Parallel Processing of Spatial and Serial Order Information Before Moving to a Remembered Target

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Smyrnis, Nikolaos, Giovanni d’Avossa, Christos Theleritis, Asimakis Mantas, Alpay Ozcan, and Ioannis Evdokimidis. Parallel processing of spatial and serial order information before moving to a remembered target. J Neurophysiol 93: 3703–3708, 2005. First published December 29, 2004; doi:10.1152/jn.00972.2004. Information storage and retrieval from working memory is limited by the capacity of storage mechanisms and attentional processes. Nevertheless, it has been shown that processing of multiple features can proceed independently in working memory. In this study we investigated how serial order and directional information are processed when executing a movement to a remembered target direction. We compared the performance of 11 healthy subjects in 3 motor working memory tasks, one with a varying spatial memory load, one with a varying serial order memory load, and one in which memory load was varied for both features. We found that the spatial information memory load does not affect the ability to store information about serial order and vice versa. Furthermore, movement response latencies indicated that retrieval of information about both features proceeds simultaneously. These results strongly favor independent, parallel working memory systems for processing space and order information in the motor system.

INTRODUCTION

Working memory is the ability to briefly hold on to information before executing a response or while performing a cognitive operation. A prominent theory separates working memory into 3 compartments: 1) a phonological loop for mental rehearsal of verbal material, 2) a visuospatial sketchpad that holds information about space and objects, and 3) a central executive that acts as a supervisory attentional system where a response is computed on the basis of some decision rule (Baddeley 1990, 1996, 2003). This supervisory system is viewed as a bottleneck for information processing that regulates the flow and content of information.

Although the capacity of visual working memory is limited (Luck and Vogel 1997), behavioral data on change-detection tasks suggested that several features can be simultaneously retained in separate, capacity-limited stores among which there is little or no competition (Wheeler and Treisman 2002). Furthermore, the processing of multiple as compared with processing of a single feature imposes no additional cost on feature-specific capacity when these features can be integrated into objects (Luck and Vogel 1997; Wheeler and Treisman 2002).

Lesion, neurophysiological, and neuroimaging studies suggest that anatomically distinct neural systems process different object features in working memory (Goldman-Rakic et al. 2000), indicating a structural correlate of the functional independence of feature processing. It is also known that neurons in cortical areas such as parietal (Chafee and Goldman-Rakic 1998; Gnad and Andersen 1998), motor (Carpenter et al. 1999; Smyrnis et al. 1992), premotor (Carpenter et al. 1998), and prefrontal areas (Chafee and Goldman-Rakic 1998; Funahashi et al. 1989) show sustained neural activity during memory delays preceding a movement.

However, it is still not known whether neural systems supporting working memory are also endowed with separate components for the storage and retrieval of spatial and serial order information, 2 basic features that need to be computed so that complex motor acts can be carried out. We hypothesized that in such tasks serial order and spatial information would be processed hierarchically, rather than in parallel, because spatial direction is a property of single elements of a sequence, whereas serial order is a property of the temporal relations between the elements in the sequence set.

We previously studied how accurately subjects move to the remembered direction of a visual target cued on the basis of its serial order within a sequence of visually presented targets (Theleritis et al. 2004) using a version of the motor memory scanning task first studied by Georgopoulos and Lurito (1991). We found that the accuracy of the recalled serial order and direction decreased with increasing number of targets. In this study, we investigate how accuracy and response latency of a movement to a remembered target depend on the number of features (serial order and direction) and the number of targets (memory load) in a sequence.

METHODS

Participants

Eleven right-handed healthy volunteers (3 women, 8 men) participated in the study. The mean age was 36.8 yr (range 25–54 yr). Participants gave informed consent, the experimental protocol having been approved by the Eginition Hospital Human Studies Committee.

Apparatus

The experimental apparatus was previously described in detail (Theleritis et al. 2004). Subjects sat in a darkened room and faced a...
computer monitor (17 in.; Hitachi CM630ET) placed at a distance of 60 cm from their eyes. Subjects held, with the right hand, a pencil-type manipulandum on a horizontal digitizing tablet (Calcomp Inc. 2000) placed in front of them. The manipulandum’s position was sampled at 100 Hz and its position displayed on the monitor as a 2.5-mm-diameter round white cursor. The ratio of manipulandum to cursor movement was 1.

