The coding and updating of visuospatial memory for goal-directed reaching and pointing

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A B S T R A C T

In this review we discuss evidence from psychophysical, electrophysiological, and neuroimaging studies that demonstrates the updating of remembered visual space in a reference frame that is centred on the eye. We then extend these findings by discussing recent work from our lab. Specifically, we address eye-centred updating of visuospatial memory for arm movements following different types of eye movements, the role of retinal versus extraretinal information in such spatial updating, and the use of allocentric versus egocentric information in coding multiple targets. We provide a conceptual model to explain the relationships among these findings.

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1. Introduction

We move our eyes 4–5 times every second, resulting in a continuously changing stream of visual information, yet we still perceive the world to be stable. Perceived stability of the world is important because it allows us to function – a continuously shifting visual world would make interaction with the environment impossible, since the spatial locations of objects in our environment are behaviourally relevant both for interacting with objects and avoiding obstacles. While this can be explained by reference frame conversions (i.e., converting visual information to a stable body-centred reference frame, such as one fixed to the head or arm), the stability of visual information regarding the locations of distal objects (i.e., those not in contact with our bodies), is more likely related to the continuous updating, or remapping, of visual space. This review will present and discuss evidence that suggests that the updating of remembered visual space occurs in a reference frame that is centred on the eye.

2. Behavioural evidence of eye-centred spatial updating

Remembered locations of pointing targets have been shown to be remapped following an intervening saccade (Henriques, Klier, Smith, Lowy, & Crawford, 1998). When subjects moved their eyes after briefly foveating a target before pointing to its remembered location, they overestimated the location of the remembered target relative to gaze. That is, when the eyes are repositioned to the right of a remembered target location, there is a leftward pointing error (and *vice versa*). This pattern of pointing error is consistent with those errors produced when pointing to targets that are only ever peripherally viewed (Bock, 1986).Since subjects showed the same pattern of errors when they foveated a target then looked away (as in Henriques et al. (1998)), as they did when pointing to a remembered target seen only peripherally – known as the retinal magnification effect – (as in Bock (1986)), it seems that remembered target locations are stored and updated in an eye-centred reference frame – the foveated target is remapped to the retinal periphery when the eyes move away. Other gaze-*independent* models (like one fixed to the head) cannot explain why a subsequent movement of the eyes following foveation (i.e., after the reference frame conversion) would lead to systematic reaching errors that are exclusively dependent on the location of the remembered target relative to gaze. Thus, these results suggest that these target locations in eye-centred coordinates are not converted to a muscle-based frame (e.g., one centred on the arm or on the hand), at least until the decision is made to generate an action toward that target (i.e., the Conversion on Demand Model, Henriques et al., 1998).

The updating of visuospatial memory relative to eye direction has also been demonstrated for a variety of different task parameters and experimental setups. These include the updating of remembered space in eye-centred coordinates for: near and far visual targets (Medendorp & Crawford, 2002; Van Pelt & Medendorp,

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2008); both explicit (distinct) and implicit (implied by the convergence point of a full field motion pattern) visual targets (Poljac & van den Berg, 2003); angular distances of the target relative to gaze produced by translating the entire body (Van Pelt & Medendorp, 2007); changing starting positions of both the seen and unseen hand (Beurze, Van Pelt, & Medendorp, 2006); multiple reaches to the same remembered target site with an intervening eye movement between reaches (Sorrento & Henriques, 2008); auditory (Pouget, Ducom, Torri, & Bavelier, 2002) and proprioceptive pointing targets (Blangero et al., 2007; Jones, Cressman, & Henriques, 2009; Pouget et al., 2002); and when judging the relative location of remembered visual and proprioceptive stimuli relative to the hand (Fiehler, Rosler, & Henriques, 2010). These studies indicate that not only are visual targets updated in an eye-centred reference frame, but non-visual targets are also stored and updated in an eye-centred reference frame.

3. Neurophysiological and functional imaging evidence

In addition to these behavioural studies, functional magnetic resonance imaging (fMRI) studies in humans and direct recording studies in non-human primates have demonstrated neural correlates of eye-centred spatial remapping. Eye-centred updating of remembered visual space has been shown (both in humans and monkeys) in many brain areas, particularly sub-regions of the posterior parietal cortex (PPC). In monkeys, neurophysiological recordings have shown remapping of reach targets specifically in the medial intraparietal (MIP) area, while predictive remapping of saccadic targets has been shown in the lateral intraparietal (LIP) area, superior colliculus (SC), frontal eye field (FEF), and extrastriate areas. We discuss this evidence in detail below.

fMRI studies using human participants have found that saccade and hand-related areas of PPC were active for memory guided saccades and reaches to peripherally viewed targets in the contralateral visual field (Medendorp, Goltz, Vilis, & Crawford, 2003). That is, a *remembered* target that was seen on the left caused activation in the right PPC. More importantly, when the eyes moved to the right (opposite) side of the remembered target, the activation in PPC shifted to the left (opposite) hemisphere, demonstrating that the target location had in fact been remapped as a function of the remembered target's new location relative to the new gaze direction. This remapping of the remembered object locations has also been shown when subjects merely had to attend to the remembered location in both the PPC (Merriam, Genovese, & Colby, 2003), and extrastriate areas (Merriam, Genovese, & Colby, 2007).

