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Research report

Slow cortical potentials during retention of object, spatial, and verbal information

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Abstract

We used event related potentials (ERPs) to examine both the specificity and the timing of slow cortical scalp potentials (SPs) elicited by the retention of object, spatial, and verbal information in working memory (WM). Participants performed a modified delayed matching task in which a task cue presented in the middle of the delay interval indicated what type of information had to be retained for a subsequent comparison with the test stimulus. The first experiment used nameable objects and spatial locations as stimuli. The retrieval mode (visual vs. verbal) was manipulated by presenting either figural information or printed words as test stimuli. Transient ensembles of frontal and parieto-occipital slow waves with different scalp topographies for object and spatial information were evoked as a function of task cues. When words rather than objects were used as test stimuli highly similar, though more pronounced, fronto-parietal slow wave patterns were obtained. The second experiment using unfamiliar objects and non-nameable spatial locations indicated that neither the left frontal negative SP nor the posterior SPs are exclusively related to verbal working memory operations. The results indicate that a parietal negative SP reflects processes of spatial selective attention whereas a parieto-occipital positive SP indexes the retention of visual object information. Left frontal negative SPs are generated by a compound of higher order frontal control processes and vary as a function of information type.

Theme: Neural basis of behaviour

Topic: Learning and memory: systems and functions

Keywords: Working memory; ERP; Slow cortical potentials

1. Introduction

Working memory (WM) refers to a brain system for temporary storage and manipulation of information, a function that is central to a large range of cognitive capabilities. The highly influential model by Baddeley [3] regards WM as a multi-component process with different working memory systems for different kinds of information. He proposed a three-omponent system of working memory with two separate storage and retention systems for verbal and visual–spatial information that are under the control of one central executive mechanism.

Behavioral measures demonstrated a further functional dissociation between object and spatial information within visual WM [24,51]. This 'What and Where' dissociation has also been demonstrated using physiological measures in monkeys [53,52].

Other psychological models, however, do not explicitly propose a information-specific architecture, e.g., the models of Cowan [7] and Engle et al. [9] regard the allocation of controlled attention on relevant information as the crucial process per se, i.e., the content of WM is identical with the information that is in the focus of attention. In accordance with this view, Awh et al. [2] identified spatial selective attention as the crucial process underlying spatial WM but not object WM by demonstrating that shifts of spatial attention selectively impair the retention of spatial information. In addition, a subsequent fMRI-study [1] showed that during retention of spatial information in WM early visual areas are modulated as they are during spatial selective attention.

Many models assume that prefrontal cortex (PFC)

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houses processes of executive control of the WM content. Goldman-Rakic [13] proposes an information specific architecture of PFC which in turn is interconnected with storage sites in posterior cortical areas. In contrast to this, Petrides [33] assumed that PFC is subdivided according to the required process, i.e., maintenance or manipulation of the contents of WM. Others, however, have argued against such a WM-specific role of PFC and rather suggest that it subserves more unspecific functions of attentional control [45], a view that is in accordance with the psychological models of Engle et al. and Cowan, as mentioned above.

The issue of which brain regions are involved in working memory processes and which cognitive functions they mediate can also be addressed using the spatio-temporal properties of event-related brain potentials (ERPs). In contrast to functional imaging techniques such as PET or fMRI, ERPs have a relative poor spatial resolution. However, the temporal resolution is in the range of milliseconds and thus can provide information on the relative timing of cognitive processes underlying working memory performance such as onset, offset, and duration that otherwise is not available.

In the present context, slow cortical potentials (SPs) of the ERP are of special interest. SPs are deflections that typically last more than 200 ms up to several seconds [37]. Negative SPs reflect the unspecific thalamo-cortical activation of a cortical area [5]. In a physiological sense, this thalamic activation can be regarded as the allocation of attentional or processing resources towards a specific cortical region [22] and therefore is predestined to investigate WM processes under the viewpoint of attention.

A number of ERP studies found ERP slow waves with a duration of several hundred milliseconds to be specific to the kind and amount of information retained in working memory [44,43,29,41,28]. Ruchkin et al. [44] employed a delayed matching-to-sample task and found a negative slow wave over left frontal brain regions in combination with a transient bilateral posterior positive slow wave for phonological working memory, with the amplitudes of both slow waves being directly related to working memory load. Since both slow waves were found in verbal working memory tasks but not in spatial or object WM they were presumably reflects of cognitive processes specific to the retention of verbal materials by means of articulatory rehearsal. Specifically, the posterior positive slow wave is assumed to reflect the conversion from visual to verbal representational formats. Spatial working memory tasks in contrast are shown to lead to bilateral or slightly right lateralized negative slow waves over posterior parietal brain regions [29]. The amplitudes of these posterior slow waves varied as a function of working memory load, and extended throughout the delay interval. Due to these characteristics the observed posterior negative slow waves were taken to primarily index retention of spatial materials in working memory. Another study of spatial WM, however, did not observe such a parietal SP [11] in a delayed-response task. The authors attribute the absence to the use of different memory strategies during delayed responses as compared to delayed matching tasks.

Frontal and parietal slow wave activity with a temporal extension of several hundred milliseconds was also reported recently in a *N*-back working memory task [26]. During serial presentation of stimuli participants had to decide whether the current stimulus matches the one that was presented *N* times before. The amplitude of both slow waves was clearly related to working memory load. However, as no difference was found between a spatial and a verbal version of the task, these slow waves were taken to reflect modality-unspecific retention processes possibly related to the higher order attentional demands of the task.

Taken together, the findings from the ERP studies can be connected to results from imaging studies [e.g., 15,6,48] in that they show that working memory for object, spatial, and verbal information relies on the combined operation of posterior and frontal cortical areas. However, they do not provide a unitary view of the particular functional role of posterior and frontal cortical regions in working memory tasks. This may be due to the fact that the different studies either focused on the retention of a particular information type, i.e., phonological, spatial, or object information or on modality differences, and that they used different tasks across the studies which makes a direct comparison difficult.

2. The present study

The goal of this study was to use the spatial-temporal properties of ERP slow waves to examine the underlying cognitive functions when object, spatial, or verbal information is retained in WM. The examination of ERP slow waves during WM tasks requires several precautions. We had to ensure that ERP slow wave activity in a retention interval can unambiguously be related to content-specific retention processes without confounding these processes with differential perceptual processes, due to physically different stimulus properties. To fulfill these criteria, we developed a modified delayed-matching-to-sample paradigm in which participants are presented with a composite stimulus consisting of two objects presented at two different spatial locations including the dimension of spatial depth.

In this task, both, object and spatial information has to be encoded into the working memory. A cue is presented after 2.5 s this stimulus (in the following: S1) that indicated whether an object-based or a spatial-based comparison will be required upon presentation of the test stimulus (in the following: S2), which is presented 2.5 s thereafter. The logic behind this manipulation is that, after presentation of the cue, participants should mainly retain the relevant type of information in working memory, i.e, object forms after the object cue and spatial locations after the spatial cue. In a third control condition the cue indicated that a perceptually-based comparison will be required upon presentation of S2. Thus contrasting ERP slow waves elicited by the task cues in the two memory tasks and the perceptual task should allow us to delineate ERP slow waves related to working memory operations for both information types.

To address the issue of separate modules for verbal working memory processes a verbal working memory condition was developed in which the objects' and spatial locations' names were presented at S2. Thus, Experiment 1 included trials in which S2 either consisted of object forms presented at particular spatial locations (figural condition) or the objects' and spatial locations' names (verbal condition). Both conditions were presented in different blocks and we assumed that in the figural condition participants hold active an image-like representation of object forms and their respective locations whereas in the verbal condition they retrieve the names and rehearse them throughout the S1–S2 interval.

Experiment 2, employing the same paradigm and testing conditions as in the figural condition of experiment 1, used unfamiliar objects and spatial locations for which verbal labels were not easily retrievable. This experiment examined whether or not the slow wave patterns obtained in experiment 1 reflect visual working memory operations per se or rather, at least in part, the use of verbal rehearsal strategies possible for the familiar (and nameable) stimulus materials employed in experiment 1.

3. Experiment 1

The objective of experiment 1 was to examine the spatio-temporal patterns of brain activation when objects forms and spatial locations are retained in WM. Moreover, we were interested in how far these retention processes are modulated when verbal rather than figural rehearsal is used. ERPs, time-locked to the cue, were recorded in the memory and the perceptual tasks. Based on prior ERP-studies we expected that the cue in the memory tasks evokes slow wave activity and that memory-related differences relative to the perceptual task were most pronounced at frontal and parietal electrode sites. An open question was how verbal rehearsal is separable from nonverbal rehearsal processes.

According to Ruchkin et al. [44], verbal rehearsal should be evidenced by a left lateralized, frontally focused negative slow wave.

3.1. Methods

3.1.1. Subjects

Twenty right-handed volunteers participated. None of the participants had prior experience with the experimental task. Due to technical artifacts the EEG-data of four participants were excluded from data analysis. The remaining 16 participants had a median age of 22 years, 8 were female and all were right-handed with either normal or corrected to normal vision.

Each participant performed a 1-h practice session followed on a subsequent day by a 3.5-h experimental session.

3.1.2. Stimuli

All stimuli were presented on a 17′ VGA monitor under the control of a P-90 computer. In both the figural and the verbal conditions S1 contained two distinct green colored objects out of the following six simple geometric forms (German labels in parentheses): circle (Kreis), diamond (Karo), star (Stern), cross (Kreuz), arrow (Pfeil), and ring (Ring). The objects were located within a box-like gray-shaded space. The positions could be: left (links), right (rechts), in front (vorne), at the back (hinten), above (oben), and below (unten). Objects varied according to their position in size, perspective, and brightness. In order to enhance the 3D-impression, the space contained a grid with the center of the screen serving as the virtual center. The mean width of an object was 3 cm at the back location, 4 cm in the middle locations, and 7 cm in the front location. The maximum visual angle was 13° horizontally and 9° vertically. (Fig. 1)

In the figural condition, S2 was the same format as S1 whereas in the verbal condition, S2 consisted of two object names and two spatial prepositions. Object names were presented using yellow proportional font within the left half of the screen on top of each other with a spacing of 1 cm whereas spatial prepositions were shown within the right half. The visual angle of all four words together was 4° horizontally and 2° vertically. Both the verbal and the figural S2 contained two digits ('1' and/or '2') in two randomly chosen corners of the screen.

