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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-

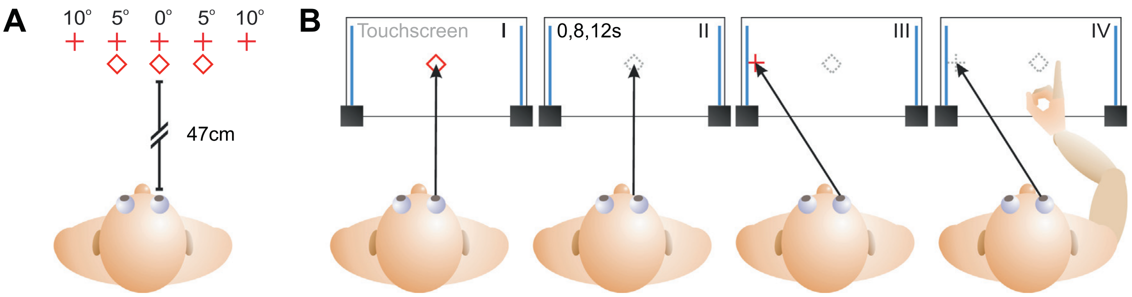

Fig. 1. Experimental setup. (A) Locations where target (diamonds) and fixation stimuli (crosses) were presented. The central position was aligned with the participant's right eye. (B) Experimental task. A target was presented for 1 s (I). After the target disappeared, subjects had to keep fixating its location throughout the delay of 0, 8 or 12 s (II). A fixation cross was then presented prompting subjects to saccade to its location (III), after which they had to point to the remembered location of the target (IV). Blue bars denote landmarks. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

tion would have increased the total duration by approximately 1 h per subject. Since delayed and immediate reaching conditions in the previous study showed almost identical error patterns and no significant differences using the same task and experimental setup, we assumed that adding the other no-landmark delay conditions would not have yielded additional results while possibly increasing subject fatigue and reducing compliance.

For consistency with earlier studies and to reduce the total duration of the experiment, target-fixation-combinations where the distance between target and fixation exceeded 10° of visual angle (e.g., −5°/+10°) were excluded. Thus, out of the possible 15 combinations of three targets and five fixation positions, 13 combinations remained. All 13 combinations were applied to each of the three delay conditions (0, 8, 12 s) as well as the no-landmark condition. Each condition was repeated 6 times, making for 78 trials per condition and 312 trials for the full experiment. The full experiment took about 2 h and was split into four sessions to avoid fatigue. Additionally, subjects could ask for breaks after each block of trials. Recording equipment was recalibrated after each break.

After each experimental session, the room lights were turned on and subjects were asked to fixate and touch each of the three possible targets in turn. This data was used to calibrate EyeLink and touch screen data, and also served as a baseline of individual pointing biases for the calculation of reach endpoint errors.

2.5. Data reduction

Eye tracking data were exported into a custom GUI written in MatLab (TheMathWorks, Natick, MA), where all data could be selected, plotted and viewed across time (Sorrento & Henriques, 2008). Trials were excluded from analysis if subjects fixated or saccaded to the wrong location, started their reach before instructed or a data recording error was detected. Across all subjects, a total number of 279 trials (6.6%) were excluded.

In all analyses, gaze relative to target or retinal error (RE) reflects the horizontal difference between target and fixation positions in visual degrees. Data from different targets but with the same gaze were combined, leading to five different gaze directions relative to target across all three targets. Pointing errors were calculated as horizontal and vertical distances between actual target locations and subjects' touch locations, corrected for bias using matching calibration data. Since only horizontal gaze direction and target eccentricity were manipulated in the experiment and vertical errors were small, we only report horizontal pointing errors. Calculations were done in MatLab.

2.6. Statistical analysis

All statistical analyses were performed using SPSS (Release 19; IBM, Armonk, NY). Data was corrected for statistical outliers by removing trials where pointing errors lay outside the range of ±2.5 standard deviations (SDs) around the mean, calculated for each subject and gaze direction relative to target. Overall, 100 trials (5.0%) from the landmark condition were outliers, as well as 85 trials (4.3%) from the no-landmark condition.

To examine whether the presence of landmarks influenced the typical pattern of pointing errors, 2 × 5 repeated measures analysis of variance (RM-ANOVA) on horizontal pointing error was conducted for cues present vs. absent, as well as gaze direction relative to target (−10°, −5°, 0°, 5°, 10°). This overall analysis was then followed up by separate one-way RM-ANOVAs in each of the two conditions on the five gaze directions relative to target. In addition, we investigated whether reach endpoint variability varied with the presence of landmarks, using RM-ANOVA with the same design on standard deviations of the same pointing errors.