The modulating PPC activity reported in the human neuroimaging studies described above is coincident with activity in the analogous MIP area in the parietal reach region (PRR) of the monkey brain, which shows evidence of eye-centred updating of visual reach targets (Batista, Buneo, Snyder, & Andersen, 1999). Other neurophysiological studies in monkeys have also shown target coding (but not updating) in MIP (Buneo, Jarvis, Batista, & Andersen, 2002; Buneo & Andersen, 2006; Pesaran, Nelson, & Andersen, 2006). However, while Batista et al. (1999) showed updating for reach targets, predictive or anticipatory updating has never been shown for reach targets, but has been for saccadic targets. Specifically, anticipatory remapping of visual space has been shown in neurons in area LIP (e.g., Duhamel, Colby, & Goldberg, 1992; Vaziri, Diedrichsen, & Shadmehr, 2006). It is anticipatory/predictive updating of visual space that allows for the perception of visuospatial constancy spoken about earlier.

Duhamel et al. (1992) propose the following mechanism for anticipatory updating. Efference copy signals of planned eye movements allow neurons to modify firing rates in anticipation of a saccade that will bring a target into, or out of, its receptive field. In response to a planned eye movement, the neuronal activity shifts accordingly with the impending shift of the retinal image. This creates a dynamic link between retinal images across the eye movement, allowing continuous remapping of visual space in eye-centred coordinates. It is in this way that predictive or anticipatory changes in firing rates contribute to the construction and maintenance of a stable representation of our visual world (Duhamel et al., 1992). The real advantage of this type of forward model is that remapping visual space anticipatorily provides an estimate of the target location prior to the availability of visual and proprioceptive feedback following a shift in gaze. In other words predictive remapping overcomes delays in sensory feedback. A predicted target location can then be compared with the sensory feedback once it is available (Vaziri et al., 2006). Predictive remapping has also been shown to occur in an eye-centred reference frame in neurons in the SC (e.g., Walker, Fitzgibbon, & Goldberg, 1995; Dunn, Hall, & Colby, 2010), the FEF (e.g., Cassanello & Ferrera, 2007; Crapse & Sommer, 2008; Umeno & Goldberg, 1997), and extrastriate areas (e.g., Nakamura & Colby, 2002).

Importantly, there is also an anticipatory response when the location of a previously displayed stimulus is about to be brought into the receptive fields of 44% of neurons recorded in LIP by Duhamel and colleagues (1992). This means even the memory of visual space is predictively remapped relative to the new position of the eyes (as shown in the analogous areas of human PPC by Medendorp and colleagues described above). The predictive remapping of *remembered* space is of critical importance because many of the tasks that we perform on a daily basis rely on visuospatial memory. For example, when someone reaches for a cup of coffee while working at a computer, they usually look to the cup and back to the screen before reaching for the coffee. This reaching movement, then, is based on the remembered location of the cup, which has since become peripherally displaced relative to gaze. This intervening eye movement would require predictive remapping of the remembered location of the cup relative to gaze, and in turn the way in which we direct our hand to it.

In addition to efference copy signals, neurons also have access to proprioceptive information of eye orientation, and of course retinal information, both of which also make a contribution to neuronal activity. For instance, neuronal firing rates in area 7a of the inferior parietal lobule (IPL) are modulated by images brought into or out of their receptive fields, by both retinal position and by the position of the eye in the head (Andersen, Essick, & Siegel, 1985). For example a neuron may fire preferentially when an image is projected on the retina 5° to the left of the fovea, and may also fire preferentially when the eye is rotated in the head to the left. If the eye were rotated in the head to the left, and while in this position there was also an image projected on the retina that was 5° to the left of the fovea, then the firing rates of these neurons would modulate multiplicatively. That is, retinal and extraretinal information (i.e., proprioception) is combined resulting in neuronal gain fields for which firing rates for varying retinal displacements are modulated in magnitude as a function of eye position relative to the head (Zipser & Andersen, 1988; Andersen, Snyder, Batista, Buneo, & Cohen, 1998; Snyder, Batista, & Andersen, 1998). While this type of activity modulation is important in the process of using visual information to direct action, it is useful at a later stage of movement generation. That is, it is likely more related to the linkage geometry comparisons required for motor implementation than it is to the updating of visual space *per se*. Visuospatial updating can be more directly related to the compensation for eye movements (resulting in changes in retinal position) by the use of efference copy signals of the eye movements (available before the eye movement is initiated) as described earlier, than by the combination of retinal and proprioceptive information described here. In

fact, predictive remapping can only be explained by efference copy signals (see Klier & Angelaki, 2008, for a review).

The findings of these electrophysiological and brain imaging studies, when taken together with the psychophysical findings discussed above, strongly suggest that target locations for both eye and arm movements are stored, and continuously updated, in eye-centred coordinates as a function of eye movement. However, a number of related questions remain unanswered in the literature. For the remainder of this review, we will discuss results from some recent behavioural experiments from our lab, and explain their contribution to our understanding of visuospatial updating. Specifically the experiments that we will discuss here address the following questions: will the eye-centred visual updating demonstrated following saccades (e.g., Henriques et al., 1998; Sorrento & Henriques, 2008) also be demonstrated after smooth-pursuit movements?; how are retinal (e.g., background movement) and extraretinal (e.g., efference copy signals of the oculomotor command) sources of information used by the brain in the eye-centred updating of visuospatial memory?; and, finally, are multiple target locations all coded egocentrically (i.e., independently, and relative to the eye) or are they coded allocentrically (i.e., relative to each other)? Through bettering our understanding of what information is being used (from experimental evidence addressing

the above questions) and when it is being used (from recent results of ongoing research that we are conducting), we present a conceptual model in an attempt to adequately describe the visual-to-motor transformation problem for goal-directed reaching and pointing.

4. Visuospatial updating following saccadic versus smooth-pursuit eye-movements

We cannot assume that targets are updated following smooth-pursuit eye movements just as they are following saccades given the different structures and pathways involved in generating and controlling the two types of movement (e.g., for saccades, the intraparietal sulcus [IPS], the junction of the IPS and transverse occipital sulcus [IPTO], and supplementary eye fields [SEF]; and for smooth-pursuit, the Pons, Cerebellum, and medial temporal complex [MT+]; see Krauzlis, 2005, for a review). So, we investigated the updating of visuospatial memory following smooth-pursuit (Thompson & Henriques, 2008).

