ± 37 in the d2 condition, and 824.8 ± 34 in the d3 condition. The tendency of reaction times to increase with delay duration did not reach the significance level (Quade test, $P = 0.08$).

It should be noticed that since the difficulty of the task was constantly modulated to maintain the subject's performance between 80 and 90% correct, it may have biased our estimation of the number of errors. To control this possibility, five additional subjects performed the task during two blocks of 90 trials, while the coefficient of difficulty was fixed at 9%. In this control behavioral experiment, the difficulty of the task was slightly increased as compared to the recording sessions, since in the behavioral sessions subjects were not required to control their eye blinks. The same increase in the number of errors in the d3 condition, compared to the d1 and d2 conditions, was observed (Quade test, $P = 0.017$; *post hoc* Conover procedures: d1–d2 $P = 0.78$ non significant, d1–d3 $P = 0.015$, d2–d3 $P = 0.009$).

Induced activities in the gamma and beta ranges

The comparison of the time-frequency analysis of single trials and of the average evoked potentials (Fig. 2) showed the existence of activities in the gamma (24–60 Hz) and beta (15–20 Hz) ranges in the time-frequency representation of the energy averaged across single trials only: these activities are induced by the stimulus, and thus disappear in the evoked potential.

Energy in the gamma band (24–60 Hz)

As in our previous experiment, the energy computed across single trials was averaged between 24 and 60 Hz. Fig. 3A shows its time course at electrodes POz and F3, in the three conditions. There was an overall good replicability of the data between conditions. At occipital electrodes, an ON response, induced by stimulus onset, peaked at about 280 ms, and an OFF response at about 700 ms (e.g. 300 ms after stimulus offset). This OFF response was followed by a sustained activity during the delay. It decreased slowly and crossed the prestimulus level at about 1500 ms in the d2 and d3 conditions. An activity during the delay could also be observed at F3 (Fig. 3A). This activity was more transient than the one observed at electrode POz. It was rising at about 500 ms, reached its maximum at about 800 ms, and fell down to baseline level at about 1200 ms.

To compare the time courses of occipital and frontal gamma activities, we tested at electrodes POz and F3 whether the 24–60 Hz energy in 200-ms moving time-windows was significantly different from prestimulus level in the d3 condition (Wilcoxon test). Fig. 3B shows that the 24–60 Hz energy in the 24–60 Hz band was significantly different from prestimulus level for a longer duration at occipital electrode POz than at frontal electrode F3. No significant enhancement of gamma activity could be observed in the EOG.

The time courses of the 24–60 Hz energy in the d1 condition and in our previous experiment were also compared (Fig. 3C, left). At electrode POz, the energy of the ON response was smaller in the present experiment, but the energy of the OFF response was similar in both experiments. During the delay, the gamma activity in the d1 condition of the present experiment was more sustained

(arrow) than in the previous experiment, where the duration of delay was fixed. On the contrary, at electrode F3, the 24–60 Hz activity seemed more transient in the d1 condition than in the previous experiment.

We tested both in the d1 condition and in our previous experiment whether the 24–60 Hz energy in 200-ms moving time-windows was significantly different from prestimulus level (Fig. 3C, right). In the d1 condition, the 24–60 Hz energy remained significantly higher than the prestimulus level until the end of the delay at electrode POz, whereas in the previous experiment it returned to baseline level about 200 ms before S2 onset. On the contrary, the 24–60 Hz at electrode F3 returned more quickly to baseline level in this experiment than in the previous one. The temporal courses of both the occipital and frontal gamma activities are thus modified depending on whether the latency of S2 onset can be predicted, but in completely opposite directions.

Energy in the beta band (15–20 Hz)

In the 15–20 Hz band, activities during the delay could be observed at POz and Fz (Fig. 4, solid lines) as in our previous experiment. At POz, only a transient increase appeared during the delay, between 600 and 1200 ms, whereas at electrode Fz the 15–20 Hz activity was more sustained, with a maximum at about 700 ms followed by a slow decrease until the end of the delay in the three conditions. The superposition of the data in the three conditions in this frequency band showed more variability than in the 24–60 Hz range. In particular, the transient response at POz seemed to be shorter in the d1 condition, and at Fz the energy seemed to be higher in the d2 condition between 1000 and 1200 ms, but the Quade test yielded no significant difference between the three conditions on the 15–20 Hz energy averaged in the 1000–1200 ms time-window, neither at Fz ($P = 0.24$) nor at POz ($P = 0.32$).

