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Event-related potentials during memorization of spatial locations in the auditory and visual modalities

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Abstract

Event-related potential (ERP) studies of working memory have used delayed S1-S2 match-to-sample tasks in which S1 is held in memory for comparison with S2. ERP negativities in the S1-S2 interval have been interpreted either in terms of working memory operations, or in terms of general preparatory motor processing. Two experiments (N = 20 each) were carried out to explore the nature of ERP negativities in a visuospatial memory task and in an auditory spatial memory task, respectively. In the experimental condition, subjects had to memorize the location of S1 (S1-memorize) so as to respond whether S2 appeared in the same spatial location (S2-memorize). In the control condition, subjects were requested to ignore S1 (S1-passive), and to respond whether S2 matched or not a target location predetermined at the beginning of the trial block (S2-pressing). Results support the two main conclusions of Martin-Loeches et al. (Electroenceph. clin. Neurophysiol., 1994, 91: 363–373). Firstly, that the encoding into memory of spatial location is associated with an ERP negative wave over the brain areas putatively associated with the processing of sensory information (i.e. right parieto-occipital for the visual task; fronto-central and left temporal areas for the auditory task). Secondly, the P300 does not seem to be an important ERP feature related to spatial location encoding and retaining into memory. Despite the distinct scalp distribution of these memory-related, modality-specific ERP negativities, they also showed a considerable degree of temporal synchronicity across modalities. © 1997 Elsevier Science Ireland Ltd.

Keywords: Event-related potentials; Spatial memory; Spatial perception; Working memory

1. Introduction

Research into the brain mechanisms of storage and maintenance of information in the human brain has benefited from the technique of scalp-recorded event-related potentials (ERPs). ERPs are useful towards the making of inferences about the timing and anatomical localization of these memory processes. Most ERP studies addressing these issues have employed variations of the delayed match-tosample paradigm. In this task the subject is presented with an initial stimulus (S1) that must be committed to memory for a delayed comparison with a subsequent stimulus (S2), following which the subject decides whether the two stimuli matched or mismatched (Lang et al., 1992; Ruchkin et al., 1992, 1995; Begleiter et al., 1993; Starr et al., 1996). Apart from its simple experimental logic, the match-to-sample paradigm has the advantage of being easily implemented with subhuman primates during single unit recording (Fuster, 1995; Ungerleider, 1995), which improves the grounds for inference on the neurophysiology of ERP results in humans.

The commonest finding across ERP studies has been a negative slow wave which differs in topography depending on the modality and the kind of information to be memorized. Thus, memorization of verbal material is generally associated with a sustained negative shift which is maximal over fronto-central and temporal regions for auditory stimuli (Patterson et al., 1991; Lang et al., 1992; Ruchkin et al., 1992; Starr et al., 1996), but is centred more posteriorly for visual material (Patterson et al., 1991; Ruchkin et al., 1992, 1995; Rämä et al., 1995).

In our laboratory a negative ERP wave was reported during the S1-S2 interval of a match-to-sample task in which the subject had to memorize the spatial location of small white vertical bars displayed on a computer screen (Martin-

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Loeches et al., 1994). Such a simple protocol was intended to keep stimulus features and task parameters to a minimum. ERPs recorded during the S1-S2 interval were characterized by a long-lasting negativity distributed bilaterally over occipital and temporal areas, and was attributed to processes specifically related to the encoding of spatial information into memory. Plausible origins for this negativity coincide with sites of maximal ERP changes related to processes of visual feature extraction (e.g., Ol and Or; Mangun and Hillyard, 1991).

More commonly, the P300 wave has been associated with memory encoding processes (Fabiani et al., 1990; Donchin and Fabiani, 1991). However, ERP results from Martin-Loeches et al. (1994) prompted their suggestion that 'the P300 is not an important ERP feature related to spatial location encoding and retaining in memory' (p. 370). Their data suggested that the memory encoding of spatial information seemed to recruit activity from neuronal networks in the primary and secondary visual cortices, rather than from third-order association and polysensory cortices (Fuster, 1995; Rösler et al., 1995). It might be argued, though, that the long-lasting negativity found by Martin-Loeches et al. (1994) was partly confounded with motor preparation, particularly as their passive task did not provide an adequate control for the S1-S2 match-to-sample memory task condition, and response preparation processes are known to develop in S1-S2 paradigms (McCallum, 1988; Birbaumer et al., 1990; Starr et al., 1996).

The present study improves and extends results from our previous study in three different ways. Firstly, ERPs are recorded during a spatial memory S1-S2 match-to-sample task in which subjects have to memorize the spatial location of S1 in order to respond whether or not S2 appears in the same spatial location. Comparisons are made against an S1-S2 passive-pressing control task, where subjects have to ignore S1, and respond whether or not S2 matched a target location predetermined at the beginning of the task. The passive-pressing task is assumed to provide an adequate control for the motor preparation processes in the spatial memory S1-S2 task. (That is, in both the memory task and the control task, motor responses have to be issued only after S2 onset). The main purpose of this design is to dissociate ERP negativities due to motor preparation from those due to memorization of simple spatial information. Secondly, spatial memory is assessed employing an openfield distribution of stimulus sources. This was intended to extend ERP results during memorization of spatial location to a more ecologically valid situation, and to establish a theoretical and empirical bridge with spatial attention studies in animals (i.e. Fuster, 1995). Thirdly, both visual and auditory modalities are examined in two otherwise methodologically identical studies. Our main hypothesis is that ERPs elicited during memorization of spatial location, devoid of motor preparation processes, will be maximal over primary cortical areas involved in the analysis of simple stimulus features (Damasio, 1990; Fuster, 1995), rather than being circumscribed to modality-independent, polysensory cortical areas.

2. Methods and materials

2.1. Subjects

Forty right-handed subjects (20 females) took part in the study, with ages between 18 and 30 years (mean 22 years, SD 3 years). All subjects had normal or corrected to normal vision, and none informed of having any audiological problems. Subjects were recruited through advertisement in the university campus magazine and were paid for their collaboration. Twenty subjects performed the visual task and another 20 subjects performed the auditory task (10 females in each).

