Locations of serial reach targets are coded in multiple reference frames

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ABSTRACT

Previous work from our lab, and elsewhere, has demonstrated that remembered target locations are stored and updated in an eye-fixed reference frame. That is, reach errors systematically vary as a function of gaze direction relative to a remembered target location, not only when the target is viewed in the periphery (Bock, 1986, known as the retinal magnification effect), but also when the target has been foveated, and the eyes subsequently move after the target has disappeared but prior to reaching (e.g., Henriques, Klier, Smith, Lowy, & Crawford, 1998; Sorrento & Henriques, 2008; Thompson & Henriques, 2008). These gaze-dependent errors, following intervening eye movements, cannot be explained by representations whose frame is fixed to the head, body or even the world. However, it is unknown whether targets presented sequentially would all be coded relative to gaze (i.e., egocentrically/absolutely), or if they would be coded relative to the previous target (i.e., allocentrically/relatively). It might be expected that the reaching movements to two targets separated by 5° would differ by that distance. But, if gaze were to shift between the first and second reaches, would the movement amplitude between the targets differ? If the target locations are coded allocentrically (i.e., the location of the second target coded relative to the first) then the movement amplitude should be about 5°. But, if the second target is coded egocentrically (i.e., relative to current gaze direction), then the reaches to this target and the distances between the subsequent movements should vary systematically with gaze as described above. We found that requiring an intervening saccade to the opposite side of 2 briefly presented targets between reaches to them resulted in a pattern of reaching error that systematically varied as a function of the distance between current gaze and target, and led to a systematic change in the distance between the sequential reach endpoints as predicted by an egocentric frame anchored to the eye. However, the amount of change in this distance was smaller than predicted by a pure eye-fixed representation, suggesting that relative positions of the targets or allocentric coding was also used in sequential reach planning. The spatial coding and updating of sequential reach target locations seems to rely on a combined weighting of multiple reference frames, with one of them centered on the eye.

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1. Introduction

Findings from psychophysical (Beurze, Van Pelt, & Medendorp, 2006; Henriques et al., 1998; Medendorp & Crawford, 2002; Poljac & van den Berg, 2003; Sorrento & Henriques, 2008; Thompson & Henriques, 2008; Van Pelt & Medendorp, 2007), electrophysiological (Batista, Buneo, Snyder, & Andersen, 1999; Duhamel, Colby, & Goldberg, 1992; Nakamura & Colby, 2002), and brain imaging studies (Medendorp, Goltz, Vilis, & Crawford, 2003), strongly suggest that target locations for both eye and arm movements are stored, and continuously updated, in eye-centered coordinates (i.e., not eye position *per se*, but as a function of gaze direction relative to the target position), every time the eyes move.

The majority of the pointing studies examining the coding of target locations (e.g., in an eye-fixed reference frame) mentioned above are conducted with minimal visual feedback, to a single target in the dark. These designs allow the elimination of external or allocentric cues that would lead to coding the reach target in a reference frame external to the body (i.e., allocentric target coding). Other studies that have specifically investigated the role of allocentric target coding report that, when available, allocentric information is used differently under different contexts depending on its usefulness in the task, and the additive value of combining it with egocentric information (see Burgess, 2006 and Desmurget, Pelisson, Rossetti, and Prablanc, 1998 for reviews). However, the majority of behavioural studies investigating the contribution of allocentric information to target localisation involve either reaching in structured environments that are secondary to the targets or strictly perceptual localisation tasks. So, it is unknown how the brain combines egocentric and allocentric information about the next reach goal when planning and executing a series of movements.

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In the real world we do not often reach to single objects, but usually make a series of arm and hand movements while continuously moving our eyes through a rich tapestry of visual cues. So, understanding the relative contributions of egocentric and allocentric target coding is of great importance in understanding how we code the locations of targets in the real world; for example the relative positions of a coffee cup to a computer mouse, the cup to the computer monitor, the mouse to the monitor, etc... Consistent with this, there is recent electrophysiological evidence that the parietal reach region (PRR) in non-human primates, is not only involved in the spatial planning of reaches to single targets, but is also involved in planning reach sequences representing both immediate and subsequent movement goals (Baldauf, Cui, & Andersen, 2008). Likewise, neuroimaging results show that when participants make sequential *eye* movements to two remembered targets (i.e., double-step saccades), the activity in retIPS (retinotopic intraparietal sulcus) reflects the location of both of these targets relative to gaze (Medendorp, Goltz, & Vilis, 2006). Yet, very few studies have explored the reference frames used by the brain when planning sequential movements to a series of targets.

It has been found recently that the planning of the first of two reaches to two targets requires, at least in part, that the second reach already be planned (Herbort & Butz, 2009). This might suggest that an intervening eye movement between the reaching movements would not influence pointing behaviour of the second reach since the reach sequence is already programmed. However, previous work has also shown that repeated reaches to the same previously foveated remembered target (with an intervening – i.e., second – saccade between reaches) result in a pattern of reaching errors consistent with the recoding of the remembered target relative to gaze following the second saccade (Sorrento & Henriques, 2008). That is, each of the two reach errors is in the opposite direction of the current gaze relative to the target – when the eyes are to the right the error is to the left and *vice versa*. This pattern of error is consistent with the retinal magnification effect (Henriques et al., 1998). But importantly, this pattern of gaze-dependent reaching errors still occurs even after a previous hand movement has been made to the same target that was originally foveated (Sorrento & Henriques, 2008). This cannot be explained by other egocentric representations like those fixed to the head or body. We, and others have also found that this eye-fixed updating applies to both near and far targets (e.g., Medendorp & Crawford, 2002; Thompson, Sharma, & Henriques, 2008; Van Pelt & Medendorp, 2008).