The time courses of the 15–20 Hz activity in the d1 condition and in our previous experiment were compared (Fig. 4A). Again, there was more variability than in the gamma range. At electrode POz, a transient increase appeared during the delay in both cases, but with a smaller amplitude in the d1 condition than in our previous experiment. At electrode Fz, the maximum of activity during the delay seemed to occur earlier.

The temporal courses of the occipital and frontal beta activities were just the opposite of those observed in the gamma band: the occipital beta component at POz was transient, ending at about 1200 ms, whereas the 15–20 Hz activity at Fz lasted longer. This is depicted in Fig. 4B: in the d3 condition, significant enhancements of beta energy compared to baseline level still occurred at late latencies at Fz, whereas they disappeared earlier at POz. No significant enhancement of the energy in this frequency band could be found in the EOG in any time-window.

Prestimulus level

Our data in the 24–60 Hz range and in the 15–20 Hz range were compared to a baseline level of energy estimated between –300 and –50 ms in each of the frequency bands studied. Therefore, we had to check whether there was a difference in the prestimulus level between the three conditions. No significant difference between conditions could be found at any electrode, neither in the 24–60 Hz band ($P > 0.51$, Quade test) nor in the 15–20 Hz band ($P > 0.27$, Quade test).

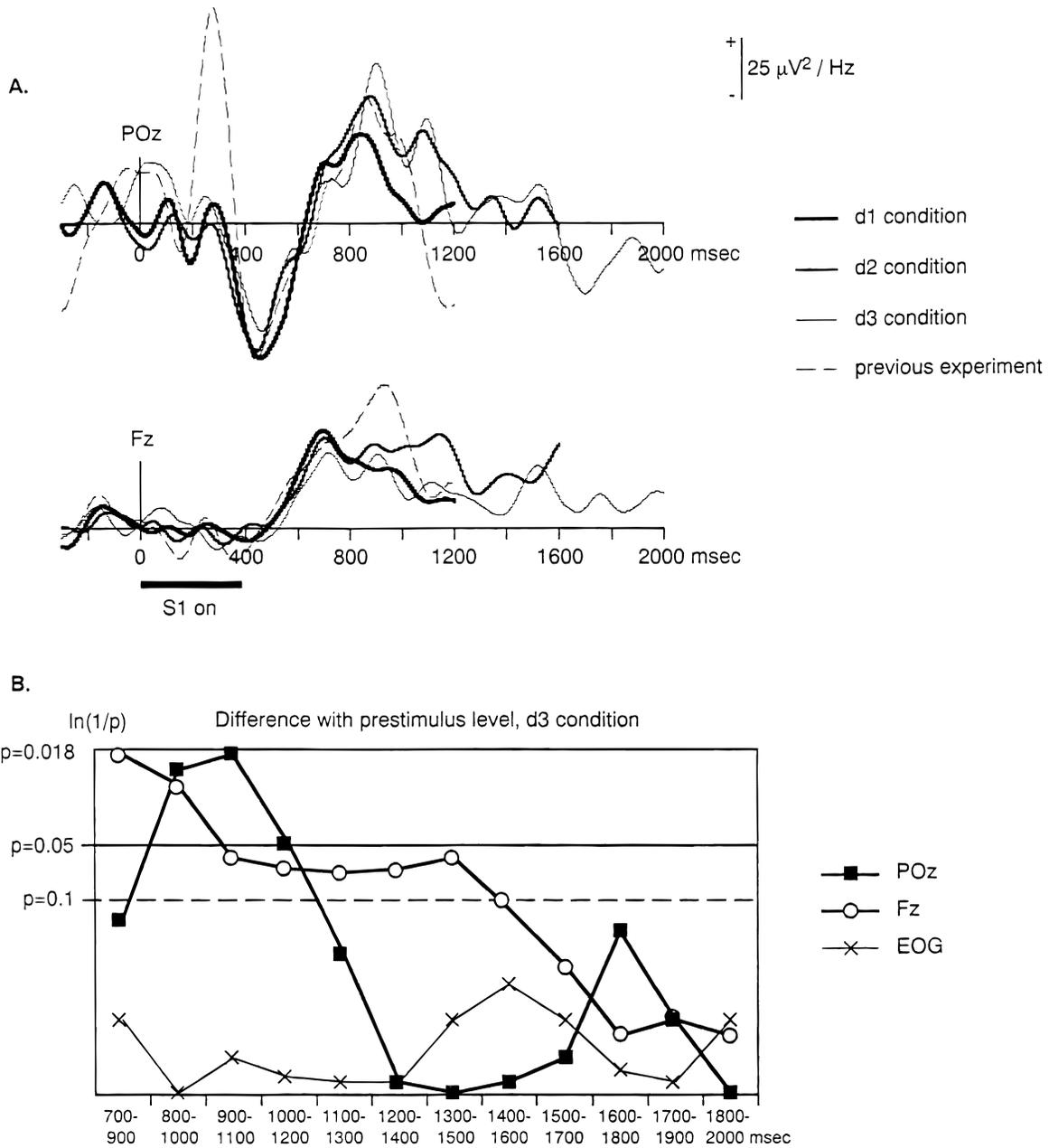


