

Allocentrically implied target locations are updated in an eye-centred reference frame

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ABSTRACT

When reaching to remembered target locations following an intervening eye movement a systematic pattern of error is found indicating eye-centred updating of visuospatial memory. Here we investigated if implicit targets, defined only by allocentric visual cues, are also updated in an eye-centred reference frame as explicit targets are. Participants viewed vertical bars separated by varying distances, and horizontal lines of equivalently varying lengths, implying a “target” location at the midpoint of the stimulus. After determining the implied “target” location from only the allocentric stimuli provided, participants saccaded to an eccentric location, and reached to the remembered “target” location. Irrespective of the type of stimulus reaching errors to these implicit targets are gaze-dependent, and do not differ from those found when reaching to remembered explicit targets. Implicit target locations are coded and updated as a function of relative gaze direction with respect to those implied locations just as explicit targets are, even though no target is specifically represented.

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1. Introduction

Systematic reaching/pointing errors opposite to gaze direction with respect to remembered target locations suggest visuospatial memory is updated/remapped in an eye-centred reference frame every time the eyes move. That is, when an eye-movement is made away from a previously displayed target before reaching to that remembered location, final leftward gaze directions (relative to the remembered target) result in rightward pointing errors and vice versa [Cf., 11]. This pattern of errors is consistent with the “retinal magnification effect” [2], demonstrating the remembered target location has been remapped to the retinal periphery, which has been shown by a great deal of previous research [see 6, and 23 for reviews]. Specifically, eye-centred updating has been shown in reach error following eye movements of varying type and speed [25], and full body translation [26] and trunk rotations [20]. This pattern of reaching error has been shown for reaches to remembered near and far targets [15,17,27], multiple reaches to the same remembered target [20], and has further been found for non-visual targets as well [1,8,12,18].

In our daily lives we perform goal-directed tasks to implicit targets such as walking through doorways, and reaching into bags,

boxes and open drawers. In all of these cases there is no explicit target, but we are able to use allocentric information (e.g., the doorframe) to guide our actions to the implied target. It has been shown that targets implied by motion (e.g., 3D full-field motion pattern) are updated/remapped in an eye-centred reference frame like explicit targets [17]. These participants perceived that they were heading toward (or away) from the centre of motion – the moving stimuli elicited a strong egocentric locus or vection. We tested how locations are coded and updated when there is *no* explicit target presented, but only simple, static “allocentric” cues to imply a target location. That is, participants self-determined the reach target as the central location between two vertical flanking stimuli (*bordered division paradigm*), or the midpoint of a horizontal line (*line bisection paradigm*), remembered this implied (personally defined) location, and (after looking away) reached to touch it with no visual feedback. Are these implicit target sites coded and updated relative to gaze? If so, reach error should vary systematically with the final gaze direction (like for remembered explicit targets). Alternatively, the absence of an explicit goal, and/or the need for relative spatial judgments, might limit/prevent the incorporation of such eye-centred representations in goal-directed movement planning.

2. Methods

2.1. Participants

The *bordered division* and *line bisection paradigms* included 7 [(3M, 4F) between the ages of 18 and 26 years (mean: 22 ± 3 years)], and 8 [(4M, 4F) between the ages of 19 and 26 years (mean:

