Gaze-related functions driving gaze anchoring in reaching

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Conceptualization (JF, JRF), Methodology (JF, JRF), Validation (JF, JRF), Formal analysis (JF, JRF), Data Curation (JF, NI), Writing – Original Draft (JF, NI), Writing – review & editing (JF, NI, JRF), Visualization (JF, JRF), Supervision (JF, JRF), Funding acquisition (JF, JRF)

Declaration of Competing Interest

The authors declare no competing financial interests.

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Abstract

In an everyday task, such as planting spring flowers, the eyes typically fixate target objects that we manipulate. When reaching to a target object, gaze shifts away from the reach target to a secondary saccade target, presented during the reach, are delayed until after the reach target has been attained—a phenomenon known as gaze anchoring. Here, we compared gaze anchoring in human participants when reaching to a visual target versus a visual-haptic target providing force feedback upon contact. We also examined gaze anchoring in a bimanual context in which participants were instructed to shift their gaze to the secondary saccade target as soon as it appeared and, at the same time, move their other hand to the secondary saccade target. We found that, during the reaching movement, gaze was anchored to the target for both visual and visual-haptic targets. Whereas in the visual condition gaze appeared to be anchored until the end of the reaching movement, in the visual-haptic condition, gaze appeared to be anchored until the hand was close to the target (i.e., the end of the directing phase). In two-handed reaching, gaze anchoring was observed but anchoring did not extend to the left hand, which started moving before the eyes. Overall, our findings indicate that the timing of eye and hand movements in object manipulation is linked to the function of target fixations.

Keywords: gaze anchoring, eye-hand coordination, reaching, saccades, visuomotor control

New & Noteworthy

When reaching to a visual target, humans commonly fixate the target throughout the reaching movement even if a competing visual target appears. Here we show that gaze remains at the reach goal until target attainment has been confirmed visually or until haptic information becomes available to guide target attainment. Whereas the eyes are always anchored to the reach goal, a secondary movement of the non-reaching hand to the competing target can be planned and initiated.

Introduction

Many natural action tasks, such as cooking, require a sequence of coordinated eye and hand movements. In goal-directed action tasks, in which people reach for and manipulate objects, gaze commonly fixates the next object that is to be manipulated at the start of the reach, and gaze shifts to the next target of interest around the time that the hand arrives at the current target (Ballard et al. 1992; Bowman et al. 2009; Epelboim et al., 1995; Wilmut et al. 2006). For example, in block stacking, gaze shifts from a given block to its placement location around the time the hand contacts the block (Flanagan and Johansson 2003).

Fixating the target serves several functions, including ‘directing’ and ‘guiding’ the hand to the target and ‘checking’ goal completion (Land et al. 1999; Land 2006; Land and Hayhoe 2001). Directing refers to the use of peripheral vision and gaze-related signals—including proprioceptive signals of the eye and/or efference copy of motor commands—to control the reaching movement towards a foveated target (Bridgeman and Stark 1991; Goettker et al. 2020; Goodale et al. 1986; Prablanc et al. 1986). During the directing phase of the reach, peripheral vision of the hand can be used to rapidly (~150 ms) and automatically correct for reach errors (Brenner and Smeets 1997; de Brouwer et al. 2018; Paillard 1996; Sarlegna et al. 2003; Saunders and Knill 2003, 2004). Guiding refers to the use of central (i.e., parafoveal) vision to control the hand movement as it approaches and contacts the reach target (Johansson et al. 2001). During the guiding phase of the reach, central vision of the hand and target can be used to adjust the hand via relatively slow feedback loops. Finally, checking refers to the use of central vision to confirm that contact between the hand and target has been achieved (Säfström et al. 2014). Many studies of goal-directed reaching have used purely visual targets, in which case central vision is required to guide the hand and check goal completion. However, when reaching to physical objects, haptic information can typically be used to guide the hand and check goal completion.

In real-world manipulation tasks, there is often competition for gaze resources between targets of action and events in the environment, such as when a brightly coloured bird appears in the peripheral vision of a birdwatcher who is reaching towards the foveated binoculars. In a series of studies, Neggers and Bekkering (2000, 2001, 2002) examined such competition using a task in which a secondary saccade target was visually cued while participants reached towards a foveated reach target. The visual target was cued at different times during the movement and the participant was instructed to shift their gaze to the saccade target as soon as it was cued. When the cue was presented during the reach, gaze remained ‘anchored’ at the reach target until around the time the hand arrived. As a consequence, the latency of the saccade—or saccadic reaction time—increased with the remaining duration of the reach movement after the cue (see thick orange trace in Fig. 1A). In the current study, we aimed to link the timing of saccades and reaching movements to the functional demands of gaze.