Fig. 4. A: Time course of the energy in the 15–20 Hz band in the three conditions (solid lines) and in the memory condition of our previous experiment (dashed line) at POz and Fz. During the delay, a transient response can be observed at POz, between 600 and 1200 ms, while at Fz a more sustained activity lasts until the end of the delay. Both the superposition of the three conditions and of the previous experiment show a greater variability in this frequency range than in the gamma range. B: Probability (Wilcoxon test for matched pairs) that the 15–20 Hz energy averaged in moving 200-ms time-windows significantly differs from baseline level (inverted logarithmic scale) in the d3 condition at posterior electrode POz (square) and at electrode Fz (circle). The 15–20 Hz energy remains higher than baseline level for a longer duration at Fz than at POz. No significant variation of the 15–20 Hz energy can be observed in the EOG (cross, thin lines).

Average evoked potentials

Average evoked potentials were low-passed filtered at 25 Hz (24 dB per octave). They were perfectly similar in the three conditions (Fig. 5). During the delay, a posterior negativity could be observed from about 600 to 1200 ms (arrows in Fig. 5).

In our previous experiment we had already identified this occipito-temporal negativity. It was combined with a more widely

distributed negativity, centered on centro-parietal locations but extending up to posterior electrodes and rising later. Fig. 6A shows the comparison of the evoked potentials in the d1 condition and in our previous experiment. The most striking feature was the complete suppression of the centro-parietal negativity in the d1 condition (thin arrows), whereas the occipito-temporal negativity was present in both experiments (thick arrows). To quantify this effect, the amplitude of the evoked potentials was averaged in 200-ms

