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Microsaccade-related brain potentials signal the focus of visuospatial attention

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ABSTRACT

Covert shifts of visuospatial attention are traditionally assumed to occur in the absence of oculomotor behavior. In contrast, recent behavioral studies have linked attentional cueing effects to the occurrence of microsaccades, small eye movements executed involuntarily during attempted fixation. Here we used a new type of electrophysiological marker to explore the attention–microsaccade relationship, the visual brain activity evoked by the microsaccade itself. By shifting the retinal image, microsaccades frequently elicit neural responses throughout the visual pathway, scalp-recordable in the human EEG as a microsaccade-related potential (mSRP). Although mSRPs contain similar signal components (P1/N1) as traditional visually-evoked potentials (VEPs), it is unknown whether they are also influenced by cognition. Based on established findings that VEPs are amplified for visual inputs at currently attended locations, we expected a selective gain-modulation also for mSRPs. Eye movements and EEG were coregistered in a classic spatial cueing task with an endogenous cue. Replicating behavioral findings, the direction of early microsaccades 200–400 ms after cue onset was biased towards the cued side. However, for microsaccades throughout the cue-target interval, mSRPs were systematically enhanced at occipital scalp sites contralateral to the cued hemifield. This attention effect resembled that in a control condition with VEPs and did not interact with the direction of the underlying microsaccade, suggesting that mSRPs reflect the focus of sustained visuospatial attention, which remains fixed at the cued location, despite microsaccades. Microsaccades are not merely an artifact source in the EEG; instead, they are followed by cognitively modulated brain potentials that can serve as non-intrusive electrophysiological probes of attention.

1. Introduction

Studies on visuospatial attention traditionally assume that covert orienting occurs in the absence of oculomotor behavior. For example, in the classical Posner task, participants are instructed to maintain fixation, while they move their attention to a location indicated by a cue (Posner, 1980). Recent studies, however, suggest that covert attention shifts often correlate with the occurrence of microsaccades, small (typically less than 1°) fixational eye movements that occur on average once or twice per second during attempted fixation (Martinez-Conde et al., 2004; Rolfs, 2009). Following the presentation of an endogenous cue (e.g., a central arrow), microsaccades are temporarily inhibited, but then tend to move into the cued direction 200–400 ms after cue onset (Engbert and Kliegl, 2003; Horowitz et al., 2007). After exogenous cues (e.g., peripheral flashes) this cue-congruency effect starts even earlier (Hafed and Clark, 2002) and is often followed by cue-opposing microsaccades (e.g., Rolfs et al., 2005).

Despite considerable debate (e.g., Hafed, 2013; Horowitz et al., 2007; Laubrock et al., 2010; Pastukhov and Braun, 2010; Pastukhov et al., 2013), the strength and nature of the link between attention and microsaccades have not been fully resolved. Do microsaccades provide a real-time index of an observer's changing attentional focus? While some authors have questioned this notion (Horowitz et al., 2007), others have suggested that behavioral cueing benefits may even be fully explained as a corollary of the execution of cue-congruent microsaccades (Hafed, 2013). An intermediate position (e.g., Laubrock et al., 2010) holds that the direction of microsaccades shortly after cue onset indexes attention, whereas that of later microsaccades is dissociated from attention and instead determined by oculomotor needs (e.g., compensation of drift).

In the current study, we introduce a new electrophysiological marker to track the focus of visuospatial attention and to investigate its relationship to microsaccades: the visually-evoked brain response generated by the microsaccadic gaze shift itself.

As microsaccades rapidly shift the gaze during fixation, the resulting changes in the retinal input evoke a volley of neural feed-forward activity throughout the visual pathway (Martinez-Conde et al., 2004, 2013;

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Rolfs, 2009). Accordingly, single-cell recordings in monkeys show modulated firing rates in striate and extrastriate areas after microsaccades (Bair and O'Keefe, 1998; Kagan et al., 2008; Leopold and Logothetis, 1998; Martinez-Conde et al., 2000, 2002; Snodderly et al., 2001).

With regard to human electrophysiological research, microsaccades have been mainly discussed as a source of measurement artifacts (Carl et al., 2012; Hassler et al., 2011; Jerbi et al., 2009; Yuval-Greenberg et al., 2008), because eye muscle spikes at movement onset can distort the gamma band. In addition, however, each microsaccade evokes a genuine brain response that can be scalp-recorded in the EEG over visual cortex (Gaarder et al., 1964; Dimigen et al., 2009). In previous studies, this microsaccade-related potential (mSRP) has been related to a bottom-up processing of the physical properties of the fixated pattern (Armington and Bloom, 1974; Armington et al., 1967; Gaarder et al., 1964).

While there is evidence that brain signal contributions from microsaccades are omnipresent in at least some experimental paradigms commonly used in cognitive neuroscience (Dimigen et al., 2009), a possible link between microsaccade-related brain activity and cognitive processes has not yet been investigated. Nevertheless, behavioral studies suggest that microsaccadic behavior is affected by task demands and contributes to perceptual processing during fixation (for reviews see Martinez-Conde et al., 2004, 2013; Rolfs, 2009). For example, microsaccades have been related to the scanning of small regions (Ko et al., 2010; Otero-Millan et al., 2013), the resolving of visual ambiguities (Laubrock et al., 2008; van Dam and van Ee, 2006), the informativeness of natural scences (McCamy et al., 2014), processes of stimulus categorization (Valsecchi et al., 2007, 2009), and task difficulty (Siegenthaler et al., 2014). Understanding whether and how the mSRP is modulated by cognitive task demands should not only provide new insights into the functionality of microsaccades during fixation, but may allow researchers to treat these potentials as signal rather than noise.