2.2. Stimuli

Five loudspeakers and 5 red light-emitting diodes (LEDs) mounted on a purpose-made semicircular campimeter 70 cm in diameter served as stimulation devices. Auditory stimuli consisted of tone pips (1.5 kHz, 90 dB SPL at head position, 100 ms in duration, 10 ms rise-fall time). Tone pips were delivered through a set of 5 hi-fi loudspeakers (Audimax). One of the speakers was placed 40 cm away and in front of the adjustable chin-rest of the campimeter (0° azimuth). The other 4 speakers were placed at equal distances from the chin-rest at azimuths 30° , 60° and -30° , -60° . The chin-rest was adjusted for each subject so that the eyes were in the same horizontal plane (0° elevation) as the loudspeakers. Flashes 2.5 cd/m² in intensity and 100 ms in duration were delivered through 5 LEDs, each mounted in the middle of one loudspeaker. Throughout the task subjects were requested to fix their eyes on a yellow spot visible 5 cm below the central LED. The sequence of presentation was programmed and controlled with the Gentask module of the STIM package (NeuroScan Inc.) installed in a Dell 486 microcomputer. Both latencies and response errors were stored on disk.

2.3. Tasks and procedure

A match-to-sample S1-S2 paradigm was employed both for the memory task and for the control task. In the memory task, the spatial location of the first stimulus had to be memorized in order to respond whether the second stimulus appeared or not in the same location as the first stimulus. In place-match (target) trials, the second stimulus (S2-memorize) appeared in the same spatial location as the first one (S1-memorize). In place-mismatch (non-target) trials, S2 did not appear in the same location as S1. Subjects were instructed to respond (YES/NO) at the onset of S2 using a two-button PC mouse. The interstimulus interval was 2 s. Intertrial intervals varied randomly between 2–3 s (mean sequence of trials. The control task consisted of the same general S1-S2 protocol as the memory task. However, subjects were requested to respond YES or NO depending on whether S2 matched or not a target location determined at the beginning of the trial block (S2-pressing condition). Subjects were instructed just to ignore S1 (S1-passive condition). Therefore, motor responses had to be issued only after the onset of S2 both in the control task and in the memory task. Half the total number of 240 trials were place-match trials. Place-mismatch trials were equally distributed across the remaining 4 locations. Target locations for the S1-S2 passive-press task changed within and across subjects to yield even numbers experiment-wise.

between blocks. Each subject received a different random

The order of presentation of the memory and control tasks was counterbalanced within groups, and the hand used by the subject to respond was swapped midway through the session. A practice session of 10 trials was carried out prior to each task, which served to acquaint subjects with the tasks, and make sure that instructions had been understood. After the experimental session, subjects responded to a debriefing questionnaire in which they described their performance, identified the easiest and most difficult aspects of the tasks, and explored the type of cognitive strategy employed. Subjects were instructed to relax their facial muscles, fixate the central fixation point, not to move their eyes and avoid blinking as much as possible. The testing room was a dimly lit, sound-attenuating chamber. Subjects were instructed that performance accuracy was more important than response speed. Feedback was provided in the practice session, but not during the experimental session.

2.4. ERP recording

Electroencephalographic (EEG) and electrooculographic (EOG) data were recorded using an electrode cap (Electro-Cap International) with tin electrodes. The electrode sites were F7, Fz, F8, T7, Cz, T8, P3, Pz, P4, P7, P8, PO3, PO4, O1, and O2 of the revised 10/20 International System (American Electroencephalographic Society, 1991). The electrooculogram (EOG) monitored eye movements using an oblique derivation from the external canthus of the right eye to the upper canthus of the left eye. Impedances were always kept below 3 k Ω . The EEG and EOG were recorded from DC, with a high frequency cut-off of 30 Hz (12 dB/octave slope). The EEG and EOG channels were continuously digitized at a sampling rate of 200 Hz for the duration of each task block. These data were stored on disk together with stimulus and response markers for offline analysis.

2.5. Data analysis

Averaging epochs of 2000 ms with a prestimulus interval of 500 ms were extracted from the continuously digitized EEG. Eye movement artifacts were removed following the method described by Semlitsch et al. (1986). Epochs that were contaminated by artifact or by remaining EOG activity after correction were rejected prior to averaging. Trials with incorrect responses were also excluded from the averages.

One separate average was computed for each of the 4 task conditions, namely, S1-memorize, S2-memorize, S1-passive, and S2-pressing. Averaged ERPs were aligned using the average amplitude in the time window 500–300 ms prior to stimulus onset as a baseline. This period was adopted as a baseline in order to assess the nature of stimulus preceding negativities which developed prior to both S1 and S2, and which were affected by the manipulation of experimental variables. An analysis of absolute mean amplitudes in the 500–300 ms time window prior to stimulus onset showed that this period was not affected by the manipulation of experimental variables, and therefore, could be considered an adequate baseline for later comparisons.

The mean amplitudes of the major waveforms were calculated in the time windows -200 ms (200-100 ms prior to onset), -100 ms (100-0 ms prior to onset), P100 (50-100 ms), N100 (100-170 ms), P200 (170-220 ms), N200 (220-270 ms), P3a (270-450 ms), P3b (450-700 ms), Slow Wave 1 (SW1, 700-1000 ms), Slow Wave 2 (SW2, 1000-1300 ms). These latency windows were chosen to be as similar as possible to the ones used in the study by Martin-Loeches et al. (1994).

Mean ERP amplitudes in these time windows were submitted as dependent variables to the BMDP/4V package for analysis of variance (ANOVAs) for repeated measurements. ANOVAs included the factors: Task (S1-memorize, S2memorize, S1-passive, S2-pressing), Hemisphere (left and right), and Electrode site (frontal, temporal, parietal, parieto-temporal, parieto-occipital and occipital). Two orthogonal contrasts were defined for the test of simple effects. The M1 vs. P1 contrast explored differences between S1memorize and S1-passive task conditions, in order to address the main hypothesis of this study. The S1 vs. S2 contrast compared an aggregate of the S1-memorize and the S1-passive task conditions against an aggregate of S2-memorize and S2-pressing task conditions, and served as a control for motor preparatory and response processes related to S2-onset. A similar statistical design was separately applied to ERP data from the 3 mid-line electrodes. Performance was assessed in terms of reaction times and percentage of errors.

The Greenhouse-Geisser method of adjusting the degrees of freedom was used where appropriate (Vasey and Thayer, 1987). When multiple comparisons were required, separate error estimates were obtained for each contrast (Keselman and Keselman, 1988), and the Bonferroni procedure was used to determine the significance level using a familyTable 1

Mean reaction times (RT) and percent of false-alarm rate (and standard deviations) for the memory and pressing tasks in the visual and auditory task groups

	Visual task gr	oup	Auditory task group			
	S2-memorize	S2-pressing	S2-memorize	S2-pressing		
RT (ms) % errors	0.601 (0.1) 0.9 (0.01)	0.533 (0.1) 3.8 (0.07)	0.609 (0.1) 3.2 (0.06)	0.548 (0.1) 3.5 (0.07)		

wise error rate of 0.05. Only comparisons that were significant are reported, unless otherwise stated.

