RESEARCH ARTICLE

Interaction between gaze and visual and proprioceptive position judgements

Katja Fiehler · Frank Rösler · Denise Y. P. Henriques

Abstract There is considerable evidence that targets for action are represented in a dynamic gaze-centered frame of reference, such that each gaze shift requires an internal updating of the target. Here, we investigated the effect of eye movements on the spatial representation of targets used for position judgements. Participants had their hand passively placed to a location, and then judged whether this location was left or right of a remembered visual or remembered proprioceptive target, while gaze direction was varied. Estimates of position of the remembered targets relative to the unseen position of the hand were assessed with an adaptive psychophysical procedure. These positional judgements significantly varied relative to gaze for both remembered visual and remembered proprioceptive targets. Our results suggest that relative target positions may also be represented in eye-centered coordinates. This implies similar spatial reference frames for action control and space perception when positions are coded relative to the hand.

Keywords Multisensory · Perception and action · Reference frames · Remapping · Space · Updating

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Introduction

To interact effectively with objects in the everyday world, the brain needs to construct a stable spatial representation. Two broad classes of spatial representations have been described: egocentric representations, in which objects and locations are coded relative to one's own body (eye, head, hand, or body) and allocentric representations, in which locations are represented with respect to the external world (external objects or locations). There is substantial evidence supporting the fact that the brain constructs multiple spatial representations in order to localize objects in space or to direct an action toward an object (e.g., Arbib 1991).

For goal-directed movements, such as reaching or pointing, the location of the target relative to the hand must be integrated into a common reference frame. There are two main accounts on spatial coding of action targets. The traditional account proposes a sequential transformation of reference frames into a common body-centered representation (for evidence in monkeys, see Andersen et al. 1985; Brotchie et al. 1995; for evidence in humans, see Soechting et al. 1991; Flanders et al. 1992). The location of a viewed target is coded in retinal coordinates, which are then immediately transformed to head-centered coordinates by adding the information of the eye position relative to the head. This representation is further transformed into body-centered coordinates by taking into account the head position relative to the body. As both the location of the visual target and the hand are represented in a body-centered reference frame, the hand-target-difference vector can be computed and an action can therefore be performed. Other target modalities are assumed to enter the transformation sequence at the corresponding stages, i.e., at the head-centered stage for audition and at the body-centered stage for proprioception. In contrast, the alternative

account suggests that the action target and the hand are represented in a dynamic retinotopic map (for evidence in monkeys, see Goldberg and Bruce 1990; Buneo et al. 2002; for evidence in humans, see Henriques et al. 1998). The target is represented in a gaze-centered frame of reference that must be updated across eye movements, and so remains stored within this reference frame until a movement is initiated.

Recent studies in humans gained further support for the dynamic model, showing that the remembered location of visual reach targets are represented relative to gaze (Medendorp and Crawford 2002; Khan et al. 2005a, b; Van Pelt and Medendorp 2007) at least prior to the movement. Participants produced systematic pointing errors toward targets in the opposite direction of the gaze shift. This means that when a person is looking left, they point slightly toward the right of the target's actual target position. This computational error is caused by the retinal exaggeration effect described by Bock (1986). He found that participants exaggerated the angular retinal eccentricity of a remembered target location viewed in the periphery. Moreover, participants made the same patterns of errors following a gaze shift from a foveated target, suggesting that remembered targets are not coded relative to the head or body, but are instead updated each time the eyes move, and are thus coded relative to gaze. In other words, if remembered targets were transformed immediately into a head- or body-centered frame (Mays and Sparkes 1980; McGuire and Sabes 2009), then any subsequent gaze shift or other change of gaze position should not affect the subsequent arm movements. Yet, this gaze-dependent updating of target location has been demonstrated for saccadic eye movements (Henriques et al. 1998; Medendorp and Crawford 2002), smooth pursuit (Thompson and Henriques 2008), and eye movements caused by body translations (Van Pelt and Medendorp 2007). Beyond vision, auditory and proprioceptive reach targets seem to be represented in an eye-centered reference frame as well (Pouget et al. 2002; Blangero et al. 2005; for evidence in patients, see Blangero et al. 2007; Jackson et al. 2009).

The posterior parietal cortex (PPC) has been proposed to play a key role in dynamic gaze-centered updating of spatial goals for actions (for a review see, Klier and Angelaki 2008). Single-cell recordings in the lateral intraparietal (LIP) sulcus of the monkey demonstrate that its receptive fields are shifted according to the associated eye movement (Duhamel et al. 1992; Colby et al. 1995). Consistent with the monkey literature, imaging studies in humans found activation of the PPC during the updating of visual target locations after gaze shifts for subsequent pointing movements or saccades toward the target (Medendorp et al. 2003, 2005), or when merely attending to the remembered target (Merriam et al. 2003). This has

been confirmed by results in patients with optic ataxia suffering from right parietal (Khan et al. 2005a) or bilateral parietal (Khan et al. 2005b) lesions who showed reach deficits in an eye-fixed reference frame that is updated after each saccade.

Besides spatial updating for action, the PPC seems to be involved in spatial updating for position judgements, i.e., perception. In a recent experiment by Wolbers et al. (2008), subjects experienced a simulated forward translation of their body after viewing objects at unpredictable positions in a virtual environment. Afterward, they were asked to point to the remembered location of one of the objects, taking body movement into account. Updating of the target location during the forward translation activated the precuneus located in the PPC. Interestingly, a similar activation was found when subjects gave verbal position judgements about remembered object position on a numerical scale. There was no differential activation in the precuneus between pointing or verbal estimates, suggesting a common cortical mechanism of spatial updating for both action and position judgements.

An effect of gaze on positional judgements has also been demonstrated for auditory (Lewald and Ehrenstein 1996a, b; Lewald 1998), visual (Lewald 1998; Eggert et al. 2001) and tactile stimuli (Harrar and Harris 2009). In the study by Lewald and Ehrenstein (1996a), participants constantly directed gaze to one of five fixation lights while they perceived an auditory target peripheral to gaze. After target presentation, they judged whether the target was located left or right to a continuously presented visual stimulus. Consistent with the results of Bock (1986), participants misperceived the auditory target in the opposite direction of any shift of their gaze. Similar results were obtained when the location of an auditory target should have been adjusted with respect to the median plane of the head (Lewald and Ehrenstein 1996b), or the location of an auditory or a visual stimulus indicated by adjusting a pointer (Lewald 1998). However, studies on localization of visual (Eggert et al. 2001) and tactile targets (Harrar and Harris 2009) relative to gaze found shifts toward gaze direction. It is important to note that in all these studies, gaze was maintained at a peripheral location until the end of target presentation. Thus, it is unclear whether targets for positional judgements were updated in a gaze-centered reference frame.