Thus, the primary goal of the present study was to investigate whether brain potentials co-occurring with microsaccades merely reflect the bottom-up processing of low-level stimulus attributes or whether they are also sensitive to aspects of higher-level cognition, specifically top-down attention. In such a case, our secondary goal was to use these mSRPs to assess the spatiotemporal profile of covert attention in comparison to biases in microsaccade direction.

To this end, eye movements and EEG were simultaneously recorded, while participants covertly attended to one side of a bilateral stimulus indicated by a central cue. In our analysis, we made use of the fact that mSRPs contain similar signal components (P1 and N1) as traditional visually-evoked potentials (VEPs) resulting from passive retinal stimulation. For VEPs, it is well-established that they are amplified for stimuli presented at cued locations (e.g., Eimer, 1993; Hillyard et al., 1998; Van Voorhis and Hillyard, 1977); for example, a concurrent stimulus presentation to the left and right hemifield results in a larger occipital P1 and/or N1 component over the hemisphere contralateral to the covertly attended hemifield (Drysdale et al., 1998; Heinze et al., 1990). Since each microsaccade refreshes the retinal image, we hypothesized that mSRPs should be similarly enhanced for stimuli in the currently attended hemifield and thereby provide an objective marker of a person's momentary attentional focus.

2. Materials & methods

2.1. Participants

Sixteen right-handed students (mean age: 28.5 years, range: 23–44 years, seven females) with uncorrected normal acuity (tested with Bach, 1996) volunteered after providing written informed consent. They received course credit or 8€ per hour for taking part in the ~2.5 hour experiment. No participants were excluded.

2.2. Stimuli and procedure

Participants were seated in an electrically and acoustically shielded cabin, at a viewing distance of 60 cm from a 22 in. monitor (Iiyama Vision Master Pro 510, vertical refresh: 60 Hz, resolution: 1024 × 760 pixel). Eye movements and EEG were recorded while participants performed a spatial cueing task requiring a speeded manual choice reaction.

Stimuli and trial sequence are illustrated in Fig. 1. A *regular* trial began with the presentation of an empty black screen for 500 ms. Afterwards, a fixation display was shown, consisting of a small red fixation point (diameter: 0.19°) in the screen center and two empty white boxes centered at an eccentricity of ±7° to its left and right. Boxes were quadratic with 2° side length and 0.35° line thickness.

After a random fixation interval between 1500–2000 ms, an additional cue stimulus appeared around the fixation point, signaling the

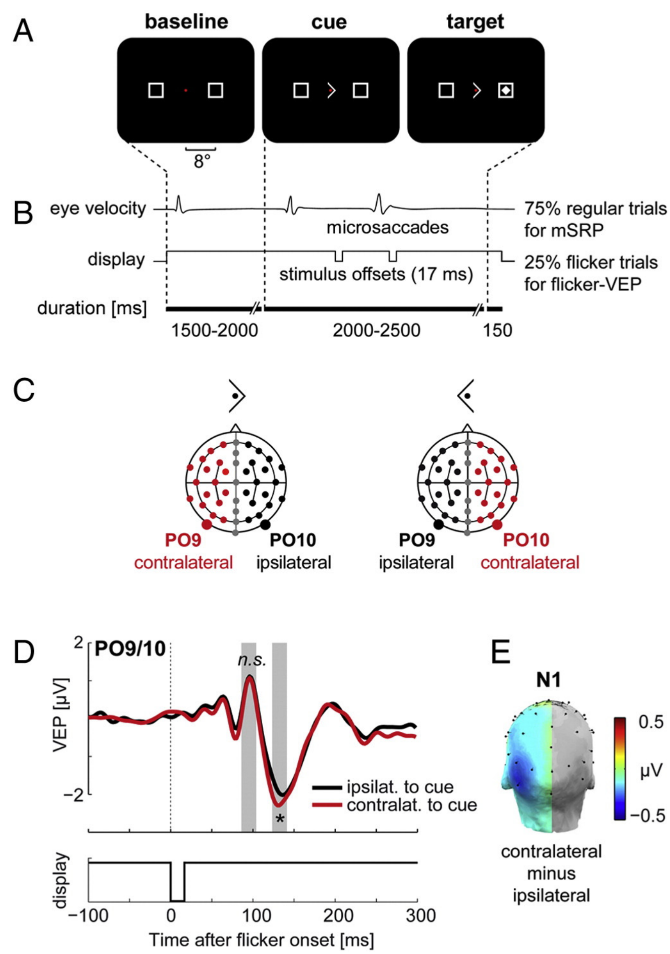

Fig. 1. Stimuli, paradigm, and flicker-VEP results. (A) Participants performed a classic spatial cueing task. After a baseline interval, a central arrow cue signaled the likely location of a target stimulus, which appeared in one of the peripheral boxes 2–2.5 s later. The task was to maintain fixation and to classify the target shape (circle or diamond) with a button press. Display items are not shown true to scale, but have been enlarged for clarity. (B) In regular trials, the EEG was time-locked to the occurrence of involuntary microsaccades during the cue-target interval (CTI). The randomly intermixed flicker trials served as a control condition with passive stimulation. In these trials, the display flickered occasionally during the CTI. Each flicker consisted of 17 ms display offset (empty black screen), which served as time-locking point for VEP analysis. (C) To study attention effects on VEPs and microsaccade-related potentials, occipital electrodes located ipsilateral to the cued visual field were compared to contralateral electrodes. (D) Effect of attentional cueing on VEPs in flicker trials. The N1 component was significantly larger over the hemisphere located contralateral to the cued visual field. (E) Scalp topography of the N1 attention effect (at 134 ms). Note, that the topography depicts only the difference between lateral EEG channels (contralateral minus ipsilateral to cued direction). The difference at midline channels is zero by necessity.