3. Results

3.1. Performance data

Comparisons of false-alarm rates between groups and across task conditions revealed that response errors were rare, with a maximum of 3.8% errors in the visual S2-pressing task condition. The auditory task group showed significantly more errors than the visual task group in the memory task condition only (t(19) = 3.41; P < 0.003; 3.2% and 0.9% errors, respectively). This can be taken as an indication of a lower accuracy of spatial localization in the auditory as compared with the visual modality (Perrot et al., 1993). There were no differences in error rates between the memory and control tasks within each group.

The analysis of reaction times to S2 revealed significantly larger response latencies in the S2-memorize than in the S2pressing task condition in both the visual (t(19) = 2.146); P < 0.045) and auditory (t(19) = 2.962; P < 0.008) task groups (see Table 1). On average, it took about 53 ms longer to issue a response in the memory task than in the pressing task. This difference is consistent with an interpretation in terms of controlled versus automatic visual search processes, and can be attributed to response and decision processes associated with S2, rather than with the perceptual

Table 2

processing of S1 (Posner and Boies, 1971; Shiffrin and Schneider, 1977).

The responses to the post-hoc questionnaire indicated that all subjects adopted a purely spatial strategy during the S1-S2 match-to-sample tasks. Indeed, none of the subjects reported having used a verbal strategy (i.e. verbal rehearsal of positions such as 'extreme right', 'right', 'centre', 'left', 'extreme-left') for retaining the spatial location of the stimulus.

3.2. ERP data

Results of the main ANOVA are shown in Table 2, and results of tests of simple effects are shown in Table 3. If both the Task \times Electrode and Task \times Electrode \times Hemisphere interactions reached significance, only simple effects for the third-order interaction are presented in Table 3. Mean ERP amplitudes for time windows -100 ms, P3a, and P3b are presented in Table 4. Fig. 1 offers a detailed comparison between grand mean ERP averages for each of the 4 task conditions (S1-memorize, S1-passive, S2-memorize, and S2-pressing) at Fz, Cz, and Pz. These mid-line averages summarize the overall pattern of ERP responding in both visual and auditory modalities, and show that the largest ERP differences were found between S1- and S2- task conditions. Fig. 2 shows memory-related difference waves which result from subtracting the S1-passive from the S1memorize ERP averages in the visual and auditory task groups, respectively.

3.2.1. Pre-stimulus periods

For the visual task group, significant differences between the S1-memorize and S1-passive conditions appeared only during the -100 ms time window at both occipital electrodes (Table 4). Significant differences between S1- and S2- task conditions were at all 3 mid-line electrodes (Fig. 1), and at both temporal electrodes for the -100 ms time window (Table 4). In all cases, pre-S2 amplitudes were significantly more negative than pre-S1 amplitudes.

For the auditory task group, S1-memorize amplitudes

	df	-200 ms	-100 ms	P100	N100	P200	N200	P3a	P3b	SW1	SW2
Visual											
Т	3,57	-	_	_	-	-	-	16.12 ^c	29.21 ^c	4.98 ^a	-
Τ×Η	3,57	-	_	-	_	-	-	5.15ª	-	_	-
Τ×Ε	15,285	-	2.64 ^a	3.07 ^a	_	-	-	7.92 ^c	13.21°	2.82 ^a	3.96 ^b
$T \times E \times H$	15,285	-	2.39 ^a	3.22 ^a	2.83ª	_	_	6.25 ^b	_	-	-
Auditory											
Т	3,57	-	_	-	_	-	9.96 ^b	31.52°	43.75°	17.15 ^c	-
$T \times H$	3,57	-	_	-	_	_	_	_	-	_	
Τ×Ε	15,285	8.62°	10.42 [°]	11.15°	10.21°	13.97°	21.19 ^e	17.25°	10.80 ^c		14.16 ^b
$T \times E \times H$	15,285	9.83°	13.83 ^c	16.26 ^c	_	7.16 ^c	_	-	3.20^{a}	-	-

T, Task; H, Hemisphere; E, Electrode.

 $^{a}P < 0.05.$

Table 3

Summary of significant simple effects and direction of differences in amplitude for the M1 vs. P1 and S1 vs. S2 contrasts in the visual and auditory task groups at each of the ERP time windows

	-200 ms	-100 ms	P100	N100	P200	N200	P3a	P3b	SW1	SW2
Visual										
M1 vs. P1	-	M1 < P1	M1 > P1	_	-	-	M1 < P1	M1 < P1	-	_
Electrodes	-	O ^a	Fz ^b ,F ^c T⁴	-	-	-	PO4 ^b ,P8 ^b P4 ^b O2 ^a	PO ^a ,O ^a P8 ^a	-	-
\$1 vs. \$2	-	S1 > S2	S1 > S2	S1 > S2	-	-	S1 < S2	$S_1 < S_2$	S1 < S2	\$1 > \$2
Electrodes	-	Fz ^c ,Cz ^c Pz ^c ,T7 ^b	Fz ^b ,Cz ^b Pz ^b ,T7 ^b	Fz⁵, T7⁵ PO7ª	-	-	All ^e but Fz, Cz	All ^c but Fz	All ^a but Fz,F	Pz ^c P ^a ,T ^c
Auditory										
M1 vs. P1	M1 < P1	M1 < P1	M1 < P1	_	-	_	M1 < P1	M1 < P1	M1 < P1	M1 < P1
Electrodes	O1 ^c , T7 ^a	O1 ^b ,T7 ^b	F7 ^a ,T7 ^a O1 ^a	_	-	-	Fz ^b ,Cz ^b F ^b ,T ^b	Fz ^b ,Cz ^b Pz ^b ,T7 ^a ,P ^b	T7 ^a	T7 ^c
S1 vs. S2	S1 > S2	S1 > S2	S1 > S2	S1 > S2	S1 < S2	S1 < S2	S1 < S2	S1 < S2	S1 < S2	S1 > S2
Electrodes	Fz ^b ,Cz ^b Pz ^b ,T7 ^c	Fz ^b ,Cz ^b Pz ^b ,T7 ^c P4 ^b	Fz ^b ,Cz ^b Pz ^b ,T7 ^c P4 ^c ,P8 ^a	Fz ^b ,T ^c PT ^a ,P ^b	Fz ^b ,P7 ^a P3 ^a	All ^b but Fz,F,T	All ^e but Fz,F	All ^c but Fz	All ^c but Fz	Cz ^c ,Pz ^c T ^a ,P ^a

M1 vs. P1, contrast between S1-memorize and S1-passive task conditions. S1 vs. S2, contrast between an aggregate of the S1-memorize and the S1-passive task conditions and an aggregate of the S2-memorize and the S2-pressing task conditions. F, frontal electrodes; T, temporal electrodes; P, parietal electrodes; PT, parieto-temporal electrodes; PO, parieto-occipital electrodes; O, occipital electrodes.