The task cues, presented in the middle of the S1–S2 interval, consisted of the strings '-Obj-' (object task), '-Pos-' (spatial task), or '-Zif-' (control task). Cues were presented in the center of the screen with visual angles of 3° horizontally and 0.4° vertically.

3.1.3. Experimental task

The participant's task was to memorize the two objects and their spatial locations provided by S1 until the cue indicated the relevant type of information. Following an object (spatial) cue, only object (spatial) information had to be retained in WM for a subsequent comparison with S2. Participants had to decide whether both objects (locations) in S2 were identical to the ones shown in S1. If this was the case they had to press the 'same' button irrespective of a possible mismatch of irrelevant information. Participants had to respond 'different' when one object (location) differed from the ones presented at S1. In the control task, no retention was necessary and upon presentation of S2 the two numbers had to be compared. A 'same'

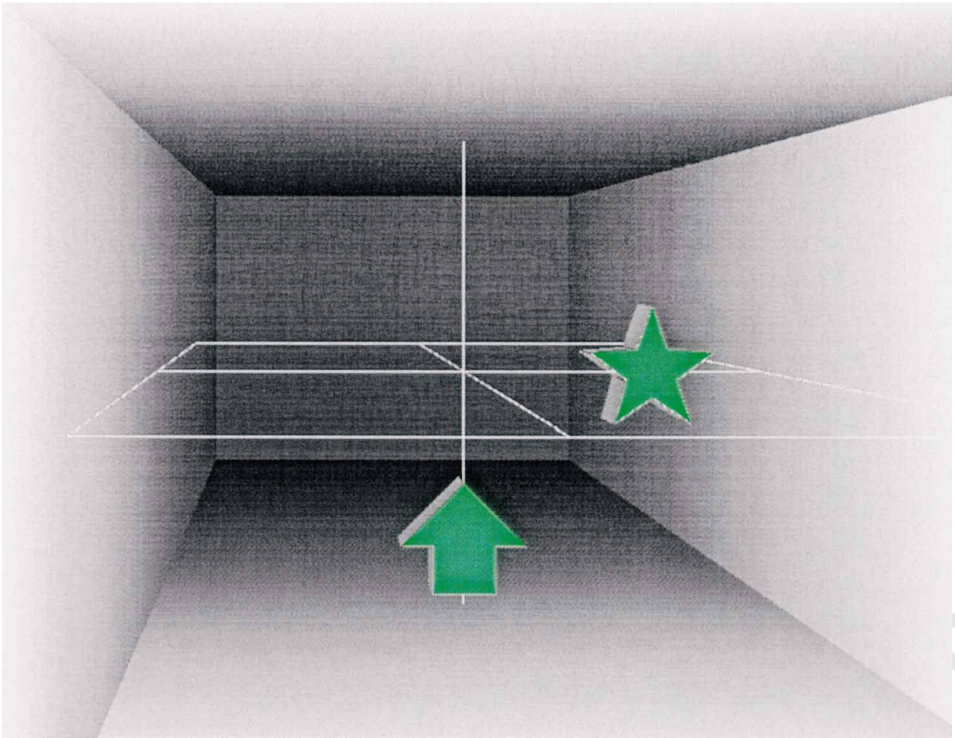

Fig. 1. Example of an S1 in experiment 1.

response was required when the two numbers were identical and a 'different' response when they were different.

The sequence of events in a single trial (depicted in Fig. 2) was as follows: trials started automatically and a break was given after each fourth trial that was terminated by the participant's button press.

Each trial began with the presentation of an empty 3D virtual space for 500 ms. Next, two objects were shown for 200 ms (S1). After an inter-stimulus interval (ISI, defined here as the onset difference) of 2.5 s the task cue was shown for 500 ms. Another 2.5 s later S2 was presented for 1 s. Participants had to respond within a 1800 ms time period after S2-onset and were instructed to respond as quickly and as accurately as possible. Feedback indicating correct, incorrect, or timeout responses was provided after each response.

To ensure that the same-different decision was based only on relevant information, in 80% of the trials the response associated with the irrelevant information was incongruent with that dictated by the relevant information. In the remaining 20% the response associated with the irrelevant information was congruent with the one dictated by the relevant information.

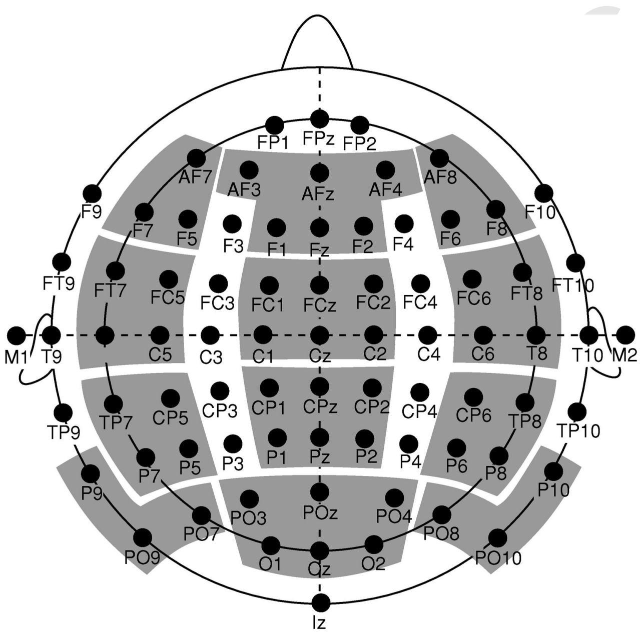

Fig. 2. Sequence of events in a single trial.

3.1.4. Experimental design and procedure

Participants were seated comfortably in a dimly lit room about 90 cm in front of the monitor screen and held a small response box on their lap.

The two levels of Format (figural and verbal) were blocked. The sequence of blocks and the assignment of response keys were counterbalanced across participants. The three levels of Task (object, spatial, and control) were pseudo-randomized. Each of the six permutations of Format×Task×Response type was equiprobable and consisted of 24 incongruent and six congruent trials, making up a total of 360 trials.

3.1.5. Recording procedure

The EEG was recorded from 74 tin electrodes referenced to the vertex (Cz) and off line rereferenced using an average reference [30]. The electrodes were mounted in an elastic cap (Electrocap International) and were positioned according to the enhanced 10–20 system based on the nomenclature described in Sharbrough et al. [46].

The ground electrode was positioned 10% of the nasion-inion distance anterior to Fz. The vertical electro-oculogram (EOG) was recorded from electrodes located above and below the right eye. The horizontal EOG was recorded from electrodes positioned at the outer canthus of each eye. Electrode impedance was kept below 5 k. The EEG and EOG were recorded continuously with a band pass from DC to 70 Hz and were A-D converted with 16 bit resolution at a sampling rate of 250 Hz. Prior to averaging, each epoch was manually scanned for eye-blinks or other artifacts. Drifts in the EEG signals were corrected by means of a modified version of the linear regression approach suggested by Hennighausen et al. [17].

3.1.6. Data analysis

3.1.6.1. Behavioral data. Response time (RT) was defined as the interval between the onset of S2 and the participant's key-press. RT averages were computed by collapsing over correct 'same' and 'different' responses of incongruent trials. Accuracy was analyzed using Pr, i.e., hit-rate minus false alarm rate [50] for incongruent trials only.

3.1.6.2. ERP data. ERPs time-locked to the onset of S1 and the cue were computed for each participant at all recording sites. Averages were computed separately for each condition.

They extended from 200 ms before stimulus onset until 2500 ms thereafter (i.e., onset of the following stimulus). Only trials containing correct responses were entered in the participant averages. The 200 ms preceding the stimulus served as a baseline, i.e., its mean value was subtracted from each data point in the waveform. To ensure that these ERPs are not confounded with systematic differences that occurred prior to the cue, averages that were time locked to S1 were also computed and no such differences were detected.

Repeated-measure ANOVAs were used to evaluate the significance of the experimental manipulations. In order to avoid the loss of statistical power that occurs when repeated measure ANOVAs are used to quantify multichannel and multi-time window data [31], electrode sites were pooled to form 12 topographical regions of interest (ROIs, see Fig. 3) [27].

ROIs represented a matrix of four levels on the anterior–posterior dimension and three levels on the left–right dimension and were defined as follows (see Fig. 2): left frontal (AF7, F7, F5), middle frontal (AF3, AFz, AF4, F1, Fz, F2), right frontal (AF8, F6, F8) left fronto-central (FT7, FC5, T7, C5), middle fronto-central (FC1, FCz, FC2, C1, Cz, C2), right fronto-central (FC6, FT8, C4, T8), left centro-parietal (TP7, CP5, P7, P5), middle centro-parietal (CP1, CPz, CP2, P1, Pz, P2), right centro-parietal (CP6, TP8, P6, P8), left parieto-occipital (P9, PO9, PO7), middle parieto-occipital (PO3, POz, PO4, O1, Oz, O2), and right parieto-occipital (P10, PO8, PO10).

Mean voltages within ROIs restricted to predefined time windows were calculated and used as dependent variables in repeated-measures ANOVAs. Thus, factors were Time-window (Time), Anterior–Posterior (Ant.-Post.), Laterality (Lateral), Task, and Format. All effects with two or more degrees of freedom in the numerator were adjusted for violations of sphericity according to the formula of Greenhouse and Geisser [14] and the Greenhouse-Geisser epsilon (ϵ) was used to adjust the P-values. In post hoc comparisons alpha-levels were corrected by means of a modified Bonferoni procedure [20].

The observations of task-specific SP-patterns were analyzed by a series of ANOVAs. Following visual inspection of the SP-effects four time epochs were selected: 600–1000 ms, 1000–1400 ms, 1400–1800 ms, and 2000–2500 ms. The first three epochs were chosen to examine task specific SP-effects whereas the fourth epoch served to examine the CNV. The analysis procedure was as follows: First, a global repeated-measure ANOVA was used to quantify the effects in the first three time windows. Then ANOVAs were conducted separately for the figural and verbal condition at anterior and posterior ROIs. More fine grained ANOVAs were conducted analyzing single time epochs and/or two-level comparisons of memory task effects when justified by significant interactions.

Topographic profile analyses were used to determine whether amplitude measurements reflected more than one pattern of brain activation. To ensure that topographic comparisons of ERP slow waves were not confounded by amplitude differences as a function of experimental condition, the RMS-standardization procedure suggested by McCarthy and Wood [25] was used.