In the present study, we investigated whether positional judgements of remembered targets relative to the hand are represented in a gaze-centered frame of reference, as they are for targets for action shown so far. In particular, we assessed estimates of position of both remembered visual and proprioceptive targets as a function of gaze using an adaptive psychophysical procedure. Participants saw (visual target) or felt (proprioceptive target) the target and

judged whether their actual unseen hand position was to the left or right of the remembered target position. To test for eye-centered updating, we applied two conditions of gaze. In the static condition, participants maintained gaze on a peripheral fixation light, thus perceiving the target in their visual periphery. In the dynamic condition, participants first directed gaze toward the target before shifting gaze away from the target to a peripheral fixation light. Because participants first directed their gaze toward the target in the dynamic condition, any initial misestimate of its location due to retinal exaggeration or misestimation of eye position (cf., McGuire and Sabes 2009) would be minimal, and thus unaffected by any subsequent eye movements if coded in a gaze-independent reference frame, i.e., head- or body-centered, or allocentric frames. Therefore, perceptual errors in the dynamic condition should not vary with the final gaze direction as they do in the static condition. However, if the position judgements of the remembered visual or proprioceptive target relative to the hand vary with final gaze in the dynamic condition, in the same way as they do in the static condition, this would suggest that positional judgments between hand and target are also coded and updated relative to gaze.

Methods

Participants

Twenty-two healthy students (11 women; mean age 21; age range 19–26) participated in this study. They had normal or corrected-to-normal vision and were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield 1971). All participants provided informed consent according to the Declaration of Helsinki (2000) before the start of the experiment and received course credits or monetary compensation.

Apparatus

The experiment took place in a completely darkened room, where participants sat in front of a table on which an apparatus was mounted. We used two programmable servomotors controlled by LabVIEW (http://www.ni.com/labview/) for driving the handle of the apparatus. Movements had two degrees of freedom (x–y-plane) and occurred across a horizontal workspace. In the experiment, the handle followed straight movements with an acceleration of 0.4 m/s^2, reaching a maximum velocity of 0.2 m/s. The handle always started at a location 25 cm in front of the participant's chest, aligned to the body midline. The movement paths consisted of linear trajectories with a length of 16 cm. A light-emitting diode (LED) was

mounted on top of the handle and was turned on depending on the experimental condition. This way, the apparatus allowed us to present visual information of a predefined location in space by positioning the handle within the workspace and turning on the LED. In addition, proprioceptive information of space could be obtained by passively moving the handle, and thus the participant's right hand, to a predefined location within the workspace in the absence of visual feedback.

Gaze was manipulated by the use of an LED array located above the table. The LED array consisted of three fixation lights placed at 0°, 15° left and 15° right horizontal eccentricity with respect to the participant's cyclopean eye. Horizontal eye movements were recorded by the horizontal electrooculogram (HEOG) with a sampling rate of 500 Hz (cf., Khan et al. 2005b). Silver/silver chloride electrodes were placed next to the canthi of the left and right eye (bipolar recording) and at the left mastoid (ground). Impedances were kept below 5 kΩ.

Procedure

Participants judged the location of their dominant right hand relative to remembered visual or proprioceptive targets. In the visual paradigm, the target was an LED mounted on top of the handle. In the proprioceptive paradigm, participants gripped the handle with their right hand as it was passively moved to the target location. After the visual or proprioceptive target had been removed, either by dimming of the LED or the return of the hand to origin, respectively, the handle moved the participant's hand near the remembered target location. The participant then judged whether their current hand position was located left or right of the previous target. The target position was always in the same position, which was 16 cm straight-ahead (y-plane) of the starting position of the handle, and was thus aligned with the body midline and the central fixation light.

Estimation of discrimination acuity and variance of position judgements

In order to assess the participants' discrimination acuity of position judgements, we determined the perceptual bias and the variance using an adaptive thresholding procedure (for a review, see Treutwein 1995). To this end, we adjusted the location of the hand relative to the previous visual or proprioceptive targets using two randomly interwoven adaptive staircases (for trial $i \leq 2$, Robins and Monro 1951; for trial $i > 2$, Kesten 1958). The staircases began by moving the hand 30° to the left or right with respect to the previous target location on the midline (0°), so that the hand would be positioned 8.28 cm left or right

of the target, respectively. These start values were clearly classifiable for all participants. According to the applied adaptive staircase algorithm, the comparison position converged toward the target position with each correct response and diverged with each incorrect response. The initial step size was set at 16°. If participants responded correctly on the first trial, the angular trajectory for the next trial was reduced to 22° (initial staircase divided by 2, see Robins and Monro 1951), but if they responded incorrect, the initial angle (30°) was re-presented. From the third trial, the angular trajectory of the next trial was determined by both the correctness of the response and response shifts. Each time the participant altered the response from left to right, or right to left along a particular staircase, the step size was decreased ensuring that participants were tested more frequently on trajectories close to their sensitivity threshold. Each staircase consisted of 35 steps, resulting in a total of 70 trials. If participants responded consistently, the two staircases converged toward the participant's position bias, i.e., the point where participants perceived their hand position (comparison position) as being in the same location as the remembered target.

To investigate whether discrimination acuity and variance of position judgements between hand and target vary as a function of gaze, we varied gaze to the left or right of the remembered target and final hand position. In the static conditions, gaze was constantly directed to the left (static-left), the right (static-right) or the center fixation light (static-center) of either the visual or proprioceptive target located at center (0°). So, while the target was presented peripherally during the static-left and static-right conditions, it was aligned with fixation (and the visual axis) for the static-center condition. This static-center condition served as a control to assess the subject's general accuracy in judging the relative position of the target and hand. In the dynamic conditions, gaze was first directed toward either the visual or proprioceptive target, but was shifted to the left (dynamic-left) or to the right (dynamic-right) fixation light after the target was removed, but prior to the comparison stimulus (hand position relative to the target) appearing. We tested the effect of gaze direction on position judgements for both remembered visual and proprioceptive targets across the static (Fig. 1a, c) and dynamic (Fig. 1b, d) conditions.

Position judgement of remembered visual targets

The static condition for the visual target proceeded in the following way (Fig. 1a). At the beginning of each trial, one of the two peripheral fixation lights (15° left or 15° right) was turned on for 3,000 ms and was followed by a high pitched tone (duration: 500 ms) signaling the start of

the trial (Fig. 1a, i). While participants fixated on the peripheral fixation light, the handle moved from the starting position to the target position (duration: 1,500 ms) where the LED of the handle radiated light for 1,000 ms (visual target) (Fig. 1a, ii). Thus, they saw the visual target peripheral to gaze. After the visual target LED was turned off, the handle returned to the starting position (duration: 1,500 ms) and the fixation light was extinguished (Fig. 1a, iii). Participants were instructed to maintain fixation on the peripheral fixation light during the time it was illuminated, and to keep gaze in this direction after the LED was extinguished. A low pitched tone (500 ms) prompted the participants to grip the handle with their right hand. According to the adaptive staircase algorithm, the participants' hand was passively guided to the comparison position (in complete darkness) where they had to indicate with a left hand key press whether this position was left or right of the remembered visual target, while maintaining gaze in the peripheral direction (Fig. 1a, iv). After the response was given, participants placed their right hand back on the resting position located 15 cm in front of their chest midline. Finally, the handle returned to the starting point (duration: 1,500 ms) and the next trial was initiated. The static-center control condition proceeded in the same way, but participants constantly fixated the central fixation and thus perceived the target on their visual axis.