Previous work on gaze anchoring during target-directed reaching has focused on tasks in which the participant moves their hand to visual targets (Abekawa et al. 2021; Neggers and Bekkering 2000, 2001). In this scenario, we would expect gaze to support both directing and guiding the hand to the target in addition to checking goal completion. However, it is unclear whether gaze anchoring is taking place in the directing phase of the reach, or whether anchoring is only taking place towards the end of the reach movement (i.e., during guiding and checking). Importantly, peripheral vision can be effectively used to direct the hand when fixating a gaze target that is displaced from the reach target (de Brouwer et al. 2017, 2018; Neggers and Bekkering 2002). Thus, it is plausible that, when a secondary saccade target is presented during the reach, participants maintain gaze at the reach target because it is critical for the forthcoming guiding and checking phases, rather than for directing per se. To examine whether gaze anchoring occurs during directing, we examined eye-hand coordination during a reaching task in which the participant moves a hand-held handle, represented as a cursor, to a 'visual-haptic' target, where contact forces between the cursor and the target are simulated by applying forces to the hand via the handle. We expected that in this situation, gaze would not be required for guiding because haptic feedback can be used to confirm that the cursor reaches the target. Thus, if gaze anchoring occurs during directing, we should find that gaze is locked to the target as the hand moves towards the target but is released (i.e., is able to shift to the secondary target) at the end of the directing phase—and the start of the guiding phase—when the hand arrives close to the target. In other words, the time from the cue (presentation of the secondary saccade target) to saccade onset should increase in lock-step with the time from the cue to the end of the directing phase (see thin solid orange trace in Fig. 1A). Conversely, if anchoring does not occur during directing, the time from the cue to the onset of the saccade (i.e., saccadic reaction time) should be constant (dashed horizontal orange trace in Fig. 1A).