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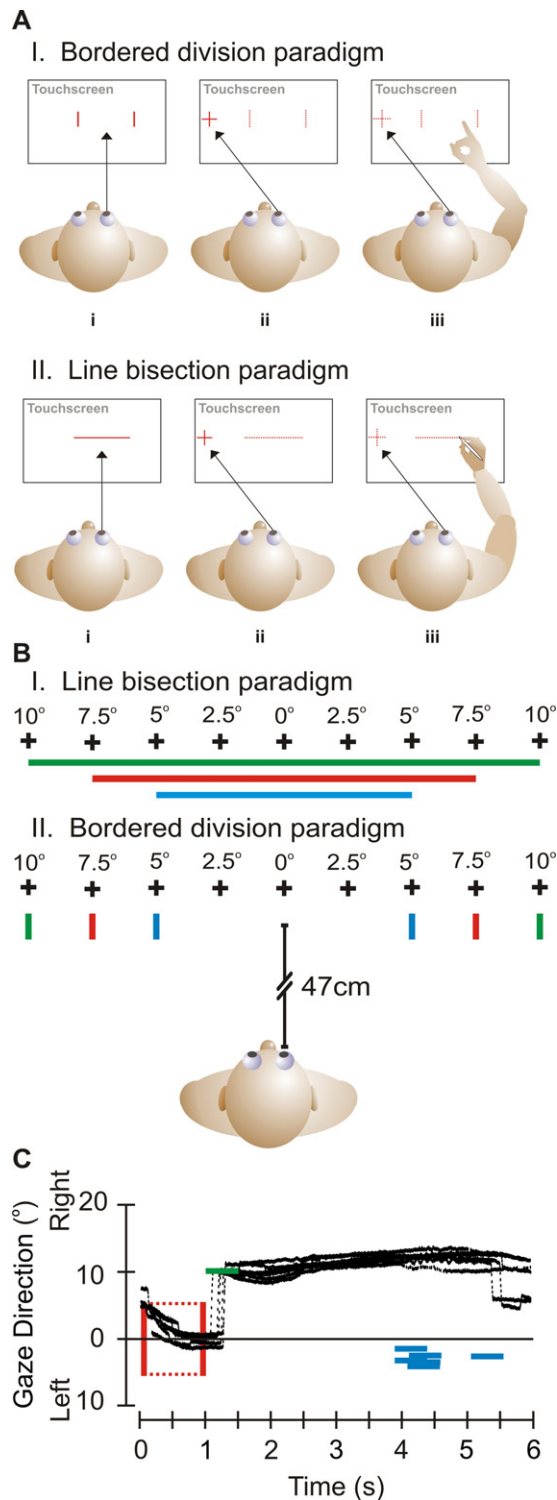


Fig. 1. (A) Sequence of events for *bordered division* (I) and *line bisection* (II) paradigms. Participants view the “target” stimuli, and visually locate the centre point either between the two vertical bars (Ii) or along the horizontal line (Iii). This implicit/allocentric stimuli disappears (Iii/Ii) and participants saccade to a briefly displayed fixation-cross. While fixating in the direction of the extinguished fixation-cross (Iiii/Ii), participants reach to touch (I) or bisect (II) as accurately as possible the remembered location of the implicit target. (B) Experimental display for the *line bisection* (I) and *bordered division* (II) paradigms. Implicit stimuli (line [I] or flanking bars [II]) varied in horizontal span: 10° (blue), 15° (red), or 20° (green) of visual angle, and were presented with their actual midpoint falling at one of five locations: 0° (i.e., centrally), and 2.5°, or 5° to the left and right of centre. Nine possible fixation locations (crosses), ranged from 10° left to 10° right of centre. All stimuli were presented in red (colour of the laser) but are colour coded here for distinction. (C) Sample data from the *line bisection paradigm*. Sample eye position (---),

23 ± 2 years)] participants respectively, with 5 participating in both paradigms. All were right handed with normal (or corrected-to-normal) vision, and no known history of visual/neuromuscular deficit. Recruitment was by word-of-mouth, informed consent was given, and no compensation was provided for participating. All procedures were conducted in accordance with ethical guidelines of York University’s Human Participants Review Subcommittee.

2.2. Apparatus

Participants sat at a table with their heads fixed by a bite bar. The seat and bite bar heights were adjusted independently so subjects were comfortably seated with an unobstructed view of the testing area. Movements of the right eye were recorded at 250 Hz via infrared pupil detection by head mounted EyeLinkII® (SR Research, Osgoode, ON, Canada). Reach endpoints were recorded by a vertically mounted touch screen panel (Magic Touch 2.0; Keytec Inc., Garland, TX, USA) ~47 cm from participants’ right eyes. This experimental setup is identical to previous experiments conducted in our lab [9,24].