The aim of this study is to determine whether the locations of targets presented sequentially would be coded relative to the first target presented (i.e., allocentrically) or if they would all be coded relative to gaze (i.e., egocentrically). To test this, we have had participants reach to two remembered targets, presented either simultaneously or sequentially, with gaze in a different direction for each reach. Since we only varied eye direction after the foveated targets have disappeared (and the head and body were fixed), we could only compare an egocentric representation fixed to the eye (rather than the head or body) with an allocentric (relative position) representation of the target. Thus, we use the terms egocentric and eye-centred/eye-fixed interchangeably. If the relative locations of these two targets are coded in this egocentric frame, then given the robust pattern of gaze-dependent errors found in studies for single reaches, the reaches to the second target should also vary systematically with gaze. Even more noticeably, the distance between the 2nd and 1st reaches should systematically vary depending on the direction of the current gaze relative to target for each reach. Yet, it is also very likely that the distances between these two targets are also coded allocentrically. This is especially true in this study where the second reach target is always 5° away (either to the left or the right) from the first target, providing a very

salient and persistent allocentric cue that can be used when programming the 2nd reaching movement. Thus if the two targets or the distance between them is coded allocentrically, then the difference between reach endpoints should not change regardless of any intervening change in gaze direction. In sum, an eye-fixed egocentric representation would predict specifiable differences in the distance between reaches depending on current gaze and target direction for each reach, while an allocentric representation would predict that this difference should not change; but remain constant independent of the two fixation and target directions.

2. Methods

2.1. Participants

Participants ($N = 8$; 3 male, 5 female) included healthy right-handed individuals between the ages of 20 and 26 years (mean: 23.3 ± 2.3 years). All participants were pre-screened verbally for self-reported handedness, and history of visual, neurological, and/or motor dysfunction. All participants had normal or corrected to normal vision, with three requiring glasses or contact lenses. Participants were recruited by word of mouth, and received no compensation for their participation in the study. All provided informed consent, and were treated in accordance with the ethical guidelines of York University's Human Participants Review Sub-committee.

2.2. Apparatus

Eye movements of the right eye only were recorded by infrared pupil identification with the EyeLink®II eye tracker (SR Research Ltd., Osgoode, ON) at a sampling rate of 250 Hz. At the start of each testing session, the apparatus was calibrated for each participant within the parameters specified by SR Research to ensure reliability of measurement.

Reach endpoint locations were measured via a 19″ touch screen panel (Magic Touch 2.0; KEYTEC Inc., Garland, TX) vertically mounted on the table top ∼47 cm from the subject's eyes.

2.3. Stimuli

All visual stimuli were generated by an Optikon XYLP-C Laser Scanner (Optikon Corporation Ltd., Kitchener, ON) and rear projected onto the touch screen panel described above. The stimuli used in the study consisted of an array of fixation-crosses and pointing targets (diamonds and squares), as shown in Fig. 1. Diamonds spanned 1.25 cm or 1.79°, squares spanned 0.9 cm or 1.29°, and the crosses spanned 2 cm or 2.86°. The central target location was located directly in front of the participant's right eye (0°), while the other two target locations were located 5° (6.1 cm) to its left and right. Crosses were located at 0°, 5°, and 10° to left and right of centre (Fig. 1).

2.4. Experimental setup

In each of the conditions described below the principle task was that participants reached to touch two briefly flashed (previously foveated) targets with no subsequent eye-movement restriction (gaze-free control conditions), or after moving their eyes to some fixed eccentric direction (remapping/experimental conditions). Participants were seated in complete darkness with their right eye aligned with the central target location, and their heads fixed by a bite bar.

Each trial began with participants pressing down on a single button mouse (Apple Canada Inc., Markham, ON) located to the
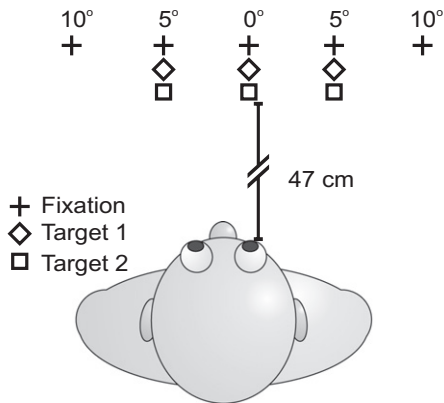
Fig. 1. Display and experimental setup for all conditions. The three pointing targets (diamonds and squares) were located directly in front of the right eye (0°), and 5° to the left and right of centre. The first target presented was always a diamond and the second target presented was always a square. The five fixation-crosses were located 10°, and 5° to the left and to the right of the central fixation cross (0°). All stimuli were rear projected onto a touch screen vertically mounted on the table surface 47 cm from the participants' right eye, and the head was fixed by a bite bar.

right of the body and within comfortable reach of the participants. The button press was used as a release switch for the display (i.e., targets only appeared when participants had their reaching hand at the start position). If the mouse was released at the wrong time (during the target or fixation display), that is if participants moved their hand too soon, the trial was aborted and repeated at a later time. Thus, the mouse ensured that participants began each trial with their right hand at the same start position, and that they did not prematurely begin a pointing movement. To prevent dark adaptation a halogen lamp was illuminated for 4 s at the end of each trial (i.e., during the intertrial interval). Experiments were otherwise performed in complete darkness.

2.5. Sequential target display task

In this task we wanted to determine how the location of a second target in a series would be coded when it was viewed immediately following another target (i.e., would the location of the second target be stored and updated relative to the remembered location of the first target, or would it be coded relative to gaze direction independent of the first target). Participants (instrumented and positioned as described above) briefly viewed a target (diamond; Fig. 2Ai; for 1 s) and then briefly viewed a second target (square; Fig. 2Aii; for 1 s), followed by a fixation cross to either side of the target presentation locations (Fig. 2Aiii). They then reached to touch (on the touch screen) the location of the first remembered target (Fig. 2Aiv). Upon completing their reach – before they could reach to the second target – the fixation cross jumped (in two thirds of all trials) to the opposite side of the target locations (Fig. 2Av). Participants then made a saccade to the second fixation cross and then touched the remembered location of the second target presented (Fig. 2Avi).

All possible target-fixation combinations were repeated 10 times for trials where the fixation jumped, and 8 times for when the fixation remained the same for a total of 260 trials. These data were collected in separate sessions of 130 trials each to avoid fatigue (pseudorandomised to ensure equal distribution of trial types across both sessions).

A separate (gaze-free) control session of 130 trials was conducted, in which participants performed an identical task without the presence of the fixation stimuli (i.e., they were free to look where they liked while reaching).

