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Kinesthetic information facilitates saccades towards proprioceptive-tactile targets

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ABSTRACT

Saccades to somatosensory targets have longer latencies and are less accurate and precise than saccades to visual targets. Here we examined how different somatosensory information influences the planning and control of saccadic eye movements. Participants fixated a central cross and initiated a saccade as fast as possible in response to a tactile stimulus that was presented to either the index or the middle fingertip of their unseen left hand. In *a static condition*, the hand remained at a target location for the entire block of trials and the stimulus was presented at a fixed time after an auditory tone. Therefore, the target location was derived only from proprioceptive and tactile information. In a *moving condition*, the hand was first actively moved to the same target location and the stimulus was then presented immediately. Thus, in the *moving condition* additional kinesthetic information about the target location was available. We found shorter saccade latencies in the moving compared to the *static condition*, but no differences in accuracy or precision of saccadic endpoints. In a second experiment, we introduced variable delays after the auditory tone (*static condition*) or after the end of the hand movement (*moving condition*) in order to reduce the predictability of the moment of the stimulation and to allow more time to process the kinesthetic information. Again, we found shorter latencies in the *moving* compared to the *static condition* but no improvement in saccade accuracy or precision. In a third experiment, we showed that the shorter saccade latencies in the *moving condition* cannot be explained by the temporal proximity between the relevant event (auditory tone or end of hand movement) and the moment of the stimulation. Our findings suggest that kinesthetic information facilitates planning, but not control, of saccadic eye movements to proprioceptive-tactile targets.

1. Introduction

In order to plan and control a goal-directed movement, the location of the target needs to be determined by using incoming sensory information from vision, audition or somatosensation, either separately or in combination. Although vision is the most reliable source of spatial information (Paillard, 1991, chap. 10), people are able to derive the location of the target also on the basis of somatosensory inputs to guide movements of the arm (e.g., Jones, Fiehler, & Henriques, 2012; Monaco et al., 2010; van Beers, Wolpert, & Haggard, 2002) or of the eyes (e.g., Blanke & Gruesser, 2001; Ren, Blohm, & Crawford, 2007; Ren et al., 2006).

The accuracy and precision of goal-directed hand movements seem to improve when proprioceptive information is available about the target location. For instance, movement endpoints are more accurate and precise when reaching to proprioceptive (i.e. the unseen hand) than to previously viewed, and thus remembered, visual targets in complete darkness (Monaco et al., 2010). Proprioceptive reaching, however, is affected when target limb joints are maximally flexed or elevated, which leads to less reliable estimates of the target location (Rossetti, Meckler, & Prablanc, 1994). Moreover, proprioceptive signals become less reliable over time and thus the location of a target that is solely derived from proprioception is shifted away from its veridical location (Cameron, de la Malla, & Lopez-Moliner, 2015; Smeets, van den Dobbelsteen, de Grave, van Beers, & Brenner, 2006).

Saccadic eye movements, on the other hand, end more accurately and precisely on visual than on proprioceptive targets (Blanke & Gruesser, 2001; Ren et al., 2006; Sullivan, Fitzmaurice, & Abel, 2004). Saccade endpoint errors increase more strongly with eccentricity for proprioceptive than for visual targets (Sullivan et al., 2004). In addition, saccades to visual targets are initiated faster than to proprioceptive (Groh & Sparks, 1996; Sullivan et al., 2004) and proprioceptive-tactile targets (Amlot & Walker, 2006). This

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difference between visual and somatosensory saccade latencies may not be due to different control processes (Amlot & Walker, 2006), but rather due to the visual information being more efficiently processed and used by the oculomotor system: visual targets are predominantly represented with respect to gaze (Crawford, Henriques, & Medendorp, 2011), whereas somatosensory targets are coded in a mixed hand- and gaze-centered representation (McGuire & Sabes, 2009). Therefore, somatosensory information may require additional transformations into a gaze-centered representation in order to be used by the oculomotor system, which may explain a longer saccade planning to somatosensory targets.

Combining sensory inputs from different modalities can be beneficial for saccadic eye movements. For instance, saccades tend to overshoot a target when its location is determined only based on proprioception, but become more accurate if both visual and proprioceptive information is provided (Ren et al., 2006). However, this combined information does not improve saccade accuracy or precision compared to when targets are determined solely on the basis of visual information (Ren et al., 2006). This suggests that visual information already provides a good estimate of the target location for saccades, which cannot be further improved by proprioceptive input signals.

