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Gaze-centered spatial updating in delayed reaching even in the presence of landmarks

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ABSTRACT

Previous results suggest that the brain predominantly relies on a constantly updated gaze-centered target representation to guide reach movements when no other visual information is available. In the present study, we investigated whether the addition of reliable visual landmarks influences the use of spatial reference frames for immediate and delayed reaching. Subjects reached immediately or after a delay of 8 or 12 s to remembered target locations, either with or without landmarks. After target presentation and before reaching they shifted gaze to one of five different fixation points and held their gaze at this location until the end of the reach. With landmarks present, gaze-dependent reaching errors were smaller and more precise than when reaching without landmarks. Delay influenced neither reaching errors nor variability. These findings suggest that when landmarks are available, the brain seems to still use gaze-dependent representations but combine them with gaze-independent allocentric information to guide immediate or delayed reach movements to visual targets.

1. Introduction

Human interaction with the environment crucially involves accurate, target-directed movements, such as reaching for a light switch or grasping a cup of coffee. The brain uses available sensory information to guide such movements in real-time. However, if the target is not currently in the field of view, remembered spatial information can also be used for guiding action.

Studies in healthy humans using perceptual illusions, such as the Müller-Lyer illusion or size-contrast effects, have argued that immediate and memory-guided movements are processed in different frames of reference. Grip aperture in grasping tasks was not influenced by perceptual illusions for immediate grasping, but varied with perceived (not real) object size when grasping was delayed by several seconds (Hu & Goodale, 2000; Westwood, Heath, & Roy, 2000). Based on these results together with findings on movement kinematics (Westwood, Heath, & Roy, 2003), the authors argue that a perceptual allocentric representation is used to guide a movement as soon as the target is no longer visible and the movement needs to be based on memory (Westwood & Goodale, 2003).

However, others have questioned the idea of two different processing systems for immediate and delayed movements and rather point to the use of a single shared representation. For example, Franz, Hesse, and Kollath (2009) also used the Müller-Lyer illusion and found an increase of the illusion effect on grasping after a delay. The authors suggest that this effect was not caused by memory but rather by a differential availability of visual feedback in on-line and delayed grasping, which influences the strength of illusion effects (Franz, Hesse, & Kollath, 2009). Thus, illusion effects in motor behavior seem to be dependent on the task and movement dynamics. There is further evidence that illusions can also influence immediate pointing movements if the visual attributes causing the illusion are relevant for the movement (de Grave, Brenner, & Smeets, 2004). Moreover, van Zoest and Hunt (2011) reported an effect of an illusion on saccadic eye movements which was even larger for immediate saccades than for saccades that began after a delay.

A recent study from our group found that reach targets were encoded and updated in a gaze-dependent, egocentric frame of reference (as has been shown for immediate reaching in numerous studies, e.g. Henriques et al., 1998; Medendorp & Crawford, 2002; Thompson & Henriques, 2008), when the movement was delayed for up to 12 s (Fiehler, Schütz, & Henriques, 2011). This suggests that egocentric target representations can persist for at least several seconds instead of becoming unavailable immediately after the target vanishes. Further evidence of persisting egocentric representations have been found in perceptual tasks such as for spatial priming in a visual search paradigm (Ball et al., 2009, 2010). These behavioral results are consistent with brain imaging studies in

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optic ataxia patients and healthy humans, which showed that brain areas engaged in immediate reaching are also active when reaches are delayed (Himmelbach et al., 2009).

In our previous study, the experiment took place in complete darkness (Fiehler, Schütz, & Henriques, 2011). One could argue that this experimental setting prevented participants from forming an allocentric representation as no external cues were available in the environment. As a consequence, they had to fall back to egocentric information to encode and maintain the target and subsequently use this egocentric representation to guide their reach. Real-world environments are seldom deprived of all visual information besides the goal of a motor act; in almost all cases, other visual cues will be present that can act as landmarks. There is evidence that spatial information from landmarks is used in controlling both immediate and delayed movements, and that precision and accuracy generally improve when landmarks are available (Krigolson & Heath, 2004; Krigolson et al., 2007; Obhi & Goodale, 2005). In a natural setting, egocentric and allocentric information are then presumably combined in a statistically optimal fashion based on their relative reliabilities (Byrne & Crawford, 2010; McGuire & Sabes, 2009). When movements are memory-guided and landmarks are available, allocentric coding tends to take precedence over egocentric coding (Lemay, Bertram, & Stelmach, 2004; Neggers et al., 2005; Sheth & Shimojo, 2004).

Given these findings, do humans still predominantly use a gaze-centered frame of reference to encode, maintain and update reach targets when additional information allows for allocentric coding? Second, if immediate and delayed actions are processed differently as detailed above, how do various lengths of delay between target presentation and reaching influence the frame of reference used?