2.6. Simultaneous target display task

The goal of this task was to investigate if the second target being presented simultaneously with the first would affect the coding of its relative location (i.e., the distance of the second target from the first). That is, if the coding of a series of targets would be stored and updated differently if all the targets were visible at the same time. The second target might be more likely to be coded relative to the first if they are both visible at the same time, since the first target would still be present as a stable visual anchor rather than a remembered location. So, in this task, participants performed the same task as described above in the previous condition. However, in this condition the two targets were displayed simultaneously before the first fixation cross was presented. That is, the first target was displayed for 1 s followed by a simultaneous presentation of the two targets for 1 s (Fig. 2Bii). This condition was again comprised of 260 trials, collected in separate sessions of 130 trials each to avoid fatigue (pseudorandomised as before). The number of trials and repetitions of each combination was identical in the sequential and simultaneous target display conditions.

A separate (gaze-free) control session of 130 trials was also conducted for this condition, in which participants performed this identical task without the presence of the fixation stimuli (i.e., they were free to look where they liked while reaching).

The order in which the experimental (remapping) and control (gaze-free) conditions were collected was counter-balanced across participants.

2.7. Data reduction

Kinematic data of the eye and the reach endpoint data were exported and combined with the command file of the laser scanner allowing the data to be temporally aligned with the appropriate stimulus presentation combination. These integrated files were then viewed in a graphical user interface (GUI) custom developed and executed in MatLab® 7.1 (The MathWorks Inc., Natick, MA).

The horizontal and vertical (2-dimensional) directions of the eyes and pointing finger were then manually selected on a trial-by-trial basis at 6 event markers: eye direction when the targets and fixation were displayed; eye direction and finger position for the first touch; eye direction following the saccade to the second fixation cross after the first touch; and the eye direction and finger position during the second touch (Cf., Sorrento & Henriques, 2008; Thompson & Henriques, 2008). Trials in which the eye moved inappropriately (i.e., at the wrong time or to the wrong location) were discarded. A custom MatLab® routine was then used to identify potential gaze or arm outliers (±2 SD of the respective mean). The identified outliers were then examined to determine if they were due to an error in selection of the data point or a mistrial to be removed from analysis (data removed as outliers accounted for approximately 3% of all data collected). Reaching errors were calculated by subtracting the 2D finger position from the coordinates at which the target was displayed (determined from full vision calibration trials to all five possible fixation locations – which includes the three target positions – conducted prior to the initiation of each session). We were specifically interested in horizontal reaching errors as a function of horizontal movement of the eyes.

2.8. Data analysis

Repeated measures analyses of variance (RM-ANOVAs) were then performed in SPSS for the remapping (i.e., experimental) and control conditions. The primary dependent measures were the horizontal reaching errors of the first and second reaches in the RM-ANOVA with levels 2 (condition: sequential, simultaneous)
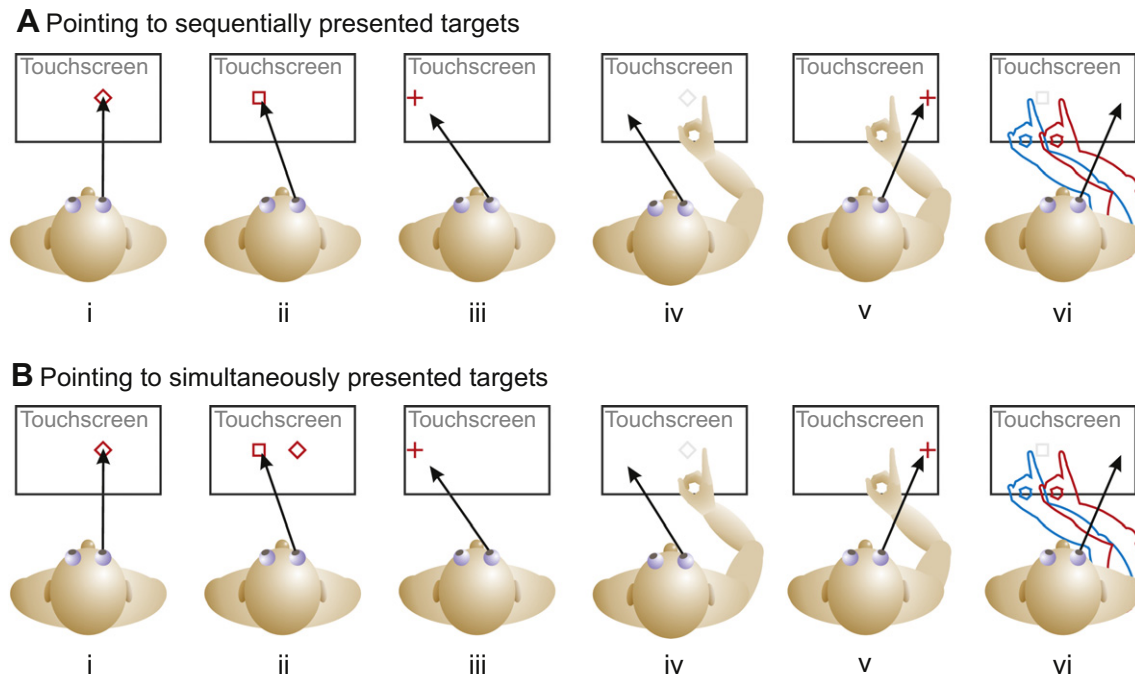
Fig. 2. Sequence of events for trials in all four conditions. A: "Pointing to sequentially presented targets" condition: In this condition subjects briefly viewed the first target (i) until the target disappeared and the second target appeared (ii). Participants then briefly viewed the second target until it disappeared and a fixation cross appeared (iii). They then reached to touch the remembered location of the first target while maintaining fixation at the remembered location of the fixation cross (iv). Upon completion of the first reach the fixation cross reappeared to the opposite side of the target locations (v; in two thirds of all trials) or reappeared in the same location (not shown; in one third of all trials), and participants reached to touch the remembered location of the second target while maintaining fixation on this spot (vi). B: "Pointing to simultaneously presented targets" condition: As in (A) but with the two targets presented simultaneously rather than sequentially (ii). All movements to the remembered target locations were made in complete darkness, with no visual stimuli of any kind, in all conditions.

by 2 (eye movement: eyes moved between reaches or remained stationary between reaches) by 2 (reach: first, second) by 6 (retinal error: −15, −10, −5, 5, 10, 15). Retinal error refers to the position of a given target relative to the corresponding gaze direction when the reach is initiated. That is, the position of the first target relative to the initial (i.e., first) gaze direction would be considered as retinal error for first reaches, and the position of the second target relative to second gaze direction (which might be the same as initial gaze if the eyes remained still) would be considered retinal error for second reaches. Negative values here refer to leftward direction. The control conditions were analysed separately in an RM-ANOVA with levels 2 (condition: sequential, simultaneous) by 2 (reach: first, second) by 3 (target location: −5, 0, 5).