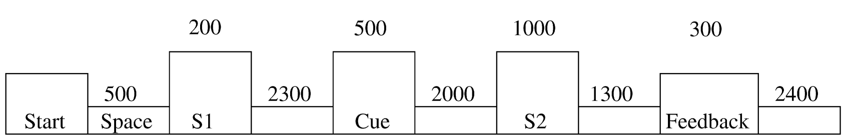

Fig. 3. Layout of electrodes and regions of interest.

3.1.7. Behavioral control experiment

A behavioral control experiment examined whether verbal rehearsal was used when words rather than figural stimuli were used as test-stimuli. A total of 24 participants performed the object and spatial working memory tasks in the verbal and figural condition as described above. In half of the trials an articulatory suppression task, i.e., counting backwards aloud in steps of one, had to be performed in the S1–S2 interval. It was proposed that interference tasks of similar kind disrupt verbal rehearsal but do not affect visuo-spatial retention processes [3].

Therefore it was predicted that articulatory suppression should disrupt memory performance in the verbal condition more than in the figural condition. Participants performed 240 trials with blocked and counterbalanced factors Interference and Format whereas the levels of Task were pseudo-randomized.

3.2. Results

3.2.1. Behavioral data

In the figural condition mean RTs were fastest in the spatial and slowest in the object memory task with the perceptual task being intermediate. In the verbal condition, RTs were comparable in the two memory tasks with the perceptual task being faster. Pr was approximately 0.8 in all memory tasks and 0.9 in the perceptual tasks. Notably, memory performance was not significantly different between the object and spatial memory task, neither in the figural ($F_{1,15}$=1.88, P>0.1) nor in the verbal ($F_{1,23}$<1) condition.

Contrasting RTs in the two figural and verbal memory tasks revealed faster RTs in the figural than the verbal memory tasks ($F_{1,15}$=69.56, P<0.0001). However, there was no difference in performance accuracy ($F_{1,15}$<1). This indicates that, though the figural stimuli could be faster encoded than words, the memory requirements were comparable in the two conditions. In order to examine the extent to which participants solely focused on the task relevant information we contrasted performance in incongruent and congruent trials in all four memory tasks. There were no significant effects of Congruence on RT but a significant main effect of Congruence on accuracy ($F_{1,15}$=10.18, P<0.01). This indicates that irrelevant information was not entirely inhibited. However, since the presence of response-incongruent irrelevant information led to more errors but did not at all delay RTs it can be assumed that participants mainly focused on the the relevant type of information.

3.2.2. Behavioral control experiment

Utilizing articulatory suppression [3], this control experiment examined the extent to which verbal rehearsal was utilized in the memory tasks of experiment 1. Pr-values were comparable in the tasks without suppression (0.81 and 0.79 in the figural object and figural spatial memory task; 0.79 and 0.80 in the respective verbal tasks) and decreased in tasks where subjects had to count backward aloud (0.63; 0.75 in the figural and 0.49; 0.62 in the verbal memory tasks) ($F_{1,23}$=105.55, P<0.0001). This decrease in performance was more pronounced in the verbal condition than in the figural condition ($F_{1,23}$=10.56, P<0.01) providing evidence for the enhanced use of verbal codes in the verbal memory tasks. This result showed that presenting S2 verbally rather than figurally subjects more relied on phonological codes in order to rehearse information provided by S1. In addition, object memory performance was more affected by the concurrent interference task than spatial memory performance in both the figural and the verbal condition ($F_{1,23}$=11.03, P<0.01), indicating that objects are more likely to be coded verbally than spatial locations.

3.2.3. EEG-data

The across-participant average ERPs from selected electrodes superimposed for the three tasks in the cue-S2 interval are displayed in Fig. 4 (figural condition) and Fig. 5 (verbal condition).

In all conditions and tasks the cue evoked a parietally focused P300 peaking around 500 ms. It was of comparable magnitude in the three figural tasks. In the verbal condition the P300 was most pronounced in the perceptual task and of comparable magnitude in the two memory tasks. Following the P300s, task dependent SPs emerged. The topographic distribution of these SPs is illustrated for the 600–1000, 1000–1400, and 1400–1800 ms time windows in the topographic maps displayed in Fig. 6.

The respective global ANOVA with factors Time (600–1800 ms, three levels), Ant.–Pos. (four levels), Lateral (three levels), Format (two levels), and Task (three levels) yielded significant interactions of the Task factor with Format, Time, and topographical factors (cf. Table 1) that allow separate ANOVAs for the verbal and figural condition and also separate ANOVAS for the six anterior and six posterior ROIs. These results are displayed in Table 1 showing significant main effects of Task and interactions with the Task factor. In the following all post hoc analyses reported below, i.e., direct comparisons of memory tasks with the perceptual task, are justified by these significant superordinate Task effects.

3.2.3.1. Figural condition

3.2.3.1.1. Anterior ROIs Starting around 700 ms in both, the object and the spatial memory task a left frontal negative and right frontal positive SP was obtained at anterior electrode sites relative to the perceptual task with the object memory task's SP being more negative than the spatial memory task's SPs at lateral frontal recording sites.

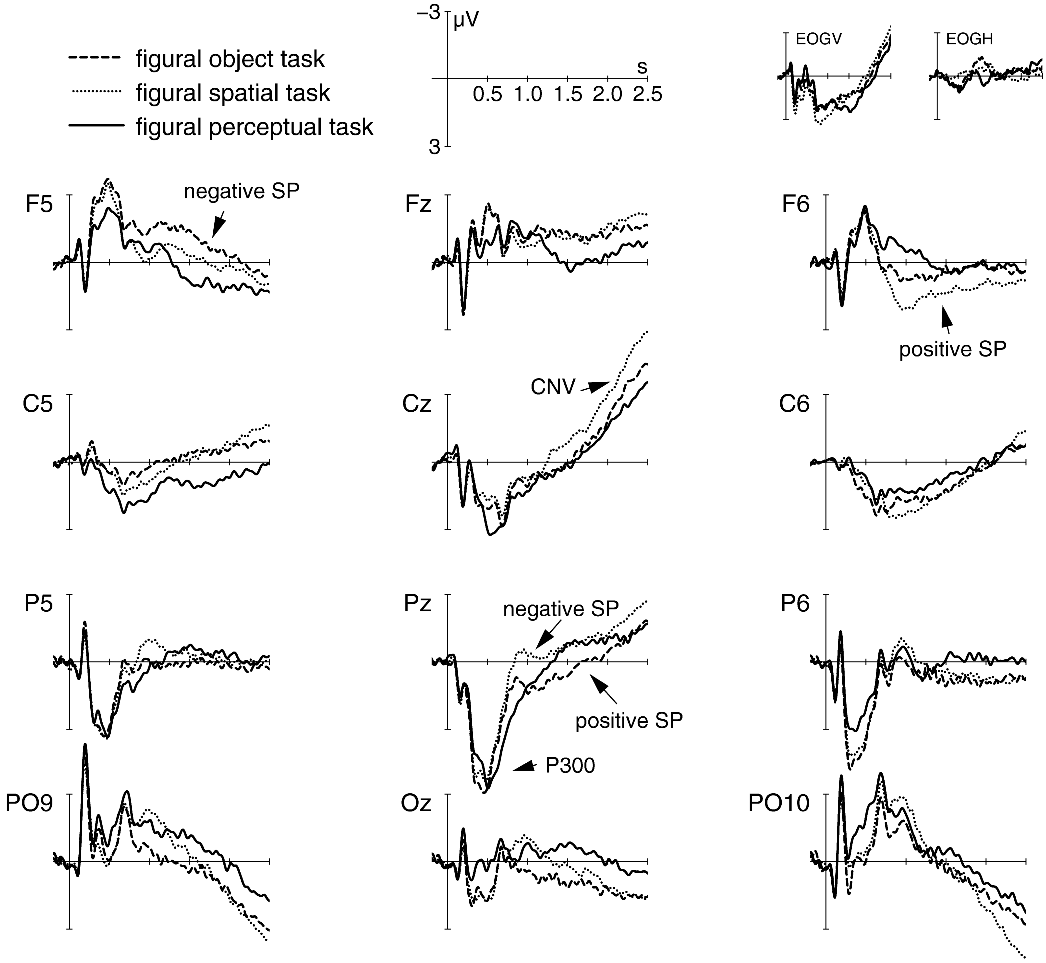

Fig. 4. Across-participant average ERPs at selected electrode sites (one per ROI) for all tasks in the cue-S2 interval in the figural condition of experiment 1. At 0 ms the cue was presented for 500 ms, at 2500 ms the onset of S2 occurred. Data were 10 Hz lowpass filtered for display purposes.

These SPs are apparent between 1000 and 1800 ms at frontal recording sites in the topographic maps (Fig. 6).

These frontal SPs were confirmed by repeated measures ANOVAs comparing either the object or the spatial memory task with the perceptual task, revealing significant interactions with the Task factor (cf. Table 1). More detailed post hoc comparisons showed that the SPs in the object memory task were significantly more negative than in the perceptual task in left ($F_{1,15}$=29.14, P<0.0001) and middle ($F_{1,15}$=5.7, P<0.05) ROIs and more positive in right anterior ROIs ($F_{1,15}$=5.53, P<0.05). Moreover, spatial memory task SPs were significantly more positive in right anterior ROIs ($F_{1,15}$=18.54, P<0.001), whereas the SPs in the left and middle ROIs were not significantly different.

A topographic profile analysis of the memory tasks' SPs at the six frontal ROIs resulted in significant interactions with the Task factor (Task×Ant.–Pos., $F_{1,15}$=6.08, P< 0.05; Task×Lateral, $F_{2,30}$=8.51, P<0.01, ϵ=0.78; Task× Ant.–Pos.×Lateral $F_{2,30}$=5.62, P<0.05, ϵ=0.93). This indicated that frontal SPs evoked by the object and the spatial memory task not only differed in magnitude but also in topography.

3.2.3.1.2. Posterior ROIs Beginning at around 1000 ms the ERP at parieto-occipital electrode sites evoked by the object memory cue was more positive than the one evoked by the perceptual task cue (Fig. 6, second panel). This positive difference was present until around 2200 ms. In contrast, in the spatial memory task a parietal SP was negative relative to the perceptual task. This negative SP was only present in an early time range (i.e. 600–1300 ms) relative to the aforementioned positive difference for the object memory task.