 ${}^{a}P < 0.05.$ ${}^{b}P < 0.01.$

 $^{\circ}P < 0.001$

were significantly more negative than S1-passive amplitudes at T7 and O1 electrodes in both pre-stimulus periods (Table 4). Pre-stimulus differences between S1 and S2 largely replicated those found in the visual modality, with S2 amplitudes being significantly more negative than those for S1 at the 3 mid-line electrodes (Fig. 1), T7 and P4 (Table 4).

3.2.2. P100 (50–100 ms)

In the visual task group, S1-memorize amplitudes reached significantly more positive values than those of the S1-passive task condition at frontal and temporal electrodes of both hemispheres (Fig. 1), as well as at Fz. This is in agreement with reports of an enhancement of early positive components of the visual ERP during target displays (Mangun and Hillyard, 1991). Differences between S1 and S2 mainly replicated those for the previous time window, with more negative amplitudes for S2 than for S1 at T7 (Table 4), and the 3 mid-line electrodes (see Fig. 1).

In the auditory task group, S1-memorize amplitudes were more negative than S1-passive amplitudes at frontal, temporal and occipital areas of the left hemisphere (see Fig. 2). Effects for the S1 vs. S2 contrast mainly replicated those found in the previous time window.

3.2.3. N100 (100-170 ms)

No significant differences appeared between the S1memorize and S1-passive task condition in the visual task group. Differences between S1 and S2 were confined to Fz, T7 and PO7, with S2 showing more negative values than S1 in all cases.

In the auditory task group, S1-memorize and S1-passive

task conditions did not differ significantly. Larger S2 than S1 amplitudes were found at temporal, parietal and parieto-temporal areas of both hemispheres.

3.2.4. P200 (170-220 ms)

No significant task effects were found in this time window for the visual task group.

In the auditory task group, S1-memorize and S1-passive task conditions did not differ significantly. Differences between S1 and S2 were confined to Fz, parieto-temporal and parietal electrodes. In every case, S2 amplitudes were significantly larger than S1 amplitudes.

3.2.5. N200 (220-270 ms)

No significant visual task effects were found in this time window.

For the auditory task group, no significant differences were found between S1-memorize and S1-passive task conditions. S2 amplitudes were significantly larger than S1 amplitudes bilaterally at all but frontal and temporal electrodes.

3.2.6. P3a (270-450 ms)

The visual S1-memorize task condition showed significantly lower amplitude values than the visual S1-passive task condition at P8, P4, PO4, and O2 electrodes (see Table 4; negative amplitudes were obtained at O2 only). By contrast, S2 amplitudes were significantly larger than S1 amplitudes at all but Fz and Cz electrodes. The S1 vs. S2 task effect was maximal over posterior areas, and was symmetrical across hemispheres (Table 4). Table 4

Mean ERP amplitudes \pm SD (in μ V) at -100 ms, P3a, and P3b time windows for task conditions S1-memorize, S1-passive, S2-memorize and S2-pressing in the visual and the auditory task groups