2.3. Stimuli

All stimuli were rear-projected by an Optikon® XYLP-C Laser Projector (Optikon, Kitchener, ON, Canada) onto a paper backing attached to the otherwise transparent touch screen. Stimuli were displayed in red (colour of the laser) at a vertical elevation roughly at eye level, and consisted of fixation cues (crosses of 2 cm diameter, subtending ~0.76° of visual angle; Fig. 1), “bisection” targets (horizontal lines of lengths 8.80, 13.16 or 17.60 cm; or 10°, 15°, or 20° of visual angle), and “bordered division” targets (vertical bars separated by varying distances equal to the lengths of the “bisection” targets to create contextually/allocentrically defined implicit target sites; Fig. 1BII). For both target presentations participants determined and remembered the central ‘target’ location (i.e., midpoint of the horizontal line or the point of equidistance from both vertical bars). The horizontal lines and vertical bars were presented so the central “target” location would fall at 0° (i.e., centre), or at 2.5° or 5° to the left or right of centre (Fig. 1B illustrates only the central target site). The locations of the fixation crosses could then fall either outside, inside, or on the boundary of the defined target area. The experiment was conducted in total darkness with no other visual stimuli of any kind.

2.4. Bordered division paradigm

Participants depressed a single-button mouse (Apple Canada Inc., Markham, ON) and briefly viewed two vertical bars separated by 1 of the 3 possible distances (Fig. 1AII). The bars disappeared after 1 s and participants saccaded to foveate a fixation-cross displayed at 1 of the 9 possible locations (Fig. 1AII). After a variable delay (1–1.5 s) the fixation-cross disappeared and participants reached to touch (with the right index finger) the remembered location directly between the previously visible vertical bars while fixating the location where the fixation-cross had been displayed (Fig. 1AIII). Participants then returned their hand to the mouse to end the trial.

A halogen lamp was illuminated for 4 s between trials to prevent dark adaptation. For task familiarization participants performed one full session without the eye tracker. The experimental

stimuli presentations (the length of the horizontal line [red hashed lines] and stimulus onset/offset [red solid lines]), and reach endpoints (blue boxes) against time for 6 trials from 1 participant. These data are representative of the behaviour of all participants in both paradigms. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

session consisted of 195 trials (5 reaches to each of the 39 possible target-fixation-location combinations; fully randomized) and lasted approximately 30 min (4–6 s per trial with a 4 s inter-trial interval). The fixation would have appeared at the physical/actual midpoint between the vertical bars in 40/195 trials by nature of the target-fixation-location combinations. In these trials no fixation-cross was displayed; participants were free to look where they had determined the target to be while reaching.

2.5. Line bisection paradigm

This paradigm was identical to the *bordered division paradigm* in every way except for 2 critical distinctions: instead of flanking visual cues (i.e., the vertical bars), a horizontal line was presented (Fig. 1AIIi); and instead of touching the remembered “target” location with their finger participants used a digital stylus (Magic Touch, Keytec Inc., Garland, TX, USA), to bisect where they remembered the midpoint of the line to have been (Fig. 1AIIiii).

2.6. Data reduction

All raw data were plotted across time and selected [Cf., 20] in a custom GUI written in MatLab 7 (The MathWorks, Natick, MA). For each trial, eye position was selected at the time of target presentation, fixation presentation, and during the reach to ensure stable and correct gaze direction. Trials where the task was not performed correctly (e.g., reach prior to command, or fixation not maintained during reaching) were excluded from analyses. Across all subjects, 15% and 10% of trials were excluded from the *bordered division line bisection paradigms* respectively because they did not meet the above criteria. Errors for each movement were computed by subtracting reach endpoint from the actual “target” location. Fig. 1C depicts sample eye traces and stimuli presentations.

2.7. Data analysis

To test the effect of gaze direction relative to the implied target site (-10° , -5° , 0° , 5° , 10°) on horizontal reaching errors we ran repeated measures analyses of variance (RM-ANOVAs) in SPSS 16 for each paradigm. To determine whether location or size/distance of the stimuli had an effect on reach errors, we also included implied target location (-5° , -2.5° , 0° , 2.5° , 5°) and bar separation distance/line length (10° , 15° , or 20°) as factors in these RM-ANOVAs. Comparisons between conditions were made using a mixed RM-ANOVA with a between subjects factor of paradigm. All omnibus effects were evaluated at $\alpha = 0.05$. Appropriate post hoc comparison procedures ($\alpha = 0.05$) were used to explore significant main effects (Holm–Bonferroni) and interactions (i.e., simple-effects ANOVA followed by Holm–Bonferroni) as necessary.