At more posterior electrodes (cf. Oz) both the object and the spatial SPs were positive relative to the perceptual task until presentation of S2. Based on interactions including the Task and the Time factor, analyses were carried out separately for three consecutive time windows.

In the first *600–1000 ms* time window a comparison of spatial memory and perceptual tasks revealed significant interactions with the Task factor. This confirmed that the

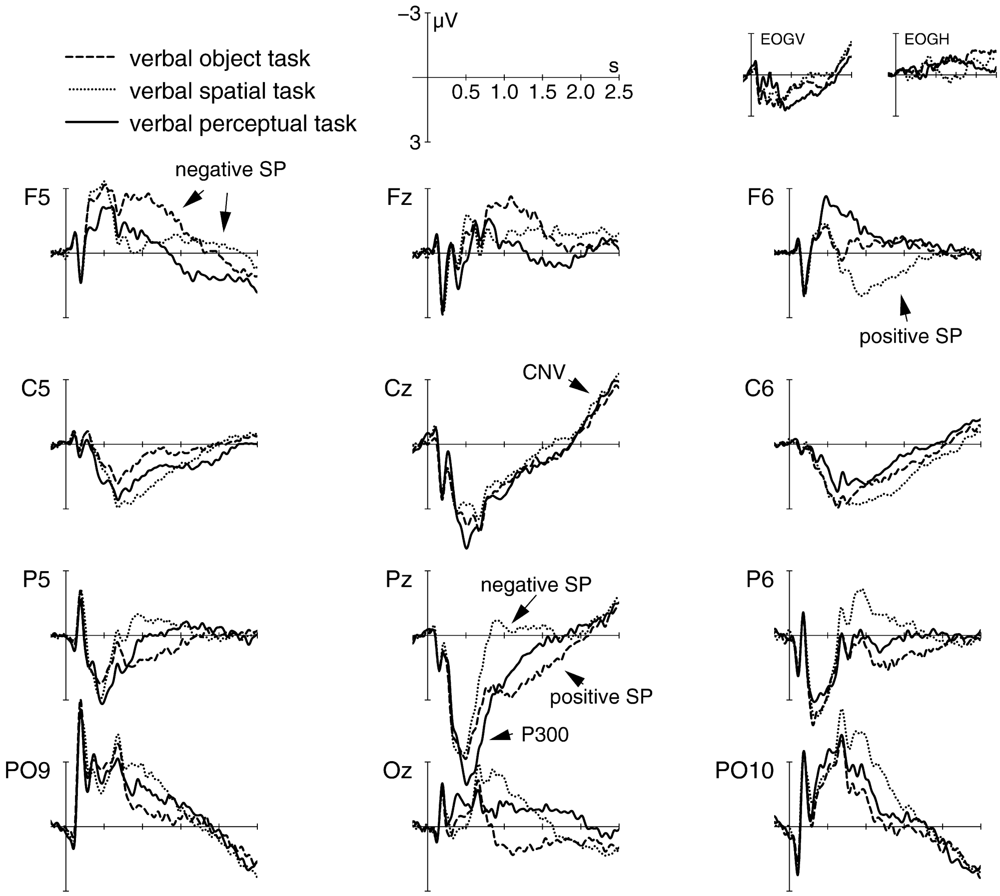

Fig. 5. Across-participant average ERPs at selected electrode sites for all tasks in the cue-S2 interval in the verbal condition of experiment 1.

SPs were more negative in the spatial memory than in the perceptual task most pronounced in the centro-parietal ROI ($F_{1,15}=17.74$, $P<0.001$). A similar pattern was achieved when object memory and perceptual tasks were compared. Again, the object task's SPs were more negative than the perceptual task's SPs in the centro-parietal ROI ($F_{1,15}=11.82$, $P<0.01$). However, examination of Fig. 4 suggests that this negative difference was substantially smaller and also restricted to a smaller time window than the corresponding difference between the spatial memory and the perceptual task.

Within the *1000–1400 ms* time window, contrasting object memory and perceptual task yielded significant Task effects. As apparent from the map (cf. Fig. 6, upper middle panel), this is caused by a positive difference most pronounced in the middle parieto-occipital ROI ($F_{1,15}=10.15$, $P<0.01$). Notably, despite a significant Task×Ant.–Pos.×Lateral interaction, there were no statistically reliable Task effects for the spatial memory task in any of the posterior ROIs.

In the *1400–1800 ms* time window, a similar pattern as in the preceding time window was obtained. In the object task, a positive difference was observed that was most pronounced in middle parieto-occipital ROI ($F_{1,15}=38.94$, $P<0.0001$). Again, there were no statistically reliable Task effects for the spatial memory task in any of the posterior ROIs.

3.2.3.2. Verbal condition. Apart from the larger P3 in the perceptual task, the ERP pattern evoked by the task cues in the verbal condition resembled the one obtained in the figural condition.

3.2.3.2.1. Anterior ROIs As in the figural condition, verbal memory tasks evoked frontal SPs that were negative at left and positive at right anterior electrode sites relative to the perceptual task. The left frontal SP in the object memory task was more negative than in the spatial memory task and emerged around 700 ms in the object memory task but not before 1200 ms in the spatial memory task. Interestingly, this left frontal negative SP was initially substantially more pronounced in the verbal object memory task than in the respective figural task.

The frontal SPs were confirmed by repeated measures ANOVAs restricted to the 600–1800 ms time interval. The left frontal negative SPs in the object and the spatial memory task relative to the perceptual task were confirmed by significant interactions with the Task factor (cf. Table 1).

More detailed post hoc comparisons showed that the SPs

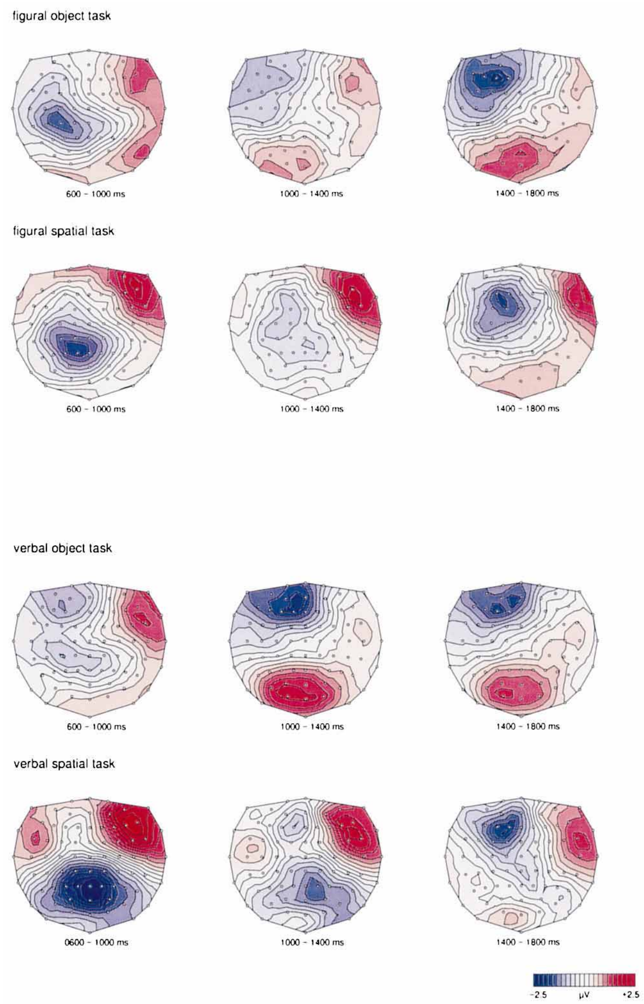

Fig. 6. Topographic maps of the SP-difference between object memory and perceptual task and the difference between spatial memory and perceptual task averaged across 400 ms time windows in the figural (upper two panels) and verbal (lower two panels) condition. Electrode positions are indicated by small circles.

in the object memory task were significantly more negative than in the perceptual task in the left ($F_{1,15}$=20.0, $P<0.001$) and the middle ($F_{1,15}$=6.31, $P<0.05$) anterior ROIs. Moreover, in the spatial memory task SPs were significantly more positive in right anterior ROIs ($F_{1,15}$=10.05, $P<0.01$) whereas the SPs in the left and middle ROIs were not significantly different.

As in the figural condition, a topographic profile analysis yielded significant interactions with the Task factor (Task×Lateral, $F_{2,30}$=3.52, $P<0.05$, ϵ=0.96; Task×Lateral×Ant.–Pos., $F_{2,30}$=4.86, $P<0.05$, ϵ=0.96) indicating that frontal SPs evoked by the object and the spatial memory tasks not only differed in magnitude but also in topography.

3.2.3.2.2. Posterior ROIs At parietal sites a negative SP followed the P300 and lasted until 1500 ms. In the object memory task, a positive SP was obtained lasting until about 2000 ms at parietal (cf. Pz) and until the onset of the S2 at occipital sites (cf. Oz). As shown in Fig. 6 (lower two panels), the posterior slow wave pattern in the verbal tasks are highly similar in their temporal and topographic characteristics to those in the figural condition.

Within the *600–1000 ms* time window at posterior ROIs, a comparison of the object memory and the perceptual tasks did not reveal significant differences whereas the spatial memory task vs. perceptual task comparison revealed significant Task effects. These results confirmed the negative SP in the spatial memory task that was most pronounced in the centro-parietal ROI ($F_{1,15}$=17.74, $P<0.001$).

In the following *1000–1400 ms* time window a comparison of object memory and perceptual tasks revealed significant Task effects confirming that, relative to the perceptual task, in the object memory task a positive SP was most pronounced in the middle parieto-occipital ROI ($F_{1,15}$=10.15, $P<0.01$). Again, a comparison of spatial memory and perceptual tasks revealed significant Task effects confirming that the negative SP of the spatial memory task extended from the 600–1000 ms into the 1000–1400 ms time interval.

In the *1400–1800 ms* time window, a contrast of object memory and perceptual tasks yielded significant main Task effects, indicating that similarly to the preceding time window the positive SP was most pronounced in the middle parieto-occipital ROI ($F_{1,15}$=38.94, $P<0.0001$). A comparison of spatial memory and perceptual tasks yielded a significant Task×Ant.–Pos.×Lateral interaction, indicating that there was a positive potential most pronounced within the middle parieto-occipital ROI and less pronounced at the lateral ROIs.