Visual task		F7	T 7	P7	P3	PO3	01
-100 ms	S1-memorize	1.13 ± 1.1	0.60 ± 1.3	-0.27 ± 1.2	-0.30 ± 1.3	-0.54 ± 1.2	-0.76 ± 1.2
	S1-passive	0.70 ± 1.4	0.46 ± 1.4	-0.13 ± 1.3	-0.22 ± 1.4	-0.34 ± 1.4	-0.13 ± 1.6
	S2-memorize	0.22 ± 1.4	-1.08 ± 1.4	-0.68 ± 1.4	-0.99 ± 1.9	-1.17 ± 1.7	-0.84 ± 1.4
	S2-pressing	0.47 ± 1.7	-1.07 ± 2.1	-0.71 ± 1.8	-1.29 ± 2.7	-1.26 ± 2.7	-1.12 ± 2.5
P3a	S1-memorize	4.13 ± 2.7	4.69 ± 3.4	1.82 ± 3.0	2.45 ± 3.0	1.90 ± 3.8	0.33 ± 3.2
	S1-passive	3.51 ± 2.8	3.72 ± 3.0	1.53 ± 3.0	2.21 ± 3.3	1.79 ± 3.6	0.65 ± 3.4
	S2-memorize	5.46 ± 2.4	6.22 ± 4.4	4.61 ± 3.4	6.57 ± 3.9	5.80 ± 4.4	4.20 ± 4.1
	S2-pressing	5.51 ± 2.8	5.94 ± 4.4	4.74 ± 3.9	6.34 ± 5.0	5.86 ± 4.8	4.04 ± 4.6
P3b	S1-memorize	0.69 ± 2.3	0.94 ± 2.6	-0.01 ± 1.9	0.59 ± 1.8	0.19 ± 1.7	-0.23 ± 1.5
	S1-passive	0.75 ± 2.3	0.87 ± 2.5	0.18 ± 1.9	0.79 ± 2.2	0.52 ± 2.3	0.34 ± 2.5
	S2-memorize	2.42 ± 2.2	4.20 ± 2.4	3.98 ± 2.7	5.69 ± 2.8	5.25 ± 2.8	4.06 ± 2.8
	S2-pressing	2.60 ± 1.7	4.03 ± 2.7	4.00 ± 2.2	5.65 ± 2.6	5.18 ± 2.4	4.07 ± 2.2
Visual task		F8	T8	P8	P4	PO4	02
-100 ms	S1-memorize	0.63 ± 1.0	0.30 ± 0.9	-0.50 ± 1.1	-0.52 ± 1.2	-0.76 ± 1.1	-0.92 ± 1.2
	S1-passive	0.32 ± 1.1	0.28 ± 1.1	-0.35 ± 1.4	-0.49 ± 1.4	-0.59 ± 1.2	-0.29 ± 1.2
	S2-memorize	-0.03 ± 1.9	-0.67 ± 1.4	-1.29 ± 1.9	-1.81 ± 2.1	-1.20 ± 2.0	-1.06 ± 2.0
	S2-pressing	0.28 ± 2.4	-0.37 ± 1.7	-1.08 ± 2.4	-1.88 ± 2.5	-1.29 ± 2.7	-1.06 ± 2.7
P3a	S1-memorize	4.08 ± 2.2	3.80 ± 2.6	0.91 ± 2.6	1.84 ± 3.0	0.39 ± 2.7	-0.71 ± 3.1
	S1-passive	3.91 ± 3.4	3.46 ± 2.8	2.33 ± 3.4	2.87 ± 3.9	1.40 ± 3.1	0.17 ± 3.2
	S2-memorize	6.57 ± 2.8	6.16 ± 3.4	5.54 ± 3.1	6.37 ± 3.5	5.54 ± 4.1	3.94 ± 4.1
	S2-pressing	6.83 ± 3.4	5.92 ± 3.8	5.81 ± 5.6	6.19 ± 5.7	5.32 ± 5.3	3.90 ± 4.1
P3b	S1-memorize	0.79 ± 2.1	1.31 ± 2.3	-0.31 ± 1.3	0.53 ± 2.0	-0.70 ± 1.5	-1.04 ± 1.5
	S1-passive	1.05 ± 2.5	1.35 ± 2.2	0.65 ± 1.8	0.91 ± 2.1	0.36 ± 1.6	-0.10 ± 1.7
	S2-memorize	3.92 ± 2.2	4.33 ± 2.1	4.17 ± 2.4	5.72 ± 3.9	4.77 ± 3.4	3.85 ± 2.4
	S2-pressing	3.96 ± 2.7	4.17 ± 2.7	4.78 ± 3.5	5.52 ± 3.3	4.92 ± 3.1	3.96 ± 2.9
Auditory task		F7	T7	P7	Р3	PO3	01
-100 ms	S1-memorize	-0.34 ± 2.4	-1.07 ± 2.2	-1.52 ± 2.6	-1.33 ± 2.4	-1.79 ± 2.6	-1.76 ± 2.6
	S1-passive	-0.08 ± 1.9	-0.22 ± 2.1	-1.03 ± 1.7	0.78 ± 1.9	-1.11 ± 1.9	-1.07 ± 1.9
	S2-memorize	-0.59 ± 1.9	-3.73 ± 2.3	-1.85 ± 1.9	-1.46 ± 1.9	-1.87 ± 2.1	-1.34 ± 2.2
	S2-pressing	0.07 ± 1.8	-3.67 ± 2.6	-1.74 ± 2.1	-1.40 ± 1.8	-1.72 ± 2.2	-1.12 ± 1.8
P3a	S1-memorize	-1.79 ± 4.4	0.40 ± 4.2	2.3 ± 3.6	1.86 ± 3.5	1.93 ± 3.7	1.49 ± 3.0
	S1-passive	-0.65 ± 3.5	1.73 ± 4.3	2.76 ± 3.0	2.62 ± 3.0	2.27 ± 3.4	2.04 ± 2.8
	S2-memorize	0.30 ± 3.7	3.12 ± 4.3	7.68 ± 3.9	6.40 ± 3.7	8.14 ± 5.0	7.58 ± 4.3
	S2-pressing	1.06 ± 3.3	3.86 ± 5.2	8.59 ± 4.8	7.50 ± 4.7	8.54 ± 5.9	8.25 ± 4.8
P3b	S1-memorize	-2.60 ± 3.8	-1.91 ± 3.4	0.08 ± 3.1	-0.36 ± 2.9	-0.50 ± 3.1	-0.41 ± 2.6
	S1-passive	-2.05 ± 2.9	-0.64 ± 3.1	0.59 ± 2.3	0.25 ± 2.4	-0.08 ± 2.4	0.06 ± 2.2
	S2-memorize	1.33 ± 3.3	3.28 ± 3.2	6.38 ± 3.6	5.05 ± 2.6	6.69 ± 3.6	5.66 ± 2.3
	S2-pressing	1.25 ± 2.7	3.57 ± 2.8	6.04 ± 3.6	5.49 ± 2.8	6.82 ± 3.9	5.81 ± 3.2
Auditory task		F8	T8	P8	P4	PO4	O2
-100 ms	S1-memorize	-0.04 ± 2.6	-0.94 ± 2.4	-1.50 ± 2.3	-1.52 ± 2.3	-1.57 ± 2.4	-1.60 ± 2.4
	S1-passive	-0.05 ± 2.3	-0.74 ± 1.9	-0.95 ± 1.9	-0.85 ± 1.9	-0.95 ± 2.1	-1.19 ± 1.8
	S2-memorize	-0.02 ± 1.4	-1.64 ± 1.5	-2.23 ± 2.2	-2.86 ± 2.4	-1.77 ± 2.3	-1.37 ± 2.1
	S2-pressing	0.09 ± 1.6	-1.41 ± 1.7	-2.29 ± 1.9	-2.88 ± 2.4	-1.81 ± 2.0	-1.31 ± 1.8
P3a				212 ± 26	2.17 ± 4.0	1.90 ± 3.6	1.79 ± 3.4
P3a	S1-memorize	-2.09 ± 5.1	-0.22 ± 3.9	2.13 ± 3.0	2.17 ± 1.0	100 ± 010	
P3a	S1-memorize S1-passive	-2.09 ± 5.1 -0.72 ± 4.1	-0.22 ± 3.9 1.00 ± 3.3	2.13 ± 3.6 2.68 ± 3.3	3.02 ± 3.8	2.60 ± 2.9	2.33 ± 2.7
P3a	S1-memorize S1-passive S2-memorize	-2.09 ± 5.1 -0.72 ± 4.1 0.13 ± 3.1	-0.22 ± 3.9 1.00 ± 3.3 2.57 ± 2.4	2.13 ± 3.0 2.68 ± 3.3 7.46 ± 4.6	3.02 ± 3.8 7.61 ± 5.1	2.60 ± 2.9 7.63 ± 4.9	2.33 ± 2.7 7.73 ± 5.0
P3a	S1-memorize S1-passive S2-memorize S2-pressing	-2.09 ± 5.1 -0.72 ± 4.1 0.13 ± 3.1 1.11 ± 3.4	-0.22 ± 3.9 1.00 ± 3.3 2.57 ± 2.4 4.00 ± 3.1	2.13 ± 3.6 2.68 ± 3.3 7.46 ± 4.6 8.20 ± 5.2	3.02 ± 3.8 7.61 ± 5.1 8.40 ± 5.8	2.60 ± 2.9 7.63 ± 4.9 8.67 ± 5.3	2.33 ± 2.7 7.73 ± 5.0 8.39 ± 5.4
P3a P3b	S1-memorize S1-passive S2-memorize S2-pressing S1-memorize	-2.09 ± 5.1 -0.72 ± 4.1 0.13 ± 3.1 1.11 ± 3.4 -3.13 ± 4.8	-0.22 ± 3.9 1.00 ± 3.3 2.57 ± 2.4 4.00 ± 3.1 -1.41 ± 3.3	2.13 ± 3.0 2.68 ± 3.3 7.46 ± 4.6 8.20 ± 5.2 -0.50 ± 2.9	$3.02 \pm 3.8 \\ 7.61 \pm 5.1 \\ 8.40 \pm 5.8 \\ -0.70 \pm 3.2$	$2.60 \pm 2.9 \\ 7.63 \pm 4.9 \\ 8.67 \pm 5.3 \\ -0.57 \pm 2.9$	$2.33 \pm 2.7 7.73 \pm 5.0 8.39 \pm 5.4 -0.32 \pm 2.7$
P3a P3b	S1-memorize S1-passive S2-memorize S2-pressing S1-memorize S1-passive	$\begin{array}{c} -2.09 \pm 5.1 \\ -0.72 \pm 4.1 \\ 0.13 \pm 3.1 \\ 1.11 \pm 3.4 \\ -3.13 \pm 4.8 \\ -2.18 \pm 3.8 \end{array}$	-0.22 ± 3.9 1.00 ± 3.3 2.57 ± 2.4 4.00 ± 3.1 -1.41 ± 3.3 -0.67 ± 2.5	2.13 ± 3.6 2.68 ± 3.3 7.46 ± 4.6 8.20 ± 5.2 -0.50 ± 2.9 -0.01 ± 2.4	$3.02 \pm 3.8 7.61 \pm 5.1 8.40 \pm 5.8 -0.70 \pm 3.2 0.25 \pm 2.6$	$2.60 \pm 2.9 7.63 \pm 4.9 8.67 \pm 5.3 -0.57 \pm 2.9 0.05 \pm 2.2$	$2.33 \pm 2.77.73 \pm 5.08.39 \pm 5.4-0.32 \pm 2.70.16 \pm 1.9$
P3a P3b	S1-memorize S1-passive S2-memorize S2-pressing S1-memorize S1-passive S2-memorize	$\begin{array}{c} -2.09 \pm 5.1 \\ -0.72 \pm 4.1 \\ 0.13 \pm 3.1 \\ 1.11 \pm 3.4 \\ -3.13 \pm 4.8 \\ -2.18 \pm 3.8 \\ 1.36 \pm 2.2 \end{array}$	-0.22 ± 3.9 1.00 ± 3.3 2.57 ± 2.4 4.00 ± 3.1 -1.41 ± 3.3 -0.67 ± 2.5 3.98 ± 1.8	2.13 ± 3.6 2.68 ± 3.3 7.46 ± 4.6 8.20 ± 5.2 -0.50 ± 2.9 -0.01 ± 2.4 6.25 ± 2.6	$3.02 \pm 3.8 \\ 7.61 \pm 5.1 \\ 8.40 \pm 5.8 \\ -0.70 \pm 3.2 \\ 0.25 \pm 2.6 \\ 6.24 \pm 3.8$	$2.60 \pm 2.9 \\ 7.63 \pm 4.9 \\ 8.67 \pm 5.3 \\ -0.57 \pm 2.9 \\ 0.05 \pm 2.2 \\ 6.26 \pm 3.5$	$2.33 \pm 2.77.73 \pm 5.08.39 \pm 5.4-0.32 \pm 2.70.16 \pm 1.95.48 \pm 3.2$