In contrast to the static condition, direction of gaze was varied within trial in the dynamic condition. In the dynamic condition for the visual target, the central fixation light was turned on for 3,000 ms and a high pitched tone (duration: 500 ms) was presented at the start of the trial (Fig. 1b, i). Participants maintained fixation on the central fixation light until it was extinguished. After the presentation of the tone, the handle moved to the target position (duration: 1,500 ms) where the LED of the handle was turned on for 1,000 ms (visual target) (Fig. 1b, ii). Thus, participants saw the target along their visual axis. At the moment that the visual target LED was extinguished, the central fixation light was turned off and one of the peripheral fixation lights (15° left or 15° right) was turned on for 1,500 ms (Fig. 1b, iii). Participants were required to saccade toward the peripheral fixation light and to keep fixation on this location even after the fixation light was extinguished. After the handle was returned to the starting position (duration: 1,500 ms), a low pitched tone (500 ms) prompted the participants to grip the handle with their right hand and to move it passively to the comparison position (Fig. 1b, iv). At the end of the trial, participants decided whether this position was left or right of the remembered visual target before the handle returned to the start position.
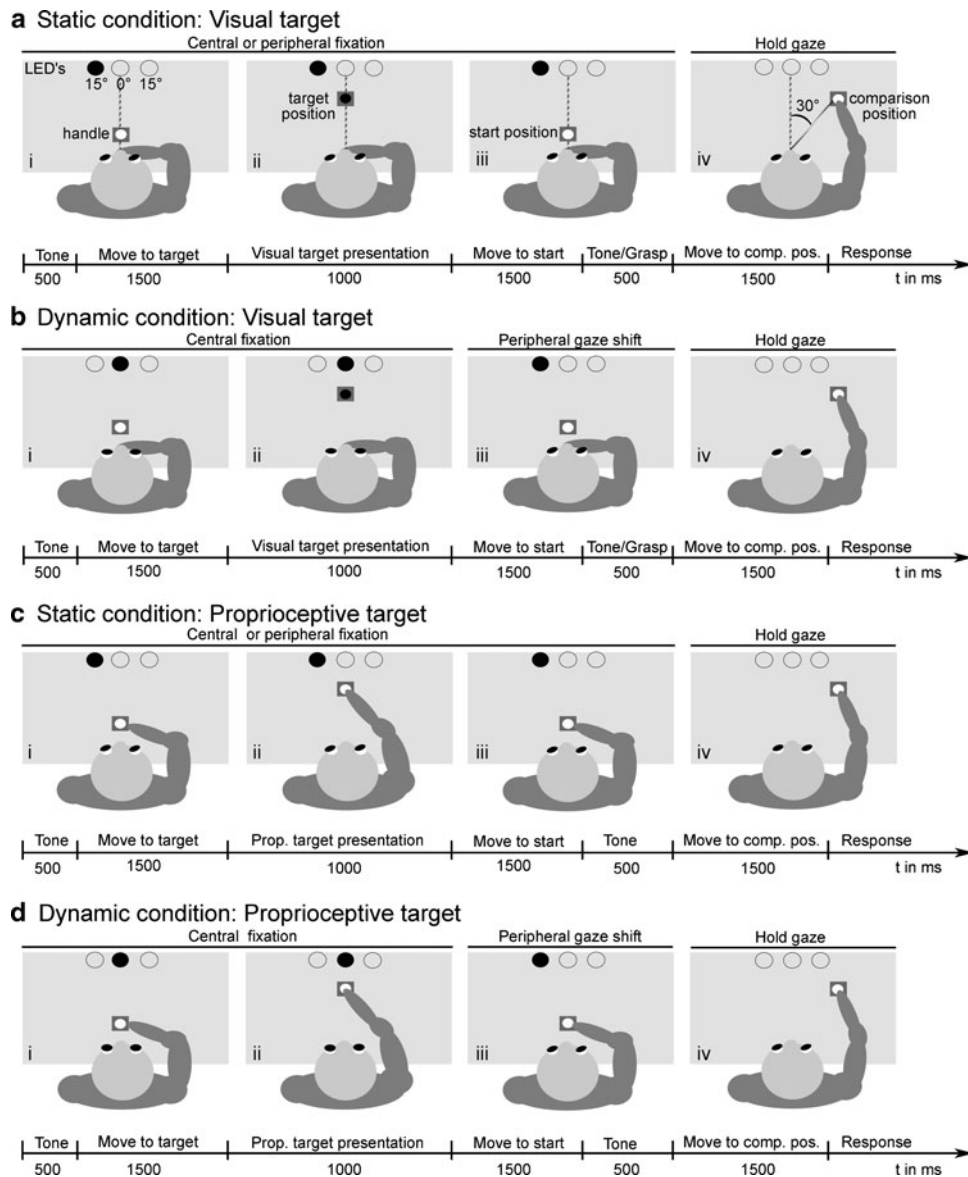
a Static condition: Visual target

b Dynamic condition: Visual target

c Static condition: Proprioceptive target

d Dynamic condition: Proprioceptive target

Fig. 1 Experimental protocol and timeline. **a**, **b** In the visual paradigm, the target position was indicated by an LED placed on the handle (*gray square*). Participants performed position judgements indicating whether the remembered target was *left* or *right* of actual hand position (comparison position). During the static condition (**a**), participants constantly fixated on one of three fixation lights (*circles*), in this example, the leftward LED (*filled circle*). During the dynamic condition (**b**), they first fixated the central fixation light, which was aligned with the visible target, as indicated by the *black circles* in the 2nd panel, then performed a saccade to the left or right fixation light (to the *left* in this example) after the target LED was turned off. Participants maintained eccentric fixation at this location until delivering the response. **c**, **d** In the proprioceptive paradigm, the participants' arm was passively guided to the target position and the unseen hand, which gripped the handle, served as the proprioceptive target. As in the visual paradigm, they judged whether the remembered target was left or right of the actual hand position. Under each row, the timing for each part of the task is shown in milliseconds. The timing and task for the static (**a**, **c**) and dynamic (**b**, **d**) conditions were identical between the visual and proprioceptive target modalities

Position judgement of remembered proprioceptive targets

For the proprioceptive target, participants permanently gripped the handle (Fig. 1c, d, i). The start of the trial was signaled by a high pitched tone (500 ms) and the participant's arm was passively guided to the target position (duration: 1,500 ms) where the handle stopped for 1,000 ms providing positional information by muscles, joints and tendons (proprioceptive target) (Fig. 1c, d, ii). In the static condition (Fig. 1c), gaze was directed either left or right relative to target during the entire presentation of the proprioceptive target and throughout the remainder of the trial. In the dynamic condition (Fig. 1d), gaze was directed toward center, and so toward the unseen

proprioceptive target (Fig. 1d, ii); and, only after the handle was returned to the start position did gaze shift to the periphery (Fig. 1d, iii). Once returned to the start position (Fig. 1c, d, iii), the handle, along with the hand, then moved to the comparison position after the low pitched tone (500 ms) was presented (Fig. 1c, d, iv) for both static and dynamic conditions. Finally, participants decided whether this position was left or right of the remembered proprioceptive target.