Fig. 1A shows the general experimental setup that was used for all the experiments that will be discussed in the remainder of this review. For these particular conditions, participants pointed to the remembered location of a briefly viewed target following either a
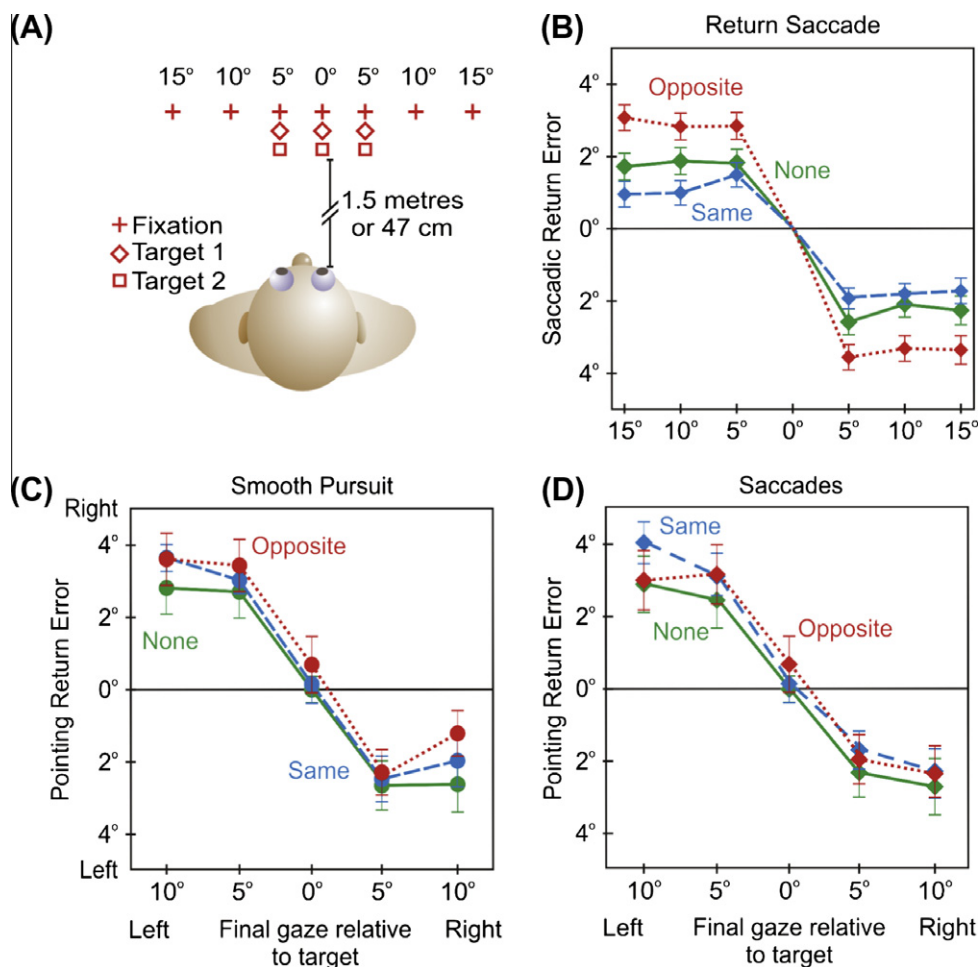

Fig. 1. A: Display and experimental setup for all experiments described here. The three pointing targets (diamonds for first reaches, and squares for second reaches when applicable) were located directly in front of the right eye (0°), and 5° to left and right of centre. The seven possible fixation crosses were located 15°, 10°, and 5° to the left and to the right of the central fixation cross (0°). All stimuli were rear projected onto a screen at a viewing distance of 1.5 m or onto a touch screen vertically mounted on the table surface 47 cm from the participants' right eye depending on the experiment. All experiments were conducted in total darkness with no visual feedback of any kind, and the head was fixed by a bite bar. B: Return saccade errors following a smooth-pursuit movement away from the target with a background moving in the same direction (blue dashed), in the opposite direction (red dotted), or not moving (green solid). C and D: Pointing errors following smooth-pursuit (C, circles) and saccadic (D, diamonds) movements made when the background moved in the same direction (blue dashed), in the opposite direction (red dotted), or not at all (green solid). In each panel, the horizontal line at 0° represents accurate pointing or accurate return saccades. Error bars are standard error of the mean. Adapted from Thompson and Henriques (2008).

saccade or a smooth-pursuit to an eccentric fixation location. In the pursuit-updating condition, a fixation cross appeared in the same location as the pointing target and then moved to one of seven fixation locations at a constant velocity of 10°/s cuing participants to smooth-pursuit. The cross then disappeared within 1 s of reaching its final location. In the saccade-updating condition, the cross appeared at one of the seven eccentric locations cuing a saccade to this location. After the cross disappeared, participants pointed to the remembered location of the pointing target (diamond) without moving their eyes from the final location of the cross.

We found the remembered locations of pointing targets are, in fact, updated following smooth-pursuit eye movements, just as they are following saccadic eye movements, as illustrated by the similar pattern of errors as a function of final gaze direction relative to the target (solid green lines) in Fig. 1C and D. This finding is consistent with recent evidence that suggests that many of the areas previously thought to be involved in only one type of eye movement or the other may in fact be involved for both (see Krauzlis, 2005, for a review).

