

Memory for proprioceptive and multisensory targets is partially coded relative to gaze

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ABSTRACT

We examined the effect of gaze direction relative to target location on reach endpoint errors made to proprioceptive and multisensory targets. We also explored if and how visual and proprioceptive information about target location are integrated to guide reaches. Participants reached to their unseen left hand in one of three target locations (left of body midline, body midline, or right of body midline), while it remained at a target site (online), or after it was removed from this location (remembered), and also after the target hand had been briefly lit before reaching (multisensory target). The target hand was guided to a target location using a robot-generated path. Reaches were made with the right hand in complete darkness, while gaze was varied in one of four eccentric directions. Horizontal reach errors systematically varied relative to gaze for all target modalities; not only for visually remembered and online proprioceptive targets as has been found in previous studies, but for the first time, also for remembered proprioceptive targets and proprioceptive targets that were briefly visible. These results suggest that the brain represents the locations of online and remembered proprioceptive reach targets, as well as visual–proprioceptive reach targets relative to gaze, along with other motor-related representations. Our results, however, do not suggest that visual and proprioceptive information are optimally integrated when coding the location of multisensory reach targets in this paradigm.

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The central nervous system (CNS) obtains sensory information about reach targets in our environment from several modalities (e.g. vision and proprioception). To guide a saccade or reach to an object, these sources of information may be integrated in such a way that a more accurate or precise estimate of target location is obtained than estimates derived from either single sensory representation (e.g. optimal integration; van Beers, Baraduc, & Wolpert, 2002). Neurophysiological research in macaque (e.g. Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Batista et al., 2007; Buneo, Jarvis, Batista, & Andersen, 2002; Caminiti, Johnson, Galli, Ferraina, & Benod, 1991; Lacquaniti, Guigon, Bianchi, Ferraina, & Caminiti, 1995) and neuroimaging studies on humans (e.g. Wu & Hatsopoulos, 2006, 2007) have suggested that the CNS uses multiple reference frames, simultaneously and/or serially, to encode target location (for both eye and hand), and that target locations are remapped each time the eyes move (e.g. Berman, Heiser,

Dunn, Saunders, & Colby, 2007; Beurze, Van Pelt, & Medendorp, 2006; Duhamel, Colby, & Goldberg, 1992; Henriques, Klier, Smith, Lowy, & Crawford, 1998; Medendorp & Crawford, 2002; Merriam, Genovese, & Colby, 2006; Quaia, Optican, & Goldberg, 1998). However, the use of any one reference frame may depend on the task and the reliability of the sensory information represented in that reference frame, at least when gaze remains stationary during target presentation and reaching (McGuire & Sabes, 2009). To date, one reference frame that has been shown to play a role in encoding reach target location (visual and proprioceptive) is a gaze-centered reference frame. The present paper sought to further explore the role of a gaze on the localization of visual, proprioceptive and multisensory reach targets by varying direction of gaze while participants reached to these targets.

Research has shown that remembered visual reach target locations are initially coded and updated relative to gaze (e.g. Beurze et al., 2006; Henriques et al., 1998; Medendorp & Crawford, 2002; Van Pelt & Medendorp, 2007; Vaziri, Diedrichsen, & Shadmehr, 2006). This work exploited an error in the brain's computation of the locations of remembered visual targets called the *retinal magnification effect* (Cf., Bock, 1986). Bock (1986) first found that participants overestimated the remembered locations of peripher-

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ally seen visual targets. Similar gaze-dependent errors were later found even after participants initially viewed the same target on their *fovea* but, before pointing to this location, rotated their eyes in darkness to a position in which, at initial fixation, the visual target *would have* fallen on the retinal periphery (Henriques et al., 1998). That is, the remembered locations of these remembered visual targets were updated or remapped when the eyes moved to another location. This remapping occurs whether the eye moves as a result of a saccade (Henriques et al., 1998; Medendorp & Crawford, 2002; Poljac & van den Berg, 2003; Vaziri et al., 2006), a smooth pursuit eye movement (Thompson & Henriques, 2008), or because of movement of the body (Van Pelt & Medendorp, 2007). Taken together, these results suggest that the brain uses, at least in part, an eye fixed reference frame to maintain and update visual-spatial memory. This has also been shown to occur for implicit target sites produced by optic flow stimuli (Poljac & van den Berg, 2003), or when participants make two pointing movements to one target site (Sorrento & Henriques, 2008).

An eye-fixed representation of spatial memory is not restricted to visual targets. In 2002, Pouget et al. found that participants systematically overestimated the locations of targets relative to gaze even when the target was auditory (a beep), proprioceptive (the participant's foot) or imaginary. Blangero, Rossetti, Honore and Pisella (2005) also found that changes in gaze direction systematically affected participants' pointing error when the target was their unseen left hand. In contrast, McGuire and Sabes (2009) found underestimates of proprioceptive target location relative to gaze, attributing these errors to misestimates of eye position during the transformation of target location into a body centered representation. However, this explanation, nor their model, cannot account for the systematic errors relative to gaze that occur even after participants fixate the target (visual or proprioceptive) before deviating gaze to an eccentric position (updating target location relative to gaze). In all of these previous studies however the proprioceptive target was at the target location while subjects were reaching/pointing to the target. Thus, while these results suggest that the brain may make use of at least one common reference frame for coding and updating the locations of different sensory targets, it is not clear whether it does so for remembered proprioceptive targets, or how the brain codes the remembered spatial location of dual modality targets.

Our two primary objectives were: (1) to explore if the CNS codes the remembered locations of non-visual (i.e., proprioceptive) reach targets relative to gaze and (2) to examine if the CNS codes the memory of a target position, from multiple sources of sensory information, relative to gaze. If visual information about target location is more reliable than the proprioceptive information in our dual modality conditions, then we would expect the CNS to assign a greater weight to visual information and reach errors for these multi-sensory targets to resemble those observed when participants reach to the remembered location of visual targets. In contrast, if proprioceptive information about target location is more reliable than visual information, the CNS might assign a greater weight to proprioceptive information and the dual modality reach errors will resemble those observed when participants reached to the current location of the proprioceptive target. Participants' reach errors could also fall in between these two outcomes if visual and proprioceptive information are equally reliable and are therefore weighted equally. Support for an optimal integration of visual and proprioceptive information can be found from each of these scenarios as in all of these cases the two types of information are combined to form a unified estimate of target location based on the reliability of each (van Beers, Sittig, & Denier van der Gon, 1996, 1999; van Beers et al., 2002). However, this study is the first to investigate optimal integration when both the visual and proprioceptive feedback about target location are remembered.

