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Working memory delay period activity marks a domain-unspecific attention mechanism

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ABSTRACT

Working memory (WM) recruits neural circuits that also perform perception- and action-related functions. Among the functions that are shared between the domains of WM and perception is selective attention, which supports the maintenance of task-relevant information during the retention delay of WM tasks. The tactile contralateral delay activity (tCDA) component of the event-related potential (ERP) marks the attention-based rehearsal of tactile information in somatosensory brain regions. We tested whether the tCDA reflects the competition for shared attention resources between a WM task and a perceptual task under dual-task conditions. The two tasks were always performed on opposite hands. In different blocks, the WM task had higher or lower priority than the perceptual task.

The tCDA's polarity consistently reflected the hand where the currently prioritized task was performed. This suggests that the process indexed by the tCDA is not specific to the domain of WM, but mediated by a domain-unspecific attention mechanism. The analysis of transient ERP components evoked by stimuli in the two tasks further supports the interpretation that the tCDA marks a goal-directed bias in the allocation of selective attention. Larger spatially selective modulations were obtained for stimulus material related to the high-, as compared to low-priority, task. While our results generally indicate functional overlap between the domains of WM and perception, we also found evidence suggesting that selection in internal (mnemonic) and external (perceptual) stimulus representations involves processes that are not active during shifts of preparatory attention.

Introduction

Working memory (WM) allows for the sustained representation of information that is no longer physically present. The neural circuits recruited by WM include prefrontal cortex (PFC; Fuster and Alexander 1971) and modality-specific perceptual brain regions (Zhou and Fuster 1996; Harrison and Tong 2009; Supèr et al. 2001). Perceptual areas are implicated in the storage of sensory information (sensory recruitment hypothesis: Emrich et al. 2013; Pasternak and Greenlee 2005; Jonides et al. 2005), and are subject to top-down biasing signals that originate in higher cortical regions such as the PFC (Postle 2006; Sreenivasan et al. 2014). The goal-dependent modulation of memory representations is implemented by modality-specific control mechanisms that modulate neural activity in sensory cortex, where sensory information is stored (e.g. Lepsien and Nobre 2006; Curtis and D'Esposito 2003). Spatially selective modulations of somatosensory neural activity are thought to indicate the attention-based rehearsal of locations in tactile WM (Katus et al. 2015b). This article addresses the question how attention is allocated to task-relevant information in mnemonic representations. In particular, we examine whether the sustained maintenance of tactile information in WM is mediated by attention mechanisms that are shared with perception.

The attention-based rehearsal account (Awh and Jonides 2001; Awh et al. 2006) states that the maintenance of task-relevant information in WM is supported by selective attention. This rehearsal process is not specific to the domain of WM, because attention plays a central role for goal-directed behavior during stimulus encoding, and in anticipation of stimuli. Three lines of evidence suggest that the attentional selection of mnemonic content is mediated by mechanisms that overlap with perceptual/preparatory attention. First, memorizing a location leads to a spatially selective bias that guides perceptual encoding of task-irrelevant events during the retention period (touch: Katus et al. 2012b; vision: Awh et al. 2000; Jha 2002). Second, selection in WM modulates ERP markers of perceptual (e.g. Kuo et al. 2009) and preparatory attention (Katus et al. 2012c; Myers et al. 2015). Third, dual-task studies that combined a perceptual task with a memory task showed that the withdrawal of attention from a memorized location impairs memory accuracy (touch: Katus et al. 2012a; vision: Smyth and Scholey 1994, but see also Belopolsky and Theeuwes 2009). In summary, these studies suggest intimate links between control mechanisms

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that allocate attention to internal (memorized) and external (perceived) stimulus representations. However, the majority of aforementioned studies examined the influence of selection in WM on neural correlates of perceptual/preparatory attention. Here, we tested whether the attentional selection of perceptually presented stimuli influences an ERP marker of WM maintenance.

The tactile contralateral delay activity (tCDA: Katus et al. 2015a) component of the ERP manifests during lateralized change detection tasks, where tactile sample stimuli are presented on both hands, but only those on one hand have to-be-compared with a test stimulus set. The tCDA is quantified by subtracting ERPs ipsilateral to task-relevant information from contralateral ERPs. The sign of the resulting difference values indicates the tCDA's polarity (which is typically negative). However, in a recent study we presented two tactile sample sets in sequence, and asked participants to memorize one stimulus per set. The tCDA's polarity changed after the second sample set, if the two memorized stimuli were located on opposite sides of the body (Katus and Eimer 2015). This finding led to the conclusion that the tCDA component indexes the allocation of attention to information in WM (see Freunberger et al. 2011; van Dijk et al. 2010 for a similar interpretation of the visual CDA component).