Surprisingly, in our gaze-free control, we found no difference in horizontal reaching errors for either reach movement when the targets were presented sequentially or simultaneously; neither for the reaching errors [$F(1, 7) = 0.117$; $p > 0.7$] nor in terms of standard deviation of the reach error [$F(1, 7) = 0.046$; $p > 0.84$]. Likewise in the remapping conditions, as in the control condition, the presentation of the targets being sequential or simultaneous also did not significantly affect reaching errors with respect to neither mean reach error [$F(1, 7) = 3.080$; $p > 0.17$] nor standard deviation of the reach error [$F(1, 7) = 1.959$; $p > 0.22$]. As, such the data were collapsed across these conditions for remaining analyses. The subsequent RM-ANOVAS for the control condition became: 2 (reach: first, second) by 3 (target location: −5, 0, 5); and for the remapping condition: 2 (eye movement: eyes moved between reaches or remained stationary between reaches) by 2 (reach: first, second) by 6 (retinal error: −15, −10, −5, 5, 10, 15).

All omnibus effects were evaluated with an alpha level of .05. Appropriate post hoc comparison procedures were used to further explore significant main effects (Tukey's LSD) and interactions (i.e., t-tests, and simple-effects ANOVA followed by Tukey's LSD) as necessary.

3. Results

3.1. Gaze-free control conditions

As a control, we had participants reach to touch the remembered locations of two targets, while freely gazing throughout the task. Fig. 3A shows the group mean horizontal reaching errors (filled symbols) to the first (open red diamond) and second (open blue square) targets at all possible locations, collapsed across sequential and simultaneous target presentation conditions. As can be seen in this figure, the presentation of the second target had no significant effect on the reaching errors to the first target regardless of the position of the second target relative to the first (i.e., right or left [$F(1, 7) = 0.96$; $p > 0.1$]). Importantly, there are also no statistical differences between reach endpoints to the same target position irrespective of whether they are presented first or second in the sequence [$F(1, 7) = 0.12$; $p > 0.7$]. The presentation of a second target, whether it is presented after the first target (i.e., sequentially) or at the same time as the first target (i.e., simultaneously), does not influence pointing behaviour to the first target in and of itself. Likewise, the distance between the two reach endpoints for these two sequential movements (highlighted by the light grey rectangle) did not vary with target location or the order of the target presentation [$F(2, 14) = 2.04$; $p > 0.1$].

3.2. Remapping conditions

After having investigated the reaching errors to two target locations while freely gazing, we will now examine the influence of gaze direction for reaching movements to two targets. In these conditions, after foveating both targets, the eyes shift away and remain fixed at some eccentric location during both reaches (a third of the trials in the experimental conditions). Fig. 3B shows 2D hor-
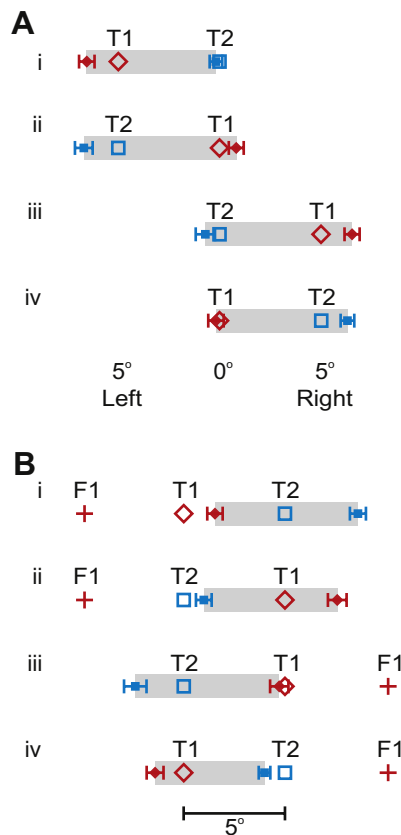
Fig. 3. Horizontal reaching errors of the first reach (small filled red diamonds) to the first presented target (large open red diamonds), and of the second reach (small filled blue squares) to the second presented target (large open blue squares), when participants could gaze freely (A), and when they maintained fixation to the same side of the target locations for both reaches (B). The distance between the reach endpoints is highlighted by the light grey bars. Error bars represent the standard error of the mean.

izontal pointing error to both reach targets when the eyes were directed either to the left of the target locations (Fig. 3Bi and Bii), or to the right of the target locations (Fig. 3Biii and Biv) for both reaches. That is, after having foveated each target as they were presented participants fixated to one side of the target locations with no further deviations in gaze. Reaching errors vary significantly as a function of gaze direction relative to target location for both reaches [$F(5, 35) = 27.03$; $p < 0.001$]. That is, when fixation is maintained to the left of the remembered target locations reach errors are rightward, and when fixation is maintained to the right of the remembered target locations reach errors are leftward. While in Fig. 3B the eccentricity of gaze is collapsed across all possible positions to the left of the target locations and all possible positions to the right of the target locations, Fig. 4A depicts horizontal reaching errors for each possible gaze direction relative to the target for the first reach (red diamonds) and the second reach (blue squares) collapsed across the three possible target positions. We can see here that the pattern of gaze-dependent reaching errors of the first and second reaches do not differ from each other significantly [$F(1, 7) = 4.39$; $p > 0.05$], and was also not influenced by the order in which the targets are reached to, or the order the targets were presented in. Yet, for the most part, the distances between the sequential reach endpoints to the two targets remained the same, and the reach endpoints are merely shifted overall in the opposite direction relative to gaze. Moreover, there was no difference in the precision (i.e., standard deviations) of reaching errors in the lateral direction between reaches to the first and

second targets [$F(1, 7) < 1$; $p > 0.1$; RM-ANOVAs], nor between either of these sequential reaches and single reaches to a single target [$F(3, 39) < 1$; $p > 0.3$; mixed-ANOVA] from a previous unpublished study conducted in our lab (Thompson et al., 2008).