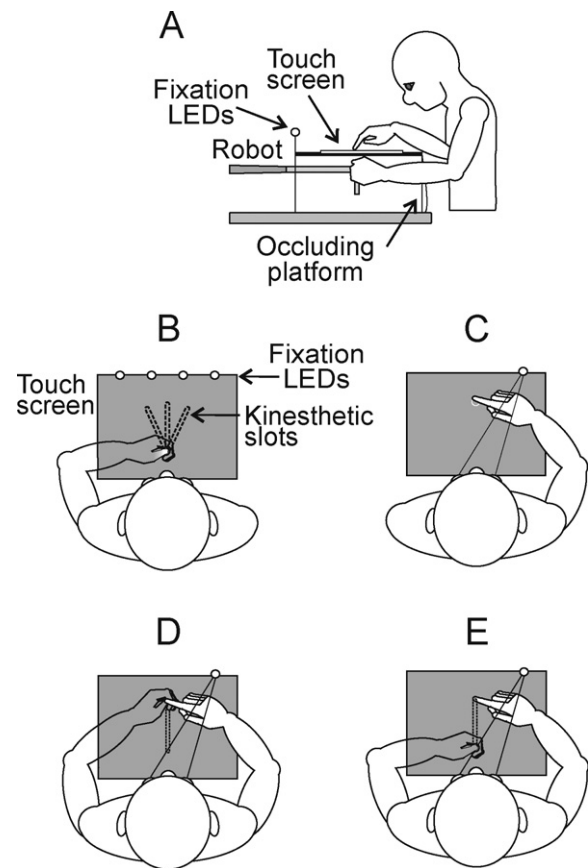


Fig. 1. Experimental setup and design. (A) Side view of the experimental setup. Participants gripped the handle of a robot manipulandum with their unseen left target hand and reached to the targets with their unseen right hand. A touchscreen recorded all reach endpoint locations. (B) Above view of the experimental step. The robot manipulandum restricted participants' active movement to a straight path from a start location to one of three target locations located 10° left, 0°, 10° right (dashed slots). Direction of gaze was varied using four fixation LEDs located 5° and 15° left and right of center (white circles). (C) In the visual memory condition, participants reached in complete darkness to the remembered location of LEDs mounted on the underside of the touchscreen (open circle). (D) In the proprioceptive conditions, participants reached to the current location of their unseen left hand in complete darkness. (E) In the proprioceptive memory condition, participants reached to the remembered location of their unseen left hand in complete darkness.

1. Materials and methods

1.1. Participants

Seven healthy human participants (2 females, 5 males) aged 20–26 (mean age = 22.28 ± 2.36) participated in this experiment. All participants had normal or corrected to normal vision and were right handed (self-reported). Written informed consent was provided by each participant prior to their participation. This experiment was approved by the York University Human Participants Review Subcommittee. Participants completed a series of five experimental conditions in which they reached to visual, proprioceptive or visual-proprioceptive targets with the right hand. These target types were selected so as to explore the effect of gaze location on reach errors when reach planning was derived from a single modality (either visual or proprioceptive) or both modalities. The order in which participants completed the experimental paradigms was randomized.

1.2. General experimental set up

A schematic of the experimental set up is presented in Fig. 1A. Participants sat on a height adjustable chair in front of a 90 cm high table. A chin rest (not shown) located 40 cm above the table top restricted movement of the head during the experiment and ensured that four red light emitting diodes (LEDs; white circles in Fig. 1) mounted horizontally on a bar in front of participants (37.5 cm in front of, and 18 cm below the eyes) were visible. These four LEDs were used to indicate to participants the fixation site on each trial; they were placed 5° and 15° to the left and right relative to the cyclopean eye. On each trial, one of these fixation positions was randomly selected to be paired with a target position.

The visual targets consisted of three white LEDs mounted on the underside of the touch screen at 10° left, 0° (center), and 10° right relative to the cyclopean eye. The proprioceptive target was the participants' left thumb, as it rested on top of the handle of a two jointed robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA; Fig. 1A), located at one of these same three target locations (Fig. 1B). The robot was programmed to constrain participants' active movement of the left hand along a straight path (dashed slots in Fig. 1B) from a common start position located 23.5 cm in front of the participant (at body midline) to one of the three target sites. The manipulandum was covered by a tinted translucent platform, so that once immersed in complete darkness, participants could not see their left forearm or hand. In addition, a curtain was placed over the remaining portion of the participant's left arm to ensure that no additional visual information concerning hand or arm position could be derived at any point throughout the experiment or testing sessions. When participants were asked to reach to visual–proprioceptive targets, the left thumb was illuminated with a white LED for one second after the left hand (proprioceptive target) reached the target location, but before the fixation LED was illuminated. This provided visual information about the proprioceptive target. All reaches to visual, proprioceptive, and visual–proprioceptive targets were made in complete darkness.

A 43 (length) × 33 (width), 3 mm thick touch screen® (Keytec Inc., Garland, TX), with a resolution of 4096 × 4096 pixels, was placed on top of the translucent platform and used to record reach endpoints (made with the right hand; Fig. 1A). An infrared head-mounted EyeLink II® eye-tracking system (SR Research Inc, Canada) was used to record the movement of the right eye at a sampling rate of 250 Hz (not shown). The EyeLink II® calibration plane included the area of visual space 7.6° above and 31.5° below the position of the fixation LEDs. All targets fell within this calibration plane, 19.1° below the fixation LEDs.

1.3. Visual memory

In the visual memory condition, participants reached to the remembered locations of visual targets. A temporal schematic of one trial is presented in Fig. 2A. Prior to the start of each trial, a start location was illuminated with one white LED. A trial began when the participant touched this location with their right reaching hand (making contact with the touch screen, usually within 1–3 s after the start location was lit). The start location LED turned off and one of the three visual targets was illuminated for one second (green box in Fig. 2A). Participants fixated this target location while it was on (red dotted line). When the visual target LED turned off, one of the four fixation LEDs (red box) was randomly illuminated for one second. Participants maintained fixation at this site during the time that the LED was illuminated, kept their gaze in this direction after the LED turned off (black dotted line indicates the auditory cue to reach), and reached with their right index finger to the remembered location of the visual target (blue dotted line). Their touch indicated the end of the trial (approximately 6 s in total). This visual memory reach is also illustrated in Fig. 1C. This condition provided a measure of reach errors as a function of target location and eye position when only visual information about target location could be used for reach planning.

1.4. Proprioceptive

In the proprioceptive condition, participants reached to their unseen left thumb as it rested on top of the robot handle (Fig. 1D). A temporal schematic of one trial is presented in Fig. 2B. At the start position for this condition and all other conditions, prior to the beginning of each trial, the left thumb was visible, lit by two white LEDs, until participants reached with their right index finger to the seen location of their left thumb in this position. This contact with the touch screen initiated the trial (i.e., it was the participants' choice when to begin each trial) and prevented drifting of the proprioceptive sense across time (e.g. Desmurget, Vindras, Gréa, Viviani, & Grafton, 2000; Wann & Ibrahim, 1992). After this initial reach to the start location, participants actively moved their left target hand to a randomly selected target location (solid green line), guided by the robot. A fixation LED was then randomly illuminated for one second (red box). Participants remained fixated on this location (red dotted line) while the LED was illuminated and throughout their reach to the felt location of their unseen left target thumb (blue dotted line in Fig. 2B and drawing in Fig. 1D). Each trial took approximately 7 s to complete.

Like in the original paradigm for visual spatial memory (Henriques et al., 1998) participants also completed a static gaze proprioceptive condition (gaze was deviated prior to target presentation and remained in this eccentric location during target presentation and reaching). However, like in the original study and as expected for eye-centered coding and updating of the targets, we found no difference in horizontal reach error or reach precision as a function of gaze relative to target or target location between the static and dynamic conditions. These two conditions were collapsed for analysis.

1.5. Proprioceptive memory

A temporal schematic of one trial in the proprioceptive memory condition is presented in Fig. 2C. Participants initiated the trial by reaching to the seen location of their left thumb. They then actively moved their unseen left hand along the kinaesthetic slot to one of the three target locations (solid green line). It remained

in this location for one second (the participant was free to look toward the unseen location of the target-hand) after which an auditory cue signalled participants to return their left hand, along the same kinaesthetic slot, to the start location (solid green line). One of the four fixation LEDs randomly illuminated for one second (red box) after which participants remained fixated on this location while they reached to the remembered location of their unseen left target thumb (blue dotted line in Fig. 2C and drawing in Fig. 1E). Each trial took approximately 10 s to complete.