In summary, in both conditions a similar task-specific pattern was observed. Relative to the control conditions, in both the object and the spatial memory tasks, left frontal negative SPs were observed that were more negative in the object tasks. In the spatial tasks, parietal negative SPs were evoked whereas in the object tasks, a parieto-occipital positive SP followed the P300. These task differences were more pronounced in the verbal than in the figural condition.

3.2.3.3. CNV. A CNV-like potential emerged in all three figural tasks (cf. Cz) at around 2000 ms. It was most pronounced in the spatial memory task and smallest in the perceptual task. Statistical analysis within the *2000–2500 ms* time window confirmed this observation. Restricted to electrode Cz a significant main effect of Task ($F_{2,30}$=24.78, $P<0.0001$, ϵ=0.96) was obtained.

The CNV-differences in the two memory tasks are in accordance with the behavioral data, i.e., the faster the upcoming response the more negative the CNV. This result is consistent with the view that CNV amplitude and RT to the upcoming trial are inversely related [35]. Conversely, CNVs were less pronounced in the perceptual task. This

Table 1
ANOVAs of SPs in experiment 1

Effect	d.f.	*F*	*P*	ϵ	Effect	d.f.'s	F	*P*<	∈
Global									
1. Task×Ant.–Pos.	6.90	8.32	<0.0100	0.35					
2. Task× Lateral	4.60	11.26	<0.0001	0.78					
3. Task×Ant.–Pos.×Time	12.180	12.08	<0.0001	0.35					
4. Task×Ant.–Pos.×Format	6.90	3.14	<0.0500	0.39					
5. Task×Ant.–Pos.×Lateral	12.180	8.41	<0.0001	0.31	VERBAL:				
					Anterior ROIs				
Figural					1.Task	2.30	7.95	0.01	.79
Anterior ROIs					2.Task×Lateral	4.60	7.83	0.001	.79
1. Task	2.30	3.77	<0.0500	0.79	3.Task×Time	4.60	12.52	0.0001	0.54
2. Task×Lateral	4.60	16.41	<0.0001	0.63	4.Task×Time×Ant.–Pos.	4.60	3.22	0.05	0.67
3. Task×Time	4.60	9.91	<0.0010	0.54	object vs. baseline				
Object vs. baseline					Task×Time	2.30	9.58	0.01	0.83
Task×Time	2.30	17.31	<0.0001	0.72	Task×Lateral	2.30	8.83	0.01	0.82
Task×Lateral	2.30	15.86	<0.0001	0.70	Task×Ant.–Pos.	1.15	9.29	0.01	
Spatial vs. baseline					spatial vs. baseline				
Task×Time	2.30	15.98	<0.0001	0.95	Task×Time	2.30	15.49	0.0001	0.9
Task×Lateral	2.30	19.29	<0.0001	0.86	Task×Lateral	2.30	10.48	0.001	0.87
Posterior ROIs					Posterior ROIs				
1. Task×Time	4.60	6.56	<0.0010	0.80	1.Task	2.30	14.96	0.0001	0.85
2. Task×Time×Ant.–Pos.	4.60	3.83	<0.0500	0.43	2.Task×Time	4.60	10.39	0.0001	0.73
3. Task×Time×Lateral	8.120	5.31	<0.0010	0.66	3.Task×Ant.–Pos.	4.60	3.59	0.05	0.97
Posterior ROIs: 600–1000 ms					4.Task×Ant.–Pos.×Lateral	4.60	3.6	0.05	0.74
1. Task×Ant.–Pos.	2.30	7.97	<0.0100	0.97	Posterior ROTs: 600-lOOOms				
2. Task×Lateral	4.60	8.07	<0.0010	0.77	1.Task	2.30	17.21	0.0001	0.82
3. Task×Ant.–Pos.×Lateral	4.60	5.99	<0.0100	0.69	2.Task×Lateral	4.60	2.78	0.05	0.98
Object vs. baseline					spatial vs. baseline				
Task×Ant.–Pos.	1.15	16.5	<0.0010		Task	1.15	16.96	0.001	
Task×Lateral	2.30	12.86	<0.0001	0.88	Task×Lateral	2.30	4.47	0.05	0.91
Task×Ant.–Pos.×bateral	2.30	4.59	<0.0500	0.81	Task×Lateral×Ant.–Pos.	2.30	4.18	0.05	0.79
Spatial vs. baseline					Posterior ROIs: l000-1400 ms				
Task×Ant.–Pos.	1.15	6.05	<0.0500		1.Task	2.30	15.14	0.0001	0.91
Task×Lateral	2.30	7.26	<0.0100	0.99	2.Task×Ant.–Pos.	2.30	5.15	0.01	0.96
Task×Ant.–Pos.×Lateral	2.30	11.6	<0.0010	0.88	3.Task×Ant.–Pos.×Lateral	2.30	4.18	0.05	0.79
Posterior ROIs: 1000–1400 ms					object vs. baseline				
1. Task×Ant.–Pos.	2.30	3.68	<0.0500	0.87	Task	1.15	7.77	0.05	
2. Task×Ant.–Pos.×Lateral	4.60	6.87	<0.0001	0.69	Task×Ant.–Pos.	1.15	4.94	0.05	
Object vs. baseline					Task×Ant.–Pos.×Lateral	2.30	3.36	0.05	0.99
Task	1.15	4.93	<0.0500		spatial vs. baseline				
Task×Ant.–Pos.	1.15	10.9	<0.0100		Task	1.15	6.27	0.05	
Task×Ant.–Pos.×Lateral	2.30	8.69	<0.0100	0.87	Task×Ant.–Pos.×Lateral	2.30	4.61	0.05	0.95
Spatial vs. baseline					Posterior ROTs: 1400-1800 ms				
Task×Ant.–Pos.×Lateral	2.30	10.8	<0.0010	0.92	1.Task	2.30	6.29	0.05	0.72
Posterior ROTs: l400–1800 ms					2.Task×Ant.–Pos.×Lateral	4.60	4.62	0.01	0.72
1. Task	2.30	5.45	<0.0500	0.75	object vs. baseline				
2. Task×Ant.–Pos.	2.30	5.88	<0.0500	0.68	Task	1.15	8.38	0.05	
3. Task×Ant.–Pos.×Lateral	4.60	8.35	<0.0001	0.83	Task×Ant.–Pos.×Lateral	2.30	4.18	0.05	0.84
Object vs. baseline					spatial vs. baseline				
Task	1.15	24.62	<0.0010		Task×Ant.–Pos.×Lateral	2.30	8.52	0.01	0.93
Task×Ant.–Pos.	1.15	21.13	<0.00100						
Task×Ant-Pos.×Lateral	2.30	10.47	<0.0010	0.99					
Spatial vs. baseline									
Task×Ant.–Pos.	1.15	5.39	<0.0500						
Task×Ant-Pos.×Lateral	2.30	10.67	<0.0010	0.90					

might reflect the fact that fewer attentional resources were required to accomplish this task [19].

In the verbal condition, the CNV-like potential was of comparable amplitude in all three tasks ($F_{2,30}<1$).

To decide whether SP-differences in this late time window are solely due to CNV differences, a global four-way ANOVA with Factors Format, Task, Ant.–Pos, and Lateral was performed using normalized data. Significant interactions involving the Task factor indicated that independent of CNV-differences and coding format topographic SP-differences due to the task were still present (Task×Lateral, $F_{4,60}=3.64$, $P<0.05$, $\epsilon=0.79$; Task×Ant.–Pos.×Lateral, $F_{12,180}=2.66$, $P<0.05$, $\epsilon=0.3$).

3.3. Discussion

Retention of both visual and verbal information elicited a frontal slow wave that was more negative at left and more positive at right frontal electrodes relative to the respective perceptual task. As revealed by the topographic profile analyses, the scalp distributions of these frontal SPs were different for the two memory tasks, indicating that distinct cortical generators were involved when objects and spatial locations were retained in WM [18].

In both the figural and the verbal condition, the frontal SP was more negative for the object memory than in the spatial memory task, a finding also reported by Mecklinger and Pfeifer [29] who examined retention processes for object forms and spatial locations in different load conditions.

Left frontal negative SPs were larger in the object than in the spatial memory tasks and was largest in the verbal object memory task. In light of the results of the behavioral control experiment, indicating that verbal rehearsal was more likely in the object memory tasks than in the spatial memory tasks, it is conceivable that the left frontal SP is associated with verbal rehearsal in the cue-S2 interval. Corroborating this view, left frontally distributed negative SPs of similar kind have been associated with verbal rehearsal processes in prior studies [44,41,40]. In light of the results of the behavioral control experiment 1, indicating that verbal rehearsal was more likely in the object memory tasks than in the spatial memory tasks, it is conceivable that the left frontal SP at least in part is associated with possible verbal rehearsal in the cue-S2 interval.

In both the figural and verbal condition, a sustained posterior positive SP was obtained in the object memory tasks starting around 1000 ms after cue-onset. In the verbal condition this positive slow wave was also present in the spatial memory task, but only in the late 1400–1800 ms time interval. An objection against the interpretation of this pattern as a posterior slow wave could be that the cue indicating the perceptual task evoked a larger P300 amplitude in the verbal condition especially at the parietal electrodes such that the memory task SP in both conditions are compared with different baseline waveforms and no comparison can be made between the SPs in the two conditions. However, the results for the slow wave pattern obtained after 1000 ms in the verbal condition were not different in any significant aspect when the SPs in verbal working memory tasks were scored against the figural baseline task. Rockstroh and McCallum [36] proposed that positive SPs may either indicate inhibition of cortical areas close to the recording sites or result from a negative potential originating in a folding of the cortex that projects positively to the scalp surface. If the former is true then posterior cortical areas might be inhibited when verbal rehearsal occurs. In the latter case, a cortical area producing positive voltages at posterior electrode sites has to be active. According to Ruchkin et al. [41] posterior positive SPs of similar kind may reflect conversions of visual to verbal representational formats. Thus, experiment 1 alone cannot decide between these alternative explanations.

In both the figural and the verbal conditions, a transient negative parietal SP starting at around 600 ms and lasting about 400 ms and 800 ms, respectively, was obtained in the spatial memory tasks. Thus, compared to the posterior positive SPs observed in the object task, the onset of these posterior negative SPs was earlier and their duration was shorter.