5. Retinal versus extraretinal information in visuospatial updating

Given that updating following pursuit movements resulted in a similar pattern of error found in updating following saccades, we were able to use smooth-pursuit movements to investigate the role of retinal information in the updating of visual space. While, there is a great deal of evidence suggesting that updating spatial memory involves efference copy signals (e.g., Duhamel et al., 1992; Heide et al., 2001; Tsotsos & Henriques, 2007), it is not known to what extent visual information might also contribute to estimating how much the eyes have moved (i.e., the magnitude and direction by which pointing targets would be remapped). Due to saccadic suppression, we would not expect retinal information during a saccade to influence updating, so we investigated updating during smooth-pursuit movements since the relatively slow velocity of the eye would allow us to ascertain the role of retinal information during the eye movement. The retinal information that we manipulated in this experiment was a cue to retinal motion in the form of a moving background.

A background moving opposite to the direction of the eye may lead to a misperception of eye movement velocity, because there is normally an inherent movement of the visual scene across the retina in the opposite direction of the eye movement during smooth-pursuit. This misperceived velocity would therefore lead to a misperception of eye movement amplitude: the perception that the eye has moved farther than it actually has exists despite an accurate efference copy of the actual movement made. Therefore, this illusory retinal motion may interfere with accurate feedback/reafference signals of the eye movements. After all, this type of illusory motion has already been shown to influence goal-directed reaching endpoints (e.g., Whitney, Westwood, & Goodale, 2003), suggesting that retinal information may be weighted more heavily in the optimal combination of information sources suggested earlier. So, the moving background condition in our experiment was to test if visual information (such as a task-irrelevant contextual moving background; c.f. Whitney et al., 2003) plays a role in estimating eye movements for updating the remembered location of pointing targets. Our experiment differed from Whitney et al. (2003) in that our background was no longer visible during the reach. That is, the motion of the background influenced only the perception of the eye movement amplitude, and had no online influence during the pointing movement.

We first established that the moving background did in fact affect the estimate of the amplitude of eye-movement away from the target (Thompson & Henriques, 2008). Participants again made smooth-pursuit eye movements away from a briefly displayed target, but the eye movements were made against a background which was stationary, or moving either with or opposite to the required eye movement direction at the same velocity as the eye. After completing the eye movement participants then saccaded back to the remembered target (i.e., starting) location. As shown in Fig. 1B, participants significantly overshot the remembered target location after they performed a smooth-pursuit against an oppositely moving background (red diamonds, dotted line). However, there was no significant effect of the background when it moved in the same direction as the eye (i.e., a static retinal image) or when it remained stationary (i.e., as the background does in the real world; represented by the blue diamonds and dashed line, and green diamonds and solid line respectively). In fact the error associated with return saccades following an outbound pursuit movement with the background moving in the same direction or remaining stationary did not differ from errors made when there was no background present at all (not shown, see Fig. 4 of Thompson & Henriques, 2008).

We then incorporated both saccades and smooth-pursuit movements away from the presented target location, and required pointing movements to the remembered location of that target rather than a return saccade. As shown in Fig. 1C and D, there was no significant effect of the background motion on horizontal pointing error for either outbound saccade movements (overlapping symbols in panel D) or smooth-pursuit (overlapping symbols in panel C). Again we found no difference in pointing error between the two types of eye movements. While visual information influences estimates of eye movement amplitudes for updating remembered saccade targets, this misestimate does not influence the updating of visuospatial memory for pointing movements. This suggests that the oculomotor and arm-motor systems may rely on different sources of information for spatial updating.

One might have argued that the low velocity of the eye as it moved away from the target would have allowed for a series of position comparisons, thus reducing the overall error in the position estimate of the target location. However, as we have shown, this is not the case which further supports that a remembered target is held in eye-centred coordinates and updated continuously as the eye moves away from a remembered target location irrespective of the speed at which the eye moves. The pointing error is not due to a sudden remapping of the target location to the retinal periphery following a saccade. Rather, the target is continuously remapped the same way regardless of movement velocity.

Despite the forgoing evidence, the similarities of structure and function in the pathways involved in saccades and smooth-pursuit discussed earlier may not be the critical feature here. It might be that no matter how the eye direction changes relative to the target the location would still be updated in eye-centred reference frame. After all, remembered visual targets are also updated in eye-centred coordinates following head movements (e.g., Medendorp, Smith, Tweed, & Crawford, 2002), and full body translation (e.g., Van Pelt & Medendorp, 2007). It may be that the updating of visuospatial memory in eye-centred coordinates can be generalised not only across different types of eye movements but also across all types of movement that displace the eye relative to the target.

6. Ego- versus allo-centric information in coding and updating sequential reach targets

We more commonly perform tasks that are much more complex than the ones described so far. Earlier we described an everyday scenario of reaching for a cup of coffee while working at a computer, but more realistically we would look to the cup and then

to several other locations before initiating the reach to the cup of coffee. We may also plan a series of reaches following our initial movement, such as returning the cup to its location on the desk and then reaching back to the computer mouse. To successfully navigate around all these objects we may also code the relative positions of the cup to the mouse, the cup to the monitor, the mouse to the monitor, etc... It becomes clear that understanding the relative contributions of egocentric and allocentric target coding is important in understanding how we code the locations of targets in the real world; particularly when coding the locations of subsequent targets in a planned sequence of movements, as in this example.