Little is known about how different information from *within one sensory modality* is being used for goal-directed eye movements. For instance, within somatosensation, different sensory information can be derived from different receptors in the skin, muscles, joints and tendons, which can fire either in isolation or in combination. This information can be classified into touch, proprioception or kinesthesia, defined as skin sensation, position sense and changes in muscle length due to movement, respectively. Adding tactile information to a proprioceptive target does not seem to improve saccade accuracy or precision (Blanke & Gruesser, 2001). It is noteworthy, that in this study the tactile input was provided to a target digit whose cutaneous receptors were continuously activated, as the digit was in direct contact with the experimental setup. Beyond proprioceptive and tactile signals, people may also use kinesthetic information to determine the location of a somatosensory target. Although kinesthetic input signals do not provide a good estimate about one's hand location in hand movement tasks (Tillery, Flanders, & Soechting, 1991), it is unknown whether and how these signals contribute to saccade planning and control.

Here, we examined the role of kinesthesia in the planning and control of saccades to proprioceptive-tactile targets. We asked participants to initiate a saccade as fast as possible towards either the index or the middle fingertip of their unseen left hand, as a response to a tactile stimulus presented to one of these two digits. Kinesthetic information was varied in two conditions. In a *static condition*, the hand remained stationary at the target location; therefore, the location of the target digit could be derived only from proprioceptive and tactile information. In a *moving condition*, the tactile stimulus was presented shortly after the hand was actively moved to the target location; therefore, additional kinesthetic information was available about the location of the target digit. If the additional kinesthetic information contributes to the planning and control of saccadic eye movements, we expect saccades to be initiated faster, and saccade endpoints to be more accurate and more precise in the moving compared to the static condition.

2. Experiment 1

2.1. Methods

2.1.1. Participants and apparatus

Eight healthy volunteers (4 females; mean ± SD: 27.5 ± 4.3 years) with normal or corrected-to-normal vision participated in the study. Three of them were authors. The others were naive as to the precise purpose of the study. Participants were right-handed according to the German translation of the Edinburgh Handedness inventory (Oldfield, 1971; mean ± SD: 82 ± 24). All participants gave written informed consent approved by the local ethics committee prior to the experiment (Declaration of Helsinki).

The experiment was performed in a dark room. Participants sat in front of a table on which a custom-made apparatus was mounted (Fig. 1). The apparatus consisted of a frame (46 × 38 × 15 cm) covered with black cardboard and of two solenoids that presented tactile stimuli to the participant's fingertips. Participants held their mouth in an individually fitted dental-impression bite-bar that was attached to the table. The bite-bar and the frame were slightly inclined so that gaze direction was approximately orthogonal to the centre of the cardboard. The eyes were at a distance of 42 cm from the centre of the cardboard. In this distance, 1 cm equals 1.28° of visual angle.

The two solenoids were mounted on a metal plate below the cardboard, approximately 30 cm in front of the participant. The solenoids were horizontally spaced by 4 cm and could be shifted along the lateral (with respect to the participant) direction to one of three different horizontal target locations: the centre of the two solenoids being aligned with the participant's midline, or 14 cm to the left or to the right of the midline, hereafter simply referred to as *centre*, *left*, and *right*, respectively. For each target location, there was also a respective hand start location (for the trials involving a hand movement). The hand start location was at the same horizontal location as the target but at the frame's close edge (approximately 15 cm in front of the participant). Thus, the hand movement amplitude was approximately 15 cm. Participants had their left index and middle fingers in two rings that were attached to a movable slider fixed to a rail below the solenoids. The slider could only be moved along the rail that restricted the movement to be orthogonal from the hand start to the target location. The slider imposed minimal resistance so that the hand movement was performed smoothly, without effort. The slider stopped exactly at the target location because the rail was extending only up to that location. When the slider was at the far-end (relative to the participant) along the rail, thus at the target location, it pressed a button that powered the solenoids and pushed out a small metal pin (diameter of 1 mm) for 50 ms. This tactile stimulus cued the participants to initiate an eye movement towards its felt location.

Visual stimuli were presented on the black cardboard via a LCD projector mounted above the frame. White noise that masked the

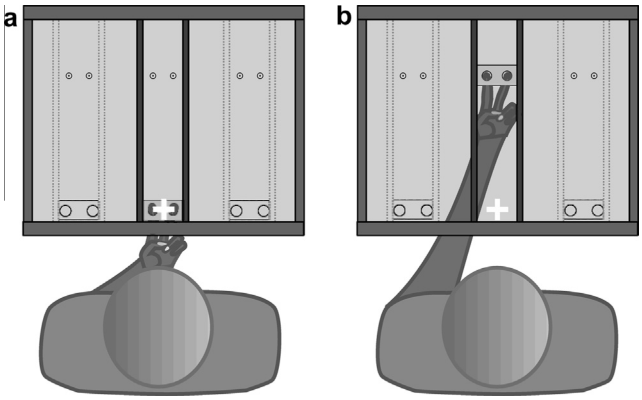

Fig. 1. Top view of the set up. A participant having the hand (a) at the central start and (b) at the target location. The two solenoids at each of the three target locations are indicated by small circles. The three rectangles at the closer edge of the frame in panel (a) are positioned at each of the three possible hand start locations. For illustration, the cardboard is drawn here transparent and the fixation-cross thicker than it actually was.