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Dorsal and ventral working memory-related brain areas support distinct processes in contextual cueing

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ABSTRACT

Behavioral evidence suggests that the use of implicitly learned spatial contexts for improved visual search may depend on visual working memory resources. Working memory may be involved in contextual cueing in different ways: (1) for keeping implicitly learned working memory contents available during search or (2) for the capture of attention by contexts retrieved from memory. We mapped brain areas that were modulated by working memory capacity. Within these areas, activation was modulated by contextual cueing along the descending segment of the intraparietal sulcus, an area that has previously been related to maintenance of explicit memories. Increased activation for learned displays, but not modulated by the size of contextual cueing, was observed in the temporo-parietal junction area, previously associated with the capture of attention by explicitly retrieved memory items, and in the ventral visual cortex. This pattern of activation extends previous research on dorsal versus ventral stream functions in memory guidance of attention to the realm of attentional guidance by implicit memory.

Introduction

When we enter familiar surroundings, our navigation is facilitated by regularities in the environment, regularities that we may not even be aware of. In the lab, this has been demonstrated in the contextual cuing paradigm (Chun and Jiang, 1998). In visual search tasks, such as searching for a 'T'-shape among distracting 'L'-shapes, half of the displays are repeated ('old displays'), whereas the other half are novel ('new displays'). Over several repetitions, observers find the target faster in the old displays. Nevertheless, when explicitly asked to discriminate between previously seen and new displays, observers are typically at a loss. Contextual cueing, therefore, is a form of incidental (observers are not told to learn) and implicit (they are not aware of learning) form of learning.

Nevertheless, contextual cueing is not a purely automatic process. While the implicit learning of search context can proceed in the absence of attentional (Jiang and Leung, 2005) or working memory (Vickery et al., 2010) resources, in contrast, the expression of learning depends on these resources. Repeated search contexts lead to a search advantage only if they are attended during search (Jiang and Leung, 2005). Likewise, the search advantage is only observed when visuospatial working memory resources are available, but not when working memory is blocked by a concurrent task (Manginelli et al., 2012).

Here, we investigated what the functional neuroanatomical basis for the working memory dependence of search facilitation in old displays might be. Previous research has implicated several areas in the posterior parietal cortex in visual working memory. fMRI-experiments have demonstrated that posterior parietal activation increased with working memory load, but only until the limit of visual working memory capacity (typically about 4 items) was reached (Todd and Marois, 2004; Xu and Chun, 2006). Increases in set size of five and more items did not lead to further increase of activation. This was taken as evidence that parts of the posterior parietal cortex represented a neural substrate of visual working memory.

In the present study, we used this logic to localize brain areas that support visual working memory. To this end, we used a visual working memory task to localize brain areas that show a BOLD-response modulated by working memory capacity. Within this neural substrate of visual working memory, we then looked for activation changes that were associated with contextual cueing. This association could take two forms. For one, we asked whether the difference in visual search-related activation between new and old displays was correlated with the size of the search advantage for old displays. This was expected for processes that were involved throughout the whole search process. Working memory is intimately related to selective attention and visual search. Many models of visual search postulate that attended display elements are kept in working memory during search (Bundesen, 1990; Duncan and Humphreys, 1989; Treisman, 1988). Beyond the visual search literature, close ties between working memory and visuospatial attention have been demonstrated (Awh et al., 1998; Griffin and Nobre, 2003; Kuo et al., 2009; Lepsien et al.,

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2005). Thus, it is very likely that working memory capacity is needed throughout the whole duration of visual search for attentional control processes that allow the utilization of the implicitly learned display configurations.

Within the posterior parietal cortex, specifically the cortex along the left horizontal and descending intraparietal sulcus has consistently shown differential activation for old (i.e. previously learned) versus new items in studies of explicit memory (e.g. Nelson et al., 2010; Wagner et al., 2005). To our knowledge, the same effect has not yet been shown for implicitly learned items. Nevertheless, this region, which also shows working-memory capacity-limited activation (Todd and Marois, 2004; Xu and Chun, 2006), may be a candidate neural structure to support the use of implicitly learned memory templates, retrieved from long-term memory and maintained in working memory, for the guidance of visual search in old displays. A similar proposition has been made by Cabeza et al. (2008), 2011 and Ciaramelli et al. (2008). They propose that the dorsal parts of the posterior parietal cortex (including the superior parietal lobule and the medial plus lateral banks of the intraparietal sulcus (IPS)) mediate top-down attentional processes guided by retrieval goals.