Consistent with our proprioceptive condition, participants also completed a static gaze proprioceptive memory condition. Again, we found no differences in horizontal reach accuracy or precision between the static and dynamic conditions as a function of gaze relative to target location or as a function of target location. These two conditions were collapsed for analysis.

1.6. Visual–proprioceptive

The visual–proprioceptive condition (temporal schematic presented in Fig. 2D) was similar to the proprioceptive condition except that participants received both proprioceptive and visual information about the location of the left target hand. Specifically, after the target hand was moved to the target site (green line) it was illuminated by another white LED for one second (yellow filled green box) prior to reaching. Each trial took approximately 8 s to complete. This condition allowed us to assess if the combination of visual-memory and proprioceptive information about target location would affect reach errors in a way that differed from the single modality conditions. If the CNS uses an optimal integration of multisensory information, we might expect that reach errors produced in response to the combination of visual-memory and proprioceptive information in this condition may be smaller and less variable than those produced in either of the single modality conditions.

1.7. Visual–proprioceptive memory

The visual–proprioceptive memory condition was similar to the proprioceptive memory condition except that the left target hand was lit for one second by a white LED at the target site (yellow filled green box, Fig. 2E) before it was returned to the start position (solid green line). Each trial took approximately 10–12 s to complete. This condition enabled us to examine integration when both sensory sources were coded in memory prior to reaching.

1.8. Gaze free control condition

The control measure was similar to the proprioceptive condition except that there were no eccentric fixation constraints, and participants were free to direct their gaze toward the unseen target site in the dark room. This task measured reach errors as a function of target location (i.e., when gaze and target location are in the same place) when the target hand could not be seen.

Each experimental condition included 10 target–fixation pairings. We paired target and fixation locations to ensure that we obtained at least two measurements of reach error for each target relative to gaze eccentricity reported (i.e., a gaze relative to target eccentricity of 5° left was obtained from the combinations of target 0° and fixation 5° right, as well as target 10° right and fixation 15° right). In addition, previous research has suggested that the retinal magnification effect (gaze-dependent errors) begins to saturate when target eccentricities are approximately 20° from the fovea (Bock, 1986; Henriques et al., 1998). To limit the number of trials, fixation–target combinations resulting in gaze relative to target discrepancies of 25° were omitted from testing. Experimental sessions took place over the course of 4 months. Participants were not provided with information about the number of target locations, nor were they given any feedback about the accuracy of their reaches. They were unlikely to have learned the location of these targets across paradigms. Participants completed two blocks of 120 trials (12 trials for each target–fixation pairing) for all conditions, except the control condition which included two blocks of 15 trials (5 trials for each target location, no eccentric fixation constraints).

Eye movement recordings were exported from the EyeLink II® system, and viewed offline in a custom developed graphical user interface (GUI) in MatLab® 7.1 (The MathWorks Inc., Natick, MA). Trials were valid if participants maintained fixation within ±2.5° of the fixation location while the fixation LED was on and after it was turned off until they completed the required reach (Sorrento & Henriques, 2008). Trials in which participants did not meet these criteria were excluded from analysis (approximately 30%). We also detected and removed trials where reach endpoints fell outside ±2 SD of the respective mean (Sorrento & Henriques, 2008; Thompson & Henriques, 2008). This resulted in removal of less than 1% of all trials.

While all reaches occurred within the horizontal plane, we will use the term *horizontal error* to refer to the difference between target locations and reach endpoints along the left–right dimension, and *sagittal error* for the difference between target locations and reach endpoints along the forward–backward dimension. In order to calculate horizontal and sagittal errors, participants completed a calibration measure following each experimental session. This calibration included one reach to each of the three target locations (visual and proprioceptive) with the room lights on, so that the targets and the reaching hand were visible during the reach. Errors were calculated by subtracting the reach endpoint location of each reach on each trial (as recorded by the touch screen) from the reach endpoint locations obtained for the same target from this baseline testing for both directions. *Horizontal and sagittal*