Procedure

In the Spatial Task (Fig. 1A) each trial began when the subject moved the cursor into a 10-mm-diameter red circle displayed at the center of the monitor. A sequence of 2, 3, or 4 targets (5-mm-diameter white filled disks) was presented at pseudorandomly chosen locations placed along a 10-cm-radius circumference. There were 16 possible target locations, regularly spaced at 22.5° intervals. Each target was presented for 1 s and was extinguished at the appearance of the following target. After all the targets had been presented, a delay of 2 s followed and then one of the target positions was highlighted for 300 ms (probe). As soon as possible the subject moved to the target whose location was nearest to the probe and maintained the position until the end of a 3-s period (Response period).

In the Serial Order Task (Fig. 1B), target presentation proceeded as in the location task but the targets were not extinguished. After the

FIG. 1. Task design. Behavioral events in (A) spatial task (the center target depicted as black in the figure was red in the actual experiment), (B) serial order task (the peripheral target changed from white to green in the actual experiment and not black as shown in the figure), and (C) conjunction task. (D) instantaneous velocity trace was used to estimate the response latency (RL).
retention period the color of one the targets changed from white to green (probe) and the subjects moved to the target that followed in the sequence. If the probe was the last target in the series the subjects had to move to the first target.

In the Conjunction Task (Fig. 1C) target presentation proceeded exactly as for the location task. After the retention period one of the targets was presented again (probe) and the subjects had to move to the recalled location of the target following in the sequence.

Each subject performed 3 separate blocks of 64 trials for each task. In each block a sequence of 2, 3, and 4 targets was presented (a total of 64 × 3 × 3 = 576 trials). The order of task and subsequent block presentation was randomized from subject to subject.

The instantaneous velocity of the manipulandum was computed by numerically differentiating the position data. This trace was used to estimate the movement onset and the end of the movement. The response latency (RL) was the time in milliseconds from the appearance of the probe target to movement onset (Fig. 1D). The position of the cursor was expressed in a polar coordinate system (direction and amplitude) with the origin at the center target (Fig. 2).

A total of 6,336 trials (11 subjects × 576 trials per subject) were obtained. We excluded all trials where subjects failed to move after the extinction of the probe target or moved prematurely before the appearance of the probe. We also excluded movements with RL <80 ms or >2,500 ms. A total of 6,088 valid trials remained that were used for all subsequent analyses (96.1% of the original data set).

Because there is a single performance measure, i.e., the angular difference between the target direction and the movement endpoint direction (Fig. 2) and because this difference could be attributable to either an error in recollecting the serial order of the target (in the serial order and conjunction task) or its direction (in the spatial and conjunction task), we used a stochastic model to estimate the uncertainty associated with the target’s serial order and direction. This was done by a maximum likelihood estimation procedure. Probability distributions of the directional data were computed using a model with 2 parameters: 1) the width of a Gaussian distribution of movement directions, that is, the SD of the variable directional error (σ); and 2) the probability of making a serial order error, p(Eserial). The conditional probability of a given trial’s movement endpoint direction, p[D_M | p(Eserial), σ], is given by

\[
p[D_M | p(E_{\text{serial}}), \sigma] = \frac{1}{\sqrt{2\pi} \sigma} \left( 1 - p(E_{\text{serial}}) \exp \left( \frac{(D_M - T_m)^2}{2\sigma^2} \right) \right)
\]

where \(D_M\) is the direction of the correct target, \(T_m\) is the direction of the

where the one predicted by the parallel model is

\[
RL_c(n_{\text{tar}}) = T(n_{\text{tar}}) + T_s + T_l
\]

where \(RL_c\) is the latency for conjunction task, \(T_s\) is the time to complete the retrieval of the target direction, \(T_l\) is the time to complete the retrieval of serial order, and \(T_l\) is the time for all other common processes. A regression analysis for each subject’s latency data in each task using as independent predictor the memory set size was performed. All regressions were significant (ANOVA for regression, \(P < 0.05\)). \(T_s\) was the RL for one target as estimated from the conjunction task data. A trial-by-trial estimate of \(T_l\) was derived by subtracting from each trial’s latency the estimated response latency for set size of one target obtained from the regression for the spatial task. In the same fashion an estimate of \(T_l\) was derived. These estimates were used to calculate latencies for the conjunction task, using the 2 models, by sampling without replacement the data from the serial order and spatial task. Finally median latencies for each subject, task, and memory load were estimated for each model and a 2-factor, repeated-measures ANOVA was used to test differences between the predicted RL values (by the parallel or serial models) versus the RL values in the conjunction task (model factor) and the effects of memory load.