To investigate whether the pattern of pointing errors varied with delay, a 3 × 5 RM-ANOVA for delay and gaze relative to target was conducted on data from the landmark condition only, as the no-landmark condition included only immediate reach movements. Again, the same analysis was repeated for SDs of pointing error to determine possible effects of delay on reach endpoint variability.

An alpha level of .05 was used for the evaluation of all effects. For all reported ANOVA results, degrees of freedom were corrected using Greenhouse–Geisser estimates of sphericity where sphericity was violated. *t*-tests were calculated one-sided unless explicitly stated otherwise. Bonferroni correction was used whenever multiple *t*-tests were performed.

3. Results

In the present study, we investigated whether the availability of allocentric visual cues influences the frame of reference used to encode visual targets for immediate and delayed reaching. Towards this end, we analyzed horizontal reach errors to remembered targets as a function of gaze (see Fiehler, Schütz, & Henriques, 2011). If the brain does use available allocentric information to encode goals for delayed reaching, reach endpoint errors in the landmark condition should be less or not at all dependent on final gaze direction compared to the no-landmark condition. On the other hand, if the availability of landmarks has no effect on the reference frame used and targets are still encoded and updated relative to gaze, reach errors in both landmark and no-landmark conditions should be comparable. Additionally, if a gradual shift from a gaze-dependent to a gaze-independent (either in a different egocentric or allocentric) reference frame occurs with increasing delay, reach endpoint errors should become less dependent on gaze direction as the delay increases. In the no-landmark condition, we expect reach errors opposite to current gaze direction as observed in our previous study (Fiehler, Schütz, & Henriques, 2011).

Fig. 2 displays horizontal reach endpoint errors averaged across subjects, plotted as a function of gaze direction relative to target for all conditions (landmark condition for delays of 0 s, 8 s and 12 s, as well as no-landmark condition).

We found systematic gaze-dependent reaching errors across both landmark and no-landmark conditions ($F_{(4,28)} = 40.8$; $p < 0.001$; $\eta^2 = .85$). Moreover, the gaze-dependent error pattern with landmarks was reduced compared to the no-landmark condition, as a significant interaction was found between gaze and landmark availability ($F_{(4,28)} = 18.8$; $p < 0.001$; $\eta^2 = .73$). We therefore performed separate follow-up RM-ANOVAs on gaze direction relative to target for the landmark and no-landmark conditions. Consistent with our previous study, RM-ANOVA in the no-landmark condition revealed the typical pattern of gaze-dependent reaching errors as depicted by the black symbols in Fig. 2 (no-landmark condition; $F_{(4,28)} = 41.3$; $p < 0.001$; $\eta^2 = .86$). Subjects overshot the target towards the right when fixating left of it and vice versa. When landmarks were available, pointing errors still significantly varied with current gaze direction (colored symbols; $F_{(4,28)} = 22.9$; $p < 0.001$; $\eta^2 = .77$), even if overall pointing errors were smaller in this condition as determined by the interaction reported above.

Adding a delay between target presentation and reaching did not significantly influence the pattern of pointing errors in the landmark condition (no interaction between delay and gaze relative to target; $F_{(8,56)} = 0.5$; $p = 0.71$), and pointing errors significantly varied as a function of gaze for all delays ($F_{(4,28)} = 26.7$; $p < 0.001$; $\eta^2 = .79$; see also Fig. 2). These results parallel those of our previous study (Fiehler, Schütz, & Henriques, 2011).

When we compared horizontal pointing errors between the landmark and no-landmark conditions, the pattern of gaze-dependent pointing errors significantly varied with the availability of landmarks (interaction between gaze and landmark availability; $F_{(4,28)} = 18.8$; $p < 0.001$; $\eta^2 = .73$). Fig. 3 plots horizontal pointing errors for immediate reaching in the landmark condition as a function of those in the no-landmark condition. If the availability of visual landmarks does not influence the type of reference frame used to encode the targets, pointing errors in both conditions should be comparable and we expect a regression slope close to the identity line (slope of one, intercept of zero). On the other hand, if landmarks do influence reach target coding, the pointing errors should differ and we expect a slope that is different from one. Linear regression as shown in Fig. 3 yielded a slope of 0.35, which falls between zero and one. This suggests smaller gaze-dependent pointing errors in the landmark condition, i.e., subjects did not overshoot the target as much as in the no-landmark condition.

