



## Gaze-centered spatial updating of reach targets across different memory delays

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### ABSTRACT

Previous research has demonstrated that remembered targets for reaching are coded and updated relative to gaze, at least when the reaching movement is made soon after the target has been extinguished. In this study, we want to test whether reach targets are updated relative to gaze following different time delays. Reaching endpoints systematically varied as a function of gaze relative to target irrespective of whether the action was executed immediately or after a delay of 5 s, 8 s or 12 s. The present results suggest that memory traces for reach targets continue to be coded in a gaze-dependent reference frame if no external cues are present.

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### 1. Introduction

Short-term storage of the location of targets allows for movement planning when the target is no longer in the field of view. It has been suggested that movements made to remembered or visible targets are subserved by distinct neural systems and thus coded using distinct spatial representations (Goodale & Haffenden, 1998; Milner & Goodale, 2008; Rossetti, 1998). The dorsal pathway projecting from primary visual areas to the posterior parietal cortex is assumed to carry out actions in real-time on the basis of egocentric representations (i.e., location of a target relative to the body). Multiple areas have been identified in the posterior parietal cortex that code action-related information in different egocentric frames of reference, such as eye-centered, head-centered, or hand-centered frames (for evidence in monkeys see, Buneo & Andersen, 2006; Colby & Goldberg, 1999; for evidence in humans see, Culham & Valyear, 2006). In contrast, the ventral pathway which projects to the inferotemporal cortex is assumed to be involved in perceptual processes and retain allocentric information (i.e., location of a target relative to the external world) over a longer time scale. Therefore, memory-driven actions are supposed to make use of a perceptual allocentric representation of the target generated by the ventral pathway.

Consistent with this account are findings in neurological patients which demonstrate that lesions in the dorsal stream lead

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to impaired grasp performance in real time and improves when grasping after a time delay, suggesting a recruitment of the intact ventral pathway (Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Milner et al., 2001). Conversely, patient DF, who has lesions in the ventral stream, shows severe deficits in grasping after a 2 s delay while on-line grasping is unaffected (Goodale, Jakobson, & Keillor, 1994; Milner, Dijkerman, & Carey, 1999). A recent study suggests that DF's deficit might be caused by impaired allocentric spatial coding irrespective of whether the task is perceptual or motor (Schenk, 2006). In line with the patient results, grasp performance in healthy humans differs depending on whether actions are guided by a remembered target representation (open loop) or by a visible target (closed loop), implying distinct transformation processes for on-line and off-line motor control (Hay & Redon, 2006; Hu, Eagleson, & Goodale, 1999). Moreover, grip aperture is affected by visual illusions for memory-guided but not for online grasping (Hu & Goodale, 2000; Westwood & Goodale, 2003). The authors propose that offline control of movements is carried out by the ventral stream, relying on a perceptual allocentric target representation sensitive to contextual information.

Other studies provide evidence for short-term storage of target locations in an egocentric reference frame tied to the eyes. Khan, Pisella, Rossetti, et al. (2005) tested for gaze-centered updating of reach targets in optic ataxia patients and healthy controls. In this experiment, participants first viewed a reaching target for 2 s and then saccaded to a fixation light which occurred for 1 s after the target was extinguished. In the immediate task, an auditory signal prompted participants to reach toward the remembered location of the target while maintaining gaze on the remembered location of the fixation light. In the delayed task, a 5 s delay was inserted before the auditory signal occurred. In support of previous findings

on immediate reaching to remembered targets (Henriques, Klier, Smith, Lowy, & Crawford, 1998; Medendorp & Crawford, 2002), healthy controls systematically overshoot the remembered target in the direction opposite to the saccade; i.e., final gaze. More importantly, this error pattern did not differ between the immediate and delayed task.

Regarding the experimental design by Khan, Pisella, Rossetti, et al. (2005), it is conceivable that the target representation was instantly updated by the saccadic eye movement resulting in a distorted target location (misestimation opposite to gaze direction) maintained across the delay period. As a consequence, whatever generated the errors in localizing the remapped reaching target would also be present even if the reach movement to that target was delayed. What happens if the saccadic eye movement is executed *after* the memory delay (such that, gaze continues to be directed toward the remembered target during the delay)? If target information is transformed from a gaze-dependent into a more stable gaze-independent egocentric (e.g., body-centered, head-centered) or even an allocentric reference frame due to time delay, eye movements occurring after the memory interval should not affect the target representation, resulting in reaching errors unrelated to gaze.