In addition, these authors propose a distinct contribution by the ventral parietal cortex (angular and supramarginal gyri, including the temporo-parietal junction area) to the stimulus-driven capture of attention by retrieved memory items (e.g. detection of memory targets). These memory-related processes are thought to occur in much the same way as the dorsal/ventral distinction that has been postulated for top-down guided shifts of attention mediated by the IPS versus stimulus-driven reorienting signals generated by the temporo-parietal junction area (Corbetta et al., 2002). Again it should be noted that the model by Cabeza and colleagues was developed to account for explicit memory processes. However, it may as well apply to the processing of implicitly learned stimuli, a topic that we want to investigate here.

Both hypothesized processes, capture of attention by memorized items in the ventral parietal cortex and maintenance of memorized search templates along the IPS can only occur after learning. Moreover behavioral data showed a dependence on visuospatial working memory of the expression of context learning, but not context learning itself. Thus, we hypothesized that such contextual cueing-associated effects should be observed not during initial learning, but at a later stage, when repeated contexts had already been learned. To investigate this question, we tested two groups of participants, one that was tested initially in a scanner and continued to work on the task in the lab and another group that was first trained in the lab and was tested in the scanner afterwards. We expected to see effects of contextual cueing only in the latter group. However, the first group was needed to rule out that any effects may have been observed right from the start. Activation differences occurring early in contextual learning have been observed in the hippocampus (Giesbrecht et al., 2012) and in the anterior prefrontal cortex (Pollmann and Manginelli, 2009). These findings show the importance of testing early activation differences in contextual cueing. However, as there is no evidence of visual working memory contributions early in contextual learning, we did not expect visual working memory-associated brain areas to show activation differences between repeated and novel displays early in learning.

Material and methods

The experiment consisted of two sessions, performed on two consecutive days. The “fMRI-last” group took part in a learning session in the lab on the first day and took part in the fMRI session the following day. For participants of the group fMRI-first the order was reversed: they participated in the fMRI session on the first day and concluded the learning session in lab the day after. Each session lasted approximately 1 h and consisted of a working memory task and a visual search task, separately performed. The order of the two tasks was counterbalanced among participants.

Participants

Twenty-six healthy volunteers were paid to participate in this study, after giving informed consent. The experiment was approved by the Ethics Board of the Medical Faculty of the University of Magdeburg. Participants were all right handed and had normal or corrected to normal sight. Participants were randomly assigned to two groups: fMRI-last (n = 13, 7 males, average age 24.3 years) and fMRI-first (n = 13, 6 males, average age 24.5 years).

Setup and apparatus

The experimental procedure was realized using the Matlab software with the PsychToolbox (Brainard, 1997; Pelli, 1997).

In the lab, stimuli were presented with a 24 inch LCD-monitor with a resolution of 1920 × 1200 pixels and a refresh rate of 60 Hz. The viewing distance to the monitor was 55 cm, ensured by a chinrest where participants were asked to lean the head. Responses were made by pressing the mouse buttons with the right hand.

In the fMRI session stimuli were displayed by a D-ILA projector on a back-projection screen mounted in the bore of the magnet behind the participants' head. Participants viewed the screen by means of a mirror positioned on top of the head coil. The screen resolution was 1280 × 1024 pixels. Responses were given by means of a two-button response pad.

Working memory task

Stimuli

Stimuli in the working memory tasks were 2–7 squares subtending 0.6° × 0.6° of visual angle (both on the lab and scanner monitors) presented on a gray background. In the visuospatial working memory task, squares were black and placed randomly on 2–7 out of 14 equidistant positions defined on an imaginary circle with a radius of approximately 4° of visual angle on the lab monitor and approximately 3.7° of visual angle on the scanner monitor, centered on a fixation cross (a white cross subtending 0.6° × 0.6° of visual angle in both sessions' monitor) in the middle of the display. Positions were chosen from a uniformly distributed pseudo-random sequence of numbers.

In the color working memory task, squares were colored. Colors were randomly chosen among 14 highly discriminable colors: black, white, red, green, yellow, blue, magenta, orange, brown, purple, light pink, dark green, light blue and dark red. All squares within the same working memory array had different colors. Squares were placed equidistantly on an imaginary circle with a 2° radius of visual angle (both on the lab monitor and on the scanner monitor) centered on the fixation cross (see Fig. 1 for an example of the stimuli).

Procedure

Working memory task in lab session. The experiment consisted of 16 blocks, 8 visuo-spatial and 8 color working memory, regularly intermixed according to an ABAB-schema. Half of the subjects started with the visuo-spatial working memory, the other half with the color working memory. Each block consisted of 6 trials, one for each set size. At the beginning of each block, a brief written instruction (“Merken Sie sich die räumlichen Positionen!” or “Merken Sie sich die Farben!”, German for “Remember the spatial positions” or “Remember the colors”, respectively) presented for 1500 ms, informed the participant about which task was to be performed. A mandatory break of 10 s was imposed after 4 blocks. Fig. 1 shows a sample trial.