Like with the visual position judgements, participants performed a static-center control condition, where they constantly fixated on the central fixation light that was aligned with the proprioceptive target.

For both visual and proprioceptive targets, gaze either remained peripheral for the entire trial, including the presentation of the target (static condition, Fig. 1a, c), or gaze was directed toward the presented target before shifting to the periphery (dynamic conditions, Fig. 1b, d). For all four conditions, the comparison stimulus, the hand position, was presented and the relative judgments made when gaze was peripheral (Fig. 1a–d, iv).

The effect of gaze direction on positional judgements for both remembered visual and proprioceptive targets was tested on separate days. For each target modality,

participants performed three static conditions (static-left, static-right, static-center) and two dynamic conditions (dynamic-left, dynamic-right) in counterbalanced order. Each of these five conditions consisted of 70 trials. The experiment took about 1 h per day.

Data analysis

Positional bias and variance

Using an adaptive staircase algorithm (left panels in Fig. 2), we assessed relative positional biases and variance between the remembered target and the hand, for each of the two gaze directions in the static and dynamic conditions and for both the remembered visual and proprioceptive targets. In order to obtain these estimates, the 70 forced-choice responses were fitted to a standard psychometric function (right panels in Fig. 2) for each condition. The 50% point of the psychometric function is the participant's position bias, i.e., the point where the participant perceived the comparison (hand) position as being equally likely to be to the left or right of the remembered target. Thus, the position bias represents the location where the participant perceived the remembered target. In the example of
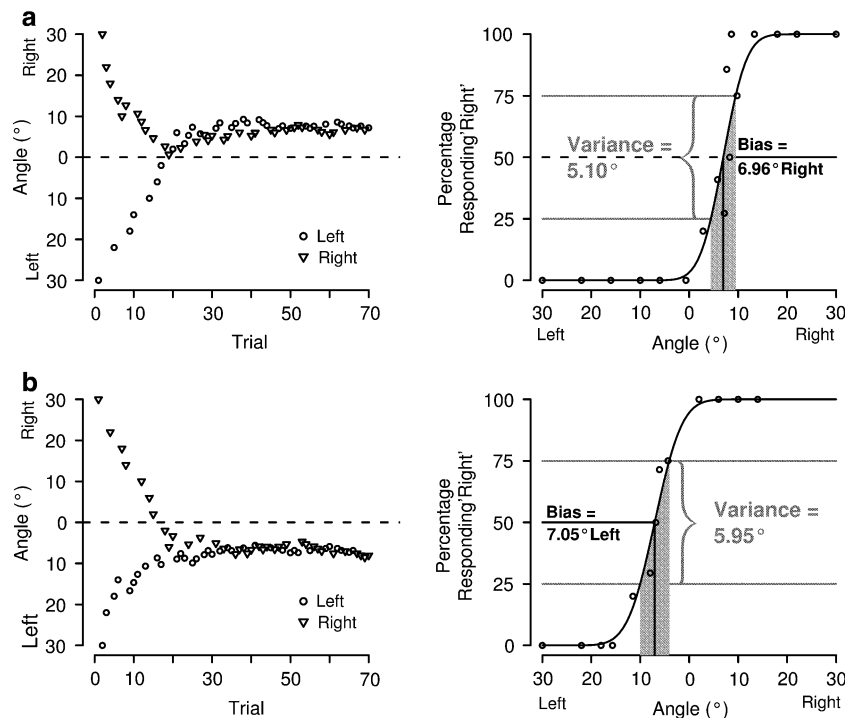

Fig. 2 Data of one representative participant for the dynamic condition during leftward (**a**) and rightward (**b**) gaze shifts for the proprioceptive target. *Left* A sequence of 35 trials from the leftward staircase (*circles*) and another 35 from the rightward staircase (*inverted triangles*) for a total of 70 trials, which were randomly positioned. Both staircases started with placing the comparison hand 30° from the remembered target position (0°). *Right* The participant's

responses were fitted to a standard psychometric function. The bias is defined as the point of 50% of the psychometric function, and the variance as the difference between the 25 and 75% of the psychometric function (*gray-shaded area*). The results show that the participant misperceived the target position to the *right* if a gaze shift occurred to the left (**a**), and misperceived the target position to the *left* if a gaze shift occurred to the right (**b**)

Fig. 2a, the bias of the dynamic condition (visual target) was 6.96° when gaze was shifted 15° left, i.e., the participant perceived the target as being 1.94 cm to the right of its actual location, and consequently would classify the actual target location as 'left' more than 50% of the time. When gaze was shifted 15° to the right (Fig. 2b), the same participant produced a similar bias but in the opposite direction (7.05° left). Here, the target was perceived 1.97 cm to the left of its actual location.

We corrected the biases of the static and dynamic conditions for the participant's general accuracy of positional judgements, as assessed by the control condition (static-center condition), by subtracting the bias of the static-center condition from each bias of the remaining conditions for both the visual target and the proprioceptive target.

To identify the variance or uncertainty range of the positional judgements, we calculated the difference between the upper and the lower difference threshold. Thus, the variance is inversely related to the steepness of the psychometric function, i.e., the steeper the psychometric function, the less variable the participant's judgements. In the example in Fig. 2a, the variance of the dynamic-left condition was 5.10°, so that hand path had to change on average 1.42 cm to the right of the bias before the participant judged with a probability of 75% that the comparison position was right of the target position. Both measures of position bias and variance indicate the participant's discrimination acuity of positional judgements.

Comparison of static and dynamic gaze conditions

To test whether gaze direction and gaze shifts affected relative position judgments for both remembered visual and proprioceptive targets, we conducted a repeated measures ANOVA with the factors gaze (left, right), condition (static, dynamic) and target modality (visual, proprioceptive) for the corrected position bias and variance. To assess whether the pattern of relative position biases for either the visual or proprioceptive targets were similar or the dynamic and static conditions were similar, we further fitted a regression for biases of each target modality.