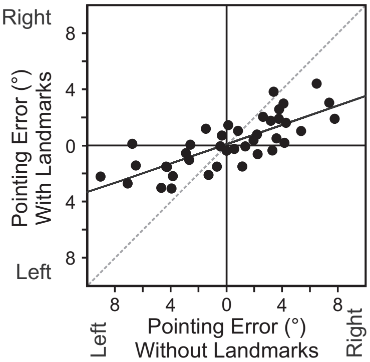

Fig. 3. Mean horizontal pointing errors in the landmark condition plotted as a function of those in the no-landmark condition. Data is shown for immediate pointing only, as the no-landmark condition did not include delays. The gray dashed line indicates the identity line (slope of one, intercept of zero).

Because the effect of landmarks on reach endpoint errors seemed to be strongest when gaze was deviated far from the target (see Fig. 2), we additionally compared pointing errors between landmark and no-landmark conditions for gaze directions between 5° left and right of target only. Here, the regression slope was 0.34. RM-ANOVA comparing pointing errors for gaze direction relative to target ±5° also showed a significant influence of landmark availability ($F_{(2,14)} = 7.0$; $p < 0.01$; $\eta^2 = .50$), suggesting that this effect is not simply caused by differences in pointing errors at the far peripheral gaze directions.

Variable errors, as defined by the standard deviations of horizontal pointing errors, were generally lower when landmarks were available than when reaching without landmarks (landmark condition: 4.95, no-landmark condition: 2.64; $F_{(1,7)} = 24.1$; $p < 0.01$; $\eta^2 = .78$). Fig. 4 illustrates average variability for the three separate delays in the landmark condition, as well as for the 0-s delay in the no-landmark condition. This finding was true for all possible gaze directions relative to target, as confirmed by post hoc *t*-tests (all $p < 0.05$, Bonferroni-adjusted).

Different amounts of delay in the landmark condition had no effect on reach endpoint variability ($F_{(2,14)} = 1.3$; $p = 0.31$). Variable errors varied with gaze direction relative to target ($F_{(4,28)} = 2.9$; $p < 0.05$; $\eta^2 = .29$), meaning that variability was lowest when gaze was aligned with the target and higher when the subject's gaze was deviated. This effect was not significantly influenced by the amount of delay ($F_{(8,56)} = 0.4$; $p = 0.78$).

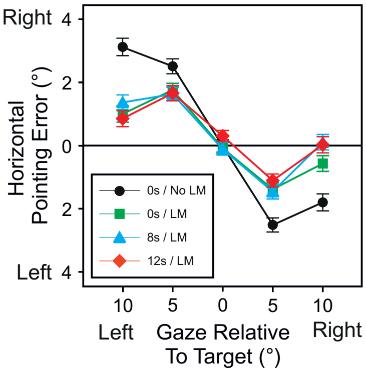

Fig. 2. Mean horizontal pointing errors plotted as a function of gaze relative to target, for the condition without landmarks and delay (black line) as well as the landmark condition with delays of 0, 8 and 12 s (colored lines). Error bars indicate ±1 standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

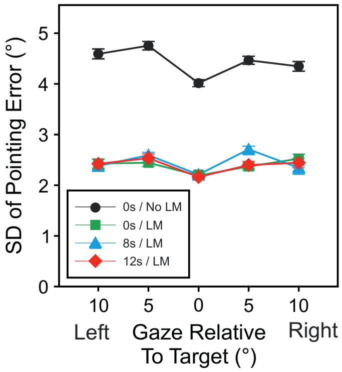

Fig. 4. Mean variable errors (standard deviations of pointing errors) for each gaze position relative to target in the condition without landmarks and delay (black symbols; mean = 4.95) as well as the landmark condition with delays of 0, 8 and 12 s (colored symbols; mean across delays = 2.64). Error bars indicate ±1 standard error. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

We investigated the effect of static visual landmarks on the reference frame used to guide immediate and delayed reaching movements, based on a paradigm used in a previous study to examine gaze-dependent spatial coding of targets for delayed reaching (Fiehler, Schütz, & Henriques, 2011). Subjects foveated each target before shifting gaze to an eccentric fixation position. Reach errors varied with current gaze direction both with and without landmarks, but were less strongly influenced by gaze when landmarks were present. This effect was the same for all delays up to 12 s. Variable errors were smaller with landmarks than without, but were uninfluenced by delay.