This negative SP presumably reflects the transient activation of a visuo-spatial store which might be accomplished by the allocation of spatial selective attention, i.e., the covert shift of attention from one location to another [2]. In support of the view that spatial selective attention is the rehearsal mechanism, similar SPs are consistently reported whenever spatial cognitive operations are required [38,39,42,16,29,28]. Since the negative SP in the present study did not extend until S2-onset it is conceivable that this negative slow wave does not represent retention operations per se, but rather the activation of a fast accessible spatial store. However, it remains unclear why a parietal negative SP was also evoked in the verbal spatial memory task.

As a conclusion, in order to resolve the functional significance of the observed SPs, it remains to be specified whether or not the left frontal slow wave is associated with verbal rehearsal operations. Another important issue is to clarify whether the positive parieto-occipital SP reflects a conversion from visual to verbal representational formats and is therefore specific for verbalizable stimulus materials. We approached both issues in a second experiment that employed stimuli for which verbal labels are not easily retrievable.

4. Experiment 2

Experiment 2 examined the extent to which the frontal and posterior slow wave pattern obtained in the figural condition of experiment 1 are generalizable to visual WM per se or rather reflect the contribution of verbal WM processes. We therefore used line drawings of abstract geometrical objects as stimulus materials.

4.1. Methods

4.1.1. Participants

Twenty-five right-handed volunteers participated. None of the participants had prior experience with the experimental task. Due to technical artifacts the EEG-data of one participant had to be excluded from the data analysis. The remaining 24 participants were between 21 and 29 years of age (median: 23), and 12 were female. All were right-handed with either normal or corrected to normal vision.

4.1.2. Stimuli

All stimuli were presented on a 17′ VGA monitor under the control of a P-90 computer. S1 and S2 contained two distinct green colored objects (‘Klingon letters’) from a set of 36. Objects were located on a virtual horizontal gray plane. One object was located in the left half of the screen, the other in the right. There were 32 locations possible, 16 on each side. The positions varied in spatial depth and on the left-right dimension. Objects were 4.5±0.7 cm wide (visual angle=2.86°±0.45°) with a height of 4.75±0.25 cm (3.02°±0.16°). Horizontal distance between the objects was 8.5±2.5 cm (5.41°±1.59°). Task cues were identical to those used in experiment 1a. (Fig. 7)

4.1.3. Experimental design and procedure

Each participant performed a practice session. Then the electrode cap was applied followed by the test session. The experiment lasted about 4 h in total.

The experimental procedure was similar to experiment 1 with the exception that S1 was shown for 400 ms instead of 200 ms because objects and locations were more difficult to encode. ISIs remained the same as in experiment 1.

In 50% of the trials the response associated with the irrelevant information was incongruent with the one dictated by the relevant one. In the other 50% of the trials this assignment was reversed. The experimental session included 384 trials. The three levels of Task (object, spatial, and control) were quasi-randomized and equiprobable. Each of the six permutations of the conditions Task× Response consisted of 32 congruent and 32 incongruent trials. The recording procedures and data analyses were identical with experiment 1.

4.1.4. Behavioral control experiment

Sixteen volunteers participated in a behavioral control experiment that used the identical dual task interference approach as behavioral experiment 1 and employed the stimuli of experiment 2. Participants performed 144 trials

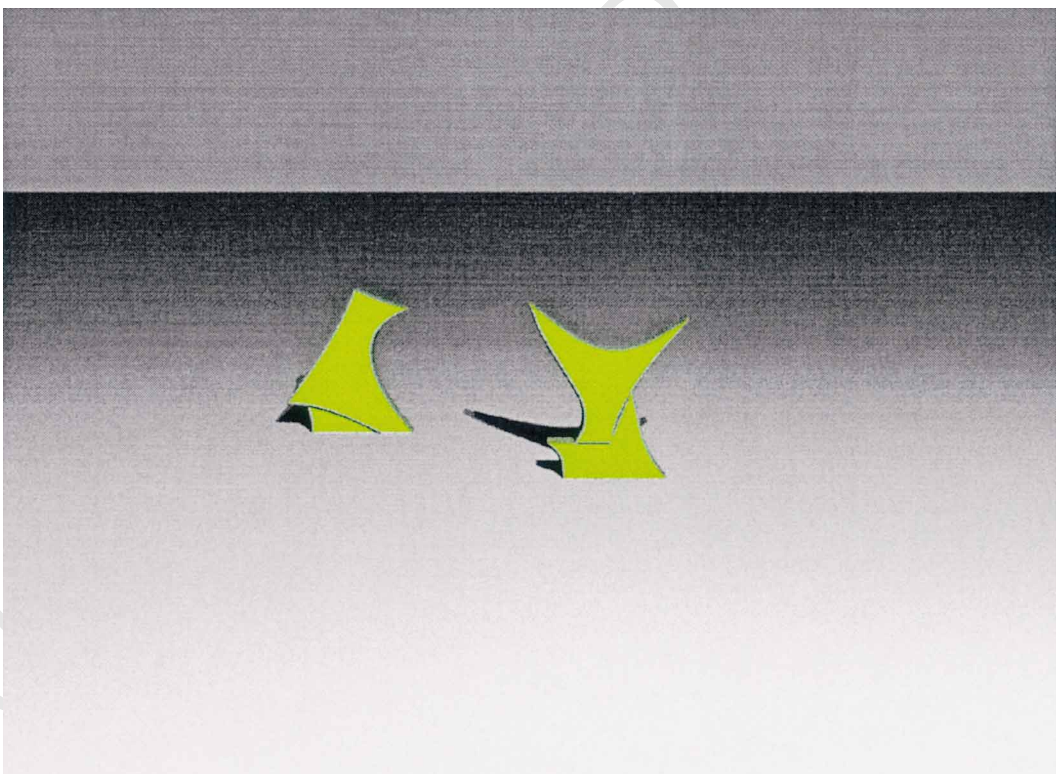

Fig. 7. Example of an S1 in experiment 2.

with a blocked factor Interference. The two levels of Task were pseudo-randomized.

4.2. Results

4.2.1. Behavioral data

In a post-experimental debriefing all participants claimed that they were not able to use verbal labels for rehearsal. The performance data for all experimental conditions are displayed in Fig. 8.

Response times were comparable in the memory tasks and fastest in the perceptual task. This pattern was confirmed by a repeated measures ANOVA yielding a main effect of Task ($F_{2,46}=7.89$, $P<0.01$, $\epsilon=0.68$). When comparing the object and the spatial memory tasks directly, the Task effect was not significant ($F_{1,23}<1$).

As expected, performance accuracy was close to perfect in the perceptual task and worse in the memory tasks. Memory performance was better in the object than in the spatial memory task ($F_{1,23}=49.0$, $P<0.0001$).

4.2.2. Behavioral control experiment

As in experiment 1, a control experiment examined to which extent verbal rehearsal was used. Memory performance was 0.48 in the object and 0.49 in the spatial memory task without articulatory suppression. With suppression Pr-values were 0.47 and 0.49, respectively. There was neither a significant main effect of interference nor an interaction with the type of information ($F_{1,15}<1$). This supports the view that visual rather than verbal rehearsal strategies were used to maintain the abstract geometrical objects and their respective locations in WM.

4.2.3. EEG-data

The across-participant average ERPs superimposed for the three tasks in the cue-S2 interval are displayed in Fig. 9.

The cue evoked a parietally focused P300 peaking around 500 ms in all three conditions. The amplitude was of comparable magnitude in the two memory tasks (Pz) but more pronounced in the perceptual task. Starting at around 700 ms slow waves at posterior and frontal electrodes emerged in the two memory tasks. The topographic distribution of these SPs is illustrated in Fig. 10.

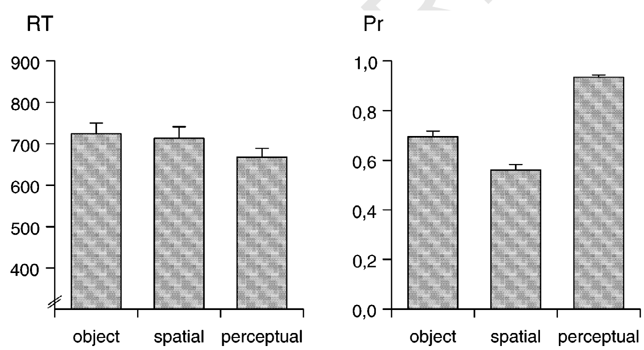

Fig. 8. RTs of incongruent and congruent trials for 'same' responses and Pr-differences collapsed over 'same' and 'different' responses in experiment 2.

The same time epochs as in experiment 1 were chosen for statistical analysis. ANOVA results are displayed in Table 2.

A global repeated-measure ANOVA with factors Time (three levels), Ant.–Pos. (four levels), Lateral (three levels) and Task (three levels) yielded a Task×Ant.–Pos.×Time interaction suggesting that the task effects were different in the three time intervals. However, since the Task×Ant.–Pos. interactions were significant in all three time windows, data were collapsed across time windows for the subsequent ANOVAs that were conducted separately for the six anterior and the six posterior ROIs (Table 2) as in experiment 1.

4.2.3.1. Anterior ROIs. At left frontal electrode sites the SPs in both memory tasks were more negative in the memory task than in the perceptual task, with this difference being more pronounced in the object memory task.

An ANOVA contrasting the object memory task and the perceptual task confirmed this observation and yielded a significant main effect of Task. Moreover, significant interactions of Task with the Ant.–Pos. and Lateral factor suggested that this difference was largest in the middle frontal ROI. Similarly, a comparison of spatial memory and perceptual tasks resulted in a significant Task×Lateral interaction. This interaction was due to larger slow wave activity in the spatial memory task in the middle ROIs ($F_{1,23}=7.27$, $P<0.05$) whereas in the left and right lateral ROIs no such difference was significant.

To test whether frontal SPs in the object and the spatial memory task differed topographically, an ANOVA with normalized data restricted to the anterior ROIs and the two memory tasks was conducted. Significant interactions including the Task factor indicated that the topographies of anterior SPs in the memory tasks were different (Task×Ant.–Pos., $F_{1,23}=18.44$, $P<0.001$; Task×Lateral, $F_{2,46}=3.75$, $P<0.05$, $\epsilon=.77$; Task×Ant.–Pos.×Lateral, $F_{2,46}=6.3$, $P<0.001$, $\epsilon=0.96$). This suggests that different combinations of neuronal sources contribute to the slow wave pattern evoked by both information types.