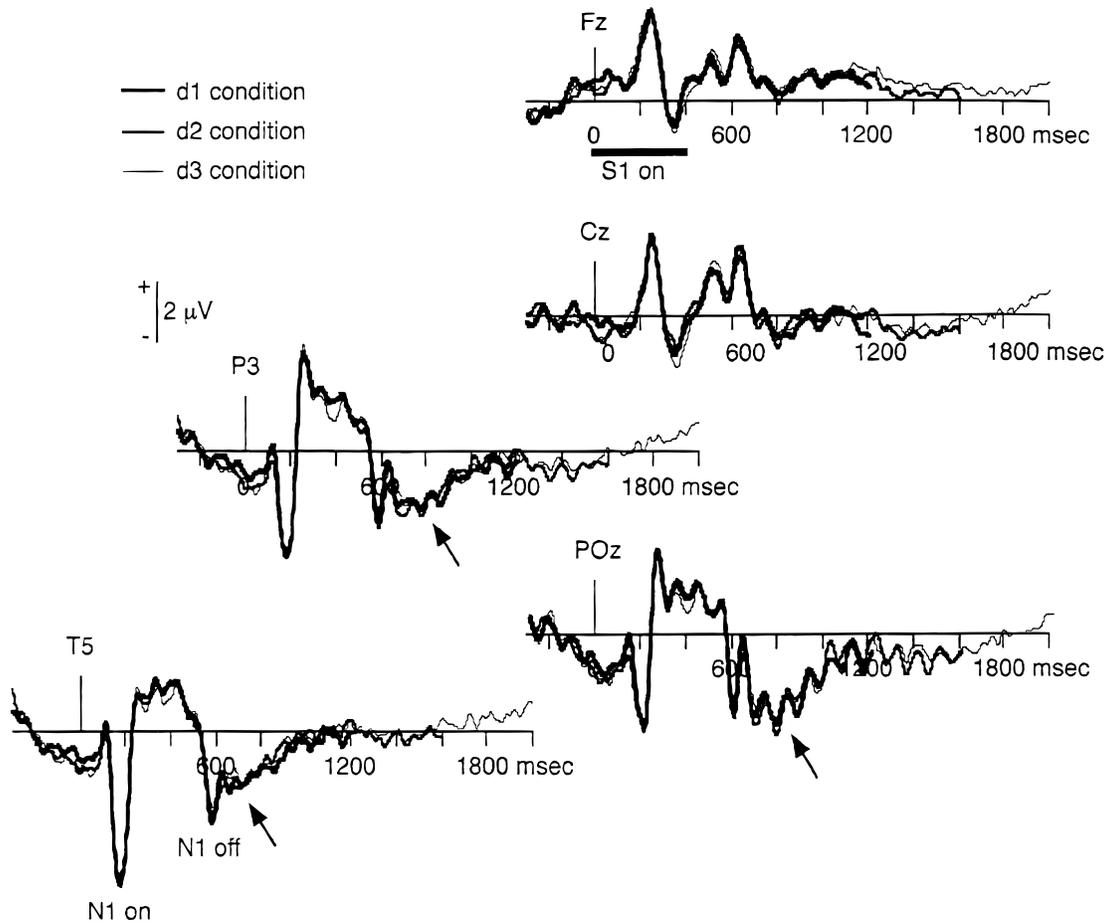


Fig. 5. Average evoked potentials in the three conditions at electrodes T5, P3, POz, Cz, and Fz. A posterior negativity develops at the beginning of the delay (arrow), but ends at about 1200 ms.

time-windows and compared to baseline level (Wilcoxon test, Fig. 6B). At electrode Cz, no activity during the delay differed from baseline in the d1 condition, whereas in our previous experiment a negativity reached the significance level at the end of the delay. At electrode O1, the negativity disappeared more quickly in the d1 condition than in our previous experiment.

Discussion

We had previously identified several components of the response during the delay that were enhanced in a memory *versus* control condition. In the present experiment, all these components could be observed again, with the exception of the centro-parietal negativity in the evoked potentials which will be discussed below. This shows the overall good replicability of the data between experiments. In addition, the data (both evoked potentials and oscillatory activities) superimposed quite well in the three conditions, corresponding to the three different delay values. No new component appeared at the end of the delay in the d3 condition, which seems to indicate that subjects had the same strategy, independent of the delay duration.

Furthermore, as we expected, the use of longer and variable delay durations allowed to discriminate between transient and sustained activities occurring during the delay. Transient components appeared at the beginning of the delay, at occipital electrodes in the

evoked potentials and in the beta band (15–20 Hz), as well as at frontal electrodes in the gamma band (24–60 Hz). Only the occipital gamma and frontal beta components showed a sustained level of activity throughout the delay, and are thus the most likely candidates to reflect the rehearsal of the first shape in visual short-term memory.

Sustained beta and gamma activities

The two sustained components (occipital gamma and frontal beta) showed a falling slope with time. In parallel, subjects' performance decreased with increasing delay. Thus, there is a parallel between the decreasing performance of the subjects and the decreasing energy of the occipital gamma and frontal beta rhythms, which provides further support for their functional role in holding an object representation active in short-term memory.

