NeuroImage 149 (2017) 114–128

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Local and interregional alpha EEG dynamics dissociate between memory for search and memory for recognition

Joram van Driel*, Eren Gunseli[1], Martijn Meeter[2], Christian N.L. Olivers

Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

A R T I C L E I N F O

Keywords:
Visual working memory
Search template
Alpha oscillations
EEG
Functional connectivity
Top-down control

A B S T R A C T

Attention during visual search is thought to be guided by an active visual working memory (VWM) representation of the search target. We tested the hypothesis that a VWM representation used for searching a target among competing information (a “search template”) is distinct from VWM representations used for simple recognition tasks, without competition. We analyzed EEG from 20 human participants while they performed three different VWM-based visual detection tasks. All tasks started with identical lateralized VWM cues, but differed with respect to the presence and nature of competing distractors during the target display at test, where participants performed a simple recognition task without distractors, or visual search in pop-out (distinct) and serial (non-distinct) search displays. Performance was worst for non-distinct search, and best for simple recognition. During the one second delay period between cue and test, we observed robust suppression of EEG dynamics in the alpha (8–14 Hz) band over parieto-occipital sites contralateral to the relevant VWM item, both in terms of local power as well as interregional phase synchrony within a posterior-parietal network. Importantly, these lateralization dynamics were more strongly expressed prior to search compared to simple recognition. Furthermore, before the VWM cue, alpha phase synchrony between prefrontal and mid-posterior-parietal sites was strongest for non-distinct search, reflecting enhanced anticipatory control prior to VWM encoding. Directional connectivity analyses confirmed this effect to be in an anterior-to-posterior direction. Together, these results provide evidence for frontally mediated top-down control of VWM in preparation of visual search.

Introduction

Searching for a specific target object among irrelevant objects requires a memory representation of the target. This representation is often referred to as the *search template* or *attentional set*, and is thought to be maintained in visual working memory (VWM), actively biasing the competition for selection towards matching objects in the scene (Duncan and Humphreys, 1989; Folk et al., 1992; Wolfe, 1994; Desimone and Duncan, 1995; Hamker, 2005; Wolfe, 2007; Carlisle et al., 2011). Such VWM-based top-down biases are likely initiated in frontal regions (Soto et al., 2008; Woodman et al., 2013; Stokes, 2015). Although current theories state that the search template is activated within VWM, behavioral evidence indicates that not just any VWM representation acts like a search template. While representations that are maintained in VWM can bias visual selection during search, they do not always do so (Downing and Dodds, 2004; Carlisle and Woodman, 2011; Olivers and Eimer, 2011; Olivers et al., 2011; van Moorselaar et al., 2014). An important question is thus what makes a working memory a template.

One approach is to compare a situation where observers know that the item they keep in memory is going to be needed for a search task, to a situation where they remember the same item, but in this case for a simple recognition task. Crucially, while a search task involves selecting an object from competing visual information, a simple recognition task simply involves the matching of the test object against the retained item, without the need for attentional biasing. We hypothesized that the expected task goal of having to search for the item in the face of upcoming visual competition signals the need for stronger top-down control over encoding and maintenance of the memory representation, thus affecting the VWM representation already prior to the task (cf. Bollinger et al., 2010; Gazzaley and Nobre, 2012; Zanto et al., 2016).

In a recent study from our lab (Gunseli et al., 2014a) we compared memory for search to memory for simple recognition on an EEG measure of VWM storage, the contralateral delay activity (CDA;

* Correspondence to: van der Boechorststraat 1, 1081 BT, Amsterdam, The Netherlands.
E-mail address: joramvandriel@gmail.com (J. van Driel).
[1] Present address: Department of Psychology, The University of Chicago, Chicago Illinois, USA.
[2] Present address: Department of Educational Psychology, Vrije Universiteit, Amsterdam, The Netherlands.

http://dx.doi.org/10.1016/j.neuroimage.2017.01.031
Received 10 October 2016; Accepted 13 January 2017
Available online 26 January 2017
1053-8119/ © 2017 Elsevier Inc. All rights reserved.

Gratton, 1998; Vogel and Machizawa, 2004; Luck, 2012). Interestingly, we found no reliable differences in CDA, which suggests that this component is not sensitive to different task goals, and that items were actively stored regardless of the subsequent nature of the task. In the present study, we tested an alternative hypothesis that posterior alpha (8–12 Hz) oscillations provide a key mechanism to prepare for top-down biasing during search. An increasing number of studies have observed suppression of alpha-band power over cortical regions that process task-relevant items, often accompanied by increases in alpha power over task-irrelevant regions (Worden et al., 2000; Sauseng et al., 2005; Thut et al., 2006; Ikkai et al., 2016). Alpha power modulations not only occur during deployment of visuospatial attention to presented targets, but also during the retention interval when items are kept in VWM (Jensen et al., 2002; Myers et al., 2014; Spaak et al. in press). These observations have led to the proposal that alpha-band oscillations reflect active, controlled attention and memory processing (Klimesch, 2012). As such, we reasoned that alpha activity may be well-suited to support stronger encoding and maintenance of items in VWM in the anticipation of search.