We have already described a number of studies that have demonstrated that the remembered locations of visual pointing targets are remapped in eye-centred coordinates following intervening eye-movements. Furthermore, previous studies from our lab have demonstrated that multiple reaches to the same remembered target location (when there is an intervening saccade between reaches), each reflect the current gaze direction relative to the target. This suggests that the remembered target locations are updated as a function of gaze direction relative to target for each reach. We have found this when reaching to point (Sorrento & Henriques, 2008), when reaching to touch (Thompson, Sharma, & Henriques, 2008), and even when the first reaching movement was made to a visible target (Fiehler, Schütz, & Henriques, 2011). In both Sorrento and Henriques (2008) and Thompson et al. (2008), participants viewed a briefly flashed target, performed a saccade to an eccentric fixation location, reached to the remembered location of the target, performed another saccade to a second fixation location and then reached again to the *same* remembered location of the target. In both studies, horizontal errors of both reaches differed by an average of 4°, since each reach was modulated as a function of current gaze relative to the remembered location of the target. But what if these multiple reaches with intervening saccades are performed to multiple target locations (such as to a coffee cup and then to a computer mouse, as in the real world example described above) rather than to the same

remembered target location (as in Sorrento and Henriques (2008) and in Thompson et al. (2008))? When more than one target is presented in sequence, are reaching movements made to subsequent targets coded relative to the first target (i.e., allocentrically), or are all targets coded independently, and relative to the direction of the eye (i.e., egocentrically)?

In this experiment (Thompson & Henriques, 2010a), participants begin by foveating a target (red diamond; Fig. 1A), followed by a second target (red square; Fig. 1A), followed by a fixation cross displayed at one of seven possible locations (Fig. 1A) to either side of the two presented targets. Participants then maintain fixation at this location while reaching to touch (on a touch screen) the remembered location of the first target (i.e., the diamond). In these same trials, the fixation cross then either remains in the same location, or reappears to the opposite side of the second target site, after completion of the first reach. Participants then either maintain fixation (if the cross remains in the same location), or make a saccade to the new fixation location (if it jumps to the opposite side of the target site), and then reach to touch the remembered location of the second target (i.e., the square).

Since the two targets are always 5° apart, if they are coded relative to each other then there should be no change in the relative distance between reach endpoints as shown in Fig. 2Av (i.e., our allocentric predictions based on gaze-free controls – gaze-free controls provide allocentric predictions because the egocentric updating that results from eccentric fixation is not present and so the only change in cue presentation is one target relative to the other). If, however, each of the targets is coded independently relative to gaze, then the relative distance between reaches to these targets would change as a function of the changes in gaze (i.e., the distance between reach endpoints would be small as in Fig. 2Ai and iii, or large as in Fig. 2Aii and iv).

In Fig. 2A we compare the actual reach endpoints with the eye-centred, egocentric predictions (i–iv). The eye-centred egocentric predictions are shown as dark grey bars, which indicate the relative distances between endpoints of reaches to the first target following a single saccade (i.e., to a single fixation direction, F1, that is
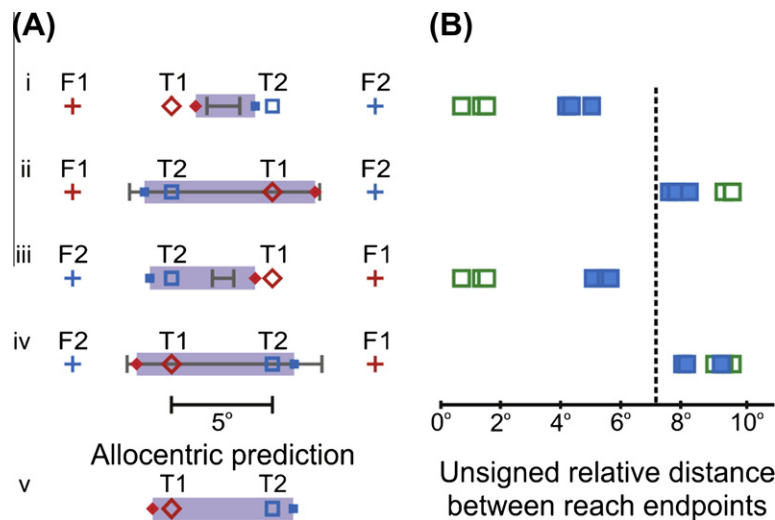

Fig. 2. A: The actual reach endpoints of the first reach (small filled red diamonds) to the first target (large open red diamonds) and of the second reach (small filled blue squares) to the second target (large open blue squares) when the eyes moved to the opposite side of the target locations between reaches for all presentation orders of fixation and targets. The relative distance between these two reach endpoints is highlighted by the mauve bars. The predicted relative distance between reach endpoints if the two targets are coded in eye-centred egocentric frame (based on actual reach endpoints to a single target following a single saccade) is represented by the dark grey bars. Panel v represents the actual relative distance between reaches with freely gazing and represents the predicted relative distance if the two targets are coded allocentrically. B: A comparison of actual and predicted data. The actual unsigned relative distance between reach endpoints with an intervening saccade between them (filled blue squares) for the four different combinations of target and gaze direction shown on the left (same as those in Ai–iv), the unsigned relative distance between reach endpoints predicted by eye-centred egocentric coding (hollow green squares; similar to dark grey bars in A) and the predicted unsigned relative distance between reach endpoints for allocentric/relative coding (vertical dashed line; equal to Av). Adapted from Thompson and Henriques (2010a).

maintained during both reaches) after viewing both targets – so the predictions are based on single reaches when the eyes do not move. As such, these bars represent what the relative distance between reach endpoints would be if the two targets were coded completely independently as a function of gaze relative to the respective targets (i.e., egocentrically in an eye-centred frame). Given that errors for reaches to a single target systematically vary as a function of gaze, the relative location of the first (T1, open red diamond) and second (T2, open blue square) targets, and the first (F1, red cross) and second (F2, blue cross) fixation crosses, leads to clear differences in the predicted relative distance between the two reach endpoints. The actual endpoints of the first (solid red diamonds) and second (solid blue squares) reaches, for the different target-fixation combinations (i–iv) are indicated with their relative distances highlighted by the mauve bands. Consistent with the eye-centred egocentric predictions, we can see that the sequence and locations of targets and fixations do impact the relative distance between the two reach endpoints. But while the pattern of errors modulates as a function of current gaze direction relative to the target, the remapping was not completely egocentric. The reach errors fell between where we would have predicted them to for egocentric and allocentric coding (Fig. 2A).