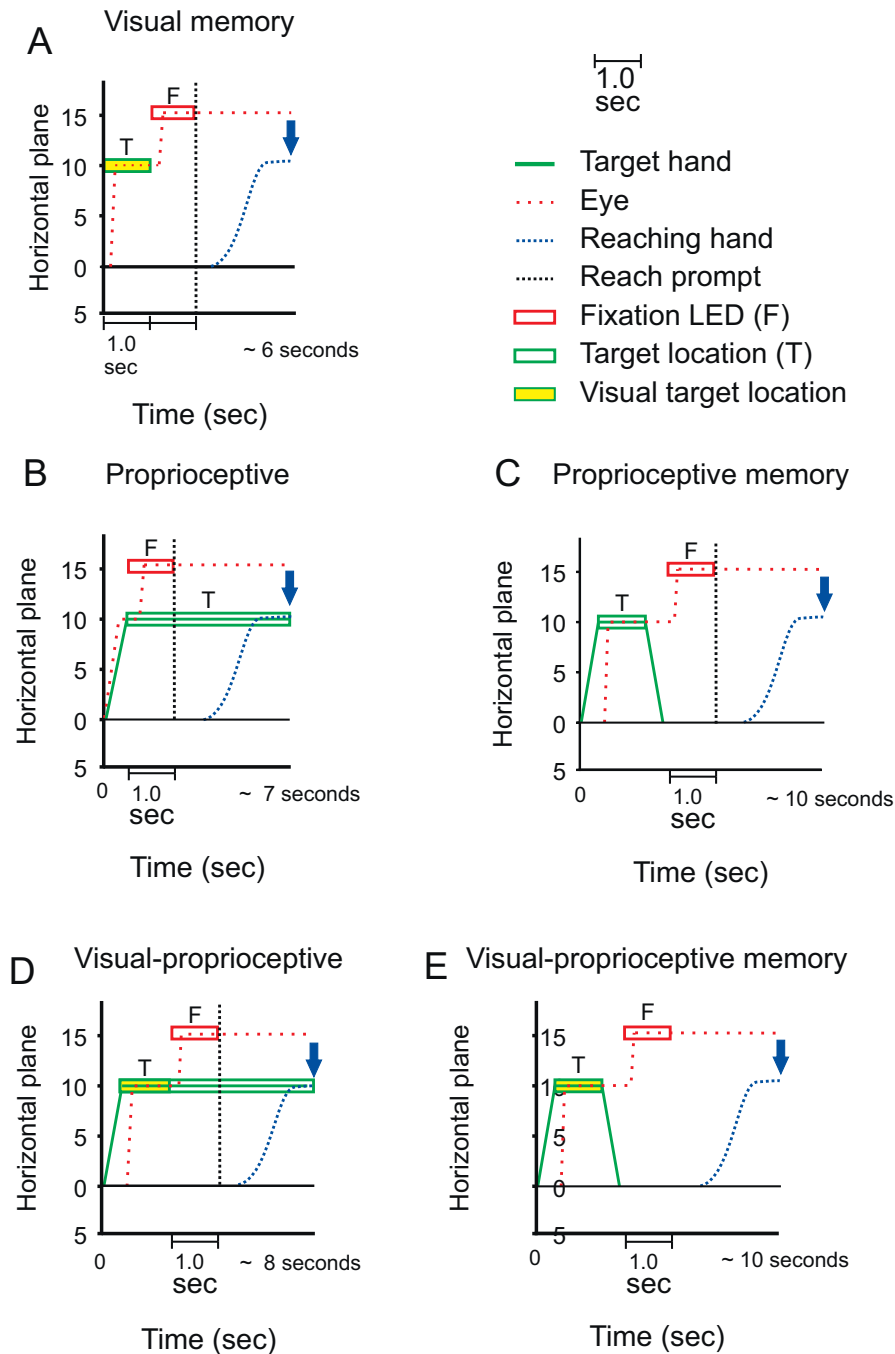


Fig. 2. Temporal schematics of one trial from each of five conditions. The red and green boxes represent the possible horizontal location and time of presentation of the fixation LED and reaching targets respectively. The yellow filled green box indicates when the target was visual. The red and blue dotted lines represent ideal gaze and arm movements respectively, while the vertical black dotted line indicates the onset of auditory prompt to reach. (A) *Visual memory*: participants reached to the remembered location of a visual target while fixating an eccentric location. For all other conditions (B–E) which used a proprioceptive target, a trial began when participants reached to the seen location of their target thumb in the start position, making contact with the touch screen. A trial ended when participants reached to the felt location of their unseen target thumb in the target position or the remembered location of their thumb shortly after it was removed. (B) *Proprioceptive*: participants reached to the current felt location of their unseen target hand. They were permitted to look to the felt position of their target hand prior to fixating an eccentric location and completing the reach. A static fixation condition was also completed (not shown). (C) *Proprioceptive memory*: participants reached to the remembered location of their target hand. They were permitted to look to the location of their unseen target hand prior to fixating an eccentric location and completing the reach. (D) *Visual-proprioceptive*: participants reached to the current felt location of their target hand while fixating an eccentric location. Their hand was briefly lit in the target position (yellow part of the green box) prior to fixation and reaching. (E) *Visual-proprioceptive memory*: participants reached to the remembered location of their target hand while fixating an eccentric location. Their target hand was briefly lit in the target position prior to returning their hand to the start location (indicated by green line), fixating, and completing the reach. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

precision will be used to refer to the variability of these reach errors in the left-right and near-far dimensions, respectively. To calculate this precision, we computed both the standard deviation and 95%-confidence interval ellipses for reach errors for each target-fixation combination for each participant.

1.9. Data analysis

As gaze was varied along the horizontal axis, we examined (and present) the effect of target location and gaze relative to target on horizontal error (sagittal error was also examined, but no systematic effects were observed). We conducted a series of one-way repeated measures analysis of variance (RM-ANOVA) to investigate the effect of these factors separately on participants' horizontal reach end point errors in each of five experimental conditions. All RM-ANOVA results are reported with Greenhouse-Geisser corrected p values. Pairwise comparisons with Bonferroni correction were used to further explore all significant effects on horizontal reach error.

The control condition, in which participants were asked to look to the felt location of the unseen left target hand while they reached to this location, was used to assess participants' general accuracy in reaching to the three proprioceptive targets (in the absence of visual information about target hand location). A one-way RM-ANOVA was used to assess the effect of target location on horizontal reach error (no target location effect was found).

1.10. Multisensory integration model

Our visual-proprioceptive guided reaching condition combined the information that participants received in our visual memory guided and proprioceptive guided-dynamic reach conditions. We, therefore, wanted to determine if the estimate of target hand location in this multisensory condition (X_{VP}) would be computed from a weighted average of remembered visual information (X_V) and proprioceptive information about target location (X_P) (see Vaziri et al., 2006):

$$X_{VP} = \alpha X_V + (1 - \alpha) X_P \quad (1)$$

where α defines the weighting given to the estimate of target location in the visual memory condition (X_V) and the weight given to the estimate of target location in the proprioceptive-dynamic condition (X_P) is the difference between α and 1. A value of $\alpha > 0$ and < 1 (significantly different from zero) would suggest that an integration of the remembered visual and online proprioceptive information has occurred. Values of 0 or 1 indicate that all weight has been assigned to one target modality and none to the other. The estimate of α was calculated by assigning an expected value of the estimate of target left hand location (that is, mean horizontal reach error) to both sides of Eq. (1):

$$E[X_{VP}] = \alpha E[X_V] + (1 - \alpha) E[X_P] \quad (2)$$

where α was estimated using a mean response model like that used by Vaziri et al. (2006):

$$\alpha = \frac{E[X_{VP}] - E[X_P]}{E[X_V] - E[X_P]} \quad (3)$$

We applied the same calculations to our visual-proprioceptive memory guided reaching condition.

To test whether these two sources of information were integrated optimally, we compared the weights for visual and proprioceptive information calculated using Eq. (3) with predicted optimal weights calculated using the following equation:

$$\alpha_{OPTIMAL} = \frac{\text{var}[X_P]}{\text{var}[X_P] + \text{var}[X_V]} \quad (4)$$

Variability in this equation is the variance of the sensory estimates of target location as indicated through reach endpoints. However, as variability in reach endpoints arises not only from the sensory estimate of target location, but also from motor noise that occurs when completing the reaching movement itself (van Beers, Haggard, & Wolpert, 2004), we included a source of variability from motor noise (α_{MOTOR}^2) in our estimates of visual and proprioceptive variability used in Eq. (4). Our estimate of motor noise was the horizontal reach variability (variance) observed from an extra baseline condition in which 10 participants (different from those who participated in the original six conditions) were asked to complete 20 reaches to the seen location of their target left hand, in each target location, while looking at their target hand. Importantly, as participants could clearly see their target hand, discrepancies between actual locations of the target hand (i.e., the location of the left target thumb resting on top of the robot handle) and reach endpoints were assumed to occur because of motor noise incurred during the reaching movement. This variability was added to the variability (variance) observed in our visual and proprioceptive conditions:

$$\text{var}[X_V] = \sigma_{MOTOR}^2 + \text{var}[X_V] \quad (5)$$

$$\text{var}[X_P] = \sigma_{MOTOR}^2 + \text{var}[X_P]$$

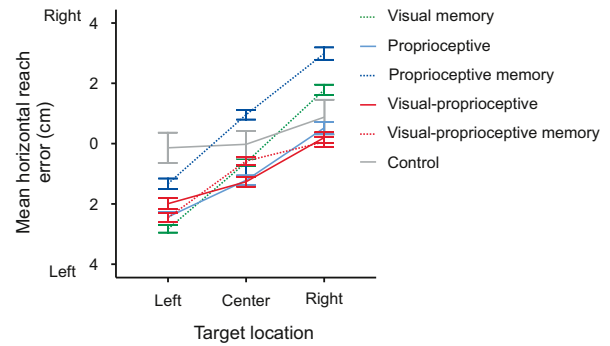


Fig. 3. Mean horizontal reach error as a function of target location, averaged across trials and subjects, for each condition. Error bars display the standard error of the mean.

These values were then plugged into Eq. (4) to calculate optimal integration weights. The same calculations were done using the visual and remembered proprioceptive conditions when calculating the optimal integration weights for the visual-proprioceptive memory guided reach condition.