We tested for the effect of delay on gaze-centered updating of reach targets by comparing reaching errors for immediate and delayed actions. Reaching was executed toward three different target locations immediately or after a variable delay of 5 s, 8 s or 12 s. In contrast to the study by Khan, Pisella, Rossetti, et al. (2005), participants were instructed to maintain gaze at the location of the previously seen target and then to shift gaze to one of five fixation points which were presented *after* the delay. If the memory trace of the target is stored in a gaze-independent reference frame, reaching errors should not systematically vary as a function of final gaze. However, if the target is maintained in a gaze-dependent frame, reaching errors should depend on final gaze direction following the saccade; in particular, reaching end points should miss the remembered target in the opposite direction of gaze. Moreover, we examined whether the use of an additional motor representation affects spatial updating of reach targets used for delayed actions. To this end, subjects either viewed or viewed and reached to the target while it was visible.

## 2. Methods

### 2.1. Subjects

Twelve volunteers (6 female) between the ages of 17 and 26 years (mean:  $22.2 \pm 2.48$  years) took part in the single-point delay paradigm and 12 participants (6 female) between the ages of 17 and 30 (mean:  $22 \pm 3.52$ ) in the double-point paradigm. Subjects were identical in both paradigms except for one person. Five of them taking part in both experiments performed the 12 s delay condition in addition to the others and had their eye movements recorded during all blocks as described below.

All participants were right-handed and had normal or corrected-to-normal vision and no known history of visual or neuromuscular deficit. They received no compensation for participating in the study. All procedures were conducted in agreement with the ethical guidelines of York University's Human Participants Review Subcommittee.

### 2.2. Equipment

Subjects were seated at a table with their head fixed by a bite bar. The heights of the chair and bite bar were adjusted independently so that they performed the task in a comfortable position

with an unobstructed view of the testing area. Movements of the right eye were recorded from five participants using a head mounted EyeLinkII eye tracking system (SR Research, Osgoode, ON, Canada) utilizing infrared pupil identification at a sampling rate of 250 Hz. The apparatus was calibrated for each participant at the beginning of each testing session according to the parameters specified by SR Research to ensure reliable measurements.

A 19" touch screen panel (Magic Touch 2.0; Keytec, Inc.; Garland, Texas), with a resolution of  $4096 \times 4096$  pixels, was mounted vertically on the table  $\sim 47$  cm from the subject's eyes, and recorded reach endpoints. A sheet of paper was attached to the back of this touch screen panel (which was only  $< 5$  mm thick and transparent), so that stimuli could be back-projected on this panel, as described in the next section. Successfully registered touches were confirmed by a beep signal. Participants used their dominant right hand for all reaching movements.

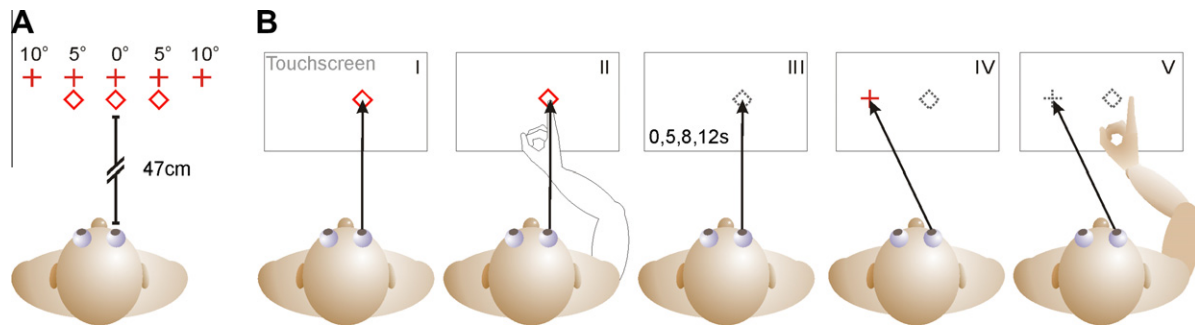
### 2.3. Stimuli

Stimuli consisted of visual targets (diamonds) and fixation stimuli (crosses). All stimuli were 1 cm in diameter. Targets were presented either centrally or at a visual angle of  $5^\circ$  towards the left or right. The central ( $0^\circ$ ) position was aligned with the participants' right eye before the experiment (see Fig. 1A). Fixation crosses were presented either centrally or at  $5^\circ$  or  $10^\circ$  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 at a consistent elevation onto the vertically mounted touch screen panel using an Optikon XYL-C Laser Projector (Optikon, Kitchener, ON, Canada). The entire experiment was conducted in total darkness with no other visual stimuli present. Verbal instructions by a computer generated voice were used to inform subjects when to start pointing and to mark the end of each trial.