In Fig. 2B, this is represented in a different way. Here, the unsigned relative distances between reaches predicted by eye-centred egocentric coding are represented by the hollow green squares (i.e., they should be similar to those distances represented by the dark grey bars in Fig. 2A, but here are shown for each of the three target locations). The unsigned relative distance between reach endpoints predicted by gaze-free controls (i.e., if the targets are coded allocentrically) is represented by the vertical dotted line. The actual unsigned relative distances between reaches with an intervening saccade are represented by the blue squares for the four general fixation-target combinations shown in Fig. 2A. Again we see that the relative distances between reaches with intervening saccades (blue squares) fall between our eye-centred (green squares) and allocentric (vertical dotted line) predictions. When the eye-centred predicted distances between reach endpoints become unrealistically small, given that the participants had viewed the two targets at a separation of 5°, it seems there is less of an influence of egocentric information and more of a reliance on allocentric information.

To determine the relative contributions of egocentric and allocentric information we fit a multidimensional mixed-model regression to the data for each subject. The equation of the model is as follows:

$$Err_2 = a_0 + a_{Err_1} * Err_1 + a_{\Delta T} * \Delta T + a_{T_2\text{-}EP_1} * (T_2 - EP_1) - a_{\Delta EP} * \Delta EP \tag{1}$$

In this equation parameters Err_1 and Err_2 represent reaching errors for the first and second reaches respectively, The allocentric component is represented by ΔT – the signed distance (in degrees) between the two target positions, the egocentric component is accounted for by T_2-EP_1 which represents the relative position (in degrees) of the second target to the first eye position, and ΔEP is the change in gaze direction (i.e., an estimate of the amount of egocentric updating of the second target location; also in degrees).

In Fig. 3 we plotted the absolute values of the coefficients representing the allocentric contribution, against those representing the egocentric contribution. In this plot exclusive allocentric coding would be represented by a steeper than unit slope (i.e., approaching infinity), whereas exclusive egocentric coding would be reflected by a horizontal slope (i.e., approaching 0). Here we see that the slope of the line of best fit falls in an intermediate position between these two extremes suggesting that both sources of information are being used. Particularly when we consider the
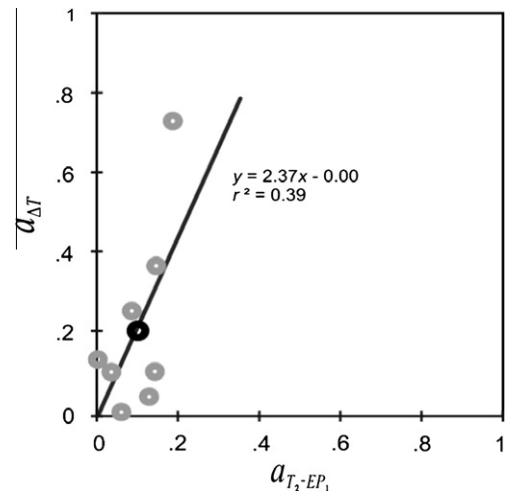

Fig. 3. The absolute values of the coefficients of representing the allocentric contribution (ΔT) as a function of those representing the egocentric component (T_2-EP_1) for each subject (grey circles) and the group mean (black circle). The dark grey line represents the line of best fit. Allocentric target coding would be reflected by a steeper than unit slope, while egocentric coding would be reflected by a shallower slope. Adapted from Thompson and Henriques (2010a).

magnitude of the modulation of eye position (as illustrated in Fig. 2B) it is clear that both allocentric and egocentric coding are used. The two sources of information are likely combined in a weighted average that shifts depending on the relative usefulness of the information source depending on the task parameters. A similar combination of egocentric and allocentric information based on the reliability of the cues provided has also been recently reported elsewhere (Byrne & Crawford, 2010).

So, when coding multiple target locations, the targets are coded both egocentrically (specifically in an eye-centred frame), and allocentrically. The task constraints of this experiment do not allow us to determine if some of the apparent influence of allocentric information on visuospatial updating is due to any other gaze-independent coding or factor, such as a seen difference between the two targets, as well as efference copy signals from the saccade between the two target locations. Likewise, some of the apparent influence of allocentric information may be egocentric, but gaze-independent (i.e., derived in some other body- or motor-centred frame). However, since the head and body are fixed here, the only changing egocentric reference frame is one centred on the eye. It is likely that multiple reference frames are used for the planning and execution of serial reaches, but clearly one of these representations is an egocentric eye-centred reference frame, and it seems that allocentric information is used to varying extents depending on its usefulness given the specific parameters of the task.