If optimal integration of visual and proprioceptive information in our visual-proprioceptive and visual-proprioceptive memory guided reaching conditions has occurred, we would expect: (1) similar weights assigned to the visual and proprioceptive sources (Eq. (4)), as those calculated from our data (Eqs. (2) and (3)); assessed using Bonferroni corrected t -tests and (2) variability in our dual modality conditions (variance) to be less than variability in either of the two single modality conditions. We also used Eq. (6) (with newly estimated $\text{var}[X_V]$ and $\text{var}[X_P]$, including motor noise estimate: α_{MOTOR}^2 , from Eq. (5)) to estimate the variability in our visual-proprioceptive (and visual-proprioceptive memory) condition that would be expected from optimal integration of visual and proprioceptive information. These estimates of variance were compared to the variance values observed in our dual modality conditions:

$$\text{Optimal variance} = \frac{[\text{var } X_P] * [\text{var } X_V]}{[\text{var } X_P] + [\text{var } X_V]} \quad (6)$$

2. Results

In this study, we examined how gaze affected the accuracy of reaches made to proprioceptive and multisensory targets. As we were most interested in the interaction between target location and eye position (gaze relative to target) on reaches to proprioceptive memory and multisensory target types (since the effect of these factors on these target types have yet to be explored), this result is described in the greatest detail. We first describe the significant target effect, followed by a description of the gaze relative to target effect, including how each of these effects differs as a function of condition (i.e., type of target). We then explore the contribution of visual and proprioceptive information on horizontal errors in our visual-proprioceptive and visual-proprioceptive memory conditions (optimal integration model).

2.1. Target location

Fig. 3 displays mean horizontal reach error (in cm) broken down by target location and condition, collapsed across trials and participants. Mean constant errors for each target location, for each condition are also presented in Table 1. Horizontal reach error varied significantly across target locations ($F_{GC}(1.12, 16.34) = 19.41$, $p < 0.05$). On average, errors were more leftward for the left target location than the center or right target locations, and vice versa for the right target location ($p < 0.05$), regardless of condition ($F_{GC}(1.37, 4.13) = 4.03$, $p > 0.05$).

2.2. Gaze direction relative to target location

Fig. 4 displays mean horizontal error (in cm) plotted as a function of all gaze and target pairings (gaze relative to target), averaged across trials and subjects for each condition. Errors for leftward tar-

Table 1

Mean horizontal constant error, averaged across participants, for each target location, gaze direction relative to target location, and condition.

Condition	Left	Center	Right	
Target location				
Visual memory*	2.83 left	0.62 left	1.78 right	
Proprioceptive*	0.01 left	0.22 right	1.51 right	
Proprioceptive memory*	1.89 left	1.06 left	0.47 right	
Visual proprioceptive*	1.96 left	1.27 left	0.20 right	
Visual proprioceptive memory*	2.46 left	0.58 left	0.06 right	
Condition	15° left	5° left	5° right	15° right
Gaze relative to target				
Visual memory**	2.34 right	0.13 right	1.29 left	3.15 left
Proprioceptive**	2.41 right	1.43 right	0.32 left	1.16 left
Proprioceptive memory**	1.12 right	0.25 left	1.40 left	2.29 left
Visual proprioceptive**	0.91 right	0.11 left	1.59 left	2.57 left
Visual proprioceptive memory**	1.27 right	0.28 left	1.73 left	2.60 left

* Target location effect significant at the $p < 0.05$ level.

** Gaze relative to target effect significant at the $p < 0.05$ level.

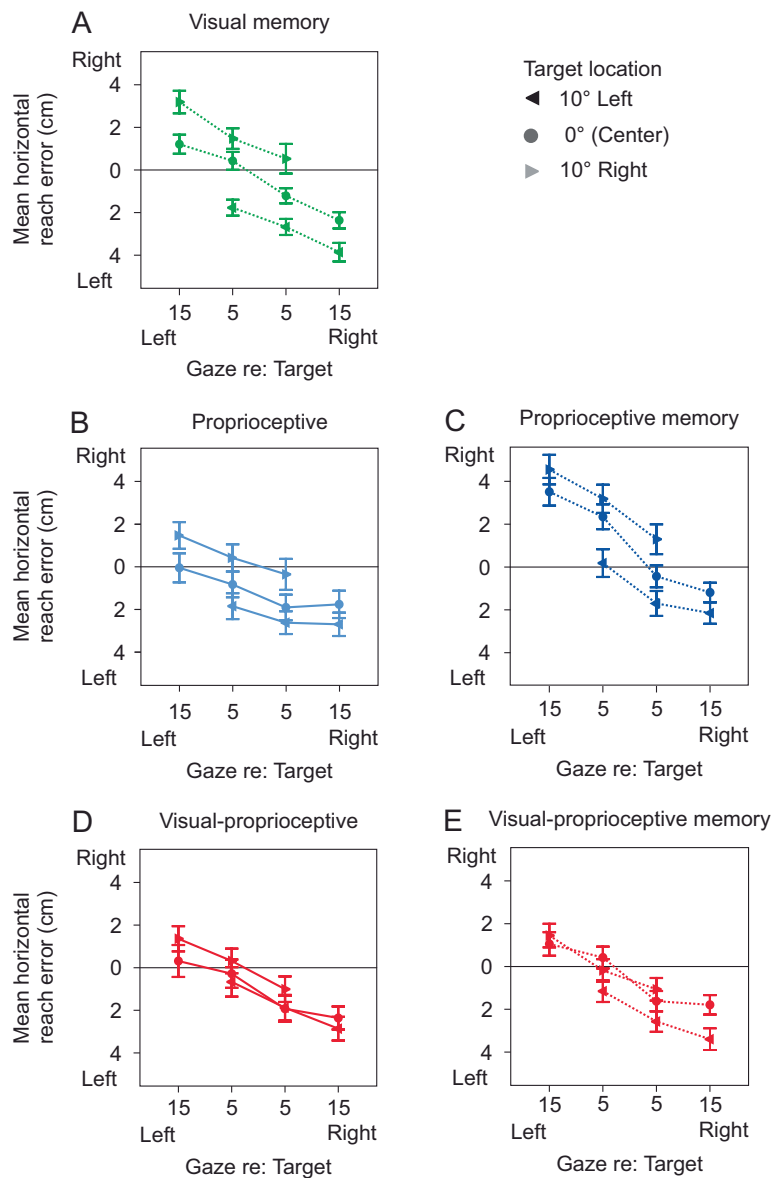


Fig. 4. Horizontal reach error for each of the three target locations, averaged across trials and subjects, as a function of the difference between gaze and target location for each condition. Errors (in cm) for leftward targets are represented using leftward pointing triangles, errors for rightward targets are represented using rightward facing triangles, and errors (in cm) for the center targets are represented using circles. The error bars display the standard error of the mean.

gets are represented using leftward pointing triangles, errors for rightward targets are represented using rightward pointing triangles, and errors for the center targets are represented using circles. Mean horizontal error for each gaze relative to target is also presented in Table 1. Horizontal error varied systematically with gaze direction relative to target location for all target types ($p < 0.05$). This effect was found to differ slightly across conditions ($F_{GG}(3.89, 23.36) = 4.91, p < 0.05$) and, as such, was explored further (below). Sagittal errors were found to differ as a function of gaze relative to target location, but not systematically ($F_{GG}(1.6, 9.6) = 7.62, p < 0.05$); participants made larger sagittal reach errors when gaze was 15° left relative to target location than when gaze was in any other location.