3. Results

Endpoint errors of reaches to implicit targets vary systematically with gaze direction relative to the target site regardless of the type of allocentric stimulus used to imply the target site (Fig. 2A and B). When participants could freely gaze while reaching (i.e., in those 40 trials per session where no fixation-cross was displayed) participants tended to reach fairly accurately (*bordered division* mean error = $0.6 \pm 2.6^\circ$; *line bisection* mean error = $1.1 \pm 2.1^\circ$) and significantly more accurately than when gaze was directed away from the target site ($p < 0.05$ for all comparisons). So, in Fig. 2A–C horizontal reach errors are normalized to 0 to demonstrate the gaze-dependent effect on reach error for all eccentricities. Horizontal reach error modulates significantly as a function of gaze direction (i.e., looking to the left of the target results in rightward error and vice versa) in both the *bordered division* (Fig. 2A; [$F(4,24) = 21.420$;

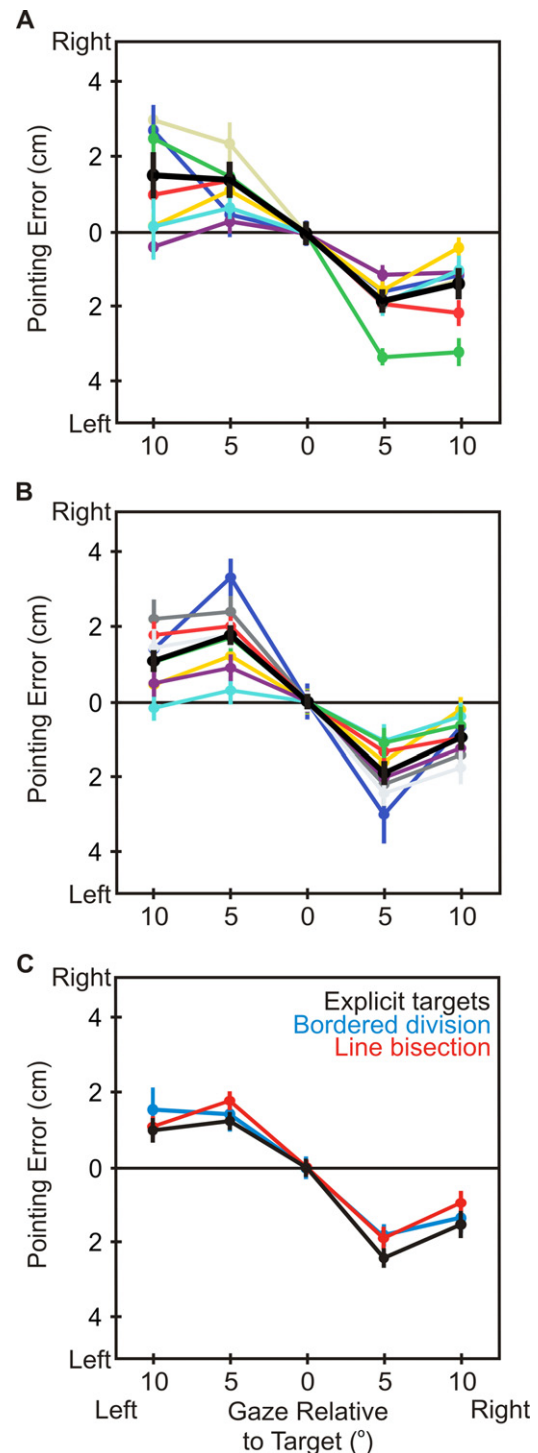


Fig. 2. Average horizontal pointing errors for all subjects (group mean in black) as a function of target-relative gaze direction (i.e., irrespective of target location, and stimulus “size”) for the *bordered division* (A) and *line bisection* (B) paradigms. (C) Group means from each paradigm against data from a previous experiment in which explicit targets were displayed. All data has been normalized to zero; where the horizontal line at 0° represents the actual central target location (i.e., accurate reaching). Error bars represent standard error of the mean (SEM).

$p < 0.05$]) and *line bisection* (Fig. 2B; [$F(4,28) = 31.392$; $p < 0.05$]) paradigms. This gaze-dependent modulation did not differ between the tasks [$F(4,52) = 2.069$; $p > 0.09$].