7. Summary and general discussion

We have shown that visuospatial memory is updated as a function of gaze direction relative to a remembered reaching target location following smooth-pursuit movements, in the same way that it is following saccades. These experiments also demonstrated that both retinal and extraretinal information are used in programming goal directed movements of both the eye and the arm; however, retinal (background) information plays a role in the spatial updating of visual memory for saccadic targeting, but not for pointing. This is likely due to the differing functional roles of the oculomotor and arm-motor systems, where the eyes move as a perceptual tool for information gathering, and the arm moves to physically interact with objects in space. This explanation is consistent with previous findings from a perception–action
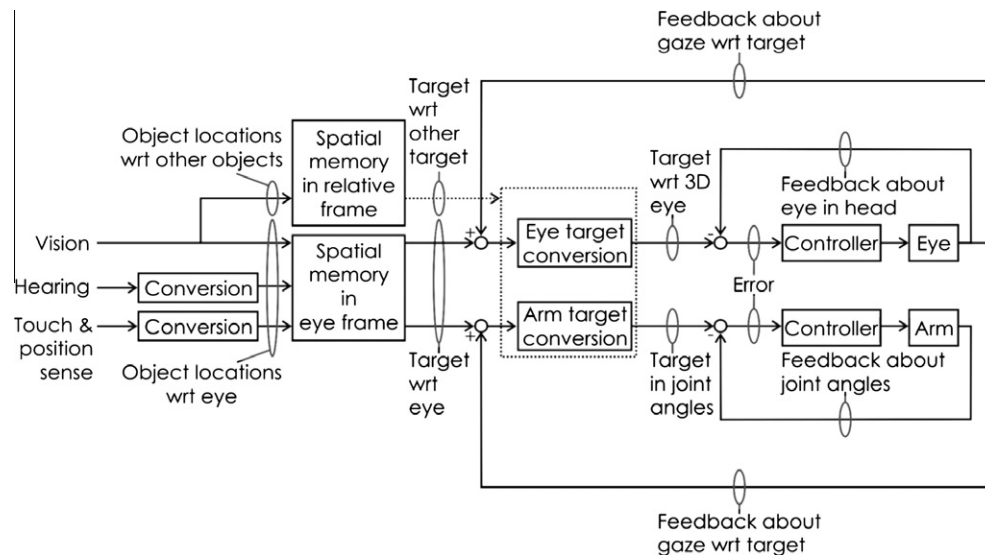
Fig. 4. A conceptual flow diagram of spatial updating. The visual target(s) is/are stored in memory in an eye-centred reference frame. Auditory and tactile/proprioceptive targets may also be converted to, and stored in an eye-centred reference frame as well. The position of the target in eye-centred coordinates is then converted to muscle based coordinates for both the arm-motor and the oculomotor systems in parallel. The error signal in the arm-motor loop is the difference between the representations of the target in arm or joint coordinates and feedback of arm position coded in the same coordinates. Similarly, there is an error signal of the 3-dimensional eye position in the head. The new position of the target relative to the eye is recomputed as the eye moves and continuously fed back to both systems. By these means, as the eyes move, the new eye position is continuously updated leading to a newly converted joint-based representation of the model. This is what allows the online updating of visuospatial memory in eye-centred coordinates even while the arm is moving.

decoupling experiment, where saccadic eye movements were affected by pictorial illusions whereas reaches to the same stimuli were unaffected (Thompson & Westwood, 2007).

Further, we have shown that both egocentric and allocentric information are used in the coding and updating of serial reach targets. Our data suggests that the two sources of information might be combined in some weighted fashion that probably depends on the usefulness of the information given the circumstances. While the brain likely uses multiple sources of egocentric information – including efferent signals from the eye and arm – when programming the second reach, the relative location of the second target to the first, and the gaze direction relative to each target both reliably and significantly influence reach error to both targets. It is clear that one of the possible multiple reference frames used to code the subsequent reach targets in this task is one that is egocentric and centred on the eye.

Fig. 4 illustrates a conceptual model of how these findings are combined. This model shows that visual targets are coded both egocentrically and allocentrically before being converted to muscle-based reference frames for both the eye and the arm. We are unable to determine what the role of allocentric information in the control of the arm and the eye are independently at this time. These data suggest that the allocentric coding is incorporated, but at this point we cannot be sure how or where, so we have left its incorporation in the model somewhat ambiguous. Proprioception of the arm is continuously compared to the desired motor outcome and the flight path is modified accordingly to reduce the error vector between hand and target to zero. In this conceptual model the position of the eye in the head is also continuously compared to the efference copy of the original motor plan. The efferent (predictive) and proprioceptive information about the eye are also continuously fed back into both the oculomotor and arm-motor systems allowing for a continuous reconversion of the target from eye-centred coordinates to the muscle-based frames. This allows the error signal of both the arm and the eye to be compared continuously to an instantaneously changing representation of the target in motor coordinates freshly converted from eye-centred coordinates as the eyes are moving [consistent with recent findings from

our lab that suggest that visuospatial memory is continuously updated in eye-centred coordinates even when the eyes move while a reaching movement is being executed (Thompson & Henriques, 2010b)].

In summary: remembered visual target locations are coded and continuously updated in eye-centred coordinates, even after the initiation of an action toward one of these remembered target locations; retinal and extraretinal (i.e., proprioception and efference copy signals) information both play a role in updating visuospatial memory, but they are used differently in the planning and execution of eye versus arm movements; and finally, egocentric and allocentric sources of information are both used in the coding and updating of serial reach targets. It is our goal to further develop our understanding of these factors and to create a model that can explain all of these complexities.

References

Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science, 230*, 456–458.

Andersen, R. A., Snyder, L. H., Batista, A. P., Buneo, C. A., & Cohen, Y. E. (1998). Posterior parietal areas specialized for eye movements (LIP) and reach (PRR) using a common coordinate frame. *Novartis Foundation Symposium, 218*, 109–122 (discussion 122–108, 171–105).

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science, 285*, 257–260.

Beurze, S. M., Van Pelt, S., & Medendorp, W. P. (2006). Behavioral reference frames for planning human reaching movements. *Journal of Neurophysiology, 96*, 352–362.

Blangero, A., Ota, H., Delporte, L., Revol, P., Vindras, P., Rode, G., et al. (2007). Optic ataxia is not only 'optic': Impaired spatial integration of proprioceptive information. *NeuroImage, 36*(Suppl. 2), T61–T68.

Bock, O. (1986). Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. *Experimental Brain Research, 64*, 476–482.

Buneo, C. A., & Andersen, R. A. (2006). The posterior parietal cortex: Sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia, 44*, 2594–2606.

Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002). Direct visuomotor transformations for reaching. *Nature, 416*, 632–636.