In the auditory task group, S1-memorize amplitudes were significantly more negative than S1-passive amplitudes at frontal and temporal areas of both hemispheres (see Table 4), as well as at Fz and Cz sites (Fig. 1). Main task effects for the S1 vs. S2 contrast were significant, indicating the presence of the full-blown P300 wave, with S2 ampli-



Fig. 1. Grand mean ERP averages at Fz, Cz, and Pz for each of the 4 task conditions (S1-memorize, S1-passive, S2-memorize, and S2-press). Upper panel: visual task group. Lower panel: auditory task group.

tudes being larger than S1 amplitudes bilaterally and at all except both frontal and mid-line Fz electrodes (Table 4, Fig. 1).

3.2.7. P3b (450-700 ms)

Significantly lower amplitudes were found during the visual S1-memorize as compared with the visual S1-passive task condition, which were confined to P8, as well as parieto-occipital and occipital electrodes of both hemispheres (see Table 4). Significant S1 vs. S2 effects appeared at all electrodes of both hemispheres (except for Fz, see Fig. 1), with S2 amplitudes being larger than S1 amplitudes.

In the auditory task group, significant differences between S1-memorize and S1-passive task conditions were found at all mid-line electrodes (see Fig. 1), as well as at temporal and parietal areas, with a significant trend towards a left temporal asymmetry (see Table 4 and Fig. 2). Significant S1 vs. S2 effects were obtained in all electrodes except Fz, with larger S2 than S1 ERP amplitudes (Tables 3 and 4).

3.2.8. SW1 (700-900 ms)

In the visual task group, only significant differences between S1 and S2 were found in all brain areas except frontal ones. ERP differences were distributed symmetrically across hemispheres.

For the auditory task group, S1-memorize amplitudes were more negative than S1-passive amplitudes only at the T7 site (see Fig. 2). S2 elicited significantly larger amplitudes than S1 at all electrode sites.



Fig. 2. Difference waveforms which result from subtracting the S1-passive average from the S1-memorize task conditions (M1 vs. P1 contrast) for the visual and auditory task groups.

3.2.9. SW2 (900-1300 ms)

A second-order interaction revealed significantly larger amplitudes for the S1 than for the S2 task condition in the visual task group. These differences were distributed symmetrically at parietal and temporal areas of both hemispheres.

In the auditory task group, S1-memorize showed significantly more negative amplitudes than S1-passive at T7 (see Fig. 2). There was a change in the pattern of results from the previous time windows, so that S1 showed larger amplitudes than S2 at Cz and Pz mid-line electrodes, as well as at temporal and parietal areas of both hemispheres.