If the distance between the endpoints of sequential reaches is not affected by gaze, then we would expect the pattern of gaze-dependent reaching errors to the second target to be the same with respect to initial fixation, independent of whether the eyes moved in between the sequential reaches or not. In Fig. 4B, we see that reaching errors to the second target when the eyes shifted prior to this second movement plotted relative to the initial fixation (blue squares), do not resemble the errors produced when the eyes remained in the same eccentric direction for both the first and the second reaches (red diamonds and blue squares respectively in Fig. 4A). However, when the same errors are plotted relative to current gaze direction (Fig. 4C) rather than the initial deviated gaze direction, we find that the pattern of errors does resemble that found in Fig. 4A, and that these errors do modulate significantly as a function of current gaze direction relative to the respective targets [$F(5, 35) = 11.66$; $p < .001$] although the magnitude of the gaze-dependent effect is smaller [$F(1, 7) = 11.71$; $p < .05$], based on the interaction of retinal error and eye movement.

This is particularly evident when the current gaze relative to the target falls at 5° to the left or right of centre. Further investigation reveals that this interaction then is driven by the reversal of the direction of modulation with respect to gaze at 5° to the left and right of centre, and is discussed in detail below.

But in order to test our hypothesis and quantify the contributions of ego- and allo-centric coding, we need to investigate if the distance between reach endpoints of sequential reaches to the two targets is affected by gaze. To do this, we calculated the predicted reach endpoints to the two targets as if they were coded completely independently of each other (i.e., exclusively/perfectly egocentrically; modulating systematically as a function of current gaze direction relative to the target) as predicted by the retinal magnification effect (e.g., Bock, 1986; Henriques et al., 1998; Thompson & Henriques, 2008). The predictions depicted here in Fig. 4D are based on the gaze-dependent reach endpoints of the first reaches depicted in Fig. 4A. That is, the mean error of the first reach (solid red diamond) in Fig. 4Di to the first target (open red diamond) when current gaze for this reach was to the left (red cross), is based on the actual first reach to the first target when gaze was to the left of both targets and target 1 was to the left of target 2 (i.e., these values are not the same as those in 4A which collapse across relative target position and represent gaze relative to the first target regardless of its relative location to target 2). The second reach errors (blue squares in Fig. 4Di) are derived from the red diamonds in Fig. 4A in the same manner from first reaches to first targets when gaze was to the right of both targets and target 1 was to the right of target 2. Thus, the predicted distance between the two reaching endpoint positions (represented by the grey line) is quite small due to the retinal magnification effect described above. Conversely, panel Dii shows that merely changing the order of the target (but not the order of gaze direction) would lead to (based on actual data of first reaches as described above) a large predicted distance between the endpoints of the two reaches. Again, in Fig. 4Diii and Div, the different current directions of relative gaze for each of the two respective reach target locations should have a strong influence on the distance between the reaching movements to these two targets (grey lines). It can be seen that simply changing the positions of the targets relative to gaze direction would result in a fivefold increase in the distance between reaching errors (i.e., comparing panels Diii–Div).

If the targets were simply coded allocentrically (i.e., the brain coded the second target as some position relative to the first),
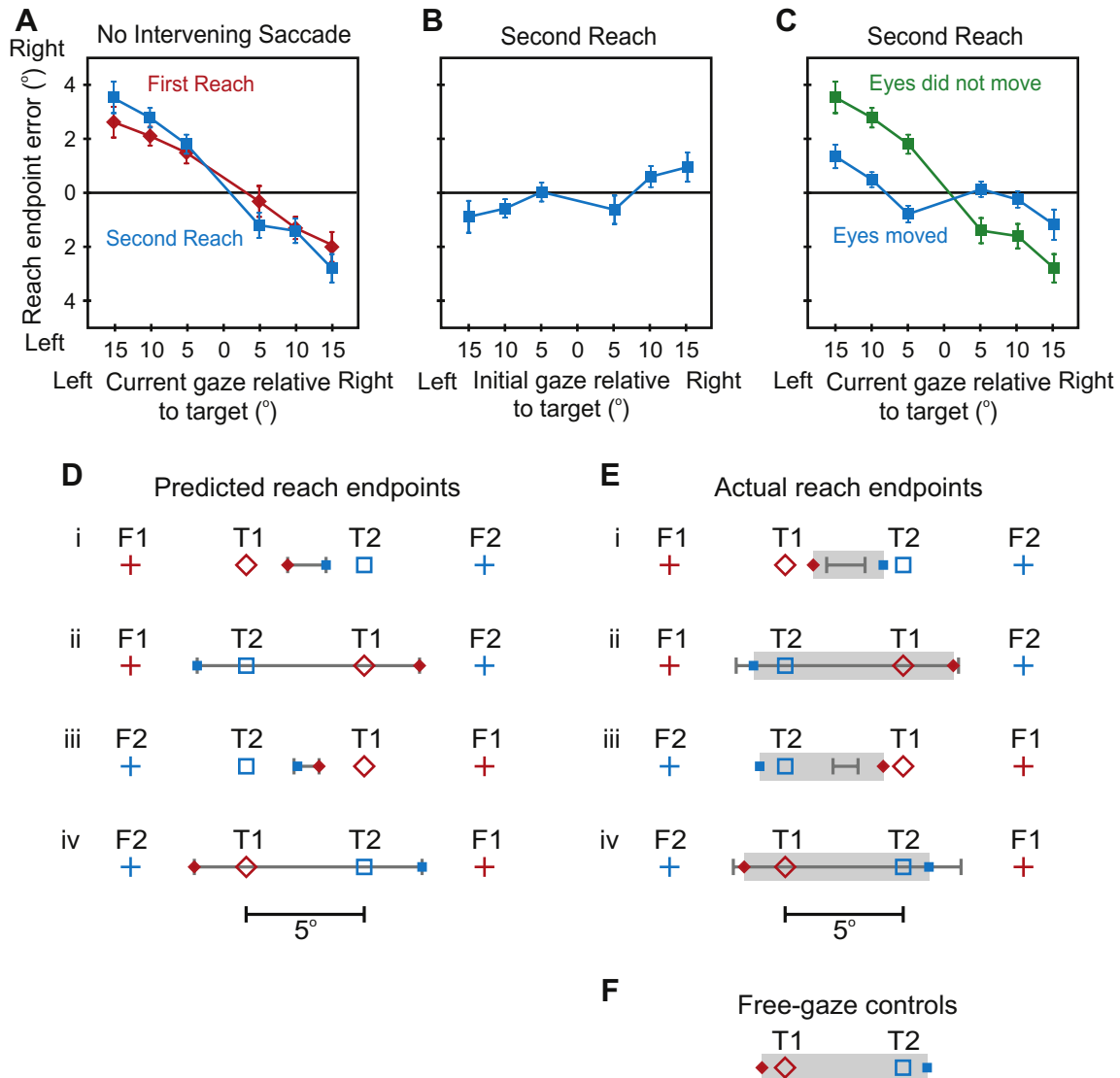
Fig. 4. A–C: Horizontal reaching errors as a function of initial or final gaze relative to target. A: Error as a function of current gaze direction relative to the target for the first (red diamonds) and second (blue squares) reaches, when gaze was deviated in the same direction for both reaches. B: Error of the second reach (blue squares) as a function of the initial gaze direction relative to the first presented target when gaze was moved between reaches. C: Errors of the second reach when the eyes moved between reaches (blue squares) and when the eyes did not move between reaches (green squares), as a function of the current gaze direction relative to the second target. Error bars in these panels represent the standard error of the mean across trials. D–F: Predicted and actual reaching endpoints (solid symbols) across the two targets for the four different combinations of gaze and target directions. D: 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) as predicted by reaching errors of the first reach from panel A. These predicted reach endpoints reflect the expected result if reach behaviour to both targets modulated exclusively as a function of current gaze direction relative to the respective target (i.e., egocentric/absolute coding). The distance between the predicted reach endpoints is indicated by the dark grey line. Note this relative difference also changes as a function of current gaze direction relative to the target. E: 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. The predicted distance between reach endpoints from panel D is again represented by the dark grey line, with the actual distance between reach endpoints highlighted by the light grey bar. F: The average 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 participants were able to gaze freely (Fig 3A). The distance between reach endpoints (highlighted by the light grey bar) is indicative of what would be expected if the second target location were coded relative to the first (i.e., allocentric/relative coding).