Byrne, P. A., & Crawford, J. D. (2010). Cue reliability and a landmark stability heuristic determine relative weighting between egocentric and allocentric visual information in memory-guided reach. *Journal of Neurophysiology, 103*, 3054–3069.

Cassanello, C. R., & Ferrera, V. P. (2007). Visual remapping by vector subtraction: Analysis of multiplicative gain field models. *Neural Computation, 19*, 2353–2386.

Crapse, T. B., & Sommer, M. A. (2008). The frontal eye field as a prediction map. *Progress in Brain Research, 171*, 383–390.

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science, 255*, 90–92.

Dunn, C. A., Hall, N. J., & Colby, C. L. (2010). Spatial updating in monkey superior colliculus in the absence of the forebrain commissures: Dissociation between superficial and intermediate layers. *Journal of Neurophysiology*.

Fiehler, K., Rosler, F., & Henriques, D. Y. (2010). Interaction between gaze and visual and proprioceptive position judgements. *Experimental Brain Research*, 55>.

Fiehler, K., Schütz, I., Henriques, D.Y. (2011). Gaze-centered spatial updating of reach targets across different memory delays. *Vision Research*, doi:10.1016/j.visres.2010.12.015.

Heide, W., Binkofski, F., Seitz, R. J., Posse, S., Nitschke, M. F., Freund, H. J., et al. (2001). Activation of frontoparietal cortices during memorized triple-step sequences of saccadic eye movements: An fMRI study. *European Journal of Neuroscience, 13*, 1177–1189.

Henriques, D. Y., Klier, E. M., Smith, M. A., Lowy, D., & Crawford, J. D. (1998). Gaze-centered remapping of remembered visual space in an open-loop pointing task. *Journal of Neuroscience, 18*, 1583–1594.

Jones, S. A., Cressman, E. K., & Henriques, D. Y. (2009). Proprioceptive localization of the left and right hands. *Experimental Brain Research*.

Klier, E. M., & Angelaki, D. E. (2008). Spatial updating and the maintenance of visual constancy. *Neuroscience, 156*, 801–818.

Krauzlis, R. J. (2005). The control of voluntary eye movements: New perspectives. *Neuroscientist, 11*, 124–137.

Medendorp, W. P., & Crawford, J. D. (2002). Visuospatial updating of reaching targets in near and far space. *NeuroReport, 13*, 633–636.

Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *Journal of Neuroscience, 23*, 6209–6214.

Medendorp, W. P., Smith, M. A., Tweed, D. B., & Crawford, J. D. (2002). Rotational remapping in human spatial memory during eye and head motion. *Journal of Neuroscience, 22*, RC196.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2003). Spatial updating in human parietal cortex. *Neuron, 39*, 361–373.

Merriam, E. P., Genovese, C. R., & Colby, C. L. (2007). Remapping in human visual cortex. *Journal of Neurophysiology, 97*, 1738–1755.

Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences of the United States of America, 99*, 4026–4031.

Pesaran, B., Nelson, M. J., & Andersen, R. A. (2006). Dorsal premotor neurons encode the relative position of the hand, eye, and goal during reach planning. *Neuron, 51*, 125–134.

Poljac, E., & van den Berg, A. V. (2003). Representation of heading direction in far and near head space. *Experimental Brain Research, 151*, 501–513.

Pouget, A., Ducom, J. C., Torri, J., & Bavelier, D. (2002). Multisensory spatial representations in eye-centered coordinates for reaching. *Cognition, 83*, B1–B11.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1998). Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. *Journal of Neurophysiology, 79*, 2814–2819.

Sorrento, G. U., & Henriques, D. Y. P. (2008). Reference frame conversions for repeated arm movements. *Journal of Neurophysiology, 99*, 2968–2984.

Thompson, A. A., & Henriques, D. Y. (2008). Updating visual memory across eye movements for ocular and arm motor control. *Journal of Neurophysiology, 100*, 2507–2514.

Thompson, A. A., & Henriques, D. Y. (2010a). Locations of serial reach targets are coded in multiple reference frames. *Vision Research, 50*, 2651–2660.

Thompson, A. A., & Henriques, D. Y. (2010b). *Online updating of remembered visual space*. San Diego, CA: Society for Neuroscience.

Thompson, A. A., Sharma, R., & Henriques, D. Y. P. (2008). *Programming repeated reaches to remembered visual targets*. Montreal, QC: Canadian Association for Neuroscience.

Thompson, A. A., & Westwood, D. A. (2007). The hand knows something that the eye does not: Reaching movements resist the Muller–Lyer illusion whether or not the target is foveated. *Neuroscience Letters, 426*, 111–116.

Tsotsos, L. E., & Henriques, D. Y. P. (2007). *Estimating the size of eye movements for updating spatial memory*. Society for Neuroscience San Diego, CA.

Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *Journal of Neurophysiology, 78*, 1373–1383.

Van Pelt, S., & Medendorp, W. P. (2007). Gaze-centered updating of remembered visual space during active whole-body translations. *Journal of Neurophysiology, 97*, 1209–1220.

Van Pelt, S., & Medendorp, W. P. (2008). Updating target distance across eye movements in depth. *Journal of Neurophysiology, 99*, 2281–2290.

Vaziri, S., Diedrichsen, J., & Shadmehr, R. (2006). Why does the brain predict sensory consequences of oculomotor commands? Optimal integration of the predicted and the actual sensory feedback. *Journal of Neuroscience, 26*, 4188–4197.

Walker, M. F., Fitzgibbon, E. J., & Goldberg, M. E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *Journal of Neurophysiology, 73*, 1988–2003.

Whitney, D., Westwood, D. A., & Goodale, M. A. (2003). The influence of visual motion on fast reaching movements to a stationary object. *Nature, 423*, 869–873.

Zipser, D., & Andersen, R. A. (1988). A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. *Nature, 331*, 679–684.