Still, none of these two oscillatory components remained statistically higher than baseline level until the end of the longest delay, whereas in the d3 condition the performance still reached 81% correct answers on average. This must not be incompatible since the baseline level chosen (energy prior S1 onset), although allowing comparison between conditions or between experiments, is not an absolute zero reference: in particular, it includes the activities induced by the appearance of the fixation point. Consequently, it is not the absolute value of the energy which should be

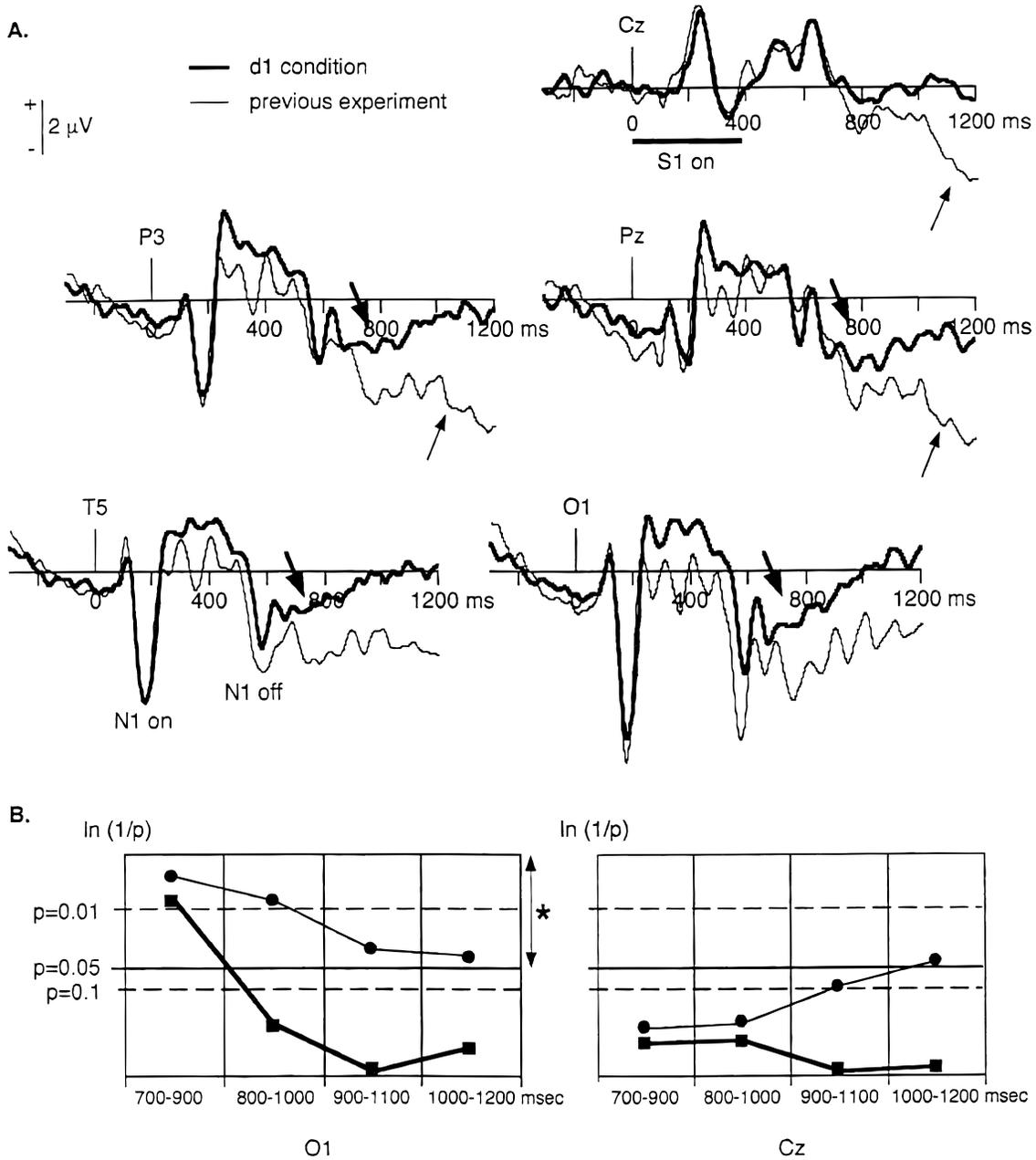


Fig. 6. A: Evoked potentials in the d1 condition (thick lines) and in the previous experiment (thin lines). The posterior negativity at the beginning of the delay can be observed in both cases (thick arrows), whereas the more centro-parietal negativity developing later is observed only when the delay duration is fixed (thin arrows). B: Significant differences with baseline (zero level) in 200-ms moving time-windows, at O1 and Cz, in the d1 condition (squares) and in the previous experiment (circles). When the delay duration cannot be predicted, the only component significantly different from baseline is the transient posterior negativity developing at the beginning of the delay.

considered, but its time course: a sustained component is characterized by a regular slope. Only the occipital gamma and frontal beta activities showed this time course.