To evaluate differences of the frontal patterns obtained in experiments 1 and 2, between-experiment ANOVAs were conducted comparing either the object or the spatial memory frontal SPs using normalized data. Significant interactions with the Experiment factor were obtained for the object memory task (Exp×Lateral, $F_{2,76}=4.64$, $P<0.5$, $\epsilon=0.92$; Exp×Ant.–Pos., $F_{1,38}=4.19$, $P<0.5$) but not for the spatial memory task.

4.2.3.2. Posterior ROIs. At posterior electrodes a positive SP focused at POz emerged in the object memory task whereas in the spatial memory task a similar positive SP

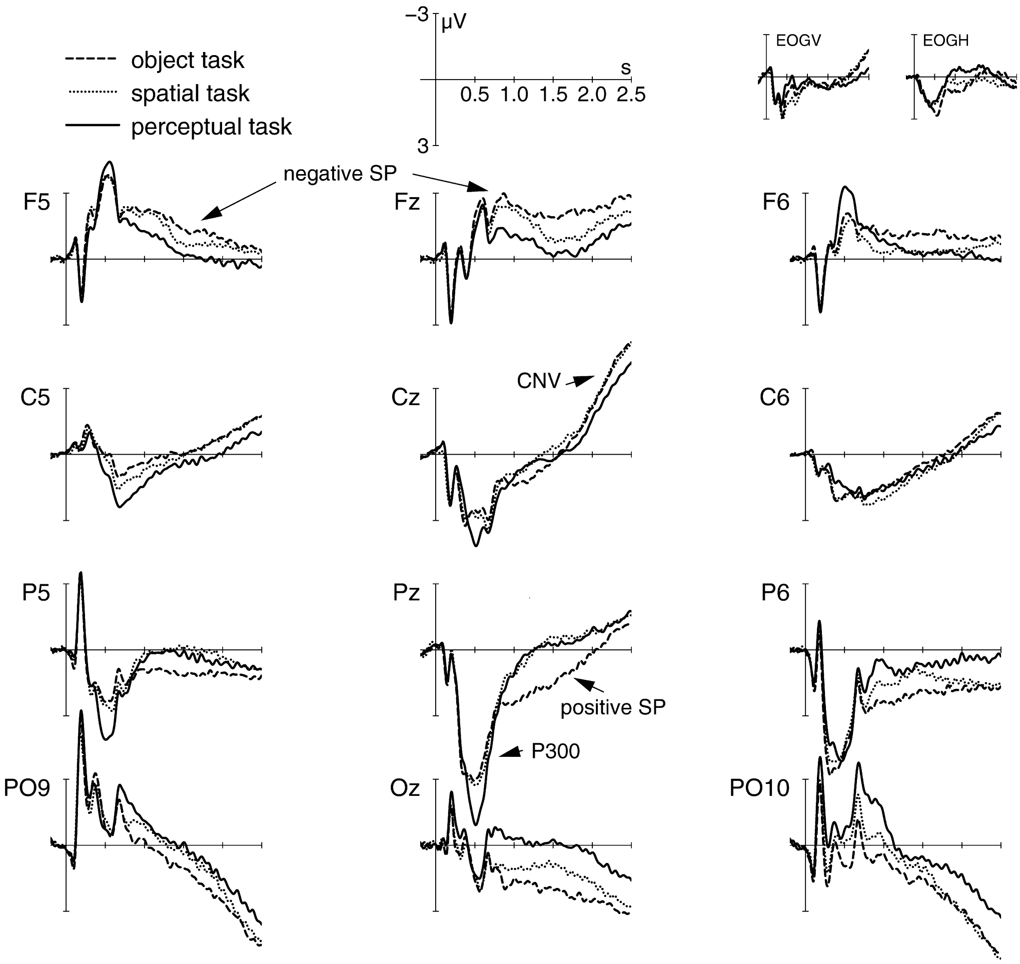

Fig. 9. Across-participant average ERPs at selected electrode sites for all tasks in the cue-S2 interval in experiment 2.

with a more posterior distribution was obtained. These positive SP were more pronounced in the object memory task than in the spatial memory task and extended until the end of the cue-S2 interval. At the six posterior ROIs, a comparison of object memory and perceptual tasks revealed a significant main effect of Task and a significant Task×Ant.–Pos interaction, i.e., the positive SP was more pronounced at parieto-occipital electrode sites. For the spatial memory task there was no significant main effect of Task but a significant Task×Ant.–Pos interaction indicating that the positive difference between the spatial memory and the perceptual tasks was significant at the three most posterior ROIs ($F_{1,23}$=6.13, P<0.05) but not at the centro-parietal ROIs ($F_{1,23}$<1).

In summary, relative to the control condition, a left frontal negative SP was elicited in both memory tasks that was more negative in the object memory task. A parieto-occipital positive SP was more pronounced in the object than in the spatial memory task.

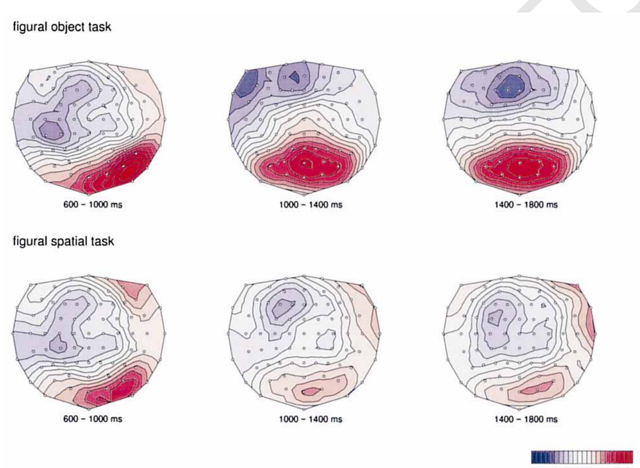

Fig. 10. Topographic maps of the SP-difference between object memory and perceptual task (upper panel) and the difference between spatial memory and perceptual task (lower panel) averaged across the 400 ms time windows.

4.2.3.3. CNV. As in experiment 1, a CNV-like potential emerged in all three tasks. It was of comparable magnitude in the memory tasks and less pronounced in the perceptual task. An ANOVA restricted to the Cz-electrode and the 2000–2500 ms time window revealed a significant effect of Task ($F_{2,46}$=5.31, P<0.01, ϵ=0.95). The contrast of

Table 2
ANOVA of SPs in experiment 2, 600–1800 ms

Effect	d.f.	F	P	ϵ
Global				
1. Task×Ant.–Pos.	6.138	10.27	<0.0001	0.38
2. Task×Lateral	4.920	5.09	<0.0100	0.71
3. Task×Ant.–Pos.×Time	12.276	3.11	<0.0500	0.32
4. Task×Ant.–Pos.×Time×Lateral	24.552	5.19	<0.0001	0.39
Anterior ROIs				
1. Task	2.46	9.26	<0.0010	0.96
2. Task×Lateral	4.92	3.96	<0.0500	0.58
3. Task×Ant.–Pos.	2.46	4.08	<0.0500	0.74
4. Task×Lateral×Ant.–Pos.	4.92	3.78	<0.0500	0.74
Object vs. baseline				
Task	1.23	17.11	<0.0001	
Task×Ant.–Pos.	1.23	5.59	<0.0500	
Task×Ant.–Pos.×Lateral	2.46	5.15	<0.0500	0.94
Spatial vs. baseline				
Task×Lateral	2.46	5.42	<0.0500	0.70
Posterior ROIs				
1. Task	2.46	10.75	<0.0010	0.99
2. Task×Lateral	4.92	3.71	<0.0500	0.60
3. Task×Ant.–Pos.	2.46	16.68	<0.0001	0.79
4. Task×Lateral×Aflt.-POS.	4.92	3.61	<0.0500	0.90
Object vs. baseline				
Task	1.23	20.61	<0.0001	
Task×Ant.–Pos.	1.23	32.60	<0.0001	
Spatial vs. baseline				
Task×Ant.–Pos.	1.23	29.61	<0.0001	

the two memory tasks was not significant ($F_{1,23}<1$), whereas both the CNV in the object ($F_{1,23}=7.08$, $P<0.05$) and the spatial memory task ($F_{1,23}=7.36$, $P<0.05$) were different from the perceptual task.

As in experiment 1 we used normalized ERP data in the 2000–2500 ms interval to examine whether between-task differences are solely due to differential CNV activity. A significant Task×Ant.–Pos. interaction ($F_{6,138}=3.92$, $P<0.05$, $\epsilon=0.42$) was obtained in an ANOVA for the normalized data. Therefore, it can be concluded that posterior positive SPs and frontal negative SP were still present in the late time window.

4.3. Discussion

The main result of experiment 2 was that a left frontal negative SP as well as a parieto-occipital positive SP were present in the object and the spatial memory task although verbal rehearsal did not play a role during retention as indicated by the behavioral control experiment. However, the focus of the left frontal negative SP was more medial (near electrode F1) than in experiment 1 (electrode F3).

Second, no negative transient parietal SP in the 600–1000 ms time interval was obtained in the spatial memory task even though this SP is consistently reported for spatial cognitive tasks such as spatial WM, mental rotation, and retrieval of spatial information from long-term memory [38,39,16,29].

The observation of a left frontal negative SP in the present experiment speaks against the view that this potential is solely related to verbal working memory processes. Rather, given that a left frontal SP was obtained in this experiment as well as in experiment 1 in which words were used as test stimuli and verbal rehearsal was likely, it is conceivable that this SP is associated with more general control operations of working memory, i.e., maintenance of the contents of WM [33] or the focusing of attention on goal relevant information [49].

However, the topographic profile analyses performed for the frontal SPs in the memory tasks provided evidence for the view that the slow wave pattern in the two tasks arose from qualitatively different neuronal activation patterns [18]. Moreover, the between-experiment comparison revealed different frontal SP patterns for the figural object memory tasks. As shown by the behavioral control experiments, additional verbal rehearsal occurred in experiment 1 but not in experiment 2, suggesting that verbal rehearsal is evidenced by a topographically distinct frontal SP component. Moreover, such a difference was not found for the figural spatial memory tasks where in both experiments the degree of verbalization was low.