Subjects' reach endpoint errors were significantly influenced by current gaze direction in both the landmark and no-landmark conditions. The overall error distribution closely resembles that found in many previous studies using this paradigm for immediate reaching (Henriques et al., 1998; Medendorp & Crawford, 2002) and delayed reaching (Fiehler, Schütz, & Henriques, 2011). While one could argue that this error might simply arise from a misestimation of eye position, pointing errors were unaffected by absolute gaze direction relative to the head, but systematically varied with current gaze direction relative to the target location at the time of reaching. If the brain simply encoded eye position relative to the head, rather than a gaze-dependent spatial representation of the target, such an encoding would also include any misestimation of eye-position at the time of target viewing. This representation would then persist throughout any subsequent eye movements, which should lead to final reaching errors that depend on initial target location, not gaze direction (Henriques et al., 1998).

The present results argue against the use of a head- or body-centered target representation in the coding and updating of reach goals prior to movement onset. Since subjects foveated each target, this representation should be accurate and subjects' reaches to the remembered target location should yield no systematic errors influenced by later gaze deviations. However, in our and many other previous studies, reaching error distributions when targets were foveated and gaze was later shifted to the periphery were no different from conditions where targets were simply viewed peripherally without any further changes in gaze direction (Fiehler, Schütz, & Henriques, 2011; Henriques et al., 1998; Medendorp & Crawford, 2002). Particularly, subjects overshot the target towards the opposite side of the gaze shift, suggesting that target locations were remapped into the periphery when the eyes moved to the opposite side. This coding might be contained within a visual representation of target location, a visual or proprioceptive representation of hand position during the reach or the calculation of the hand-target difference vector.

Our finding poses the question as to why the visuo-motor system would rely primarily on a gaze-centered representation when it has access to more stable visual information. Some researchers have argued that allocentric information is more suited for long-term storage, such as during a memory delay (Hay & Redon, 2006; Obhi & Goodale, 2005), and that egocentric representations are more variable and show rapid decay after target offset (Bradshaw & Watt, 2002; Chen, Byrne, & Crawford, 2011; Hesse & Franz, 2009, 2010; Westwood & Goodale, 2003). However, many behavioral and imaging studies point to a gaze-centered coding as the basis for reach movements (Crawford, Henriques, & Medendorp, 2011; Fiehler, Schütz, & Henriques, 2011; Henriques et al., 1998; Medendorp & Crawford, 2002), which is then transformed into limb- or body-centered motor commands immediately before movement onset (Byrne, Cappadocia, & Crawford, 2010; Crawford, Henriques, & Medendorp, 2011; Henriques et al., 1998). If a gaze-centered egocentric representation is used to control movement, keeping and updating target coordinates in this frame of reference would be computationally less costly than transforming them into allocentric coordinates to be combined with landmark information and then back into a gaze- or limb-centric representation when the movement is initiated.

The reach endpoint errors found in the present experiment fell between the expected patterns of a purely gaze-centered coding, which would have yielded identical error patterns in both landmark and no-landmark conditions (i.e., a regression slope of one as e.g. found in Fiehler, Schütz, and Henriques (2011) for immediate vs. delayed movements), and that of a purely allocentric coding based on landmarks, which would have resulted in pointing errors independent of gaze (i.e., a slope of zero). While it has been argued that allocentric information tends to dominate over egocentric information for memory-guided actions when both are available (Lemay, Bertram, & Stelmach, 2004; Sheth & Shimojo, 2004), more recent studies suggest that both types of information are combined before movement execution based on their relative reliabilities (Byrne & Crawford, 2010, 2012; McGuire & Sabes, 2009). In this case, a smaller gaze dependency of pointing errors when landmarks were present may well be explained by a combined use of gaze-centered and allocentric reference frames when consistent information from landmarks is available.

The differences in reach endpoint errors between landmark and no-landmark conditions are most apparent for more eccentric gaze directions relative to target (see Fig. 2). Because our landmarks were physical light tubes placed in front of the stimulus display instead of mere two-dimensional cues projected next to the targets, a possible explanation for the reduced eccentricity of pointing errors in the landmark condition might be that subjects tried to avoid the tubes by reaching closer to the midline. Such effects have been reported in both grasping and reaching studies where subjects tended to deviate their hand trajectories away from potential obstacles in the workspace (Chapman & Goodale, 2008, 2010; McIntosh et al., 2004; Tresilian, 1998). However, in the present study we placed the light tubes with a safety margin left and right of the outer targets, taking the expected gaze-dependent reach errors of previous studies into account. It is important to note that none of our subjects reported feeling that their reaches were impeded by the light tubes in any way. Reach endpoint errors were pooled across all three target positions for analysis, thus hiding possible target-specific reach endpoint deviations. If subjects reached closer to the midline with landmarks present, reaches to e.g. the left target (at −5°) with gaze deviated 10° further right should lead to smaller gaze-dependent errors than reaches to the center target at the same gaze deviation (i.e., at 10°). The same should be true for the right (5°) target with gaze deviated 10° left of the same. However, when we compared error differences between landmark and no-landmark conditions for each target pair using paired-samples *t*-tests, we did not find any difference in reaching errors for the left or right target compared to the center target ($p > .11$). Therefore, the reduced gaze-dependent effect for more eccentric gaze-target positions does not seem to be caused by object avoidance in the reach space but is rather due to differential processing of the reach targets with and without landmarks.