In summary, memory-related negativities revealed by the M1 vs. P1 contrast were confined to the -100 ms, P3a, and P3b time windows in the visual modality, and involved mainly occipital, parieto-occipital and parieto-temporal areas of the right hemisphere. In the auditory modality, memory-related negativities started earlier and lasted longer in the recording epoch, and were focused at fronto-central midline electrodes, as well as at frontal, temporal and occipital areas of the left hemisphere. The topographical distribution of effects for the S1 vs. S2 contrast did not conform to this pattern of effects. It is worthwhile noting the synchronicity of the peak amplitude of the memory-related negativities displayed in Fig. 2, which appeared almost simultaneously in both modalities around 450 ms post-stimulus. The scalp distribution of this peak clearly differs across modalities.

4. Discussion

There is a good deal of agreement between the present results and those reported by Martin-Loeches et al. (1994). This is in spite of considerable modifications in the type of stimuli used, the open-field mode of presentation, the use of a S1-S2 passive-pressing control task, and even an altogether different EEG system of data acquisition and analysis. All in all, the two main conclusions from the previous study still hold. Namely, that the encoding into memory of spatial location is associated with a negative wave over the brain areas putatively associated with the sensory processing of stimulus features. Also, that the P300 does not seem to be an important ERP feature related to spatial location encoding and retaining in memory. An improved task design allowed us to qualify and complement these two earlier conclusions in several respects. Firstly, memoryrelated negativities were experimentally dissociated from motor preparation negativities in the S1-S2 interval, and both show distinct patterns of brain activation. Secondly, the brain topography of memory-related negativities differed across modalities. Thus, a post-stimulus memoryrelated negative wave was centred over right parieto-occipital, parietal and occipital areas in the visual task, but it focused over midline fronto-central and left temporal areas in the auditory task. Thirdly, these memory-related negativitics peaked synchronously in both the visual and auditory tasks at around 450 ms post-stimulus. Finally, the presence of stimulus-preceding negativities (SPN) suggests that sensory preparation processes manifest themselves over the same cortical areas activated during storage and maintenance of spatial information in working memory.

Match-to-sample tasks have been successfully employed in ERP studies of human memory (Lang et al., 1992; Ruchkin et al., 1992; Ruchkin et al., 1995). However, slow ERP waves obtained during the S1-S2 interval of this kind of task also reflect motor preparation processes prior to S2 responding (McCallum, 1988; Birbaumer et al., 1990; Rämä et al., 1995; Starr et al., 1996). In this study, we assumed that both S1-memorize and S1-passive task conditions are equally affected by motor preparation processes, and therefore, their difference wave should reflect processes related to the encoding of spatial information into memory devoid of motor preparation processes (Fig. 2). Basically, these difference waves can be taken to reflect memory-related negativities at brain areas devoted to the perceptual analysis of stimulus features, and hence, can be regarded as modality-specific. Such a topography is clearly in contrast with the modality-independent midline fronto-central maximum of CNV waves (McCallum, 1988) (see Fig. 1). Using a similar task design, Ruchkin et al. (1995) reported significant effects of information load upon the amplitudes and topography of slow waves during the S1-S2 interval, thus ruling out motor preparation as the sole explanation (see also Ruchkin et al., 1992).

The memory-related negativities revealed by M1 vs. P1 difference waves in Fig. 2 might reflect two distinct types of processes. On the one hand, stimulus-preceding negativities (SPN) may reflect anticipatory activation of primary sensory areas. On the other hand, poststimulus negativities during the 2 s memorization interval may reflect processes related to the storage and maintenance of spatial information. Both the prestimulus and poststimulus parts of these memory-related negativities show scalp distributions which are largely dependent on stimulus modality. Other working memory studies have analyzed ERP activity preceding a stimulus to which an open motor response is required (Gevins and Cutillo, 1993; Starr et al., 1996), thus leaving open the possibility of a contribution of motor preparation processes to their reported SPNs. By contrast, our M1 vs. P1 difference waves reflect ERP activity around the first stimulus in the delayed S1-S2 match-to-sample task, which demanded no motor response. The following discussion refers to ERP waves preceding and succeeding S1.

4.1. Memory-related stimulus-preceding negativities (SPN)

The earliest significant negativity effects reported by Martin-Loeches et al. (1994) appeared 150 ms after stimulus onset, but there was a gradual development of this negativity starting several milliseconds before stimulus onset. Although their prestimulus negativity did not reach statistical significance, a prestimulus preparatory activation was surmised. The use of a 100 ms prestimulus baseline, however, precluded a suitable assessment of this conjecture. The present data confirm our previous suspicion that memoryrelated SPNs develop in the visual modality, and suggest that the same happens with auditory stimulation. SPNs appear bilaterally at occipital leads in the visual modality; and at left occipital and temporal leads in the auditory modality. In both modalities these SPNs might be indexing preparatory activation of those sensory areas subsequently involved in the memorization of spatial information. A similar SPN was reported by Ruchkin et al. (1986) who related it to some operation in the domain of expectancy, anticipation, or 'mental preparation' for the incoming stimulus.

SPNs prior to task-relevant stimulation have been studied by Damen and Brunia (1994). These authors propose a psychophysiological model of attention to account for their SPN effects in terms of the activation of the reticular nucleus of the thalamus. This would inhibit all modalityspecific thalamic projection nuclei not related to the task and would leave open only the task-related thalamic relay centres. In case of the anticipation of a visual stimulus, this system would allow only the passage of signals to the occipital cortex. The finding of a SPN at left temporal cortex in the auditory task could be interpreted in a similar way. SPNs have also been reported in association with working memory tasks (Gevins and Cutillo, 1993; Starr et al., 1996). However, these two studies considered ERP activity from a time window preceding and following a self-paced movement, which makes it likely a contribution from motor preparation and expectancy processes to the reported negativity. This possibility has been ruled out in the present task design. Thus, even if some might argue about the different nature of our SPNs due to considerable disparities in task design, we are quite confident to underscore the nonmotoric character of the SPNs described here. This is apparent from the scalp distribution of peak amplitudes of difference waves over areas devoted to perceptual analysis in their respective modalities.

Somewhat less expected was the finding of a concurrent SPN at left occipital cortex in the auditory task. One possible explanation for this effect can be put forward considering the primacy of the visual over the auditory modality in the perception of spatial relationships. Thus, when visual and auditory spatial information is discordant, humans perceive the auditory stimulus as originating from the location of the visual stimulus (Knudsen and Brainard, 1995). This kind of visual-auditory interactions in the formation of spatial maps in the brain have been discovered all the way up from the tectum to the forebrain. In fact, as much as 40% of individual neurons in striate and extrastriate visual cortices are responsive to convergent spatial information from both visual and auditory modalities (Knudsen and Brainard, 1995).