The gaze-dependent pattern of reach errors shown in Fig. 2A and B is consistent across the different implied target locations and the size of the implied target area in that these factors either did not

significantly influence (or interact with) target-relative gaze direction, or the interaction only modulated the size of the effect of gaze without changing the overall pattern (described below). Specifically, there was no interaction of location with target-relative gaze direction in either the *bordered division* [$F(8,48) = 1.252$; $p > 0.2$] or *line bisection* [$F(8,56) = 0.944$; $p > 0.4$] paradigms, nor was there an effect of line length in the *line bisection paradigm* [$F(2,14) = 0.809$; $p > 0.4$]. The only significant interaction found was for the *bordered division paradigm*, where the gaze-dependent pattern of error was significantly affected by the separation distance of the vertical bars [$F(8,48) = 3.818$; $p < 0.002$]. In particular the effect of gaze was a bit smaller (by ~52%) for the bar separation distance of 20° , compared to errors for the other two bar separation distances. Also, there is a main effect of bar separation distance [$F(2,12) = 39.483$; $p < 0.001$], which is due to reaching errors (again only for the bar separation distance of 20°) being shifted ~2 cm left as a whole compared to reach errors for other bar separation distances. The leftward shift is perhaps due to a previously observed effect of pseudoneglect when working with stimuli of such size [Cf., 14], but the gaze-dependent pattern of error remains unchanged despite the shift, so it is not important to our overall question. Thus, neither the length of the horizontal lines displayed nor the separation distances of the vertical bars affected the overall pattern of errors as a function of gaze direction. Consequently, we collapsed across implied target locations, and line lengths and bar separation distances in the analyses above which address the main question of our study.

In Fig. 2C we compare the gaze-dependent pattern of reach errors to these implied targets with that for reaches to explicit visual targets previously collected in an identical experimental setup [9]. Reach errors for both the *bordered division* and *line bisection paradigms* do not differ significantly from reach errors to explicit stimuli in direction or magnitude [$F(8,96) = 0.636$; $p > 0.5$], nor do they differ in precision [$F(8,96) = 1.674$; $p > 0.1$].

4. Discussion

The primary goal of our study was to determine if remembered implicitly defined reach target locations are coded and updated in the same way explicitly defined targets are. Participants presented with allocentric cues, visually determined and remembered the centre point of the stimuli, and reached to this remembered location. Reach endpoint errors to these implicit target sites vary systematically and significantly as a function of gaze direction with respect to the remembered “target” location (regardless of the type of stimulus provided). This pattern of errors (i.e., overshooting the remembered target location in the opposite direction to final target-relative gaze), is consistent with findings for explicit visual targets [e.g., 11,15,25]. Thus, it seems implicit targets (defined only by allocentric cues) are coded and updated in an eye-centred reference frame, just as explicit targets are. That is, we have found gaze-centred updating of a location that is not explicitly visible. These findings demonstrate similarities in processing of two conceivably distinct types of visual information.

It is conceivable that making such relative spatial estimates (i.e., determining the midpoint between vertical bars or along a horizontal line) should not require eye-centred coding at all. If this were the case any subsequent gaze shift after viewing these stimuli should not have systematically affected reaching accuracy. Our results suggest this is not the case – at some point estimates of centre of this/these stimulus/stimuli were coded relative to gaze and remapped in an eye-centred reference frame when gaze shifted eccentrically before reaching. This is consistent with previous findings that reach errors to targets implied by a 3D full-field motion pattern varied with gaze indicating eye-centred updating of the reach goal [17]. But since full-field motion elicits a strong egocentric illusion, perhaps this is not surprising. Our task entails making

relative spatial judgments involving allocentric coding, except that our participants reached to the target site which requires egocentric coding of that location. While it is not surprising that the allocentrically defined location is converted to an egocentric representation for motor planning, it is surprising that the egocentric representation is an eye-centred one (at least initially). In an eye-centred reference frame, any subsequent eye movements before reaching require appropriate remapping of the reach goal (i.e., as a function of the new gaze direction relative to the target); other egocentric reference frames would not require this eye-centred remapping.