Eye movements

Eye movements were recorded by HEOG and processed offline by means of VisionAnalyzer Software (http://www.brainproducts.com). First, HEOG signals were corrected for DC drifts and low-pass filtered with a cut-off frequency of 50 Hz. Second, time windows of interest were segmented. For the static condition, we ensured that participants constantly fixated the LED from its start until the subject's response. Therefore, the time window of interest was set from turning on the LED at trial start (with a

400 ms delay to direct gaze to the LED) until 8,000 ms after. For the dynamic condition, we controlled that participants performed a saccade to the left or right LED after target presentation, and hold fixation until after responding. To this end, the time window of interest was set from 400 ms before until 5,000 ms after the switch of the fixation light prompted gaze shift. Third, the segmented signals were baseline corrected using the first 400 ms of each HEOG segments. In the static gaze condition, no HEOG signal change is expected because participants hold fixation on the LED. In the dynamic condition, saccadic eye movements to the left or right should occur that are reflected by positive (downward deflection) or negative voltage change (upward deflection), respectively.

We carefully inspected each HEOG segment of each experimental condition in order to guarantee that participants followed the task instruction. We detected no trial in any of our participants where eye movements deviated from the correspondent fixation schedule. For illustration purposes, we averaged the HEOG signals across trials and participants per gaze condition. Averaged eye movements recorded during the static and dynamic gaze conditions are depicted in Fig. 3.

Results

We investigated the effect of gaze on positional judgements of remembered visual and proprioceptive targets. Figure 4a–b illustrates the results of the corrected position bias for visual and proprioceptive targets in the static and dynamic conditions. For both the visual (Fig. 4a) and proprioceptive targets (Fig. 4b), the biases varied with the direction of gaze so that participants mislocalized the remembered target relative to the hand as being more to the right when looking to the left (black circle), and as being more to the left when looking to the right (gray circle). The biases significantly differed across the gaze directions for both visual targets ($t_{(21)} = 6.24$; $P < 0.001$) and proprioceptive targets ($t_{(21)} = 5.27$; $P < 0.001$). More interestingly, we found this pattern of gaze-dependent misperceptions even when participants first look toward the target before shifting their gaze peripheral in the dynamic condition (gaze shift left: black cross; gaze shift right: gray cross); this effect of gaze was significant for both visual targets ($t_{(21)} = 7.65$; $P < 0.001$) and proprioceptive targets ($t_{(21)} = 9.05$; $P < 0.001$).

Overall, these positional judgements significantly varied as a function of gaze, irrespective of condition and target modality ($F_{(1,21)} = 102.05$; $P < 0.001$). This was supported by post hoc t-tests showing significant deviations from zero for each condition (for all t-tests, $P < 0.05$). The effect of gaze varied as a function of condition, such that
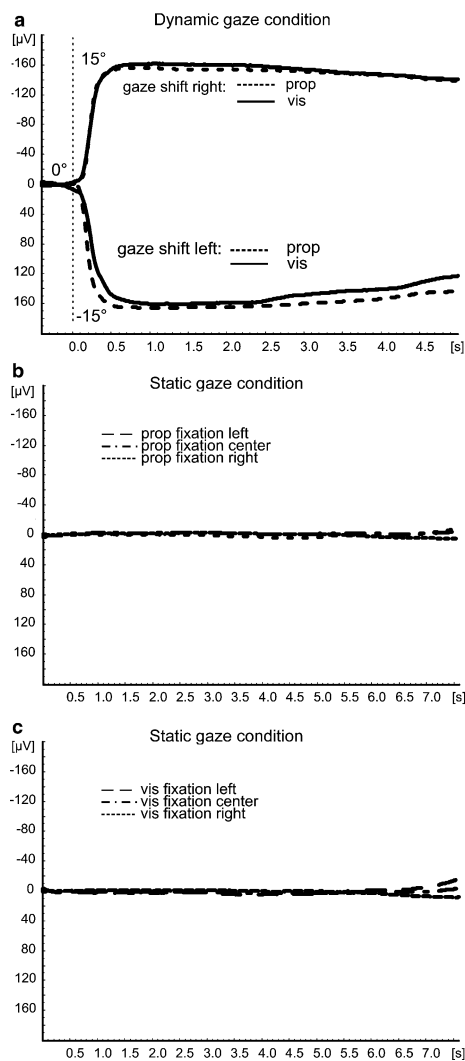
Fig. 3 Horizontal electrooculogram (HEOG) averaged across participants. **a** During the dynamic gaze conditions, participants performed a saccade from the central fixation light (0°) to the peripheral fixation light, positioned 15° *left* or *right*, following target presentation (at 0.0 s). After the fixation light extinguished (at 2.0 s), participants were instructed to maintain gaze toward this location until the response was given. Negative values (plotted upward) indicate a rightward gaze shift while positive values (plotted downward) indicate a leftward gaze shift. For both the proprioceptive and the visual targets, participants correctly followed the fixation schedule as reflected in the clear HEOG signal changes. **b-c** In the static gaze conditions, participants were instructed to keep their gaze attached to one of the three fixation lights until responding. As a consequence, no signal deflection was expected. Consistent with the fixation schedule, the HEOG signals recorded during the proprioceptive (**b**) and the visual paradigm (**c**) showed a flat line indicating no gaze shift

Fig. 4 The effect of gaze on position judgements for remembered visual (**a**) and proprioceptive (**b**) targets. *Gray circles* indicate the mean positional biases when participants maintain fixation 15° right, while *black circles* are those when they fixated 15° left in the static condition. *Gray* crosses mark the mean positional biases when participants shifted their gaze 15° right, while *black* crosses are those biases produced after participants shifted gaze 15° left in the dynamic condition. The open diamond depicts target location. (**c**) The mean positional bias and the corresponding variance are shown for the proprioceptive (*upper rows*) and visual (*lower rows*) targets in the static and dynamic conditions

this effect was even larger for the dynamic (Fig. 4a, b, crosses) than the static condition (circles) ($F_{(1,21)} = 24.53$; $P < 0.001$; gaze left: $t_{(21)} = 3.73$; $P < 0.001$; gaze right: $t_{(21)} = -4.04$; $P < 0.001$).