One might argue that the difference between landmark and no-landmark conditions could be caused by the horizontal distance between target or fixation positions and the spatial location of the landmarks, instead of their physical presence as potential obstacles. In this case, reaching errors in the landmark condition should also vary with target location relative to the landmarks. However, we did not find significant differences when we compared reaching errors within the landmark condition between the center and each eccentric target at gaze deviation of 5° left or right of the target (paired-samples *t*- tests, all $p > .16$). Moreover, we could not find any evidence for a general bias introduced into the movement created by the landmarks. This fits with previous studies which have reported no difference in absolute horizontal errors when subjects reached to remembered targets with and without landmarks (Obhi & Goodale, 2005). In sum, these previous reports and our statistical verifications suggest that most likely the differences between landmark and no-landmark conditions in our experiment cannot be attributed to obstacle avoidance.

In the present study, delays of up to 12 s had no influence on the gaze-dependent pattern of pointing errors when landmarks were present, which is in agreement with our previous study where we observed the same effect without landmarks but the same amounts of delay (Fiehler, Schütz, & Henriques, 2011). This result is also consistent with studies on visuo-spatial perceptual tasks showing that egocentric representations can persist over seconds (Ball et al., 2009, 2010). Thus, our findings do not support a sudden switch from an egocentric representation used for on-line movement control to an allocentric representation used for memory-guided movements when the goal of the action is no longer visible (cf., Westwood & Goodale, 2003). In sum, our results suggest a continued use of a gaze-dependent reference frame for immediate and delayed reach movements and support the idea of a single shared representation.

Reach error variability did not vary with different delays when landmarks were present. Previous findings point to a gradual decay of egocentric visual information across time (Chen, Byrne, & Crawford, 2011; Hesse & Franz, 2009, 2010; Westwood, Heath, & Roy, 2003), usually reflected in increasing variable errors for longer amounts of delay. Since such decay processes are supposed to set in quickly, most likely immediately after the target disappears from view (Westwood & Goodale, 2003), it seems unlikely that we would have seen an effect of gaze-dependent errors using delays even longer than 12 s.

In a previous study from our group, we demonstrated an increase in variable errors for delayed compared to immediate movements (Fiehler, Schütz, & Henriques, 2011). This increase has also been found in other investigations (Obhi & Goodale, 2005) and fits with the idea of a gradual decay of the remembered egocentric representation instead of a sudden switch of reference frames (Chen, Byrne, & Crawford, 2011; Hesse & Franz, 2009, 2010; Obhi & Goodale, 2005). Crucially, our subjects in the Fiehler, Schütz, and Henriques (2011) paradigm relied exclusively on remembered egocentric target locations to guide their reach, and no other visual cues or landmarks were present during the delay and reach phase. In the present experiment, landmarks were continually visible and might therefore have compensated for the loss in precision otherwise expected due to decay of a remembered egocentric representation. This assumption is also supported by a recent study, in which variable errors increased with time delay in a purely egocentric reaching task, but were constant across delays in the corresponding allocentric condition (Chen, Byrne, & Crawford, 2011).

When we compared variable errors between the landmark and no-landmark conditions, subjects' reaches showed lower variability when landmarks were available than when reaching in total darkness, which suggests that they were not only able to use the landmarks to improve reach accuracy in the form of absolute endpoint errors, but also reach precision. This finding is in line with other reports where variable errors in reaching tasks diminished when allocentric cues were available (Byrne & Crawford, 2010; Chen, Byrne, & Crawford, 2011; Krigolson et al., 2007; Obhi & Goodale, 2005).

To conclude, our results suggest that the brain still uses a gaze-dependent target representation to code and update target locations for reaching movements even when landmarks are present and reaching is delayed by up to 12 s. This gaze-dependent target representation seems to be combined with allocentric information when environmental cues are available.

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