then we should see no difference in the distance between reach endpoints for any of the gaze shifts or relative target positions (i.e., the four possible combinations depicted in Fig. 4D) – and the distance between reach endpoints should also resemble the relative difference in reach errors from the free-gaze controls shown in Fig. 3 (the average distance between reach endpoints in the gaze-free condition across target locations are shown in Fig. 4F).

The actual reach endpoints of the first reach (red diamond), and of the second reach (blue square), with the second reach endpoint relative to the first reach endpoint (i.e., difference in point-

ing error) indicated by the light grey bar, when the eyes moved between reaches are shown in Fig. 4E. Notice that none of the second reach endpoints relative to the first reach endpoints (i.e., the distance between reach endpoints; depicted by the light grey shaded bars) are of the same magnitude as each other, across all possible combinations and orders of target and fixation location presentations (i.e., the distances between reach endpoints are all significantly different from each other; $F(3, 21) = 113.16$; $p < .0001$; post hoc analyses using Tukey's LSD result in $p < .001$ for all comparisons). This indicates that reach endpoints of the second reach did in fact modulate with the intervening change

in gaze direction relative to the remembered target location, as described (and confirmed statistically) above.

Moreover, we do see the general predicted pattern of smaller versus larger distances between reaching errors between the first and second reaches, as predicted by the gaze-dependent (egocentric) model (Fig. 4C), in that the actual distances between reach endpoints (light grey bars in Fig. 4E) for the combinations of fixation and targets in subpanels Eii and Eiv are smaller than those for subpanels Ei and Eiii, like they are in the predictions shown by the dark grey lines in Fig. 4D and E. However, the second reach endpoints do not perfectly match the predictions of egocentric coding depicted in Fig. 4D, and represented again by the dark grey lines in Fig. 4E, either.

In Fig. 5 we compare the contributions of allocentric (i.e., the difference in target position) and egocentric (i.e., the current gaze direction relative to the second target position) information, by comparing the unsigned distance between reach endpoints for all three target locations (averaged across subjects) collapsed across gaze directions relative to target locations (blue squares in Fig. 5) with the predicted relative differences of the two models. The dashed vertical black line indicates the predicted distance if the targets were coded using allocentric information ($\sim 7°$ while the targets were actually separate by 5°), while the green squares indicate the distance between the two reaches predicted if the targets were coded exclusively relative to gaze (as in Fig. 4D). Like the horizontal bars shown in Fig. 4D, the distance between reaches predicted by eye-fixated coding would be relatively small for gaze-target combinations in rows in i and iii, but much larger for those combinations in rows ii and iv. So, the relative magnitude of the distance between the sequential reach endpoints changes as a function of the gaze direction relative to the target location as shown in our predictions in Fig. 4D and reflected in the actual data in Fig. 4E. However, in Fig. 5, it is clear that the actual distances between reaching errors are closer on average to the allocentric predictions, than they are to those predicted by eye-centred coding [paired samples t-test: $t(11) = 2.3$; $p < 0.02$]. This test compares the absolute/unsigned difference between the actual difference between reach errors (blue squares) and the predicted egocentric difference values (green squares), and the absolute difference between the actual reach endpoints (blue squares) and the allocentrically predicted difference between reach endpoints (vertical dashed line). This result further suggests that both ego- and allocentric information are used in the coding of the second target location.
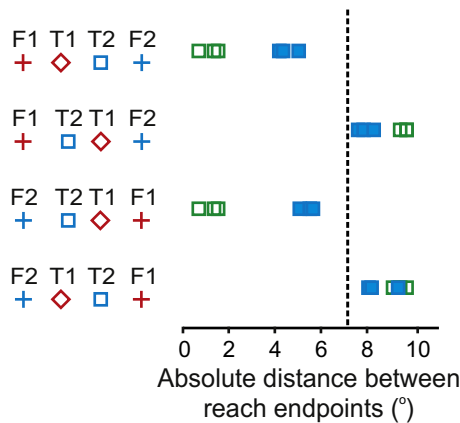

Fig. 5. The actual absolute distance between reach endpoints (filled blue squares) with the predicted distance between reach endpoints for egocentric/absolute coding (hollow green squares), and for allocentric/relative coding (vertical dashed line) for the four different combinations of target and gaze direction shown on the left (same as those in Fig 4D and E).