In general, positional judgements did not vary with target modality ($F_{(1,21)} = 0.04$; $P = 0.84$), but the gaze-dependent
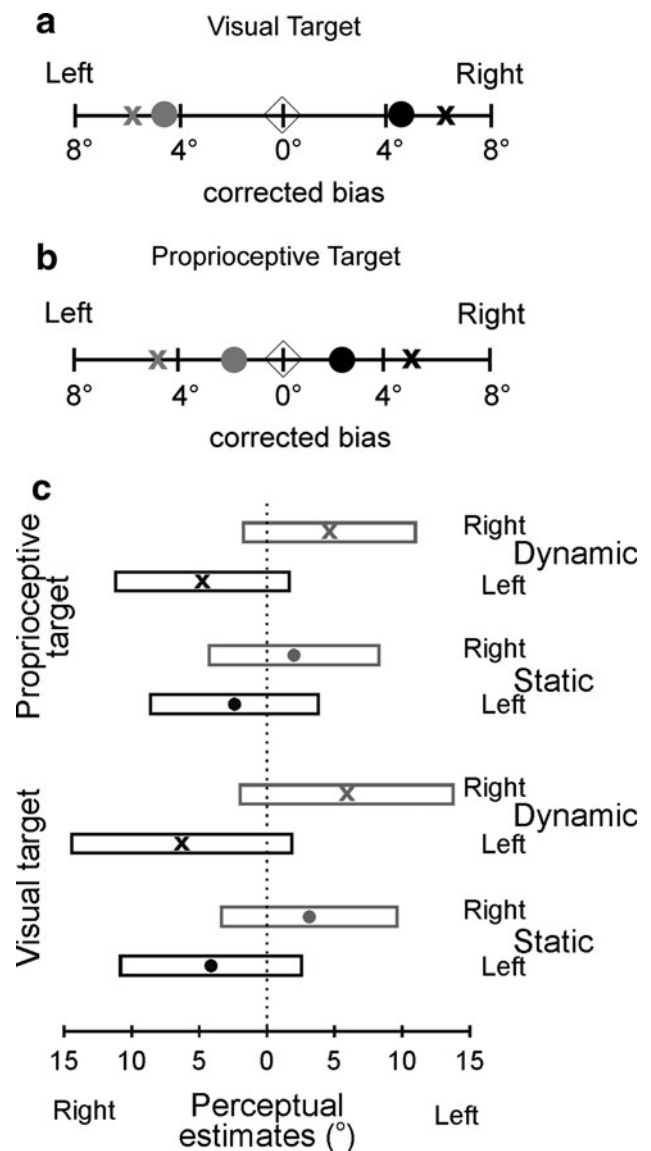
effect did interact with target modality ($F_{(1,21)} = 5.64$; $P < 0.05$), such that gaze modulation appears to be slightly larger for the visual target (Fig. 4a) than the proprioceptive target (Fig. 4b). However, this was not confirmed by post hoc *t*-tests.

The variance of the positional biases, as illustrated by the boxes in Fig. 4c, did not significantly differ as a

Table 1 Means and standard deviations (SD) of the bias, corrected bias, and variance of positional judgments of the five gaze conditions for the visual and proprioceptive targets in degrees

Gaze condition	Visual target						Proprioceptive target					
	Bias		Corrected bias		Variance		Bias		Corrected bias		Variance	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Static-center	−4.20	5.04	–	–	−7.90	5.22	−3.84	3.79	–	–	−7.05	4.38
Static-left	−0.06	4.60	4.13	5.03	−6.67	3.98	−1.45	3.00	2.39	4.20	−6.22	4.14
Static-right	−7.33	5.53	−3.14	4.89	−6.46	2.81	−5.84	3.47	−2.00	1.98	−6.27	3.66
Dynamic-left	2.07	4.07	6.30	5.37	−8.08	5.01	0.92	4.44	4.76	3.54	−6.44	3.16
Dynamic-right	−10.11	6.20	−5.91	5.49	−7.82	4.00	−8.46	4.23	−4.62	3.41	−6.37	3.98

function of gaze, condition or target modality. This result indicates that positional judgements varied comparably across gaze direction, for both the static and dynamic conditions, and for both visual and proprioceptive target modality. Table 1 provides a summary of the means and standard deviations of the corrected position bias and variance.

In the next step of the analysis, we tested first whether the positional judgements were similar between the static and dynamic conditions, and second, whether the positional judgements were similar between the visual and proprioceptive targets. If the pattern of perceptual estimates for judging the relative position in the dynamic condition were similar to those of the static condition, this would suggest that relative position of the target to the hand is coded and updated in a gaze-centered reference frame (slope of 1). If the perceptual estimates were not similar, the slope would be close to 0, suggesting that relative target position is coded in a reference frame independent of gaze, such as a head or body, or integrated, or even allocentric, reference frame. Figure 5 shows the individual positional biases of the dynamic condition as a function of individual positional biases of the static condition for each of the target modalities. Open circles indicate 15° leftward gaze and black circles 15° rightward gaze. The regression fit to the mean across-subject bias (solid line) revealed for the visual target (Fig. 5a) a slope of 1.06 and a correlation of 0.80 ($P < 0.001$), and for the proprioceptive target (Fig. 5b) a slope of 0.97 and a correlation of 0.65 ($P < 0.001$). The slopes for both the visual and proprioceptive targets were close to the identity with an intercept of 0 and slope of 1 (Fig. 5, dashed line). This clearly supports the hypothesis that perceptual judgements are coded and updated in a gaze-centered frame of reference.

Discussion

The present results demonstrate that participants code and update the location of targets in a gaze-centered reference

frame in order to perform positional judgements. We found gaze-centered updating for remembered visual and remembered proprioceptive targets. Together with previous findings on spatial updating for action control, our results suggest that the brain represents spatial locations in eye-centered coordinates for judgements about space as well.