In addition to power, the phase of ongoing alpha oscillations may provide a mechanism to transiently link distant cortical regions through interregional phase synchronization (Palva and Palva, 2007; Klimesch et al., 2008; Palva and Palva, 2011; van Driel et al., 2014). Such functional connectivity has been considered a hallmark of top-down control (Engel et al., 2001; Varela et al., 2001; Siegel et al., 2012). Alpha-phase synchronization within a frontoparietal network has been observed during visuospatial attention and VWM maintenance (Schack et al., 2005; Crespo-Garcia et al., 2013; Capotosto et al., 2015), but also in anticipation of cued stimulus features (Zanto et al., 2010, 2011), as well as trials that require effortful control such as task-switching and errors (Phillips et al., 2014; van Driel et al., 2012). Our hypothesis was thus that synchronized alpha oscillations, linking frontal control regions to posterior stimulus processing regions, are key to preparing VWM for search.

Here, we present new EEG analyses of our previous work (Gunseli et al., 2014a) that support this hypothesis. We investigated the oscillatory dynamics during VWM maintenance of lateralized Landolt squares, while we manipulated the goal for which these items were needed: Single-item recognition or search among competing distractors. We find that anticipated search clearly resulted in more strongly expressed alpha-band activity related to the memory item, already prior to encoding, both in terms of local posterior power suppression, and long-range interregional phase synchronization – lending support to the hypothesis that stimulus competition requires stronger memories to bias selection.

Materials and methods

For this study we re-analyzed the data of Experiment 1 described in Gunseli et al. (2014a). For clarity and completeness, we also include the information regarding participants and task settings here.

Participants

Twenty-one healthy human participants with normal or corrected-to-normal vision participated in this study for course credit or monetary compensation. Data of one participant were excluded from analyses due to excessive horizontal eye movements (as revealed by the electro-oculogram, see below). Final analyses were thus conducted on 20 participants. The study was conducted in accordance with the Declaration of Helsinki and was approved by the faculty's Scientific and Ethical Review Board (VCWE). Written informed consent was obtained.

Task

Participants performed three versions of a VWM-guided visual detection task, in a blocked design. The tasks differed in the presence and type of competing stimuli that accompanied the target item at test, and thus in the amount of search that was involved to find it. The following task settings and stimulus parameters were identical across these three versions. Each trial started with a fixation cross (0.23 degrees of visual angle [dva]) presented on a gray-colored computer screen. The fixation cross remained visible throughout the entire trial. After a randomly jittered duration of 800–1200 ms, a cue display appeared, consisting of two Landolt squares (0.7 by 0.7 dva) with a gap on one side (top, bottom, left or right, 0.68 dva) presented 1.17 dva left and right from fixation on the horizontal plane. One Landolt square was red, the other green. In one half of the entire experimental session, participants were instructed to encode the red Landolt square, as it served as the relevant VWM cue (i.e. it indicated the target), and ignore the green Landolt square, which was thus irrelevant and only served for sensory balancing purposes. Relevant and irrelevant color mapping was reversed for the other half of the session, with the order of mapping counterbalanced across participants. The cue display was presented for 100 ms, followed by a 900 ms delay period during which only the fixation cross was visible. Next, a target display was presented. The participant's task was to maintain fixation until the target display was presented and then to indicate, as fast as possible without risking accuracy, whether the target was present or absent.

Crucially, the target displays differed depending on condition (Fig. 1). In the Simple Recognition condition, a single item, i.e. a Landolt square of similar size and in the task-relevant color (with either the same [present] or different [absent] gap location), appeared at fixation and the participant had to make a present/absent judgment (which, since there was only one item present, is equivalent to a same/different judgment). This procedure is also known as a delayed match-to-sample task. In the Distinct Search condition, the target display consisted of a search array of nine Landolt squares presented equidistantly on an imaginary circle with a radius of 3.0 dva. The participant's task was to search for the Landolt square that matched the cue with respect to its color, and then determine whether the location of the gap corresponded to the cue. All other items were black, except one distractor, which carried the to-be-ignored color (e.g. green when the target was red, or vice versa). The presence of a salient distractor in the target display meant that there was clear visual competition (Theeuwes, 1992, 2013), but at the same time, as the target was the only item carrying the relevant color, it could be relatively easily detected. In the Non-distinct Search condition, the target display consisted of a similar search array, except that now all items carried the relevant color and thus were potential competitors for the target, resulting in serial search. Importantly, the position of the search target on the search array was varied randomly over trials, thus precluding any preparatory spatial attention during the delay period.

With this design, the three conditions not only differed in the type of search, but also in overall task difficulty, from easy (Simple Recognition) to difficult (Non-distinct Search). On the one hand, this is inevitable, because the very nature of competition is that it makes detection more difficult. On the other hand, our design allowed us to dissociate the effects of competition and difficulty to some extent. That is, the Distinct Search condition involved competition, yet was relatively easy (as the behavioral results showed; Gunseli et al., 2014a). Thus, for any effects driven by difficulty, the Distinct Search condition should group more with the Simple Recognition condition. In contrast, for any effects driven by competition, the results of the Distinct Search should group with those of Non-distinct Search.

Importantly, prior to the target display, all three conditions were identical with regard to the cue display and delay period. Because of our blocked design with preceding task instructions, any difference during (or before) the delay period between the conditions can be attributed to the difference in anticipated competition. In all three conditions, the target display was presented until response, and auditory feedback was given regarding accuracy. The experiment used

Download English Version:

https://daneshyari.com/en/article/5631238

Download Persian Version:

https://daneshyari.com/article/5631238

Daneshyari.com