While we, and others [17], find no differences in the way gaze affects localization of implicit and explicit targets for reaching, some have shown that movements guided by allocentric stimuli and explicit/egocentric stimuli do differ. For example, several experiments [e.g., 21,22] comparing egocentric and allocentric movements have found that reach accuracy and precision both differ between these tasks (although gaze direction did not change in these studies). But these disparate findings are likely because the goal-directed movements to implicit targets used in the current study, and in [17] are different from the “allocentric movements” used in [21], which better resemble mimicking gestures and reproducing drawings. Specifically, the “allocentric movements” involved assessing distances between two points in one area of the workspace, and moving the hand the same distance and direction in a different area of the workspace starting from a different location. This is a task which people may not be well calibrated for; thus especially difficult to perform. In our paradigms, the tasks are more similar to well-calibrated everyday tasks like locating the centre of an object (e.g., grasping a pencil) or the centre of some visually defined region of space (e.g., reaching into a drawer). So, there appears to be a similarity between movements made toward the “centre” of objects (or/and the centre of the space between objects) and those made to a single remembered object, which in this context suggests that planning allocentrically and egocentrically defined movements may not be different.

People seem to convert allocentric representations to egocentric representations at an early stage of processing – perhaps at the earliest possible opportunity [5] – and explicit information is not required to hold a specific region of space in memory. So, it might be that in our study the implicit representation is converted to an explicit representation, in a similar way as allocentric information is converted to egocentric information [5]. It may also be that the vertical bars are “bound” in some Gestalt representation, the centre of which can be retrieved from memory for reach planning [Cf., 19]. Alternatively, efference copy of exploratory eye movements during the viewing period could also allow for a reasonable egocentric representation of the stimuli which could again allow the determination of the centre/“target” location in memory. In any event, our results indicate remembered implicit target locations, defined by allocentric information, are coded and updated in an eye-centred reference frame as remembered egocentrically/explicitly defined target locations are (Fig. 2C).

But what are the implications of implicit and explicit information about target location both being available concurrently? How would a gaze shift affect reaches made to an explicit target located between flanking vertical bars? If implicit targets (i.e., the midpoint between the two bars) are coded in eye-centred coordinates, as we have found here, then reach errors to explicit targets that are surrounded by allocentric cues (the bars) should still vary with final gaze direction in the same way. If the errors or biases are the same for both sources of information as we have shown, then the average of these two statistically identical patterns of errors would not be different. Only, the variance would likely be reduced (proportional to the weighed variance of each source) as would be the case whenever multiple sources of spatial information about target location are simultaneously available [e.g., 28].

When allocentric information is visible during reaching movements, gaze-dependent reach errors to targets in the left visual hemifield seem partly reduced [4]. This is not the case in the right visual hemifield though, suggesting allocentric cues do not necessarily diminish the gaze-dependent effects on reach error. It could be that the allocentric cues used (four dots in a square formation) were providing additional information for coding the explicit target in gaze-independent coordinates. Alternatively, the target location implied by these allocentric cues (which corresponds to the explicit target displayed) could also be coded relative to gaze, but the gaze-dependent effect of these visible allocentric cues was somewhat smaller than the modulation effect produced by the explicit target (at least for the left side). Thereby when the allocentric stimuli is combined with the remembered explicit target, the overall combined gaze effect on reaching was smaller. Other studies also indicate allocentric/relative coding is used in parallel with egocentric/absolute coding and not instead of it, with allocentric information typically being used in more complicated situations where egocentric coding can be enhanced by the additional information [see 3, and 7 for reviews]; specifically allocentric information can improve reach accuracy when it provides some structured environment to the target [e.g., 10,13,16]. In these studies, it could be that the more structured or informative the allocentric cues, the less likely that interpolated locations within this structure would be coded relative to gaze, and thus the less likely to show gaze-dependent modulation of error. Of course these studies do not involve systematically varying or shifting gaze, so whether this is indeed the case, and how or if these enriched surrounding cues would subsequently affect updating the explicit target, are unknown.

We have shown previously that “allocentric information”, in the form of relative distance between sequential explicit reach targets, does indeed reduce, but does not eliminate eye-centered representation of each remembered target [24]. In that study, the errors fell between those predicted for gaze-centred representation and those predicted for gaze-independent representation of the target [24], and more so when the purely eye-centred coding would have resulted in a very small relative reach distance to the second target compared to the actual distance between the two target locations. Other cues about relative location of the targets, such as efference copy of the eye movements made between the two targets, may also have reduced the effect of gaze-representation, as may have been the case here. Regardless of how/when implicit cues might be converted to explicit representations, or under what circumstances allocentric and egocentric information might be treated the same or differently, our results show that reach errors to implicit targets are gaze-dependent in the same way and to the same extent as in reaches to explicit targets.

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