### 2.4. Single-point delay paradigm

Subjects began each trial depressing 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 target locations. Subjects had to fixate the target (Fig. 1B, I) and to keep their gaze at this location for a variable delay of 0 s, 5 s, 8 s or 12 s after the target disappeared (Fig. 1B, III). After the delay, a fixation cross was presented at one of the five possible locations, which prompted participants to saccade to its position (Fig. 1B, IV). This was followed by a verbal instruction, 750 ms after the onset of the fixation cross, asking to point at the remembered target location while keeping their gaze on the fixation position (Fig. 1B, V). The fixation cross was extinguished as the mouse button was released, so that the reaching movement was done in total darkness. The trial ended when the right hand was brought back onto the mouse. Trials with the three different delays and the no-delay (0 s) prior to updating were randomly interspersed.

In order to reduce the length of the experiment, we did not use all possible combinations of the three targets and five fixation positions but included a subset of them. Trials with a distance between target and fixation of larger than  $10^\circ$  of visual angle were not included into the experiment (target  $-5^\circ$ /fixation  $+ 10^\circ$  and vice versa). The remaining 13 combinations were presented for each of the four delay conditions (0 s, 5 s, 8 s and 12 s), resulting in 52 trials per experimental block. The experiment consisted of six blocks, and thus six repetitions of each combination for each of the four delays, for a total of 312 trials. These six blocks (each made up of 52 trials) took on average a total of 90 min to complete and were run over 2 or 3 days to avoid fatigue. To ensure that participants were comfortable with the bite bar and eye tracking equipment, they could opt to take breaks after each block or continue on a



**Fig. 1.** Experimental setup. A: Three target (diamonds) and five fixation (crosses) positions were randomly presented. The central location was aligned to the subject's right eye. B: In the single-point paradigm (panels I, III, IV and V), subjects were shown a target for 1 s (I), followed by a delay varying between 0 s, 5 s, 8 s, or 12 s during which subjects kept their gaze at target location (III). Afterwards, a fixation cross was shown and the subjects performed a saccade toward its location (IV) and then pointed to the remembered target location (V). The double-point (panels I–V) paradigm differed from the single-point paradigm in that in phase I the target stayed visible until subjects had pointed to it for the first time before returning the hand to the same start position (panel II).

different day. In the case of a break, a calibration was done to correct for EyeLink camera shift during the break.

### 2.5. Double-point delay paradigm

At the start of every trial in the double-point delay paradigm, a target was displayed at one of the three target locations. Subjects were instructed to point at the visible target, which disappeared after the touch was recorded, as illustrated in Fig 1B, II. Subjects then had to bring their hand back to the mouse. One of the four delay periods described above was then applied, during which participants had to keep their gaze fixed on the location of the now absent target. Like in the single-point paradigm, a fixation cross was presented after the delay, whereupon participants directed their gaze to its location and then pointed at the remembered target location again while keeping gaze on the fixation position. The trial ended when the right hand pressed the mouse.

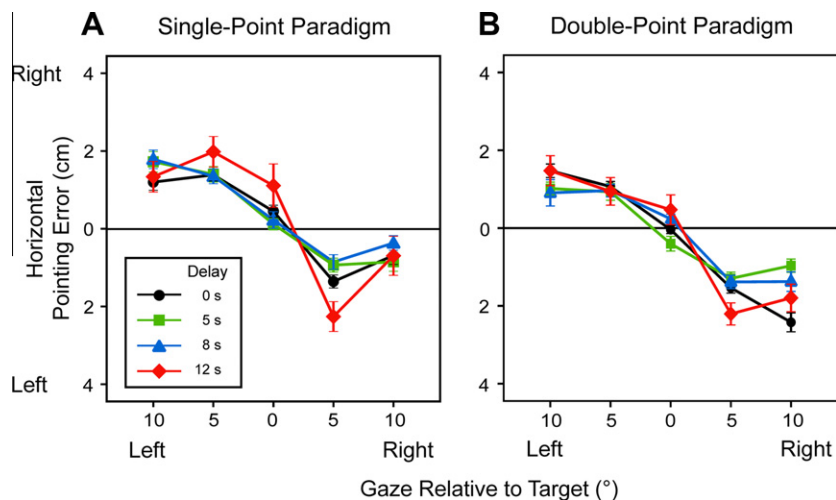
As in the single-point paradigm, each experimental block consisted of 52 trials including all four delay conditions and the thirteen combinations of target and fixation described above. Because of longer runtime of this paradigm due to the first reaching movement, each subject completed four blocks, so four repetitions for each fixation-target combination and delay, resulting in a total of 208 trials recorded and about 90 min of runtime per subject. Like in the single-point experiment, subjects could take breaks after each experimental block and equipment was recalibrated.

After every block for both paradigms, the room was lit, and participants fixated and touched (with their now visible hand) each of the five visible targets/fixation crosses to calibrate eye tracking and touch recording. The single touches to each of the three visible target location were used as a baseline measure of ideal reaching, in order to calculate reaching errors across the experimental conditions.