We tested whether somatosensory delay period activity reflects a rehearsal process that is specific to the domain of WM, or alternatively, a process that relies on attentional resources that are shared with perception. In a dual-task study, participants performed a perceptual task during the retention period of a WM task. The tasks were always performed on opposite hands. In different blocks, participants prioritized the memory task over the perceptual task or vice versa. Delay period activity (tCDA) was quantified as the difference of contra- minus ipsilateral ERPs, relative to the hand where the memory task was performed. If the tCDA reflects a rehearsal process that is specific to WM, a sustained negativity should emerge contralateral to the memory task, regardless of whether or not the memory task is prioritized. If the tCDA however marks the allocation of domain-unspecific attention resources, its polarity should indicate the hand where the prioritized task is performed. This would lead to a relative positivity contralateral to the memorized sample in blocks where the perceptual task has high-priority. To confirm that participants performed both task simultaneously (but with different priority) we additionally examined behavioral data and the modulation of transient ERP components triggered by stimulus material of the two tasks (cf. Katus et al. 2012a; Katus et al. 2015b). Larger attentional modulations were expected for stimuli associated with the currently prioritized task.

Materials and methods

Participants

Twenty healthy right-handed participants with normal or corrected-to-normal vision participated in the experiment. One participant was excluded due to excessive drifts in the EEG. A further participant did not comply with the instructions to perform both tasks simultaneously (no responses were given to the perceptual task in priority of WM blocks). Eighteen participants remained in the sample (14 female, age range 20–33 years, average 24 years). All participants gave informed written consent prior to the experiment and received payment or course credit. The experiment was conducted in accordance with the Declaration of Helsinki.

Task design and stimulation procedure

Participants were seated in a dimly lit electrically shielded recording chamber and performed a memory task with an interleaved perceptual task (Fig. 1). The two tasks were always performed on different hands. On the hand relevant for the memory task, observers judged whether the locations of sample and test stimulus matched (same finger) or differed (different fingers). Additionally, participants searched for transient irregularities (events) in the vibrotactile stream on the perceptually attended hand. In different blocks, the memory task had higher – or lower - priority than the perceptual task. Participants were asked to devote 90% of their attention resources to the currently prioritized task. Half of the participants were instructed to prioritize the memory task in the first six experimental blocks and the perceptual task in the remaining six blocks; the other participants started with priority of the perceptual task. In each trial, a visual cue signaled whether the high-priority task was located on the left or on the right hand. During the recording of brain potentials, participants were asked to fixate on the centrally presented fixation cross and avoid movements. Participants were however allowed to blink at any time, and were explicitly instructed to immediately respond to events that were behaviorally relevant to the perceptual task. Artifacts caused by eye blinks and vocal responses were corrected offline using independent component analysis (ICA).

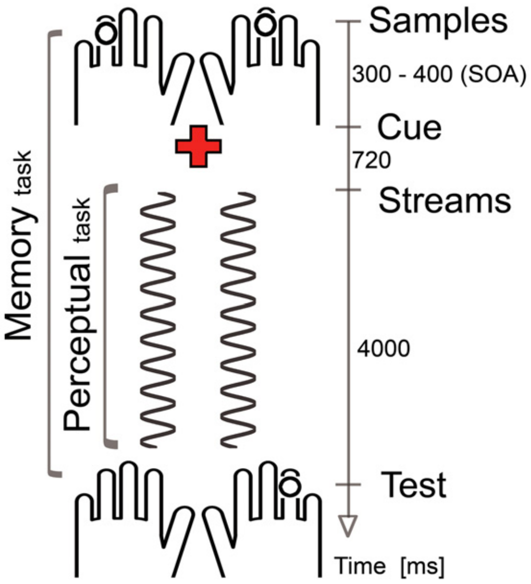

Fig. 1. Task design. Participants concurrently performed a perceptual task and a memory task that were located on opposite hands. On the hand relevant for the memory task, participants memorized the sample pulse's location and compared it with the location of the test pulse. During the retention period, participants searched for transient irregularities (events) in the vibrotactile stream on the perceptually attended hand. In different blocks, participants prioritized the memory task over the perceptual task, or vice versa. The visual cue indicated the hand where the currently prioritized task was located via an arbitrary color/hand mapping rule (e.g. a red cue might signal the need to perform the prioritized task on the left hand).

Fig. 1 illustrates the stimulation protocol. A trial started with the bilateral presentation of tactile sample stimuli. The visual cue stimulus was shown for 150 ms after a random interval of 300 to 400 ms relative to sample onset. Vibrotactile streams were presented bilaterally for 3500 ms, and started 720 ms after cue onset. Events (see below) were embedded into the streams at three latencies (500 ms, 1500 ms or 2500 ms relative to stream onset; i.e. 1220 ms, 2220 ms or 3220 ms after the cue). A single test stimulus was presented to the hand of the memory task 4720 ms after the cue. The response period for the memory task was indicated by a question mark, shown on the monitor for 2000 ms. The next trial started after a random interval between 0 and 100 ms. The experiment consisted of 480 trials, divided into 12 blocks (duration 4 min 30 s each). Feedback about average hit and correct rejection rates was given after each block. Observers performed 40 training trials with priority of the memory task, and 40 trials with priority of the perceptual task prior to the main experiment.

Stimulus material

Tactile stimuli of the memory task were delivered by electromagnetic stimulators (Dancer Design, St. Helens, UK) that were adhered to the