Research has consistently shown that participants make the same pattern of pointing errors when pointing to a remembered target seen in their retinal periphery as they do when they first foveate a briefly flashed target but then shift their gaze so that the memory trace of the target would fall on the same retinal periphery (Henriques et al. 1998; Medendorp and Crawford 2002; Khan et al. 2005a, b). These pointing errors, which vary systematically with the distance between gaze and target site, cannot be explained by a head- or body-centered reference frame, or even an integrated frame; foveating the target should immediately lead to a reliable and stable representation of the target in these reference frames that would not be affected by any subsequent eye movement following target offset. Thus, gaze-centered updating seems to be an important and viable way for maintaining spatial constancy for the control of action. Our current results demonstrate that gaze-centered updating may also be responsible for maintaining spatial constancy for judging or comparing the relative position between objects, specifically that of the target and the unseen hand. In our study, we found a similar pattern of errors when participants performed positional judgements, again, both when the targets were viewed in the periphery, and more importantly, when the remembered target was remapped to the periphery when gaze was shifted. As with pointing movements, if the remembered targets had been transformed immediately into a head- or body-centered frame (Mays and Sparkes 1980; McGuire and Sabes 2009), then any subsequent gaze shift or other change of gaze position should not affect the subsequent position judgement. The mean perceptual biases we found for remembered visual targets in the dynamic (6.30° right when gaze was shifted left, and 5.91° left when gaze was shifted right) and static (4.13° right when gaze was maintained left and
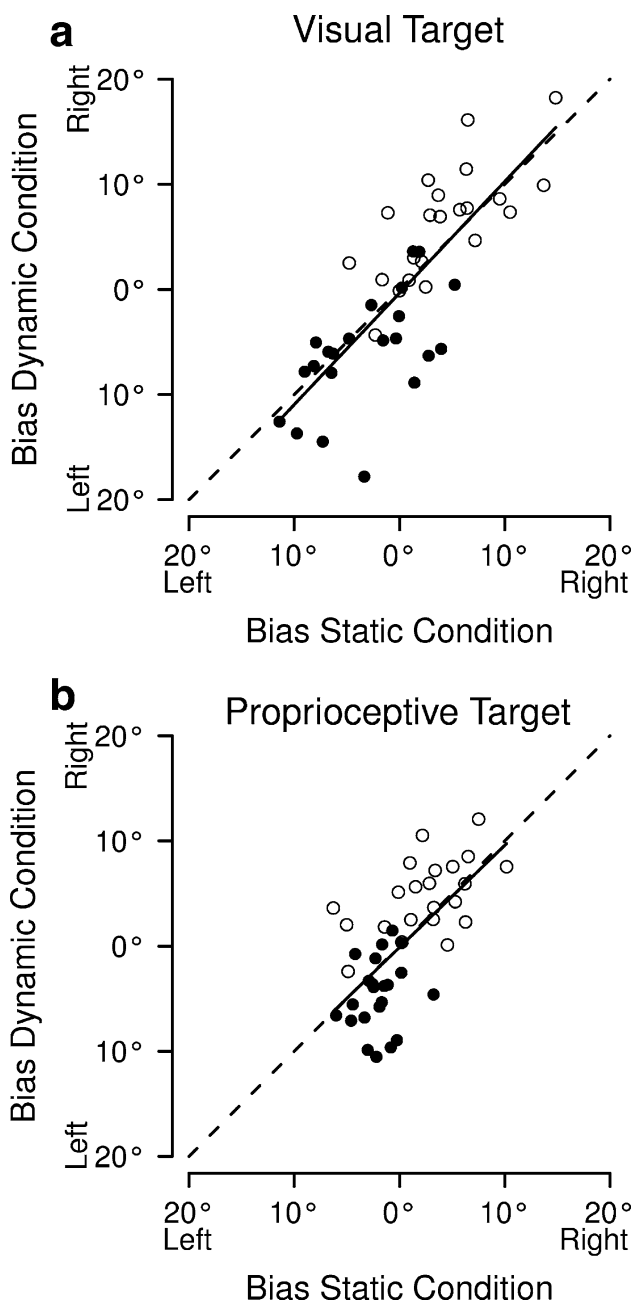
Fig. 5 Bias of position judgements of each subject in the dynamic condition are plotted as a function of those in the static condition for remembered visual (**a**) and proprioceptive (**b**) targets. *Open* and *closed circles* indicate relative position biases for 15° leftward gaze and 15° rightward gaze, respectively. The regression (*solid*) line fitted to these biases was close to the identity (*dashed*) line

3.14° left when gaze was maintained right) conditions were comparable with the pointing and reaching errors in previous studies, ranging from 2° to 7° right, when gaze was directed or shifted to the left, and 1° to 5° left when gaze was directed or shifted to the right (Henriques et al. 1998; Medendorp and Crawford 2002; Sorrento and Henriques 2008; Thompson and Henriques 2008). The present results

suggest that visuospatial memory is updated in a gaze-centered map by taking the eye movement signal into account. This map is then used by the brain to make relative judgements of space.

Position judgements of remembered proprioceptive targets varied as a function of gaze as well. Similar results have been shown for pointing (Pouget et al. 2002; McGuire and Sabes 2009) and reaching (Blangero et al. 2005) to proprioceptive targets. However, these studies only tested for the effect of gaze on online targets, i.e., participants were constantly provided with positional information of the proprioceptive target while acting to it. As a consequence, there was no way to test whether these targets were updated as a function of gaze since updating or remapping target positions requires that the fixated target vanishes prior to deviating gaze. In the experiment by Blangero et al. (2005), participants reached with the right hand to the location of their unseen left index finger while maintaining gaze peripheral to the target. They observed reaching errors of about 2° to 3° opposite to the direction of gaze, which are comparable to the values reported here (static eyes left, 2.39° right; static eyes right, 2.00° left). Pouget et al. (2002), instructed participants to point to the location of their unseen right foot while fixating a peripheral LED. The pointing errors were less than 1° in the opposite direction of gaze, and were significantly smaller than pointing errors obtained for the visual target. In the study by McGuire and Sabes (2009), participants pointed to their unseen left hand (proprioceptive target) and produced systematic errors that were of similar magnitude. But, unlike in the previous studies, participants systematically underestimated the location of proprioceptive targets relative to gaze, while systematically overestimating remembered visual targets and visual-proprioceptive targets. That is, the patterns of errors as a function of gaze relative to target for proprioceptive targets were opposite to that produced to remembered visual targets in their own study, as well as all other studies for visual and proprioceptive targets. In our current study, gaze-dependent perceptual biases also varied with target modality, but in the same direction relative to gaze (overestimation), thereby indicating the difference between target modalities was due to a slightly larger mislocalization in the opposite direction of gaze for visual compared to proprioceptive targets.

It is not clear why the angular difference between gaze and targets would lead to different sizes of perceptual biases (or motor errors) for the different target modalities, since it is not known what exactly produces this systematic mislocalization of targets relative to gaze. Bock (1986) originally described this systematic overestimation of reaches relative to gaze in a static condition as a magnification of the retinal distance of the target relative to the fovea. Results by Henriques and Crawford (2002) suggest

this retinal magnification effect may have arisen because of miscalibrations in eye-head coupling when pointing to distant targets with deviated gaze. Recently, McGuire and Sabes (2009) suggested that this systematic effect of gaze relative to target on reaching errors may be due to misestimates of eye position (gaze direction is misjudged as being closer to the visual target than it really is). While this is possible, such a misestimate of eye position cannot explain similar reaching errors produced when the target is foveated, and then its memory trace is remapped following an intervening eye movement (Henriques et al. 1998; Khan et al. 2005a, b; Sorrento and Henriques 2008; Thompson and Henriques 2008), or even a change in eye position following translation of the body (Van Pelt and Medendorp 2007). Nor could a misestimate of eye position explain how they found opposite systematic effects for visual and proprioceptive targets. Whatever the reason for this systematic mislocalization of target as a function of the distance of the target relative to gaze, the fact is that the pattern is similar both when the target is presented in the periphery and when it is remapped into the periphery following a gaze shift. This suggests that the location of both proprioceptive and visual targets is coded and updated in a gaze-centered reference frame. It is possible that the other reference frames and sensorimotor transformations used to represent and convert these targets for spatial localization and action may also subsequently influence this initial error, and may do so differently for different target modalities.