### 2.6. Data reduction

Raw touch screen and 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). For every trial, eye position at the time of target and fixation directions, as well as the pointing movement(s), was selected to ensure subjects' compliance with the instructions. Trials were excluded from analysis when subjects fixated the wrong location, shifted gaze before reaching or started to reach before instruction. Trials with faulty data recordings were also removed. Across the subjects that were tested with eye tracking, 141 trials (9%) of the single-point paradigm and 68 trials (7%) of the double-pointing paradigm were excluded.

Gaze relative to target or retinal error (RE) was computed for each trial as the angular difference between target and fixation locations. Pointing errors for each movement were computed as the difference between finger position at reach endpoints and



**Fig. 2.** Horizontal pointing error plotted as a function of gaze relative to target for 0 s, 5 s, 8 s and 12 s of delay in the single-point (A) and double-point (B) paradigms. The zero-line marks the target location. Error bars show  $\pm 1$  standard error.

subjects' perceived target location as determined by matching calibration data. Specifically, pointing errors were calculated by subtracting the 2D finger position when subjects reached to each visible target at the end of each experimental block (baseline reaches) from the 2D finger positions collected during the experimental conditions for the corresponding targets. Given that gaze and target location only varied in the horizontal (left–right) direction, for brevity, we only report the horizontal pointing errors.

### 2.7. Statistical analysis

All analyses were performed in SPSS (SPSS Inc., Chicago, IL). After removal of outliers (two standard deviations above or below the mean for each subject) and trials previously marked invalid, 3697 trials (=96%) remained for analysis in the single-point paradigm; 2060 trials (=97%) were analyzed in the double-point paradigm. Since we found no significant difference between subjects tested with eye tracking and those without, data were collapsed across the two groups for all future analysis.

In order to test whether the typical gaze-effect (target relative to gaze,  $-10^\circ$ ,  $-5^\circ$ ,  $0^\circ$ ,  $5^\circ$ ,  $10^\circ$ ) on horizontal pointing error varied as a function of delay, repeated-measures analysis of variance (RM ANOVA) were conducted for the different delays and across delays. To further examine whether variability in pointing increased with delay, an RM ANOVA was calculated for each target-fixation combination to test for an effect of delay on standard deviation of horizontal pointing error. 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.

## 3. Results

### 3.1. Horizontal pointing error for different delays

We investigated the effect of introducing a temporal delay between target presentation and a saccade away from the target site on subsequent reaching errors to determine whether spatial memory continued to be updated in a gaze-dependent reference frame, or was converted into a more stable gaze-independent frame during the delay. Fig. 2 shows horizontal pointing errors (averaged across subjects) as a function of gaze eccentricity relative to target

for each delay period for both single-point paradigm (A) and double-point paradigm (B).

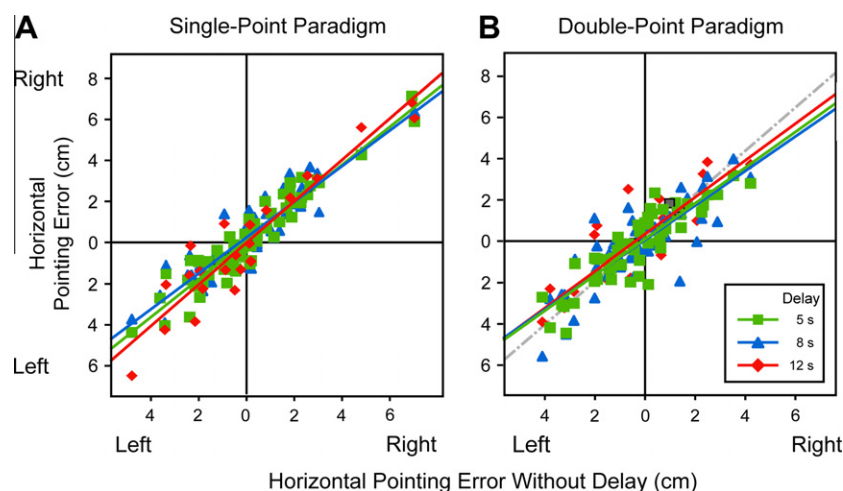
In the *single-point paradigm*, horizontal pointing errors systematically varied with gaze relative to target for the 0 s, 5 s and 8 s delays ( $n = 12$ ;  $F_{(4, 44)} = 51.9$ ;  $p < 0.001$ ), as well as for the five subjects who were additionally tested in the 12 s condition ( $F_{(4, 16)} = 38.6$ ;  $p < 0.01$ ). Specifically, horizontal pointing errors were directed towards the opposite side of the target relative to the fixation position (i.e., fixating left of the target resulted in a rightward pointing error and vice versa) for all four different delays (Fig. 2A). No difference was found in gaze-dependent errors between delays for the group who underwent all delay conditions ( $F_{(12, 48)} = 2.3$ ;  $p > 0.123$ ) and the group tested with 0 s, 5 s and 8 s of delay ( $F_{(8, 88)} = 2.6$ ;  $p > 0.051$ ). Thus, gaze-dependent errors did not vary systematically with delay in that the pattern remained quite similar and does not appear to diminish with longer delays.