2. Methods

To investigate these questions, we added static visual landmarks that served as permanent external cues and thus provided additional allocentric information, and included delays of 0, 8 and 12 s between target presentation and reaching. The experimental paradigm was based on that used in our previous study (Fiehler, Schütz, & Henriques, 2011).

2.1. Participants

Eight right-handed volunteers (3 female) between the ages of 22 and 27 (mean: 24.5 ± 2.07 years) participated in the study. All had normal or corrected-to-normal vision and no known history of visual or neuromuscular deficit. Subjects received no compensation for participating in the experiment. All procedures were conducted in agreement with the ethical guidelines of York University's Human Participants Review Subcommittee.

2.2. Equipment

The present task, along with the equipment and stimuli, was similar to that in our previous study (Fiehler, Schütz, & Henriques, 2011). Subjects sat at a table with their head immobilized by a bite-bar. The heights of the chair and bite bar could be adjusted independently, so that the participants had an unobstructed view of the testing area and were comfortably seated. To ensure compliance with the experimental paradigm, movements of the right eye were recorded using a head mounted EyeLink II eye tracking system (SR Research, Osgoode, ON, Canada) utilizing infrared pupil identification at a sampling rate of 125 Hz. All recording equipment was calibrated using the parameters specified by their respective manufacturers before the start of the experiment.

Reach endpoints were recorded using a 19″ touch screen panel (Magic Touch 2.0, Keytec, Inc., Garland, Texas) at a resolution of 1280×1024 pixels. The thin transparent touch screen panel was mounted vertically at a distance of 47 cm from the subjects' eyes. Successfully registered touches were confirmed by a beep signal.

2.3. Stimuli

Stimuli consisted of visual targets (diamonds) and fixation stimuli (crosses), each of which was 1 cm (1.2°) in diameter. Fig. 1 details possible stimulus locations. The central (0°) position was aligned with the participant's right eye before the start of the experiment. Targets were then presented either centrally or at a visual angle of 5° towards the left or right, while fixation crosses were presented centrally or at 5° or 10° towards the left or right. In case the target and fixation fell onto the same location, no separate fixation stimulus was displayed.

All visual stimuli were rear projected using an Optikon XYLP-C Laser Projector (Optikon, Kitchener, ON, Canada), at a consistent elevation and onto a sheet of white paper attached to the back of the touch screen. Verbal instructions by a computer generated voice were used to inform subjects when to start pointing and to mark the end of each trial.

Two blue-colored cold cathode fluorescent light tubes (CCFLs; Conrad Electronik, Hirschau, Germany) were placed in front of the touch screen to serve as landmarks. The light tubes were mounted vertically and parallel at a distance of 7 cm from the touch screen, and arranged 10.6° left and right of the central target to allow subjects an unrestricted view of all visual stimuli and to not impede reaching. Landmarks created by this setup extended vertically from 6 cm to 31.5 cm above table surface. The diameter of the light tubes was 1.2 cm, while the actual luminous filament had a diameter of 0.2 cm (0.24°). To prevent illumination of the reaching hand, the lights were wrapped in three layers of 95% opaque car window tinting foil, making for a total light transmission of 0.0125% and ensuring that subjects could not see their hand when reaching. With the exception of the light tubes and laser-projected target and fixation stimuli, the entire experiment was conducted in total darkness.

2.4. Experimental paradigm

To start each trial, subjects depressed a single-button mouse (Apple Canada Inc., Markham, ON) with their right hand. A target was displayed for 1 s at one of the three possible positions (Fig. 1B, I). Subjects were instructed to fixate the target and then to keep their gaze at this location for a variable delay of 0 s, 8 s or 12 s after the target disappeared (Fig. 1B, II). Delays were presented in random order. After the delay, a fixation cross appeared at one of the five possible locations for 750 ms prompting participants to saccade to its location (Fig. 1B, III). This was followed by a verbal cue which asked participants to point at the remembered location of the target while keeping their gaze on the fixation position (Fig. 1B, IV). When the mouse button was released, the fixation cross was extinguished so that reaching took place in total darkness. The trial ended when the right hand was brought back onto the mouse. Between trials, a computer-controlled halogen desk lamp was switched on for 2 s to prevent dark adaptation.

Participants performed two experimental conditions. In the landmark condition, the light tubes were present for the whole duration of the experiment. In the separate no-landmark condition, subjects were instructed to execute immediate reaching movements (delay 0 s) while no landmarks were present. This condition was otherwise identical to the landmark condition. As we did not find any influence of delay on gaze-dependent reaching errors in our previous experiment (Fiehler, Schütz, & Henriques, 2011), we only included immediate reaching in the no-landmark condition. Moreover, adding delays of 8 and 12 s to the no-landmark condi-