3.3. Modelling the relative contributions of ego- and allo-centric coding

Using similar logic to previous studies (Cf., Beurze et al., 2006; Scherberger, Goodale, & Andersen, 2003) we fit a multidimensional mixed-model regression to the data for each subject. With this we were able to investigate the relative contributions of egocentric and allocentric information in target coding. The equation of the model is as follows:

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

Reaching errors for the first and second reaches are represented by Err_1 and Err_2 respectively, ΔT is the signed distance (in degrees) between the two target positions (i.e., the location of the second target relative to the first; accounting for the allocentric component of target coding), T_2-EP_1 is the relative position (in degrees) of the second target to the first eye position (i.e., the egocentric component of target coding), 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). The parameters of the model for each subject are shown in Table 1.

Parameter a_0 (the intercept) quantifies the pointing bias, and was small on average (-0.17 ± 0.1) and not significantly different from 0 [one sample t-test: $t(7) = -0.65$; $p = 0.52$]. When we plot the absolute values of the coefficients of ΔT against those of T_2-EP_1 (Fig. 6) we see that the slope falls in an intermediate position between exclusive relative position or allocentric coding (which would be represented by a steeper than unity slope; i.e., approaching infinity) and exclusive egocentric coding (which would be represented by a horizontal slope; i.e., approaching 0). While the slope in Fig. 6 is steeper than unity (indicating a greater reliance on allocentric cues), just as the actual distances between reach endpoints are closer to those predicted by allocentric coding as in Fig. 5, when the magnitude of eye position modulation is considered, it can be clearly seen that both allocentric and egocentric coding are used (as discussed above).

4. Discussion

We have found that when participants move their eyes to the opposite side of two previously foveated remembered targets between reaches to those locations, their reach errors vary systematically with their current gaze direction relative to the respective target locations for each reach. This is evidenced by a systematic change in the distance between these two sequential reaches as predicted by an eye-centred representation of each target (Figs. 4E and 5). However, the change in the distance between the reach endpoints did not match either our egocentric or allocentric coding predictions (which predict changes in the distances between reach endpoints dependent solely on gaze direction, and no change in these distances respectively), but fell between the two. So, our results suggest that while the distances between reach errors for the sequential reaches do vary systematically as a function of current gaze at the time each reach was initiated, the distance between the first and second targets does provide a salient allocentric cue for guiding the second reaching movement. Further, when participants gazed to some eccentric location to either side of the two target locations – and maintained fixation there for both reaches – the direction of reach error was dependent on the current gaze direction relative to the target for both reaches. That is, when looking to the right participants exhibited leftward pointing error for both reaches and *vice versa*.

When the eyes are maintained at a single fixation for both reaches we might expect the errors of the second reaches to be

Table 1
Best-fit parameters for each subject in the remapping conditions, fitting Eq. (1).

| Subject	a_0	a_{Err_1}	$a_{\Delta T}$	$a_{T_2\text{-}EP_1}$	$a_{\Delta EP}$
as	−1.268 ± 0.129	0.686 ± 0.051	0.742 ± 0.033	−0.183 ± 0.021	0.222 ± 0.013
cg	0.786 ± 0.126	0.685 ± 0.050	0.375 ± 0.027	−0.143 ± 0.021	0.222 ± 0.011
cw	−0.924 ± 0.102	0.665 ± 0.044	0.107 ± 0.019	−0.031 ± 0.015	0.038 ± 0.009
ds	0.294 ± 0.159	0.727 ± 0.048	0.111 ± 0.024	−0.141 ± 0.014	0.101 ± 0.009
jn	−0.571 ± 0.066	0.813 ± 0.029	−0.004 ± 0.016	−0.057 ± 0.011	0.093 ± 0.007
ok	0.748 ± 0.085	0.446 ± 0.032	−0.045 ± 0.019	−0.125 ± 0.014	0.129 ± 0.009
sj	−0.044 ± 0.090	0.657 ± 0.036	0.262 ± 0.017	−0.081 ± 0.012	0.079 ± 0.008
zl	−0.414 ± 0.069	0.724 ± 0.034	0.139 ± 0.014	0.0002 ± 0.010	0.015 ± 0.007
Mean	−0.174 ± 0.103	0.675 ± 0.040	0.211 ± 0.021	−0.095 ± 0.015	0.112 ± 0.009
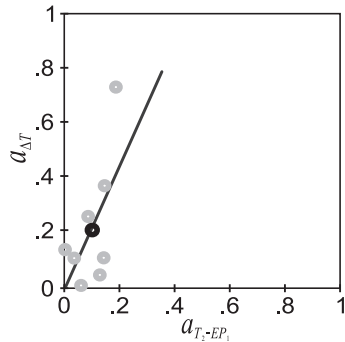
Fig. 6. The absolute values of the coefficients of ΔT as a function of those of T_2-EP$_1$ for each subject (grey circles) and the group mean (black circle). The dark grey line represents the line of best fit. Allocentric target coding would be reflected by a steeper than unity slope, while egocentric coding would be reflected by a shallower slope.

smaller and less variable if the brain used relative (i.e., allocentric) coding along with the absolute (i.e., egocentric) position coding – this additional information may be combined in an optimal manner to increase precision and accuracy (e.g., Vaziri, Diedrichsen, & Shadmehr, 2006). Alternatively, if there were an accumulation of error in subsequent reaches as previously reported (Bock & Arnold, 1993), then the error of the second reach should be significantly greater than that of the first. However, we found that there was no reduction or accumulation of error between the two reaches. Rather, the magnitude of errors of second reaches did not differ from those of first reaches, and the magnitude of errors from both of these reaches did not differ from those errors produced when there was only one reach target presented (Thompson et al., 2008). This was true not only when gaze was fixed at some eccentric position for reaches to both targets, but also for gaze-free double reaches. In the case of the gaze-deviated reaches it might be that the errors did not differ because gaze direction remained the same relative to the targets – so the errors for both reaches vary in a similar pattern. As described above, the precision also did not differ between reaches, or between either of these reaches and the precision of single reaches to single targets (Thompson et al., 2008). So, it is unlikely that absolute/egocentric and relative/allocentric coding were optimally integrated. If they had been the precision should have been greater for the second reach where both sources of information were available.