**RESULTS**

**Memory storage**

We first consider the data on the probability of serial order errors in the serial order and the conjunction tasks. As shown in Fig. 3A the probability of serial order errors increased with memory load in both tasks \(F(2,9) = 21.53, P < 0.0001\), but there was no overall difference in serial order error probability between the 2 tasks \(F(1,10) = 0.08, P > 0.7\) and, more important, the memory load effect on serial order error prob-
ability was not different in the 2 tasks [load × task interaction, $F_{(2,9)} = 0.21, P > 0.8$]. We conclude that the capacity for serial order information was the same in the serial order and the conjunction task. Interestingly, Fig. 3A suggests that subjects occasionally moved to a target different from the one also cued in the spatial task and that the probability of such errors increased with memory load [$F_{(2,9)} = 13.3, P < 0.03$]. There are at least 2 possible explanations for these errors: either subjects used the wrong strategy in choosing the target, such as basing their choice on the serial order of the cue and target, or the spatial location of target was retained inaccurately. To distinguish between these alternative interpretations, we analyzed the directional error for trials with a memory load of 4 targets in which the probability that the subjects had moved to a wrong target was greater than the probability that they had moved to the correct one. The SD of the directional difference between the movement endpoint and the correct target was significantly smaller in the spatial task (79 deg) than in the conjunction task (114 deg) (one-tailed bootstrapped $t$-test, $P < 0.05$). This result suggests that choosing the wrong target in the spatial task was more likely to depend on inaccurate spatial information than a faulty strategy, such as using the serial order of the cue.

We next consider the data on the directional error in the spatial and conjunction tasks. Figure 3B shows the SD of the directional error. The directional error increased with memory load in both tasks [$F_{(2)} = 16.82, P < 0.0001$] with no significant difference between tasks [$F_{(1,10)} = 0.52, P > 0.4$]. Furthermore, memory load had very similar effects on directional error in the 2 tasks [load × task interaction, $F_{(2,9)} = 0.32, P > 0.75$]. As expected, in the serial order task, in which the targets were continuously visible, the SD of directional error was much smaller than that in the other 2 tasks (Fig. 3B).

In summary, the results showed that the simultaneous storage in working memory of both features in the conjunction task does not affect the capacity to store serial order and spatial information compared with the feature tasks.

**Retrieval from memory**

We measured response latencies in the 3 tasks to infer the time taken to retrieve serial order and spatial information from memory. Although response latencies increased with memory load overall [$F_{(2,9)} = 49.44, P < 0.0001$], a significant task effect [$F_{(2,9)} = 9.01, P < 0.01$] and a memory load by task interaction [$F_{(4,7)} = 8, P < 0.01$] indicated that response latency and its modulation by memory load differed among tasks. Figure 3C shows pooled response latencies as a function of memory load in the 3 tasks. These data indicate that response latencies in the serial order and conjunction tasks were greater and that they increased at a faster rate with memory load than response latencies in the spatial task.

**FIG. 3.** Errors and response latencies in the 3 tasks. A: probability of making a serial order error, averaged across subjects, vs. memory set size for the 3 tasks (error bars indicate bootstrap estimates of 95% confidence intervals). B: variable directional error vs. memory set size for the 3 tasks (error bars indicate bootstrap estimates of the 95% confidence intervals). C: mean of the median response latencies (RL) vs. memory load for the conjunction task and the 2 latency models (error bars indicate SEs of the means). D: mean of the median response latencies (RL) vs. memory load for the conjunction task and the 2 latency models (error bars indicate SEs of the means).
To gain better insight into the relation between retrieval times in the different tasks, we modeled the response latency in the conjunction task using the data from the 2 feature tasks. In the first model we assumed that the retrieval of serial order and spatial information take place sequentially (serial model) and therefore the retrieval time in the conjunction task is the sum of the retrieval times in the feature tasks. In the second model we assumed that the retrieval of direction and serial order information proceed simultaneously (parallel model) and therefore the retrieval time in the conjunction task is equal to the time taken by the slower of the 2 retrieval processes. Figure 3D shows the latencies predicted by the serial and parallel models and the RL in the conjunction task as a function of memory load. The latencies in the conjunction task and those predicted by the parallel model were not different \(F_{(1,10)} = 0.48, P > 0.5\) nor were they affected differently by memory load [interaction \(F_{(2,9)} = 2.34, P > 0.1\)]. In contrast the latencies predicted by the serial model were significantly greater than those found in the conjunction task \(F_{(1,10)} = 13.66, P < 0.01\). These results are not consistent with the hypothesis that serial order and directional information are retrieved sequentially, but rather indicate that spatial and serial order information retrieval proceed simultaneously and independently.

