

RESEARCH NOTE

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Electrophysiological localization of brain regions involved in perceptual memory

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Abstract Event-related potentials (ERP) were recorded during perceptual discrimination and short-term memory, varying the interstimulus interval (1–10 s) in delayed spatial frequency discrimination. Accuracy of discrimination remained unimpaired across this time interval, but choice reaction times increased. A brain source localization (BESA) model showed that the activity of the parietal and right temporal sources increased with long retention intervals in a sequential activation pattern where a long-latency component of the parietal source specific to the memory condition was observed, the latency of which matched a memory-related increase in choice reaction times in the cognitive task. It is suggested that the temporal sources are involved in encoding and storage of visual information, and the parietal source is involved in memory retrieval.

Key words Event-related potentials · Memory · Spatial frequency · Human

Introduction

The importance of visual representations in human memory has been generally acknowledged (Farah 1995). However, it has proved difficult to develop experimental strategies that isolate the encoding, storage, and retrieval processes of the visual component of memory, as pictorial information is coded in both visual and verbal or categorical representations (Paivio 1995). One approach is to use complex, hard-to-name fractal-type patterns (Klingberg et al. 1994). A second approach, used in the present paper, is to simplify stimuli and study storage of those elementary visual attributes shown by visual neurophysiology

and psychophysics to be the building bricks of visual images, such as the spatial frequency, orientation, contrast, and movement of visual stimuli (De Valois and De Valois 1990).

Recent psychophysical experiments measuring discrimination thresholds for spatial frequency against memory representations of reference stimuli have demonstrated high-precision storage in short-term memory, with discrimination thresholds around 5% for retention intervals in the range of 1–60 s (Magnussen et al. 1996; Magnussen and Greenlee 1998), suggesting that spatial frequency information is important in storing visual images. The type of memory mechanism that might achieve this high-fidelity memory performance is not known, but the perceptual representation system (PRS) proposed by Tulving and Schacter (1990) is a likely candidate. The PRS, which is largely non-declarative and reveals its influence through implicit memory tests, is believed to be composed of a number of subsystems distributed in the brain, each of which stores information about particular structural properties or features of the visual image. PET studies show that brain regions involved in perception are also recruited in imagery tasks (Farah 1995), suggesting a close relationship between perception and memory.

Neurophysiological studies indicate that the temporal lobes and especially the inferotemporal regions are important in linking on-line perceptual analysis to memory representations (Miyashita 1993). Neuropsychological studies have confirmed this for the specific task of delayed spatial frequency discrimination (Greenlee et al. 1993), and event-related potential (ERP) studies (Begleiter et al. 1993) conclude that the same regions, especially in the right hemisphere, are involved in short-term memory for abstract line patterns. In the present experiment, we have studied ERP correlates of short-term memory for spatial frequency in a delayed discrimination task where perception and memory measurements are distinguished only by the time factor, allowing differences in ERP patterns to be exclusively tied to the memory component. The search for a memory component in the ERP pattern was guided by the recent demonstration of a reaction time component

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that is specific to memory retrieval (Magnussen et al. 1998).

Method

Cognitive task

Stimuli were vertical, sinusoidal luminance gratings generated on a high-resolution color monitor by a Cambridge Research Systems graphic card, presented in a circular window subtending 5° visual angle. The grating contrast was modulated by a temporal Gaussian within a 200-ms time window, with a maximum contrast of 20%; previous cognitive studies of memory for spatial frequency have employed both Gaussian (Greenlee et al. 1993; Magnussen et al. 1996) and rectangular (Magnussen et al. 1998) modulation. For the ERP recording, a Gaussian modulation has the advantage that it contains no higher harmonic components.

