



Revising the link between microsaccades and the spatial cueing of voluntary attention



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ABSTRACT

Microsaccades – i.e., small fixational saccades generated in the superior colliculus (SC) – have been linked to spatial attention. While maintaining fixation, voluntary shifts of covert attention toward peripheral targets result in a sequence of attention-aligned and attention-opposing microsaccades. In most previous studies the direction of the voluntary shift is signaled by a spatial cue (e.g., a leftwards pointing arrow) that presents the most informative part of the cue (e.g., the arrowhead) in the to-be attended visual field. Here we directly investigated the influence of cue position and tested the hypothesis that microsaccades align with cue position rather than with the attention shift. In a spatial cueing task, we presented the task-relevant part of a symmetric cue either in the to-be attended visual field or in the opposite field. As a result, microsaccades were still weakly related to the covert attention shift; however, they were strongly related to the position of the cue even if that required a movement opposite to the cued attention shift. Moreover, if microsaccades aligned with cue position, we observed stronger cueing effects on manual response times. Our interpretation of the data is supported by numerical simulations of a computational model of microsaccade generation that is based on SC properties, where we explain our findings by separate attentional mechanisms for cue localization and the cued attention shift. We conclude that during cueing of voluntary attention, microsaccades are related to both – the overt attentional selection of the task-relevant part of the cue stimulus and the subsequent covert attention shift.

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1. Introduction

There is widespread consensus that microsaccades – miniature saccades during fixation – are related to covert shifts of attention (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Hafed, Lovejoy, & Krauzlis, 2013; Yuval-Greenberg, Merriam, & Heeger, 2014). The microsaccade attention link is commonly investigated in spatial cueing tasks (Posner, 1980), where participants orient their attentional focus toward a peripheral target location indicated by a cue while maintaining fixation. Participants show a sequence of attention-aligned and attention-opposing microsaccades in response to exogenous (e.g., a peripheral flash) and endogenous cues (e.g., a central arrow) with a time course that directly relates those effects to the distinct dynamics of reflexive (exogenous) and voluntary (endogenous) orienting, respectively (Müller & Rabbitt, 1989; Posner & Cohen, 1984): With exogenous cues, a movement bias toward the cued location starts within the first 100 ms (i.e., ‘attentional capture’; e.g., Hafed & Clark, 2002; Laubrock, Engbert,

& Kliegl, 2005; Rolfs, Engbert, & Kliegl, 2005) and can be followed by a bias away from the cued location (i.e., ‘inhibition of return’; Galfano, Betta, & Turatto, 2004; Rolfs et al., 2005). In contrast, with endogenous cues, a bias toward the cued location emerges not before 200 ms after cue presentation (Engbert & Kliegl, 2003).

Biases in microsaccade orientation have been linked to attention-related activities in the superior colliculus (SC) (Engbert, 2012; Hafed, Goffart, & Krauzlis, 2009; Hafed et al., 2013; Rolfs, Kliegl, & Engbert, 2008). The SC integrates multisensory bottom-up signals with top-down demands and generates motor commands for saccadic movements (Fecteau & Munoz, 2006; Krauzlis, Lovejoy, & Zenon, 2013). During spatial cueing, neurons of the peripheral SC representing the cued location exhibit a transient activity increase (Fecteau, Bell, & Munoz, 2004; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004). The resulting asymmetric SC activation was suggested to affect the rostral SC that is involved in the generation of microsaccades (Engbert, 2012; Hafed et al., 2009). By implementing this coupling mechanism in a computational model of microsaccade generation (Engbert, Mergenthaler, Sinn, & Pikovsky, 2011), Engbert (2012)

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was able to predict various effects on microsaccade orientation observed with endogenous and exogenous spatial cues.

Here we argue that a potential confounding factor has been neglected in previous experimental studies on the effect of voluntary covert attention on microsaccades: In these investigations it is common to use spatial cues that are asymmetric by design (e.g., an arrow), where the task-relevant part of the stimulus (e.g., the arrowhead) is located within the visual field to-be-attended (Engbert & Kliegl, 2003; Hafed, Lovejoy, & Krauzlis, 2011; Hafed et al., 2013; Hermens & Walker, 2010; Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007; Laubrock, Engbert, Rolfs, & Kliegl, 2007; Laubrock, Kliegl, Rolfs, & Engbert, 2010; Meyberg, Werkle-Bergner, Sommer, & Dimigen, 2015; Pastukhov & Braun, 2010; Pastukhov, Vonau, Stonkute, & Braun, 2013). In such a cue arrangement, microsaccades might be directed toward the task-relevant part of the cue symbol, in addition to or instead of being aligned with the cued attention shift. Importantly, this confounding factor is not restricted to stimuli with inherent asymmetric shapes as in case of arrow cues (Engbert & Kliegl, 2003; Hermens & Walker, 2010; Horowitz et al., 2007; Laubrock et al., 2007, 2010; Meyberg et al., 2015), but also applies to symmetrically shaped cues as long as only one of several stimulus parts is more informative about the target location (Hafed et al., 2011, 2013; Pastukhov & Braun, 2010; Pastukhov et al., 2013). Examples are the bright arm of a centrally presented fixation cross (Pastukhov & Braun, 2010) or the odd-colored ring among peripherally presented rings, indicating target locations (Hafed et al., 2011, 2013). In fact, encoding the directional information from those unbalanced spatial cues requires a top-down selection mechanism favoring those stimulus parts that are most informative about the target location while ignoring the irrelevant parts. In this situation, spatial cues may drive an additional well-known attentional mechanism commonly investigated in the visual search task in which a target stimulus needs to be extracted among distractor items (Van Velzen & Eimer, 2003).