The *double-point paradigm* revealed similar results (Fig. 2B). Horizontal pointing errors varied systematically as a function of gaze relative to target for the 0 s, 5 s and 8 s conditions ( $n = 12$ ;  $F_{(4, 40)} = 29.3$ ;  $p < 0.001$ ) as well as for the 12 s condition ( $n = 5$ ;  $F_{(4, 12)} = 19.0$ ;  $p < 0.05$ ). In both cases, no significant difference was found between the different delays ( $n = 12$ ;  $F_{(12, 36)} = 1.0$ ;  $p > 0.422$ ;  $n = 5$ ;  $F_{(8, 80)} = 1.9$ ;  $p > 0.118$ ).

In Fig. 3, mean horizontal pointing errors are plotted for the different delays (5 s, 8 s and 12 s) as a function of mean horizontal pointing error in the no-delay condition (averaged across all subjects) for both the single-point paradigm (A) and double-point paradigm (B). If the remembered target continues to be updated as a function of gaze regardless of delay, a slope close to 1.0 is expected for every delay condition. However, if delay leads to converting a gaze-centered target representation into a reference frame independent of gaze, the slopes should be close to zero. In the *single-point paradigm*, slopes for the separate delays ranged from .87 to 1.01, with correlations ranging from .93 to .95. Again, the *double-point paradigm* showed similar values. Individual slopes ranged from .84 to .90 with corresponding correlations of .83 to .89.

### 3.2. Combined data from both paradigms

When we analyzed the combined results of both the single-point and double-point paradigms, the gaze-dependent pointing errors did not differ across the two paradigms or across the delays for both the subjects that were tested with 0 s, 5 s and 8 s of delay



**Fig. 3.** Horizontal pointing errors when pointing after a delay of 5 s, 8 s or 12 s plotted as a function of those errors for immediate pointing in the single-point paradigm (A) and the double-point paradigm (B). The solid lines represent the regression fits for errors in the 5 s, 8 s and 12 s delay conditions, while the grey dot-dashed line marks the identity line with a slope of 1 indicating equivalent gaze-centered updating with and without delay.

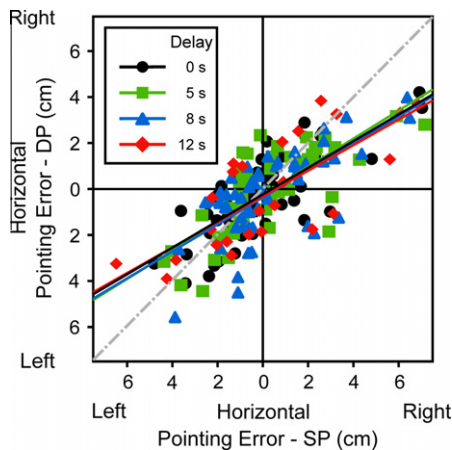


( $F_{(8, 168)} = 2.2$ ;  $p > 0.064$ ) and the subjects also tested with 12 s of delay ( $F_{(12, 84)} = 0.8$ ;  $p > 0.531$ ).

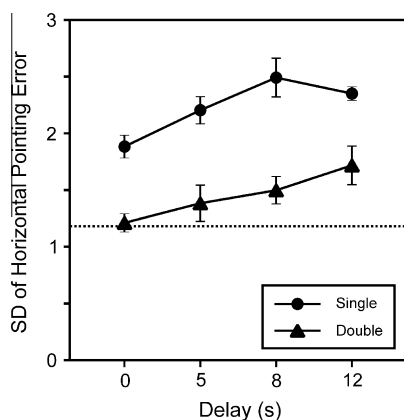
In Fig. 4, we plot mean horizontal pointing errors for each delay in the double-point paradigm (averaged across all subjects) as a function of mean horizontal pointing error for the corresponding delay in the single-point paradigm. Regression slopes for the different delays ranged from .56 to .61 with correlations of .69 to .76. This result indicates that the pattern of gaze-dependent pointing errors may have been smaller in the double-point paradigm than in the single-point paradigm, as may be expected given the preceding reach movement, although this difference did not reach significance in the ANOVA comparing the data of both paradigms.

### 3.3. Variability of horizontal pointing errors

Fig. 5 displays averaged standard deviations of horizontal pointing errors across subjects for each delay for the single-point paradigm and the double-point paradigm. For comparison purposes, the mean standard deviation of horizontal pointing errors for the first reach movement in the double-point paradigm (during which the target stayed visible for the whole movement) is displayed as dotted black line (mean SD for all subjects: 1.18).