Spatial frequency discrimination was measured by a two-interval forced choice procedure, where the subject decided which of two successively presented gratings had the higher spatial frequency. The difference in spatial frequency between test and reference gratings were individually adjusted to produce around 75% correct responses, and varied between 5% and 15%. Two reference spatial frequencies, 1.25 cycles/° and 5 cycles/°, were randomly mixed in a single run. In addition, a $\pm 10\%$ random jitter of reference spatial frequency was introduced to prevent a build-up of long-term representations of particular spatial frequencies. Thus, each trial introduced two fresh gratings, with the computer randomly assigning the higher spatial frequency to the first and second interval. The interstimulus interval (ISI) was either 1 s or 10 s, fixed within a single run of 40 trials; between stimulus exposures the subject kept her/his gaze at the blank screen. The subjects completed three runs for each ISI in an approximate counterbalanced order; giving a total of 120 trials in each ISI condition. Accuracy and choice reaction times (RT) were recorded together with ERP measurements. The subject was sitting comfortably in a easy chair with a small response box resting in the lap and the left and right thumb on two response buttons. They pressed the left button if the first grating of the pair had the highest spatial frequency and the right button if the second grating had the highest spatial frequency and were instructed to respond as fast and accurately as possible. The response triggered a new trial after 3 s. The experimental session, including preparation for ERP recording, lasted about 1.5–2 h. A brief practice run preceded the experiment.

ERP recording

Continuous EEG activity was recorded with a Synamp (Neuroscan) DC amplifier, and after epoching, the single sweeps were high-pass filtered above 0.1 Hz (24-dB attenuation). The trigger for the sweeps was placed at the onset of the sinusoidal stimulus envelope, so the latencies of conventional ERP deflections may be expected to be longer than in otherwise comparable studies. The procedure for measuring ERP was modeled on that of Begleiter et al. (1993), with 31 recording electrodes referenced to Cz. In addition to the conventional channels of the 10–20 systems, we interposed electrodes between the F and C lines (FC3, FC5, FC4, FC2), between the C and P lines (CP3, CP5, CP2, CP4), and between the P and O lines (PO3, PO5, PO2, PO4). Bipolar electrodes placed above and below the left eye and at the outer canthi of the eyes were used for recording eye-movement artifacts. Impedance was kept below 5 k Ω , and the continuous recording was epoching into sweeps from 100 ms pre- to 800 ms poststimulus trigger onset. Epochs with amplitudes above 70 μ V on the eye-movement or EEG channels were rejected, and baseline adjustment was employed, with mean activity during the 100 ms preceding stimulus onset set to zero.

Subjects

Nine healthy students and staff members were recruited; all signed an informed consent. Three subjects were excluded from further analysis because performance on the cognitive task was close to chance performance (less than 60% correct).

Results

Confirming previous experiments (Magnussen et al. 1998), the behavioral data showed no memory loss in terms of accuracy. Subjects performed as well when discrimination was made with reference to a 10-s-old memory image (73% correct) as they did in immediate discrimination (74% correct), but there was an increase of 115 ms in RT for correct responses in the memory condition (950 ms compared with 1065 ms, in the 1-s and 10-s ISI conditions, respectively ($F=59.27$, $P=0.0001$)). While it is conventional in cognitive psychology to calculate RTs for correct responses only, it should be noted that, in a two-alternative forced choice task where chance probability is 0.5, it is not possible to separate “correct” trials based on guessing from those based on perceptual discrimination. Control statistics of RTs including incorrect trials gave the same picture (see also Magnussen et al. 1998), and correct and incorrect trials were therefore collapsed in the analyses of the ERP data.

Grand mean waveforms observed for test stimuli at 1-s and 10-s ISIs are shown in Fig. 1. Since there are no essential differences in the occipital visual evoked potential to spatial frequencies in this frequency range (Plant et al. 1983), data for the two spatial frequencies have been collapsed. The experimental conditions resulted in ERPs characterized by a negative complex starting about 250 ms after trigger and lasting until about 600 ms after trigger. Subcomponents varying according to experimental condition (time) and electrode are suggested by the panels. The waveforms resemble the complex labeled peaks 3–5 by Begleiter et al. (1993), except that the present latencies are about 150 ms longer. This is probably due to the Gaussian temporal envelope of the stimulus contrast in the present experiment. As an initial check on the reliability of the differences, we selected the recording from the Oz electrode in the 1-s and 10-s ISI and defined peaks labeled P250, N340, P410, and N500. When the maximum amplitudes for each subject in appropriate time windows centered on the peaks were measured, reliable quantitative differences between test stimuli in the 1-s and 10-s delay condition for the N340, P410, and N500 subcomponents were observed in all subjects ($P=0.023$, Wilcoxon signed rank test), indicating that the grand mean waveforms represent stable tendencies across individuals and justifying the use of group data in the search for cerebral sources underlying discrimination and memory.