In the present study, we investigated whether microsaccades do not only align with the cued direction of the voluntary attention shift, but also (or alternatively) with the location of the cue stimulus – as a second attentional mechanism. Therefore, microsaccades were measured in a spatial cueing task with an endogenous cue arrangement that was visually symmetric (<> or ><) but unbalanced with respect to task-relevance: To independently manipulate the direction of the cued attention shift and the position of the cue, only one side of the stimulus indicated the target location and needed to be selected over the task-irrelevant side. If microsaccades align with the cued attention shift, we expected to observe a movement bias toward the cued target location regardless of the position of the task-relevant cue. Alternatively, if microsaccades align with the position of the cue, a bias toward the cued location would be expected when the task-relevant cue is placed in the to-be-attended visual field, whereas the bias should be reduced or inverted when that cue is placed in the not-to-be-attended visual field.

We further related microsaccadic behavior to task-related performance and estimated the effective size of both mechanism – cued covert orienting and cue localization – in a recent computational model on microsaccade generation (Engbert, 2012; Engbert et al., 2011).

2. Materials and methods

2.1. Participants

Participants in the experiment were 32 healthy volunteers. After excluding one participant due to excessive artifacts in the

eye tracking signal (data loss >50%), 31 participants remained in the final sample (mean age: 24.7 years, range: 18–36 years, ten males, one left-hander). All participants gave informed consent, had uncorrected normal vision (tested with Bach, 1996), and received course credits or 8 € per h of testing. This work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Data collection comprised parallel eye movement and EEG recording. Here we only present the eye movement data.

2.2. Stimuli and procedure

Participants sat in an electrically and acoustically shielded cabin facing a 22-inch CRT monitor (Iiyama Vision Master Pro 510, 160 Hz, 1024 × 768 pixel, viewing distance: 60 cm) and performed a spatial cueing task. Stimuli and procedures are depicted in Fig. 1. All stimuli were presented on a 1/f noise background (37.9 × 28.4°; omitted in Fig. 1) that changed after ten trials each. Low-level image properties such as luminance and frequency spectra were kept constant across noise patterns using the SHINE toolbox (Willenbockel et al., 2010).

A trial began with the presentation of a small central fixation point (diameter: 0.15°) and two peripheral white squares, serving as placeholders (2 × 2°, line thickness: 0.37°). Placeholders were positioned in the lower visual field (top of square was 1° below

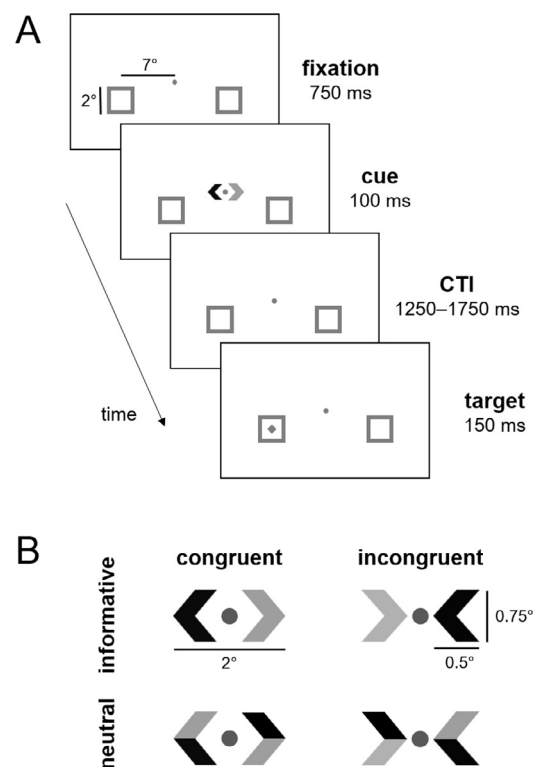


Fig. 1. Paradigm and cue arrangements. (A) In a spatial cueing task, two central arrowheads of different color (red and blue) appeared. Only one arrow was task-relevant and signaled the likely location of a target stimulus. The color of the task-relevant arrow was instructed at the beginning of the experiment. Participants maintained fixation, shifted attention covertly toward the cued target location, and classified the target shape (circle vs. diamond) with a button press. (B) For (informative) congruent cues, the direction of the cued attention shift (e.g., the task-relevant arrow pointed leftwards) was congruent with the position of the cue (e.g., the arrow appeared left to the fixation point). For (informative) incongruent cues, the cue pointed toward the visual field opposite to cue position. In a neutral cueing condition, the cue was non-informative with respect to the target location. CTI = cue-target interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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