4.2. Memory-related post-stimulus negativities and P3-like waves

Memory-related post-stimulus negativities in the P3a and P3b time windows also revealed distinct patterns of brain activation across modalities. In the visual modality this negativity appeared bilaterally at occipital, parieto-temporal and parieto-occipital areas, but with significantly larger amplitudes over the right hemisphere (see Table 4). In the auditory modality, the memory-related post-stimulus negativity was manifest over midline fronto-central, temporal and frontal leads, but with significantly larger amplitudes over the left temporal area. These hemispheric differences in memorization of visual and auditory material are consistent with reports that slow waves are largest over midline fronto-central and left temporal areas during phonological and/or auditory working memory operations (Ruchkin et al., 1992; Chao et al., 1995), but largest over the right parietal sites during visuospatial working memory operations (Ruchkin et al., 1995). Gevins and Cutillo (1993) reported that the pattern of evoked potential covariances for a match detection task requiring maintenance of numeric information in working memory was more complex at the left hemisphere both prior to the stimulus, and in a postimulus interval spanning the P300 peak.

Memory-related negativities were found up to 700 ms post-stimulus in the visual modality. This is partly consistent with data from our previous study, where a slow wave memory-related negativity was reported in the 550-822 ms latency range (Martin-Loeches et al., 1994). In the auditory modality, memory-related negativities outlasted those in the visual modality, continuing up to the end of the recording epoch over the left temporal site. Except for the lack of a late slow wave negativity in the visual task, our data show a good amount of agreement with those of Ruchkin et al. (1992), considering differences in stimulus material, and the much shorter interstimulus interval used by us. It is not clear, though, why the S1-memorize negativity did not reach the end of the recording epoch in the visual task, as is often the case in similar studies (Ruchkin et al., 1992; Ruchkin et al., 1995). Perhaps the sheer simplicity of the visual stimuli used (dim red lights) made redundant part of the working memory operations necessary to retain spatial information during the S1-S2 interval, or made these operations last for a shorter time. On the other hand, there was an intriguing temporal synchronicity in the peaks of maximal memory-related negativity across both modality groups (see Fig. 2). If we agree that these difference waves reflect processes of encoding and retaining of spatial information, then their synchronous temporal courses might be indexing the manifestation of a common underlying mechanism. Such type of mechanism would set the tempo of working memory operations, and/or would coordinate the information from different sensory systems (i.e. like the central executive of Baddeley's model). But then further research would be required to explore these various possibilities suggested by the observed differences and similarities between memory-related negativities across modalities.

In any case, neither P3a nor P3b waves seemed to be associated with the storing and retention of spatial information in working memory. This is consistent with reports from studies using match-to-sample paradigms that memoryrelated negative slow waves develop immediately after the P300 wave (Ruchkin et al., 1992). It also supports the view that working memory is largely independent of classical limbic memory networks associated with P300 elicitation (Chao et al., 1995; Knight and Grabowecky, 1995). The timing and scalp distribution of the peak amplitudes of memory-related negative waves are consistent with current neurophysiological models of working memory based on specialized brain systems for short-term, data-driven storage of sensory information (Fuster, 1995). These models consider that the memory of things cannot simply be allocated to one polymodal area just because that memory is usually anchored in several sense modalities (Damasio, 1990; Fuster, 1995). These data are also consistent with current psychological models of working memory in terms of separate systems for phonological and visuospatial information (Baddeley, 1992). It seems reasonable that such a simple stimulus feature as spatial location is encoded in cortical areas devoted to primary perceptual processing.

In agreement with our earlier study too, a P300 wave was elicited during the S1-memorize task condition, which showed a significantly lower amplitude and a different brain distribution than the one elicited by the S2-memorize task condition. On the contrary, the S1-passive task condition also elicited a P3 wave which mimicked the amplitude and topography of the S1-memorize P300 wave. Although a P3a wave in the S1-passive task condition might appear as counterintuitive, it should be noted that S1 forewarns the incoming target stimulus S2 and can hardly be 'ignored'. These P3a waves may reflect the process of keeping count of the order of presentation in the S1-S2 paradigm, which of course was necessary both in the S1-passive and in the S1memory task conditions alike. In this respect, the S1-passive task condition can be regarded as an adequate control for the S1-memorize condition, and it can be assumed that both task conditions elicited the same amount of perceptual processing regarding S1. Both the S1-passive and S1-memorize P300 waves displayed a maximum over fronto-central areas, and therefore, could be best described as P3a waves in clear contrast with the P3b waves elicited by the S2memorize task condition (Knight and Grabowecky, 1995). In the visual task, P3a waves were more conspicuous over frontal areas and decreased in amplitude posteriorly (cf. Martin-Loeches et al., 1994). In the auditory task, P3a waves were more evenly distributed, with a maximum over centro-parietal areas.

The scalp distribution of post-stimulus memory-related negativities does not show a common frontal locus as would be expected from reports about the implication of the dorsal prefrontal cortex in working memory operations (Smith et al., 1995; Ungerleider, 1995). One possible explanation for the lack of prefrontal effects could be that the encoding of spatial information during our simple match-tosample task required the activation of neural networks in the lower levels of the hierarchy of perceptual processing, with minimum requirements made upon prefrontal working memory systems of higher levels of the hierarchy (Fuster, 1995). Most studies reporting prefrontal activation during working memory operations have typically employed more complex stimulus material and/or made higher demands during task performance. Also compatible with this explanation is that prefrontal cortex was activated to a similar extent both during the S1-passive and S1-memorize task conditions; hence the lack of frontal ERP differences between both task conditions.

5. Conclusions

The presence of distinct scalp topographies across modalities for the memory-related negativities reported here could be taken as an indication that different configurations of neural sources were active during storage and retention in working memory of visuo-spatial and auditory spatial information. In the main, the present data show a good deal of agreement with our previous study in that input to memory takes place in the same cortical areas devoted to feature extraction of simple stimulus characteristics (Martin-Loeches et al., 1994). This lends support to models of working memory based on specialized brain systems for shortterm, data-driven storage of visuo-spatial and audio-spatial information (Damasio, 1990; Baddeley, 1992; Fuster, 1995). Consequently, our ERP evidence is consistent with single cell studies of working memory which suggest that the storage and retaining of simple visuo-spatial and audiospatial information recruit activity from neuronal networks in the primary and secondary visual cortices, rather than from third-order association and polysensory cortices. This reinforces the view that sensory processing and memory representation probably share largely the same cortical substrates (Fuster, 1995).

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