2.3. Gaze direction relative to target location: comparison across conditions

We compared the pattern or modulation of reaching errors as a function of gaze re: target across the conditions. Fig. 5 shows horizontal error (this time averaged across the three target locations) as a function of gaze relative to target for all experimental paradigms. The horizontal grey dotted lines represent the mean horizontal errors for each of the three target locations in the control condition (these errors did not differ as a function of target location, $p > 0.05$).

We did not find a difference in gaze dependent error between the proprioceptive condition (light blue-solid curve Fig. 5) and the proprioceptive memory condition (dark blue-dashed curve; $F_{GG}(1, 6) = 5.01, p = 0.07$, Table 1). This suggests that storing the

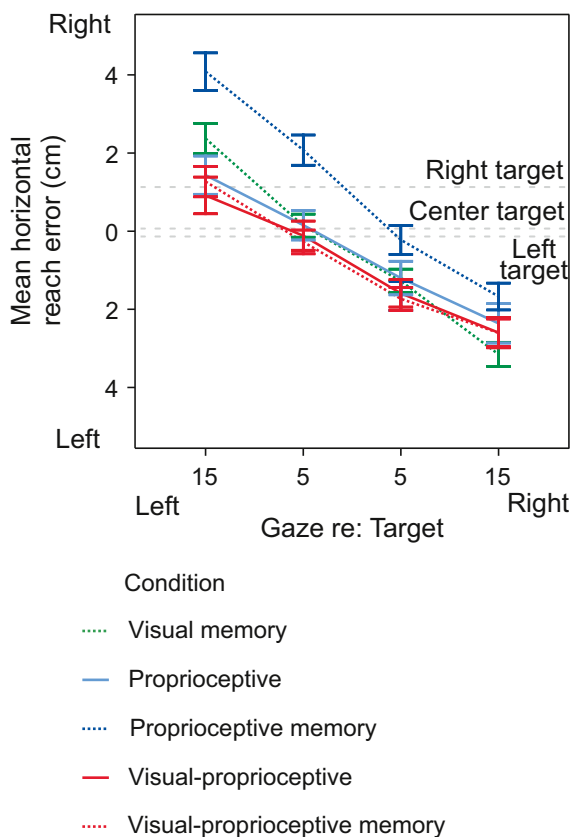


Fig. 5. Mean horizontal reach error as a function of gaze relative to target location, averaged across trials, targets, and subjects, for all conditions. Participants' mean horizontal error, for each target location in the control condition (when gaze was not varied), are represented by the horizontal grey dotted lines. Error bars display the standard error of the mean.

proprioceptive target location in memory does not affect the pattern or magnitude of gaze dependent error. No difference was found between the visual memory (green-dashed curve in Fig. 5) and proprioceptive conditions either (light blue-solid curve Fig. 5; $F_{GG}(1,6) = 0.002, p = 0.96$). We also found no significant difference between the single and dual-modality conditions ($F_{GG}(1, 6) = 0.15, p = 0.71$, Table 1).

We then made the same comparisons between the single-modality and dual-modality conditions when the proprioceptive target was remembered. We found that gaze-dependent errors for the visual memory condition (green-dashed curve, Fig. 5) significantly differed from the proprioceptive memory condition (dark blue-dashed curve; $F_{GG}(1, 6) = 9.84, p < 0.05$); although the pattern of reach errors as a function of gaze appears the same (negative slope), these errors were larger in the proprioceptive memory condition. Gaze dependent errors in the visual memory condition did not significantly differ from those in the visual-proprioceptive memory condition ($F_{GG}(1,6) = 0.23, p = 0.88$). But gaze dependent errors in the proprioceptive memory condition did differ from those observed in the visual-proprioceptive memory condition ($F_{GG}(1,6) = 52.24, p < 0.05$). Once again, gaze-dependent reach errors were larger in the proprioceptive memory condition (1.0 ± 0.47 cm) than in the visual-proprioceptive memory condition (0.63 ± 0.80 cm). This result suggests that the addition of visual information may allow for more accurate localization when the proprioceptive target is remembered.

2.4. Gaze direction relative to target location, and target location

Our next step was to compare the pattern of horizontal errors as a function of gaze relative to target across the three target locations (different curves in each panel of Fig. 4). While horizontal reach errors systematically varied as a function of gaze direction relative to target location, this pattern of gaze dependent error did not vary with target location ($F(4,60) = 0.25, p = 0.90$). The curves for each target in each panel of Fig. 4 are parallel to each other.

2.5. Multisensory integration

The gaze dependent error differences observed between the visual-proprioceptive memory and proprioceptive memory conditions suggest optimal integration of vision and proprioception. To further examine this possibility, we calculated the relative weighting of visual and proprioceptive information in our dual modality conditions for each participant separately, the averages of which are presented below. We also assessed changes in reach endpoint variability between the single and dual modality conditions, as shown in Fig. 6A. Fig. 6B plots observed and predicted variance values (that might be expected from optimal integration of visual and proprioceptive information sources, Eq. (6)) for the visual-proprioceptive and visual-proprioceptive memory conditions, broken down by participant. These variances (collapsed across participants) are compared to average variance in our single modality conditions in Fig. 6A.

Visual-proprioceptive. Eqs. (2) and (3) were used to calculate the relative weighting of visual and proprioceptive information in our visual-proprioceptive condition for each participant. The average visual (0.67 ± 0.56 , 95% confidence limits) and proprioceptive (0.33 ± 0.55 , 95% confidence limits) weights differed from zero ($p < 0.025$) but not from one another ($p > 0.05$), suggesting some type of integration of these two sources. Eqs. (4) and (5) were used to determine if the integration of visual and proprioceptive information was optimal. Although we found no difference between the actual (listed above) and predicted optimal weights assigned to visual (predicted: 0.54 ± 0.12 ; $t(12) = 0.57, p > 0.05$) and proprioceptive (predicted: 0.46 ± 0.13 ; $t(12) = -0.57, p > 0.05$)

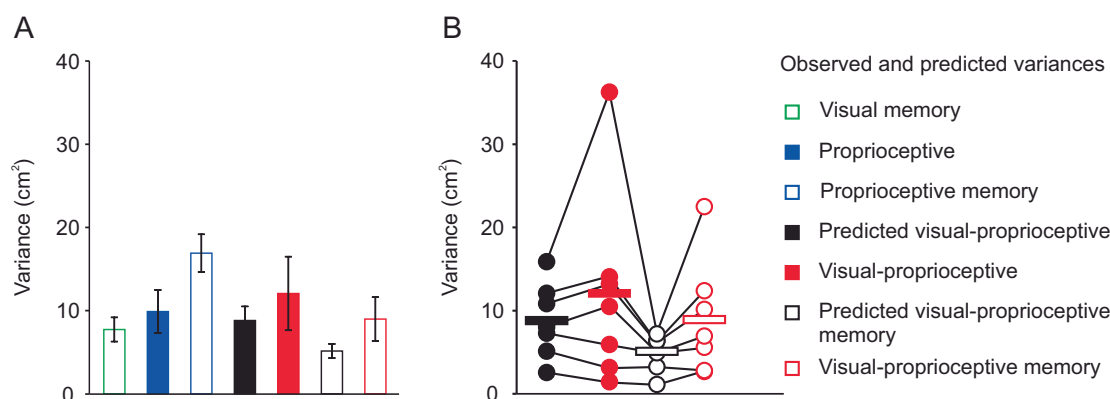


Fig. 6. Observed variance, as measured by the elliptical area fitted to reach endpoints, and the predicted variance according to the optimal integrated model. (A) Observed variance, computed for each target–fixation pairing for each participant for the visual-memory (solid green bar), proprioceptive (solid blue bar), proprioceptive memory (blue open bar), visual proprioceptive (solid red bar) and visual–proprioceptive memory (open red bar) conditions and predicted variance for the visual–proprioceptive (solid black bar) and visual–proprioceptive memory (open black bar) conditions. (B) Observed and predicted variance for the visual–proprioceptive (solid red and black circles) and visual–proprioceptive memory (open red and black circles) conditions, broken down by participant (indicated by the joined circles). The rectangles represent the averages of these participants' observed and predicted variances.