With a source analysis approach (BESA; Scherg 1996) to ERP data, the selection of recording sites and particular curve segments for analysis is avoided and a solution for the whole curve complex from 200 to 600 ms is explored. We used an approach constrained by anatomical assump-

Fig. 1 Grand mean waveforms across subjects for selected posterior electrodes, showing time-related changes in event-related potential amplitudes to the test stimulus for 1-s and 10-s interstimulus intervals (*ISIs*)

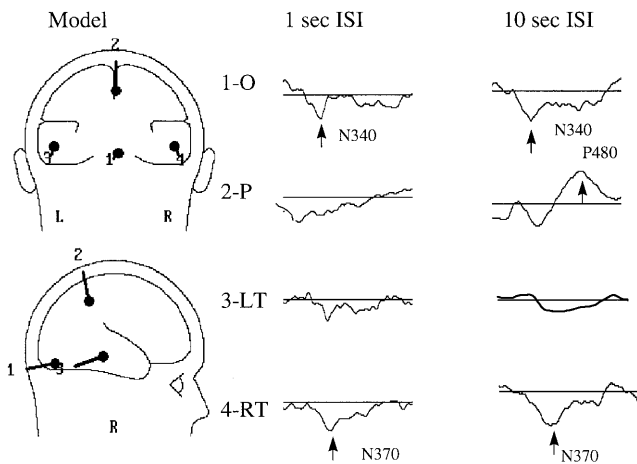
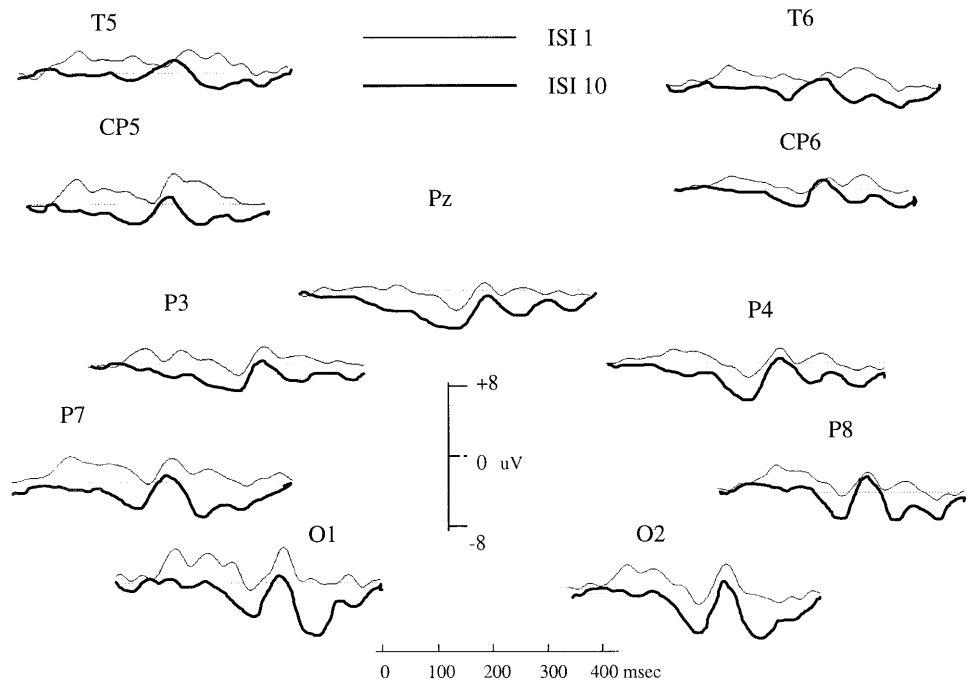


Fig. 2 Source localization model used to explain the observed event-related potential curves: 1, occipital; 2, parietal; 3, left temporal; 4, right temporal. Derived source waveforms for the 1-s ISI and for the 10-s ISI. Arrows denote latency, polarity (*N*; negative; *P*, positive) and source strength at observed maxima

tions about location of sources, assuming initially regional occipital and temporal sources, where the temporal source has a symmetrical right and left side representation to allow for hemispheric asymmetries, and an additional source located along the anterior-posterior axis. Testing alternative locations for this source indicated that a parietal source gave the best explanatory model.