**Fig. 4.** Horizontal pointing errors in the double-point paradigm for each delay plotted as a function of those in the single-point paradigm for corresponding delays. The solid lines represent the regression fits for errors in the 0 s, 5 s, 8 s and 12 s delay conditions, while the grey dot-dashed line marks the identity line with a slope of 1 indicating ideal correspondence of gaze-centered updating with and without delay.



**Fig. 5.** Variability (standard deviations) of horizontal pointing error plotted as a function of delay for the single-point (circle) and double-point (triangle) paradigms. The dotted line represents average standard deviation for pointing when the target was still visible. Error bars show  $\pm 1$  standard error.

Variability increased significantly with increasing delay, both in the single-point and the double-point paradigm. This was true for the subjects tested with three different delays ( $F_{(2, 42)} = 27.9$ ;  $p < 0.001$ ) as well as the subjects that also participated in the 12 s delay condition ( $F_{(3, 21)} = 13.2$ ;  $p < 0.001$ ). Variability in the single-point paradigm was consistently higher than in the double-point paradigm in both cases (subjects with 0 s, 5 s and 8 s delay:  $n = 23$ ;  $F_{(1, 21)} = 18.2$ ;  $p < 0.001$ , subjects with 0 s, 5 s, 8 s and 12 s delay:  $n = 9$ ;  $F_{(1, 7)} = 27.8$ ;  $p < 0.001$ ). However, the effect of delay on this variability pattern was not significantly different between experimental conditions ( $n = 23$ :  $F_{(8, 168)} = 1.7$ ;  $p > 0.154$ ;  $n = 9$ :  $F_{(12, 84)} = 1.3$ ;  $p > 0.299$ ).

## 4. Discussion

Our results demonstrate that reaching errors systematically vary with gaze direction irrespective of whether reaching is executed immediately after target presentation or after a time delay. This error pattern is consistent across different delay intervals ranging from 5 s to 12 s and does not differ from errors in immediate reaching. However, the variability of these reaches increases with increasing delays. Moreover, reaching toward the target during its presentation and again when the target is no longer visible leads to a lower variability than solely reaching to a previously seen target.

The present findings suggest that remembered reach targets used for memory-guided actions are represented in a dynamic gaze-centered reference frame if no other external cues are available. They parallel results that we and others have found for immediate reaching (Henriques et al., 1998; Medendorp & Crawford, 2002) and observations by Khan, Pisella, Rossetti, et al. (2005) in healthy subjects on updating of reach targets after 500 ms and 5000 ms delays. These gaze-dependent errors, following a gaze shift between viewing and pointing to the remembered target (independent of delay), cannot be explained by a gaze-independent representation of the remembered target, such as one anchored to the head, body or stored within an allocentric frame. Nor can they be due to misestimates of eye position. As we showed in our original study, Henriques et al., 1998 (and in subsequent studies from our lab and other labs since), the errors are not due to the eye position itself (eye-in-head) since they vary as a function of gaze relative to target, not relative to eye position. If this were the case, then we could explain reach errors as being due to a conversion from retinal signal to a head- or body-centered representation of the target, since these conversions involve incorporating information about this “misestimated” eye-in-head position. Yet, reaching does not vary consistently with the eye-in-head, but it varies consistently with the distance between the target and gaze. Moreover, if this error occurred during the conversion to a gaze-independent reference frame, we should not find any gaze-dependent errors. The reasoning is as follows: any conversion of the target into a reference frame fixed to the head or body would occur once the target is viewed (in this study when the target is foveated and the distance between the target and gaze is zero and therefore not exaggerated or distorted). But if the brain converts this foveated target into a stable head- or body-centered (or even allocentric) representation, then any subsequent eye movements following the disappearance of the target should have no effect on reaching since the brain has already coded the location of the target relative to the body. The key behavioral evidence for gaze-centered coding and updating of spatial memory is that pattern of reach errors as a function of final gaze (re: target) is the same whether the target is only viewed in the periphery or when the foveated target is remapped to the periphery following a subsequent gaze shift. No gaze-independent reference frame

(head-, body-, allocentric) can account for this similarity in reach errors, so we conclude that the spatial memory of the target is being remapped relative to gaze, and so stored in gaze-centered coordinates. However, our results and the results of others cannot distinguish whether these systematic errors are due to the remembered target being coded and updated relative to gaze, or whether it is the goal of the hand movement and/or the target-hand vector that are being updated instead or in addition to.