**DISCUSSION**

There were 2 main findings in this study. First, the accuracy of the retrieved serial order and direction information gradually decreased, as memory load increased from 2 to 3 to 4 items. This result is in contrast with previous findings showing that the accuracy of the recalled information does not decrease when the number of targets is increased. These earlier observations have been used to suggest that working memory capacity is object based and does not depend on the amount of information that is stored per object, which constituted 3–4 objects for the visual component (Luck and Vogel 1997) and even more (5–6 items) for spatial information (Wheeler and Treisman 2002). However, a recent study that manipulated the complexity of the memorized feature information found that the capacity of the visual component of working memory can vary from 3.2 to 7.5 items according to the feature retained: the smaller the capacity, the larger the complexity of the feature (Alvarez and Cavanagh 2004). The conclusion of that study that the effective memory load depends both on the complexity of the feature memorized and on the number of objects is consistent with our data that indicate a gradual decrease of accuracy with target number.

The second finding was that the directional and serial order accuracy did not change when memorizing either feature in isolation or both features simultaneously. In addition, the response latencies in the conjunction task were consistent with a model that assumed that they were determined on each trial by the slower of the 2 retrieval processes. These results were not entirely expected. Although spatial direction is a property of each individual target, determining the serial order of a target in the sequence also implies being able to distinguish it by some means other than its serial order (i.e., its direction) from the other targets. Therefore we hypothesized that knowledge of the serial order of a target should also encompass knowledge of its distinguishing feature. Thus we predicted that in the conjunction task, when both directional and serial order information need to be jointly stored, we would observe a loss in the amount of retrieved feature information compared with the single-feature tasks. However, this prediction was not confirmed by our results.

On the contrary, our results suggest that the targets’ serial order and direction information are stored in separate feature-specific, limited-capacity systems. This hypothesis, previously promoted by Wheeler and Treisman (2002) in the context of storage in working memory of simple visual features, would explain why the storage of serial order does not interact with the storage of direction information. Clearly, this account does not address how information is combined to form a single movement plan. If binding takes place after, rather than before, the appearance of the probe then one would expect that serial order information would be retrieved before selecting the appropriate direction information. This serial retrieval would yield retrieval times in the conjunction task equal to the sum of the retrieval times in the feature tasks. However, our data showed that the retrieval of both features occurs in parallel, rather than serially, in the conjunction task. Thus we must conclude, somewhat paradoxically, that serial order and spatial information are stored as bound features, but in separate stores. How this could be accomplished computationally remains unknown. Nevertheless, neural recordings in the motor cortex during a version of the motor memory-scanning task have demonstrated the existence of signals related to both independent and bound representations of serial order and spatial information during the delay period of a working memory scanning task. More specifically some neurons were found to be responsive only to serial order information, whereas others were responsive only to direction information and still others were responsive to a combination of the 2 features (Carpenter et al. 1999).

A potential confound in this study is that subjects may have used the same strategy in all 3 tasks. It should be noted that during retrieval subjects must have used different strategies. In fact, using the same strategy would have resulted in chance performance in one or more of the tasks with respect to the criteria used by us to define the target and the distractors. Second, the response latency in the serial order and conjunction tasks was significantly higher than that in the spatial task and increased linearly with memory load as shown by previous studies (Sternberg 1969), clearly indicating that subjects used different retrieval strategies in the different tasks. Third, in the spatial task the direction of the movement in trials in which the subject had probably moved to a target different from the one cued were closer to the probe location than the direction of the movements in the conjunction task (see RESULTS), thus suggesting that errors in the spatial task were attributed to faulty spatial information rather than to a faulty strategy. Whether it is possible that during the delay period subjects maintained both types of information is a thornier issue. Blocking of task conditions and randomization of the order of task presentation across subjects minimized this possibility. Furthermore, in the serial order task, where targets were continuously visible, the idea that subjects would have used working memory to store spatial information is not consistent with the finding that the internal representation of the environment relies on a short-lived, unlimited-capacity memory system (Sperling 1960). Nevertheless, we cannot definitely rule out that serial order information may have been retained in all 3 tasks, even though
there would be no obvious advantage in doing so and the data indicate that this information was not used when it was task irrelevant.

In conclusion we showed that separate stores hold targets’ direction and serial order information in working memory. Nonetheless, direction and serial order are probably also maintained in bound representations because there is no time cost when retrieving both features beyond that taken to retrieve each feature in isolation.

REFERENCES