information in this condition (with Bonferroni correction), we failed to observe an improvement in precision that might be expected if optimal integration was occurring. That is, variance in our visual–proprioceptive condition (solid red bar in Fig. 6A and solid red circles in Fig. 6B) was not less than an average of the variances observed in the single modality conditions (open green and blue bars in Fig. 6A). Yet there was no difference between the observed (solid red bar in Fig. 6A and solid red circles in Fig. 6B) and predicted variability (predicted optimal integration variability calculated from Eq. (6), solid black bar in Fig. 6A and solid black circles in Fig. 6B) in this condition ($t(12) = 0.68, p > 0.05$). Overall, these results suggest that while there may be some type of integration of visual and proprioceptive information in our visual–proprioceptive condition, this integration may not be optimal.

Visual–proprioceptive memory. In our other multimodal condition, when both visual and proprioceptive information about the targets was removed prior to the memory-guided reach, the average visual (0.55 ± 1.17 confidence limits (95%)) and proprioceptive (0.45 ± 1.22 confidence limits (95%)) weights did not differ from zero ($p > 0.025$) or one another ($p > 0.05$), suggesting that visual and proprioceptive information in this condition are not being integrated across subjects. Consistent with our visual–proprioceptive condition, the actual and predicted optimal integration weights assigned to remembered visual (0.75 ± 0.10 ; $t(12) = -0.15, p > 0.025$) and remembered proprioceptive (0.34 ± 0.07 ; $t(12) = -0.15, p > 0.025$) information did not differ, nor did the actual (open red bars and circles in Fig. 6) and optimal predicted (open black bars and circles) variances ($t(12) = -1.48, p > 0.05$). Despite this, we failed to observe variance values that would suggest optimal integration; variance in our visual–proprioceptive memory condition (open red bar in Fig. 6A and open red circles in Fig. 6B) was not less than an average of the variances observed in the single modality conditions (open green and open blue bar in Fig. 6A).

3. Discussion

We found that horizontal reach errors to online and remembered unimodal and multisensory targets varied systematically with gaze relative to target. On average, participants overestimated target location to the left when gaze was to the right of the target and overestimated target location to the right when gaze was to the left of the target. This gaze dependent effect was consistent across target locations, and occurred both when the visual and/or

proprioceptive target appeared in the visual periphery, and when participants first looked toward the target site before shifting gaze away. Reach errors were also deviated more leftward when the hand was in the left target position and more rightward when the hand was in the right target position. Reach accuracy, gaze dependent errors, and variance were similar across conditions. We failed to observe variance values in our two dual modality conditions that would suggest optimal integration of visual and proprioceptive information.

3.1. Target effect

We found that horizontal errors were related to the location of the target, regardless of the type of target. An effect of visual target position on reaching errors has been previously found (e.g. Bock & Eckmiller, 1986). Also, in two other proprioceptively guided reaching studies of ours (Jones, Fiehler, & Henriques, 2009; Jones, Cressman, & Henriques, 2010) where gaze was not constrained, we found similar target-dependent errors for the same target locations used in this study. Since we do not see these target-related biases when pointing with the extended arm to aim at distant visual targets (Henriques et al., 1998; Sorrento & Henriques, 2008; Thompson & Henriques, 2008), these target-dependent errors may be partly due to the setup—moving the finger to a surface in the horizontal plane. These errors may also be due to biomechanical factors or errors in representing or converting the target representation in a body or hand or motor-related coordinates (McIntyre, Stratta, & Lacquaniti, 1998).

3.2. Coding target location: multiple reference frames

Neurophysiological research in macaque (e.g. Avillac et al., 2005; Batista et al., 2007; Buneo et al., 2002; Caminiti et al., 1991; Lacquaniti et al., 1995) and neuroimaging studies on humans (e.g. Wu & Hatsopoulos, 2006, 2007) have supported the suggestion that visual target locations are coded using multiple reference frames (Beurze et al., 2006; Bock & Eckmiller, 1986; Graziano, 2001; Khan et al., 2007). While multiple reference frames may contribute to movement planning, the reliability of each reference frame may decide how they are used or weighted to obtain the best estimate of target location (McGuire & Sabes, 2009; Sober & Sabes, 2003, 2005). The reliability of an estimate of target location in a given reference frame may be associated with the type and quality of sensory information that is available to plan and execute the movement (e.g.

target modality). And transformations from one reference frame to another may introduce errors that were not present when the target was coded in any one particular reference frame (McGuire & Sabes, 2009; Sober & Sabes, 2003, 2005), prompting the CNS to form the most accurate and parsimonious (fewest transformations) representation of target location, given the available sensory information. As has been shown in the current study, when participants first fixate toward the proprioceptive and multisensory targets and then deviate their gaze to an eccentric location, or kept their gaze eccentric during the entire trial, they systematically overestimate target location relative to gaze, even when the targets were removed. This suggests that a gaze-centered reference frame is one of the frames used to encode and update target location (in addition to a head or body centered reference frame as suggested by our target effect). These errors are not found when participants are permitted to fixate the target location during movement planning and throughout the reach (grey curve, Fig. 3 and horizontal grey lines, Fig. 5). Our gaze dependent effects are consistent with those that have been reported for visual (Henriques et al., 1998), proprioceptive (Blangero et al., 2005, 2007; Pouget, Ducom, Torri, & Bavelier, 2002), and auditory targets (Pouget et al., 2002) and under varying motor (Medendorp & Crawford, 2002; Poljac & van den Berg, 2003; Sorrento & Henriques, 2008; Thompson & Henriques, 2008; Van Pelt & Medendorp, 2007; Vaziri et al., 2006) and relative judgement tasks (Fiehler, Rosler, & Henriques, 2010). The following section will further discuss these gaze dependent effects.

3.3. Coding target location relative to gaze

Behavioural and neurophysiological research has suggested that the brain represents visual spatial memory, at least partially, relative to gaze (Batista, Buneo, Snyder, & Andersen, 1999; Buneo et al., 2002; Henriques et al., 1998). Batista et al. (1999) found that neurons in the parietal reach region (PRR) of macaque exhibited the same pattern of activity for different reach targets when they had the same retinal location, but not the same pattern of activity when the target locations (or the reach goals) were the same, but gaze differed (i.e., so that the retinal location differed). These results suggest that the PRR codes the location of visual reach targets in an eye-fixed reference frame. Buneo et al. (2002) later recorded cells in area 5d and found that the activity of these neurons was modulated by changes to the eye-centered coordinates of the reach targets and the initial reaching hand location, suggesting that area 5d encodes initial hand and reach target locations (or perhaps the movement or hand-target vector) in eye-centered coordinates, as opposed to a body-centered coordinate reference frame.