While shifting gaze direction after foveating both targets lead to a general shift in reach error in the direction opposite to gaze for both reaches, the distance between these reach endpoints did not differ as shown in Fig. 3B. This could suggest that the brain codes the second reach goal using allocentric cues about the distance between the two targets. But, if both reach targets are updated and coded in eye-centred coordinates, then introducing an intervening eye movement between sequential reaches should lead to a predictable change in the distance between endpoints. Our results

show that this is indeed the case (Figs. 4E and 5) consistent with an eye-centred egocentric representation of the target. However, the change in the distance between the reach endpoints, when the eyes moved between reaches, did not vary to the extent or magnitude predicted by egocentric (i.e., eye-centred) coding. This means that gaze-independent cues, such as those used for allocentric coding, were also incorporated when programming the second reach. This makes senses considering the targets were always the same distance apart for all trials (5° or 6.1 cm), and also considering that participants saccaded to both targets while they were still visible, allowing an oculomotor efference copy of the distance between the two. This also meant that in cases where eye-fixed representations of the two targets would predict a very short distance between the two reaches (<2 cm, as shown by the horizontal bars in Fig. 4Ci and Ciii, and the green squares in the first and third rows of Fig. 5), the actual distance between the two reaches fell closer to the distance predicted by allocentric (or gaze-independent) coding. So, it is clear that the relative position of the second target to the first (and perhaps the efference copy signals of the saccade between the target locations) helped to overcome the erroneous (even absurd) coding provided by the gaze-centred updating of the target locations.

It is also possible that the remembered locations of the two foveated targets (and their relative positions) were converted to a head, body, or integrated reference frame based on these being the most reliable (egocentric) representations (McGuire & Sabes, 2009). However, as with allocentric coding, these other egocentric representations of the target pairs cannot explain the gaze-dependent errors, or the distances between reach endpoints, associated with subsequent reaches. Likewise, neither such gaze-independent representations (allocentric or egocentric), nor the integrated model of McGuire and Sabes (2009), can account for reaching errors produced after a briefly foveated target has been remapped as the result of a subsequent eye movement, for either single or sequential targets. Foveating the targets should have provided the most reliable representation of the target locations, yet this did not prevent gaze-centred errors when coding and updating the target locations for reaching. This is despite the fact that coding peripheral targets in eye-centred coordinates is generally less reliable and less accurate (e.g., Ariff, Donchin, Nanayakkara, & Shadmehr, 2002; Henriques et al., 1998). Moreover, viewing both targets, either simultaneously or in close succession, should have also provided another reliable allocentric representation of the second target (as well as the oculomotor efference copy signals produced when foveating these visible targets). But, we still found that reaching errors, as well as the distances between reaching endpoints, systematically varied as a function of current gaze direction relative to the targets. Our results suggest that despite these various, stable, and more reliable gaze-independent cues, these targets are at least partly coded and updated in an egocentric reference frame that is centred on the eye.

But what is the exact contribution of the eye-centred representation of the targets, in relation to the multiple sources of information, or even multiple reference frames used for relative target coding? As can be seen in Fig. 5, the distance between actual reach endpoints resembles those predicted by relative or allocentric coding (i.e., approaching the vertical dashed line in Fig. 5) especially when the predictions of the egocentric coding were "unreasonably" small. When we fitted a multidimensional mixed-model regression to the data for each participant, we found that the error of the second reach was influenced by the distance between the initial gaze direction and the second target, the shift in relative gaze between reaches, and the location of the second target relative to the first. The contributions of each source of information in the coding of the second target seem to be similar, with a small, but significantly, greater importance placed on the allocentric or relative coding information. Similar weightings of egocentric and allocentric information have also been recently reported elsewhere (Byrne & Crawford, 2010).

As discussed briefly in the introduction, allocentric information can influence spatial localisation when the allocentric information adds some benefit to the task performance. In addition to the studies discussed earlier, it has also been found that reach error due to mislocalisation of a target is reduced when a structured background is provided (Bridgeman & Graziano, 1989; Matin et al., 1982; Velay, Roll, Lennerstrand, & Roll, 1994). But, this advantage is only found when the egocentric representation of the target has been compromised due to unreliable information about the position of the eye-in-head. It seems likely then that the presence of reliable allocentric information reduces the relative weighting of the egocentric information when it is made unreliable. After all, it has been shown elsewhere that when there is no noise in the egocentric signal (i.e., ocular proprioception was not perturbed) the addition of allocentric information did not influence reaching and pointing behaviour (e.g., Blouin et al., 1993; Bridgeman, 1991; Carey, Dijkerman, & Milner, 2009; Neggers, Van der Lubbe, Ramsey, & Postma, 2006; Obhi & Goodale, 2005). More recently Byrne and Crawford (2010) have also reported that the reliability of cue stability is a critical component in the relative weighting of allocentric cues. Matin and colleagues (1982), Bridgeman and Graziano (1989), and Velay et al. (1994) also stressed that the relationship between allocentric and egocentric coding was not linear, and greatly depended on the richness of the contextual scene. In our study, we did not use a rich contextual scene, but instead used a single but very relevant allocentric cue – the distance of one movement goal or target with respect to the final reach goal. Even in this case (i.e., when the allocentric cue was relevant but not contextually rich), the brain incorporates allocentric information in programming the second reach in a sequence. However, given that reach errors also varied systematically with gaze, the brain seems to also incorporate the updated eye-fixed (i.e., egocentric) representation of this second target.

The contribution of an allocentric cue that is a target itself has not been investigated before. We have shown that the position of the second target relative to the first has a significant contribution in localising the second reach endpoint. This distance between subsequent reach targets could be coded in an allocentric reference frame. But, given that both targets were used in action, their relative position could have been coded in a gaze-independent egocentric reference frame such as one anchored to the head or body, or could even be partly based on oculomotor efference copy signals produced when each target was foveated. The current task constraints do not allow us to distinguish between these possible cues or reference frames. Rather, our results and model are consistent with the idea that multiple reach targets are coded relative to each other but also coded and updated in an eye-centred frame of reference. In summary, when coding two serial reach targets, the brain continuously uses both egocentric (specifically eye-centred) and allocentric information. The brain likely uses multiple reference frames for planning and executing these complex sequential movements, but it is clear from our results that one of these representations is an egocentric eye-centred reference frame.

Acknowledgments

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