Figure 2 shows the model and the resulting solution with optimal orientations of the sources with reference to the test stimulus in the delayed discrimination task, providing solutions that accounted for 9.9% and 9.5% residual variance in the 1-s and 10-s ISI conditions, respectively. In the 1-s ISI condition (center panel, Fig. 2), the

source waveforms (mathematically derived curves representing the underlying sources) indicate an early activity in the parietal (*P*) source, and then maxima in the time frame 340–370 ms for both the occipital (*O*), left temporal (*LT*), and right temporal (*RT*) sources, with the *O* source leading in latency. We assume that the amplitudes reflect strength and, in the 340- to 370-ms time frame, the *O*, *P*, *LT*, and *RT* sources account for 35%, 10%, 24%, and 31%, respectively, of the total activity. The ratio of left to right temporal activity is 0.78, indicating a stronger right-hemisphere involvement.

The source waveforms in the 10-s ISI (Fig. 2, right panel) display a maximum in the time frame 340–370 ms as observed for the 1-s ISI, with two notable differences. First, the parietal source is more active and the relative contributions of *O*, *P*, *LT*, and *RT* are 29%, 21%, 20%, and 30%, respectively. Secondly the ratio of *LT* to *RT* activity decreases to 0.68, indicating a stronger hemispheric asymmetry in memory compared with the perception condition. Readings at 480 ms showed that the relative contributions of *O*, *P*, *LT*, and *RT* were 25%, 40%, 9%, and 16%, respectively.

The stability of the regional source model described was tested by adding another source in a frontal location and by postulating two laterally symmetric parietal sources. None of these strategies resulted in solutions with improved explanations.

Discussion

Perception and memory for visual spatial frequencies involve a topographically distributed set of posterior brain regions. Focusing on ERP segments showing a systematic effect of memory interval, the BESA analyses indicate an

asymmetric temporal lobe activity in favor of the right side and an increase in asymmetry in the memory (10-s ISI) condition. These activity patterns include activity peaks in a time frame of 340–370 ms poststimulus, which probably correspond to the visual memory potential (VMP) described by Begleiter et al. (1993). The results further confirm their finding of a dominant right temporal involvement in visual memory, obtained with different stimulus material, different test procedure, and a different method of localization analysis. The direction of the hemispheric asymmetries observed for low-to-medium spatial frequencies in both the perception and memory conditions in the present study is consistent with the spatial frequency hypothesis of hemispheric asymmetry in visual processing (Christman 1997).

The four-source model is equally successful with 1-s and 10-s ISIs, suggesting that the same set of regions are active but with adjustments of relative strengths and with a more pronounced sequential activation pattern as ISI increases. Comparisons of the activation patterns in the perception (1-s ISI) and memory (10-s ISI) conditions, distinguished only by the time factor, might thus indicate underlying processes specific to memory. The present results demonstrate a well-defined parietal component with long latency (480 ms) that is specific to the memory condition. Interestingly, this component has a comparable time relationship to the maxima, centered at 360 ms, observed in both perception and memory conditions, to the increase in the choice RT observed behaviorally (115 ms compared with 120 ms) and is probably related to the retrieval of information from perceptual memory. This interpretation assumes that the components identified by the model reflect either perceptual encoding (occipital and temporal sources) or memory retrieval (parietal source); the decision process which is based on the output of these mechanisms is not identified by the model.

In conclusion, the present results suggest that while encoding of basic stimulus dimensions in short-term memory involves several brain regions, the parietal lobe has a unique role in retrieving information from perceptual memory; the RT increase as well as the appearance of the long-latency ERP component may index these retrieval-related cognitive mechanisms. The absence of a frontal source is a typical finding in PET studies of priming

(Cabeza and Nyberg 1997) and is consistent with the idea the perceptual memory is associated with the PRS (Tulving and Schacter 1990).

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