Using fMRI, Medendorp, Tweed, & Crawford (2003) found that when participants made saccades or reached to a remembered target, following a gaze shift to the opposite side of the briefly seen target, the activity in PPC associated with the memory traces of the target were remapped to the contralateral PPC. This lateralization of activity suggests that the PPC codes and *remaps* the remembered locations of saccade and reach targets relative to gaze and further supports that the brain, at least partially, codes and updates visual-spatial memory in an eye-fixed reference frame. This finding is further substantiated by patients with unilateral optic ataxia (a disorder associated with damage to the PPC) who exhibit deficits in the ability to accurately reach to peripheral targets that are remapped in the visual field contralateral to their lesion when the eyes move between viewing the target in their intact field and reaching to its remembered location (cf. Khan, Pisella, Rossetti, Vighetto, & Crawford, 2005). Moreover, these same patients do not have any reach deficits when they see the target in their contralesional visual field, but move their eyes so that this memory trace is being remapped to their intact visual field prior to reaching. The same deficits were found when these patients also reached to

proprioceptive targets (opposite hand) when the target-hand was placed in their contralesional field compared to their ipsilesional field (Blangero et al., 2007). Such gaze-dependent effects have also been previously found for proprioceptive targets in healthy people (e.g. Blangero et al., 2005; Pouget et al., 2002).

3.4. Reaching to proprioceptive targets: accuracy and precision

Several studies have reported greater reach accuracy (Lovelace, 1989; Sarlegna & Sainburg, 2007) and/or precision (Adamovich, Berkinblit, Fookson, & Poizner, 1998; Lovelace, 1989) when reaching to a proprioceptive target (i.e., a body part), in the absence of visual information about target location, than when reaching to visual targets. In our study, precision of reach errors did not significantly differ between the visual memory and proprioceptive conditions. This may not be so surprising given that participants were able to actively and directly place their hand to the target site (guided by the robot) in the proprioceptive conditions. Moreover, the proprioceptive target was continuously “on”, while the visual target disappeared after one second. We did find that reaching to remembered proprioceptive targets was significantly less precise than that for the online proprioceptive targets, suggesting that, as expected, no longer having the hand at the target site may have led to a noisier estimate of the movement goal. Reaches to remembered proprioceptive targets were also less precise than reaches in the visual memory condition, suggesting that noisier estimates of hand location are derived from remembered proprioceptive information than from remembered visual information (discussed further in the visual-proprioceptive section).

3.5. Coding visual-proprioceptive targets

Although research has suggested that the CNS may rely more heavily on visual information when it is available (e.g. Balslev, Miall, & Cole, 2007), when given visual and proprioceptive information about a targets' location, reaches to that target have been found to be more precise than when either sensory modality alone is used (van Beers et al., 1996), although this does not always occur (e.g. Laufer & Hocherman, 1998). van Beers, Sittig and Denier van der Gon (1998) found that more weight is placed on visual signals than proprioceptive ones for multisensory targets when they are located along the azimuth (along the radial axis of the target shoulder), so that final endpoints tend to more closely resemble those made to visual-only targets than those made to proprioceptive-only targets. Thus, we wanted to test whether the same was true when targets (either visual, proprioceptive, or both) were remembered (they were continuously available during pointing in van Beers et al., 1998), and if combining two sources of information would lead to a change in the size of the gaze modulation on pointing.

We did not find any difference in the overall errors or gaze dependent errors, nor the variance in reach errors, between visual memory, proprioceptive and the visual-proprioceptive conditions. It could be that our sophisticated technique for generating online proprioceptive targets, using the robot for precisely controlling the active displacement of the target hand, allowed our participants to localize these proprioceptive targets with the same precision and accuracy as localizing briefly flashed visual targets. In addition, usually studies that show greater reliance on vision compared to proprioception have the visual target continually on during the task (e.g. Sober & Sabes, 2003; van Beers et al., 2002). But likely, visual-memory (even after a short delay) would be noisier and so a less reliable than continuous vision, and as a consequence people should not necessarily show better performance or greater reliance on remembered visual information about the target compared to proprioceptive information. And this is what we found. The visual (0.67) and proprioceptive (0.33) weights were comparable and sig-

nificantly different from zero and the predicted and observed visual and proprioceptive weights were also comparable, but the overall and gaze-dependent errors and variances for visual–proprioceptive targets were not smaller than those for the single-sensory targets. It could be that both modalities (visual–memory and proprioception) may be equally reliable and so contribute equally (but not necessarily optimally) to multisensory guided movements.

Variance when reaching to visual memory targets was less than that for proprioceptive memory targets, but the visual memory (0.55) and proprioceptive memory weights (0.45) were comparable (but not significantly different from zero), suggesting that remembered visual and remembered proprioceptive information in this condition are not being optimally integrated. Overall error and variance were larger in the proprioceptive memory condition than in the visual–proprioceptive memory condition, but this difference was not found between the visual memory and visual–proprioceptive memory conditions. As constant and gaze dependent errors between this bimodal condition and the visual memory condition are so similar, perhaps visual information is being used to guide the reach to the remembered visual–proprioceptive target. That is, when the target hand is removed prior to reaching, only the visual and not the proprioceptive memory of hand position was used to guide reaching. Yet, the calculated weights do not reflect this greater reliance on visual information.

Reach errors in our visual–proprioceptive condition suggest that the CNS may not optimally integrate visual and proprioceptive memory traces for planning reaches to these multisensory targets. However, the combination of remembered visual and remembered proprioceptive information did lead to significantly more precise (less variance) movements to the remembered visual–proprioceptive targets than to the proprioceptive memory targets alone. Again, this suggests that remembered visual information may be being used to the exclusion of remembered proprioceptive information because remembered visual information (even though remembered) may still be more reliable than remembered proprioceptive information. Or these slight discrepancies may be because integration is occurring repeatedly and separately for the different stages of the sensorimotor transformation or motor planning, (Sober & Sabes, 2003) and/or for different reference frames, in a complex way that cannot be easily deciphered with our current paradigm. For example, perhaps visual and proprioceptive information are being optimally integrated, but this integration could be masked by the gaze dependent effects for visual and proprioceptive targets that are not being integrated.

3.6. Summary

The present study presents a comprehensive examination of, and further supports, at least in part, a gaze-dependent localization of reach targets. Participants systematically overestimated the locations of remembered visual, proprioceptive, remembered proprioceptive and visual–proprioceptive targets relative to gaze. These results suggest that similar mechanisms may be used by the CNS to code and update the location of reach targets, independent of sensory modality. In addition, we also found that the goal of the reach (target location) also influenced reaching accuracy as consistent with other studies, for visual (Bock and Eckmiller, 1986), proprioceptive, and remembered proprioceptive targets (Jones et al., 2009).

We found little difference in overall and gaze-dependent reach errors, and variance, between the single-sensory and multi-sensory targets when the proprioceptive target was online (at the target site during reaching). When reaching in complete darkness with gaze deviated, participants performed similarly when reaching to briefly

seen targets, or felt targets, and to targets that were briefly seen and felt. While this systematic gaze dependent pattern also held for remembered proprioceptive targets, the effect of gaze on reaching was a bit larger (when gaze was left) and overall less precise for these targets. Our results do not conclusively suggest an optimal integration of visual and proprioceptive information in our dual modality conditions, especially for proprioceptive–memory traces. However, the similarities among target dependent and gaze relative to target dependent errors observed across our conditions indicate that the difference in precision or reliability between the two single modality sources may not have been large enough to lead to substantially greater weighting for one modality.

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