Gaze-centered updating has consistently been associated with activations in the posterior parietal cortex (for a review see, Klier & Angelaki, 2008; Medendorp, Beurze, van Pelt, & van der Werf, 2008). Single-cell recordings in the lateral intraparietal (LIP) sulcus of monkeys demonstrate that receptive fields of LIP neurons are shifted during, and even before, the eyes have moved (Colby, Duhamel, & Goldberg, 1995; Duhamel, Colby, & Goldberg, 1992). In line with monkey literature, imaging studies in humans found activation of the posterior parietal cortex during updating of visual target positions after gaze shifts for subsequent pointing movements or saccades towards the target (Medendorp, Goltz, Crawford, & Vilis, 2005; Medendorp, Goltz, & Vilis, 2003). These findings confirm the assumption that the dorsal stream, which covers the posterior parietal cortex, represents targets in an egocentric gaze-dependent reference frame. However, this assumption is supposed to be restricted to targets engaged in online control of movements (Goodale & Haffenden, 1998; Goodale, Westwood, & Milner, 2003).

Our results suggest that spatial memory for movement planning continues to be represented in an egocentric gaze-dependent reference frame which implies an involvement of the dorsal stream in both online and off-line motor control. This apparent discrepancy between our results and those suggesting that the memory trace of target location (which is built up as soon as the target had disappeared) is stored in the ventral stream, could be resolved by considering the refined pathway model put forward by Rizzolatti and Matelli (2003). They assume an anatomical and functional division of the dorsal pathway into the dorso-dorsal stream (nodal point in the superior parietal lobe) for online motor planning and the ventro-dorsal stream (nodal point in the inferior parietal lobe including AIP and LIP), which acts as the interface of perception and action subserving space perception, action observation, and other higher cognitive functions in addition to motor planning. Hence, the ventro-dorsal stream seems to be a suitable candidate for short-term storage of target location. This view has gained support from previous electrophysiological (Murata, Gallese, Kaseda, & Sakata, 1996) and neuroimaging research (Fiehler, Burke, Engel, Bien, & Rösler, 2008; Fiehler et al., 2011). Furthermore, findings in optic ataxia patients who mainly suffer from lesions in the superior parietal lobe imply that the dorso-dorsal stream may be involved in coding target location for immediate actions (an unilateral and an asymmetrical bilateral optic ataxia patient show a pattern of reaching deficits in the affected visual field that is consistent with gaze-centered updating of reach targets), while the ventro-dorsal stream is involved in spatial memory of target location used for offline planning of movements (gaze-centered updating did not occur for immediate reaches for the bilateral optic ataxia patients but was recovered when reaching after a 5 s delay) (Khan, Pisella, Rossetti, et al., 2005; Khan, Pisella, Vighetto, et al., 2005). Information may be re-routed through the ventro-dorsal stream allowing patients to update targets relative to gaze when reaching after a time delay, while the bilateral lesioned dorso-dorsal stream affects spatial updating for immediate reaching movements. This hypothesis is strengthened by recent neuroimaging results in a bilateral optic ataxia patient exhibiting activation in the intact parts of the ventro-dorsal stream, adjacent to the patient's lesions, during delayed reaching (Himmelbach et al., 2009). Together with previous findings on reference frames

in online motor control, we suggest that both the dorso-dorsal and the ventro-dorsal stream code targets for immediate and delayed movements in gaze-centered coordinates, with a stronger contribution of the ventro-dorsal stream in delayed motor acts.

We found an increasing variability in reaching endpoints with prolonged time delay; however, with no impact on the systematic reach errors that varied with final gaze direction relative to target. Such an increase in movement variability has been reported in many previous studies (e.g., Chieffi, Allport, & Woodin, 1999; Elliott & Calvert, 1990; McIntyre, Stratta, & Lacquaniti, 1997; McIntyre, Stratta, & Lacquaniti, 1998; Westwood, Heath, & Roy, 2003) and point to a gradual decay of spatial memory of the target over time. This argues against a sudden switch between two distinct processing pathways and suggests that the memory trace of the target persists within the same cortical network subserving motor control, viz., we propose in the ventro-dorsal stream (for a similar argumentation, see Bradshaw & Watt, 2002; Hesse & Franz, 2009; Himmelbach & Karnath, 2005; Rogers, Smith, & Schenk, 2009).