Since both these components (1) disappeared when no memorization was required (previous experiment) and (2) showed a sustained time course when the delay duration was increased (present experiment), they are very likely to reflect the continuous rehearsing of S1 in memory. As revealed by the comparison with our previous experiment, the time course of the occipital gamma com-

ponent is strongly affected by the fact that the delay duration is fixed or not. In our previous experiment, it tended to decrease before the end of the delay. This was probably due to an active anticipation of S2 onset, because this onset could be easily predicted.

A sustained time course would also be expected for activities reflecting two other processes, namely expectancy and motor preparation. It seems unlikely that the occipital gamma or the frontal beta activities reflect motor preparation because in that case they should increase until movement onset (Pfurtscheller et al., 1994),

whereas they are slowly decreasing. Furthermore, these activities disappeared in the control condition of our previous experiment, in which motor preparation was required. An activity reflecting expectancy would also be expected to increase during the delay. In addition, the contingent negative variation we observed in our previous experiment disappear here. This could indicate that both expectancy and motor preparation are reduced in this experiment compared to our previous one, whereas both the occipital gamma and the frontal beta activities during the delay show amplitudes which are similar in both experiments. For all these reasons, it seems unlikely that these sustained oscillatory activities during the delay reflect only motor preparation or expectancy.

As underlined in the Introduction, gamma activity peaking at occipital electrodes in response to a coherent visual stimulus (Lutzenberger et al., 1995; Müller et al., 1996, 1997; Tallon-Baudry et al., 1996, 1997) could reflect the synchronization of the areas participating in the representation of this object. Here, the occipital gamma activity during the delay may reflect the holding in memory of the sensory trace of S1 that is needed to achieve later the matching process with S2. The functional interpretation of the sustained frontal beta rhythm is less clear. Nevertheless, frontal areas have been repeatedly shown to be involved in short-term memory processes in humans (Swartz et al., 1995; Courtney et al., 1996, 1997) and in monkeys (for review, Goldman-Rakic, 1995; Desimone, 1996). Furthermore, this frontal beta activity was shown to disappear when no memory process is required (Tallon-Baudry et al., 1998).

Transient beta and gamma activities

Transient oscillatory activities appeared at the beginning of the delay at frontal sites in the gamma band and at occipital sites in the beta band. In our previous experiment, they disappeared when no memorization of the stimulus was required. Thus, they may play a role in the initial transient phase of the memory process. Nevertheless, since data on oscillatory components of the response in similar paradigms are lacking, it is difficult to be more precise on their functional role.

The existence of different time courses for spatially distinct activities (occipital and frontal), both in the gamma and in the beta ranges, shows that induced oscillatory activities should not be considered as a whole, but analyzed as distinct spatial and temporal components. This observation does not preclude functional relationships between these components: for instance, whether these occipital and frontal oscillatory activities are transiently synchronized at the beginning of the delay remains an open issue.

Evoked potentials

In the evoked potentials, two negativities overlapping in time seemed to be related in the memory condition in our previous experiment: an occipito-temporal one and a more centro-parietal one, developing later. These two negativities during the delay of such a task had already been observed by Ruchkin et al. (1995) in a paradigm where the delay duration was also fixed. When, as in the present experiment, the delay duration varies, the occipito-temporal negativity appears more clearly as a transient component, and the centro-parietal negativity is completely suppressed. This latter negativity thus probably rather reflects an anticipatory process due to the strict contingency between S1 and S2 than an activity related to memory rehearsing. Both its topography and time course suggest that it belongs to the family of contingent variation negativ-

ities (for review, Tecce & Cattanach, 1987). The transient occipito-temporal negativity appearing at the beginning of the delay may reflect part of the initiation of the memory rehearsal.

Conclusion

The time course of the occipital induced oscillatory activity in the gamma band suggests that it is related to the maintenance of the sensory trace which is necessary for the delayed matching process. The functional role of the sustained frontal beta activity is less clear, but it could be related to the known involvement of prefrontal areas in such delayed matching-to-sample tasks. These results support the hypothesis that oscillatory synchronization serves to bind distributed sets of neurons into a coherent representation of memorized contents.

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