Since we tested for remembered proprioceptive targets, we were able to investigate spatial updating for proprioceptive positions as well. Consistent with the results of the visual target, we found that participants mislocalized the proprioceptive target relative to their unseen hand position in the opposite direction to peripherally maintained gaze (static condition) as well as to peripheral shifts of gaze (dynamic condition). The present results indicate that targets are updated across eye movements irrespective of target modality. Since there was no visual input about hand position, proprioceptive information seemed to be recomputed in eye-centered coordinates using eye position signals in order to perform position judgements. In accordance with our findings, there is recent evidence of a similar mechanism for updating remembered proprioceptive targets for upcoming actions (Jones and Henriques submitted).

Participants were equally precise when they judged the position of visual and proprioceptive targets relative to the hand when the target was presented in the visual periphery (static condition) or the target was remapped into visual periphery (dynamic condition). This is in line with our recent findings showing similar precision for angle judgements based on a dot of light moving along trajectories (visual) and passive hand movements (proprioceptive)

following the same trajectories (Reuschel et al. 2010), and with studies on reaching that found no difference in the variability of errors in movement distance toward visual and proprioceptive targets (Sarlegna and Sainburg 2007). Our results do not confirm the results of Van Beers et al. (1998), which indicate that proprioceptive-guided reaches are more precise in radial (depth) than azimuth (horizontal) directions, while the reverse is true for visually guided reaches, plus the variances for these reaches were overall smaller. In the present task, the comparison position of the hand only varied in azimuth direction relative to the target, yet we did not find a smaller variance for judging relative positions of visual targets as compared to proprioceptive targets. This discrepancy could be due to differences in the task, reaching versus relative spatial judgment, as well as the fact that both types of targets were continuously available in the van Beers study, while they were only briefly presented in our study. Furthermore, there is some evidence that visual spatial memory decays quicker than proprioceptive spatial memory (Chieffi and Allport 1997; Chieffi et al. 1999; Desmurget et al. 2000; Goodale et al. 2004), so it is possible that this may explain the equivalence we find in precision localization between the two target types.

Other studies have demonstrated that the direction of gaze also influences perceptual judgements of spatial locations of visual and tactile targets, with some studies finding that spatial positions are mislocalized toward the direction of gaze (Eggert et al. 2001; Harrar and Harris 2009). It is important to note that these studies were performed with gaze maintained peripheral to the target, i.e., corresponding to the static condition of the present study (and so cannot be assessed whether these perceptual representations are updated in eye-centered coordinates). Harrar and Harris (2009) asked participants to report the position of touches presented between the elbow and the wrist while maintaining eye positions at various eccentricities. Position judgements were given verbally using a ruler, which was placed next to the arm and was illuminated after each touch. Eggert et al. (2001) presented a brief visual target followed by a visual test flash (comparison position) in the retinal periphery, while participants fixated the center of the screen. Participants then reported whether the test flash had appeared left or right of the target. Both studies required to compare the target with an external reference (location on a ruler or another visual stimulus). In the present study, however, the participants' arm was passively guided to the comparison position and they were then asked whether the target had appeared left or right of the unseen position of their dominant hand. Coding the relative location between the hand and the target is the exact kind of information that is needed in order to produce a goal-directed movement. Therefore, our

task seems to resemble a passive version of a goal-directed action task, like "passive reaching", more so than a purely perceptual task, where the target has to be compared with an external stimulus. Similar to reaching tasks, here, participants received proprioceptive feedback about the movement of the arm to the comparison position as well the comparison position itself. This could explain why we found a misestimation of the target in the opposite direction of gaze like previous studies on pointing and reaching (e.g., Henriques et al. 1998).

Coding and updating the location of targets in a gaze-centered reference frame as previously shown for goal-directed actions, and as shown here for relative position judgements, is likely being implemented in the posterior parietal cortex (PPC), the nodal point of the dorsal visual stream. Electrophysiological studies in monkeys (Duhamel et al. 1992; Colby et al. 1995), and brain imaging studies in humans (for a review see, Culham and Valyear 2006), found areas along the dorsal visual stream that code spatial locations in eye-centered coordinates. In particular, LIP in monkeys and an area in the posterior superior parietal lobule in humans have been associated with coding saccade direction (Koyama et al. 2004; Sereno et al. 2001), and spatial updating of saccade targets when gaze changed (for evidence in monkeys, see Zhang and Barash 2004; for evidence in humans see, Medendorp et al. 2003, 2005; Merriam et al. 2003). Spatial coding of reach targets is supposed to be implemented in the parietal reach region (PRR) located in the dorsal aspect of the PPC superior to area LIP (Cohen and Andersen 2002). Monkey data suggest that remembered reach targets are coded with respect to both the eye and the hand, with both locations represented in eye-centered coordinates (Batista et al. 1999; Buneo et al. 2002). At least two reach-related areas have been identified in humans, i.e., the human PRR situated in the anterior part of the PPC, medial to the intraparietal sulcus (medial IPS), and the superior parieto-occipital cortex (SPOC) (for a review, see Culham et al. 2007). Activation in both human PRR (Medendorp et al. 2003) and SPOC (Culham et al. 2007) for visual reach targets have been shown to be modulated by gaze distance, thus providing information about target location with respect to gaze for action. According to the findings of Prado et al. (2005), these two areas have different functional properties: the human PRR (medial IPS) responds to reaching movements regardless where the eyes are directed; and a subregion of SPOC, namely the parietal-occipital junction (POJ) responds during reaching movements to peripheral but not foveated targets. Since the PPC does not only process visual but also proprioceptive information of space (Fiehler et al. 2008), it seems to be suitable for gaze-dependent updating of both visual and proprioceptive targets. In line with this

assumption, activation in area POJ has been found when individuals reach to proprioceptively defined target locations (body parts) without visual feedback (Pellijeff et al. 2006). This suggests that area POJ may not only participate in the dynamic representation of the visual world but also of the body schema.

Results of patients with optic ataxia further support an eye-centered representation of visual and proprioceptive targets in area POJ. Blangero et al. (2010) showed in both unilateral left- and right-brain damaged patients that reaching movements to visual targets in the contralesional field produce systematic errors directed toward the eye fixation position, the so-called field-effect. Consistent with these findings, gaze-dependent reach errors has been also demonstrated for proprioceptively defined targets (index fingertip of the ataxic hand) in a patient with right-parietal optic ataxia (Blangero et al. 2007). Corroborative results have been reported of patient JJ with optic ataxia who suffered from a bilateral posterior parietal lesion (Jackson et al. 2009). He exhibited a clear bias toward the point of fixation when reaching to extra-foveal visual targets. Similar results were found when he reached to extra-foveal proprioceptive targets (index fingertip) with and without vision.

To conclude, position judgements of visual and proprioceptive targets relative to the unseen hand are coded in a gaze-centered frame of reference. This extends previous findings on targets for action. Our results imply that there may be a general mechanism for updating space as a function of each eye movement, and thus maintaining spatial constancy for both action and space perception when positions are coded relative to the hand.

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