Besides our assumption that target representations remain in the same gaze-dependent reference frame independent on whether the movement is performed with or without a delay, there are at least two alternative interpretations of the present results. First, one could presume that for delayed actions the memory trace of the target is transformed from a gaze-dependent representation into a gaze-independent egocentric or allocentric one and then re-transformed into a gaze-dependent egocentric reference frame just before the movement is executed. This possibility has been put forward recently by Cohen and colleagues (2009) who believe that the dorsal stream carries out actions either on the basis of a real-time representation or a perceptual memory representation which is held in the ventral stream and forwarded to the dorsal stream on demand (see also, Milner & Goodale, 2008). Using transcranial magnetic stimulation (TMS), they found that a disruption of the ventral stream area lateral occipital (LO) cortex impaired grasping kinematics when movements were executed after a memory delay but not when they were executed immediately. The TMS pulse was delivered simultaneously with the start of the movement; i.e., after movement planning. In our experiment, participants saccaded to a fixation cross after the delay, and then 750 ms later they reached toward the remembered location of the target. Since we found that the reach errors were systematically affected by an intervening gaze shift, it would imply that if the memory trace of the target location had been stored in a gaze-independent reference frame, it would then have to have been re-transformed into a gaze-dependent representation before the saccadic eye movement. In this case, the re-transformation would have to result in a gaze-fixed egocentric representation of the target site since any other gaze-independent reference frame would not be susceptible to changes in gaze.

It is conceivable that the re-transformation of the remembered target representation from a gaze-independent into a gaze-dependent frame may only apply to targets for grasping, where target features such as size, shape or material, rather than target location, may be critical for movement planning. Such target features have been shown to be coded within LO; i.e., in the ventral stream. However, so far there is no evidence that areas within the temporal lobe devoted to the short-term coding of the location of a single target exist (like they are for coding target features), and thus whether a reciprocating transformation occurs for delayed goal-directed movements, for either the arm or the eyes.

Second, it is likely that the target is represented in multiple frames of reference that either completely or partly contribute to movement control (e.g., Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003; Blohm, Keith, & Crawford, 2009). In support of this, Sober and Sabes (2003, 2005) have shown that both visual and proprioceptive information serve motor planning but at different

planning stages. Determining the movement vector primarily relies on visual representations of the target and arm, whereas computing the motor command depends more on proprioceptive coding. Furthermore, recent work suggests that egocentric and allocentric information is integrated for reaching movements by weighting each single input with respect to its reliability (Byrne & Crawford, 2010a). Nonetheless, the same authors in another study (Byrne & Crawford, 2010b) found that allocentric cues do not consistently nor substantially diminish gaze-dependent reaching errors made when reaching to a single remembered target after a delay of about 3 s. Since we do not see any reduction in the pattern of reach errors with increasing delay, it implies that the brain is not incorporating these additional representations when coding the target in memory for delayed reaches.

Here, we provide evidence that reach targets guiding immediate and delayed movements are stored and updated in gaze-centered coordinates, at least when no additional external cues are present. Overall, we do not presume that the gaze-dependent reference frame is the exclusive framework for coding goal-directed movements in real-time or based on spatial memory. Previous studies also argue for short-term storage of target information in an egocentric reference frame tied to the head, hand or arm based on variable error. For instance, reaching errors, measured after 3 s and 30 s memory delays, consistently varied with the starting position of the hand (Chieffi et al., 1999). Moreover, reaching to remembered targets maintained for 0.5 s, 5 s or 8 s produced error patterns aligned toward the persons' head and body and remained stable across the different delay lengths (McIntyre et al., 1997, 1998). However, spatial coding with respect to gaze in contrast to other egocentric reference frames, or even an allocentric reference frame, seems to dominate our representation of space for motor control especially in the absence of additional environmental cues. Further studies are necessary to investigate how memory delay alters how different spatial representations (allocentric, egocentric) are weighted and combined in order to contribute to goal-directed movements.

We further examined the impact of gaze direction in goal-directed reaching under two task conditions where participants either reached toward the visible target prior to a second memory-guided reach (double-point condition) or simply viewed the target while it was visible, before they reached to its remembered location (single-point condition). While both conditions exhibited the typical gaze-effect, the first reach to a visible target lead to a decrease in variability in both subsequent immediate and delayed memory-guided reaching movements. Our result indicates that motor-related information from the preceding arm movement, such as proprioceptive and efferent signals, are used to produce more precise reaching for subsequent aiming movements; this is not surprising since reproducing arm movements can be fairly precise (replicating endpoints within an average of less than 2° or 2 cm) even without visible feedback (Adamovich, Berkinblit, Fookson, & Poizner, 1998; Darling & Miller, 1993; Jones, Henriques, & Fiehler, 2010). This initial visually-guided reaching movement improved precision even after longer memory delays. Yet, it did not lead to improved accuracy; reaching endpoints in the double-point paradigm varied as a function of gaze, much to the same extent they did for the single-point condition. This result extends our previous findings suggesting that multiple reaching movements to the same remembered location are mainly based on updated gaze-fixed representations of the target (Sorrento & Henriques, 2008). Since the effect observed for offline control of movement mimics those of immediate movement guidance, it further implies that delays prior to a movement do not result in visuospatial memory being converted in a gaze-independent reference frame but continues to be represented in gaze-dependent coordinates at least until movement onset.

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