These findings are evidence against the view that this ERP pattern reflects a higher order monolithic function and rather suggests that frontal SPs reflect in part information-specific WM retention systems. This view is consistent with a model of WM recently proposed by Goldman-Rakic [12]. In her view, distinct frontal areas subserve maintenance functions depending on the type of information (i.e., spatial, object, or verbal).

Similarly, the finding that the parieto-occipital positive SP was present even when participants did not verbally rehearse the stimulus material argues against the view that this SP reflects operations solely related to verbal WM such as a transformation from visual to verbal representation formats. The topographic differences of this parieto-occipital SP, with a clear focus at electrode POz in the object memory task and a more posterior focus (Oz) in the spatial memory task again suggest that this SP is associated with information-specific retention operations.

The posterior positive SP obtained in the spatial memory task, however, was unexpected. It was less pronounced and more posterior than that for the object memory task. A possible explanation of the absence of the predicted parietal negative SP in the spatial memory task is that a positive SP was superimposed. Most probably, this positive SP was due to a possible maintenance of object information in the spatial memory task which may have occurred simultaneously. A hint towards this interpretation is that the focus of the SP in the object memory task was in the vicinity of the POz electrode whereas the focus in the spatial memory task was near Oz. This is exactly the pattern to be expected if a negative SP with focus near Pz is superimposed with a POz-focused positive potential.

5. General discussion

The present experiments examined the spatial-temporal pattern of brain activation underlying working memory with object, spatial, and verbal memory contents by means of high density ERP recordings. In order to be able to examine ERP slow waves during the retention of different information types without confounds due to differential perceptual processes, we developed a modified delayed matching task in which a task-cue, presented in between the S1–S2 interval, indicated the kind of information to be retained in working memory for a subsequent comparison with a test stimulus. ERP slow waves evoked by the cue in the memory tasks were contrasted with those evoked by a cue indicating a perceptually based comparison at S2.

5.1. ERP data

The analysis of the ERP data revealed that retention object forms and spatial locations in working memory was associated with a combination of slow waves over frontal and over parietal-occipital recording sites.

5.1.1. Frontal slow waves

Relative to the perceptual tasks, there was negative slow wave activity at left frontal recording sites that was modulated by the type of information (object vs. spatial) and by the degree of verbalization.

These SPs started at around 700 ms and extended throughout the cue-S2 retention interval. In experiment 1 in which nameable object forms and spatial locations had to be retained in WM it was larger in amplitude for object forms than for spatial locations at left frontal recordings, whereas in experiment 2 in which abstract object forms and unnameable spatial locations had to be retained, the negative SP in the object memory task was most pronounced at medial frontal recordings. Notably, in both experiments the frontal slow wave activity evoked by the object and spatial task cue differed in scalp topography, indicating that the retention systems for verbalizable and non-verbalizable objects and spatial locations were neuroanatomically distinct.

In contrast, Ruchkin and colleagues (e.g. [43]) proposed that the frontal negative SP reflects processes related to the maintenance of phonological information. Additionally, there is a more central frontal SP associated with the retention of lexical information [40]. In experiment 1 where verbalizable objects and spatial locations were utilized as stimuli, the left frontal slow wave pattern observed in the verbal condition was delayed for about 300 ms for the retention of location names compared to the retention of object names. As left frontal activation may be related to verbal processes a possible explanation for the observed latency difference might be that object names (nouns) are more easily retrievable than location names (prepositions). However, the view that the frontal slow wave pattern is solely associated with verbal rehearsal processes was contradicted by experiment 2, in which topographically different negative slow wave patterns were obtained for unnameable objects and for spatial locations in the memory tasks. Nevertheless, the between-experiment comparison suggested a distinct neuronal generator associated with verbal rehearsal. Therefore, the present data indicate that the two components found by Ruchkin and colleagues are not sufficient to explain the observed patterns. Rather, in all memory conditions a left frontal negative SPs were evoked with topography, onset, and amplitude varying as a function of format (figural vs. verbal) and content (object vs. spatial).

What WM functions are then reflected by this SP-'family'? Recent specifications of executive functions emphasize that attentional control is crucial when information has to be kept in a WM buffer system comprising attention and inhibition [49], selective attention [4], and the control of the focus of attention [7]. Baddeley and Logie [4] regard the allocation and the switching of attention as crucial executive processes. Similarly, in the framework proposed by Engle and coworkers [e.g., 9], controlled attention plays a crucial role in WM.

This includes controlled processes of maintenance, focusing, and the shifting of attention, a function that presumably is carried out by prefrontal cortex. The view that slow potentials are directly connected to attentional processes is supported by, e.g., a neurophysiological model of Skinner and Yingling [47] and a more recent model of LaBerge [22]. They emphasize the role of thalamo–cortical connections that in turn are necessary for the generation of slow cortical potentials [5]. Therefore, the present data provide evidence that the neuronal generators involved in attentional control depend on the type of information.

5.1.2. Posterior SPs

Similar to the information-specific slow wave pattern at frontal recording sites qualitatively different information-specific slow waves were obtained at parietal and occipital recording sites in both experiments. First the retention of spatial locations was associated with a transient negative slow wave between 600 and 1200 ms at parietal recordings. Based on the fact that negative slow wave patterns of similar kinds have been reported in a large variety of tasks requiring spatial operations [44,39,38,29] and based on its short duration we take this ERP pattern to reflect the activation of a transient visuo-spatial buffer system or the allocation of spatial selective attention as a rehearsal mechanism [2]. Except for the figural condition in experiment 1, this negative slow wave in the spatial tasks was followed and partially overlapped by an occipitally focused positive slow wave that extended until the end of the recording interval. A similar long lasting positive slow wave was also obtained when object forms had to be retained in working memory. Since this positive slow wave was also present for both information types in experiment 2 in which verbal rehearsal presumably did not occur, it appears unlikely that this brain response is solely associated with the conversion of visual to verbal formats. Its extended duration until the end of the recording interval rather suggests that this positive slow wave reflects more perceptually oriented aspects of working memory such as the retention of image-like representations, i.e., object information. In support of this view Farah et al. [10] found positive posterior SPs in imagery tasks.

The absence of a parietally-focused negative slow wave in the spatial task of experiment 2 most probably was caused by the maintenance of object information that occurred simultaneously. Thus, presumably any parietally focused negative differences at parietal recording sites between the spatial and the perceptual task were cancelled out due to the superimposition of a positive slow wave.

Awh et al. [2] identified spatial selective attention, i.e., covert shifts of attention to memorized locations, as the rehearsal mechanism for spatial information. It is conceivable that this attention modulated rehearsal process is evidenced by parietal negative slow waves because this is a consistently observed SP whenever spatial operations in WM are required.

However, it is still at issue whether there is a separate rehearsal mechanism for object form information. We observed a positive posterior SP during object retention and assume that this SP is the prime candidate to reflect aspects of the object rehearsal mechanism. (The observation of a similar positive SP in the later time range in experiment 1 might be due to the fact that, similar as in experiment 2, subjects did not exclusively focus on the relevant spatial information.) This explanation receives support from an experiment by Farah et al. [10] who found similar positive SPs during imagery tasks. Furthermore, the occipito-parietal focus is in line with the assumption, that posterior sensory areas are involved in the generation of mental images [21]. Therefore, imagery, i.e., the active restoration of visual information from long term memory is a plausible candidate for being part of the rehearsal circuitry for visual object information. Kosslyn [21] proposed that such a mechanism comprises the repetitive activation of a compressed image representation that is controlled by prefrontal cortical areas.

We conclude that there are in fact two distinguishable storage mechanisms within visual working memory evidenced by posterior slow waves, one related to object information and one related to spatial information. From experiment 1 we learned that these two mechanisms have different timing properties. The spatial mechanism seems to be faster in onset and due to its transient existence mainly active during the initiation of maintenance whereas the object mechanism appears to be slower and used during the entire retention phase.

Finally we want to comment on the brain activation patterns found in the verbal working memory conditions. Prior neuroimaging studies revealed that verbal working memory is mediated by a left lateralized network composed of posterior parietal and inferior frontal regions [32,34]. Similarly, verbal working memory studies with ERP recordings found a left anterior negative slow wave that is assumed to index verbal rehearsal operations [44,23]. Although a direct comparison of the ERP response in verbal and visual working memory conditions may be weakened by the fact that both conditions were performed in different blocks in the present study, the results nevertheless suggest that rehearsal in the verbal condition in experiment 1 did not lead to qualitatively different slow wave patterns compared to the figural condition. Rather, in the verbal condition we found more pronounced frontal and parieto-occipital slow wave patterns for both memory tasks relative to the perceptual task. Note that this effect cannot be attributed to differential task difficulties, as task performance in both the object and the spatial working memory tasks was not different in the verbal and figural testing conditions.

Moreover, the application of verbal rehearsal operations should not result in any differences between the rehearsal of object names and spatial prepositions because both should be maintained in the same phonological format. However, a SP-pattern was observed that is topographically similar to that of purely visual WM as shown by experiment 2.

This allows the conclusion that the SPs in the verbal condition of experiment 1 are due to the rehearsal of figural information and the rehearsal of phonological information did not evoke a separable SP-component. However, it remains to be clarified why the SPs in the verbal condition of experiment 1 are more pronounced than in the respective figural condition.

A possible interpretation of this finding is that the verbal memory tasks required the construction of phonological representations from figural ones.This process includes the identification of a visual scene, its semantic content, and its transformation to phonological word representations via the lexicon [8] which in turn may presuppose the maintenance of visual information in WM. This transformation might have additionally loaded WM. The data from the present experiments suggest that the conversion from visual to phonological representations requires additional access to the same visual storage sites that are also accessed by visual rehearsal processes. Though speculative, this interpretation might account for the enhanced fronto-parietal ERP slow wave pattern in the verbal memory tasks as compared to the figural tasks. More research will be required to further clarify the issue of the interface between visual and verbal WM.

6. Conclusion

The present results provide several lines of evidence for a clear dissociation of both executive (frontal SPs) and lower order storage processes (posterior SPs) according to the type of information to be held in WM. The parietal negative SP reflects processes of spatial selective attention whereas the parieto-occipital positive SP indexes the retention of visual object information. Left frontal negative SPs presumably are generated by a compound of higher order frontal control processes and are not solely due to verbal rehearsal processes. Rather, the data suggest that different frontal generators are involved in a content specific manner.

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