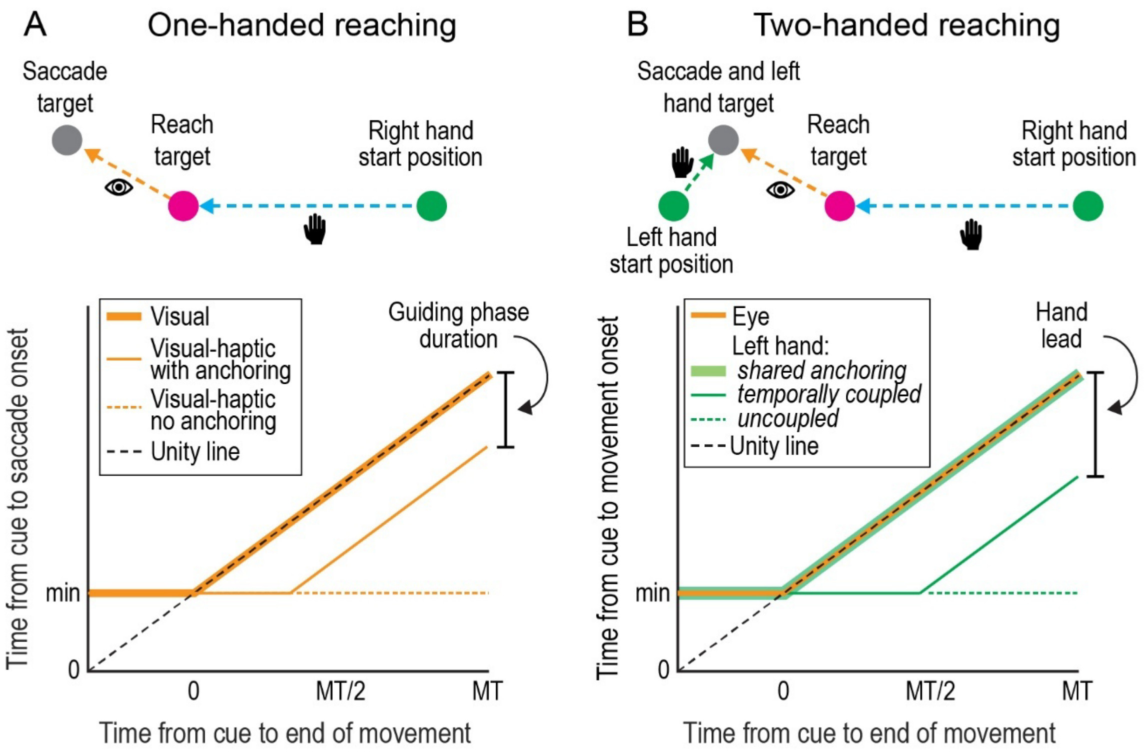

Figure 1. Expected and hypothesized eye-hand coordination in virtual reaching tasks. (A) In the one-handed task, the participant is instructed to shift their gaze from the reach target to a secondary saccade target, which is cued at different times during the right-hand reach. For visual targets, the time from the cue to saccade onset is expected to increase in lock-step with the time from the cue to the end of the movement (thick orange trace). For visual-haptic targets, we predict that gaze anchoring will occur during the directing phase of the reach, such that the time from the cue to saccade onset will increase in lock-step with the time from the cue to the end of movement minus the duration of the guiding phase (thin solid orange trace). However, if gaze anchoring does not occur during the directing phase, saccade latency for visual-haptic targets should be constant and not depending on the time of the cue during the movement time (dashed horizontal orange trace). (B) In the two-handed task, the participant is instructed to move their gaze and left hand to the secondary (saccade+left hand) target, which is cued at different times during the right-hand reach to the initially foveated reach target. Three possible outcomes can be considered: shared anchoring of the left hand and saccade may occur (thick green trace); the left-hand onset may be temporally coupled with the saccade onset with the hand leading the eye (thin solid green trace); the left-hand latency may be constant and independent of saccade latency (dashed horizontal green trace).

In addition to testing whether gaze anchoring occurs during the directing phase of visually guided reaches, we asked whether anchoring extends to movements of the other hand. In a two-handed version of our reaching task, participants used their right hand to reach to a foveated visual reach target, just as in the one-handed task, and were instructed to move both their eyes and their left hand to a secondary target as soon as it was cued. We expected saccade latencies in the two- and one-handed tasks to be similar because the visual and gaze-related functional demands of the right-handed reach should be the same. We can consider three alternative hypotheses about left-hand movement latencies. First, the left hand and gaze may exhibit shared anchoring, in which case the left hand and saccade latencies should be similar (see thick green trace in Fig. 1B). Second, the left-hand movement may be temporally coupled with the saccade but start moving at a different time. For example, participants may time the onset of the left-hand movement such that the hand arrives at the secondary target around the same time as gaze. In this case, we would expect the left-hand onset to lead to the saccade onset by a consistent time interval (see thin solid green trace in Fig. 1B). Third, the left hand may start moving at a fixed latency relative to the cue and therefore be decoupled from the saccade onset (see dashed horizontal green trace in Fig. 1B).

Methods

Participants

Twenty-eight individuals participated in the experiment (18-51 years of age; mean age 25). Participants were primarily recruited from the Queen’s University undergraduate and graduate student population. All participants were eligible for monetary compensation ($10 per hour) or course credits towards a psychology course. Each participant provided written consent prior to participation and received a debriefing once the experiment was completed. Participants were required to be 18 years of age or older, and have no history of psychological, neurological, or eye disease. The experiment was approved by the Queen’s General Research Ethics Board (TRAQ #: 6003707) and complied with the Declaration of Helsinki.

Apparatus

Participants were seated at a desk with their head placed on a mounted chin and forehead rest in front of a vertical monitor (70 × 39.5 cm in size; 1920 × 1080 resolution) on which the visual stimuli were displayed. Eye movements were recorded using a desktop mounted eye tracker (EyeLink 1000; SR Research, Ltd., Kanata, ON, Canada). Unimanual and bimanual reaching movements were performed in a horizontal plane using the handles of a robotic manipulandum (End-Point robot, KINARM, Kingston, ON, Canada). The position of the hand was represented as a cursor on the vertical monitor with forward and rightward hand movements mapped onto upward and rightward cursor movement (as with a standard mouse). There was a 1:1 relationship between hand movement displacement and cursor movement displacement, i.e., a 10 cm movement of the hand resulted in a 10 cm movement of the cursor. The viewing distance from the right eye to the monitor was 37 cm, such that a 1 cm displacement on the monitor corresponded to 1.5 visual degrees.

Stimuli and Procedure

Three conditions (one-handed visual, one-handed visual-haptic, and two-handed visual) were examined with 108 trials per condition. Fourteen participants performed the one- and two-handed visual reaching conditions, and 14 separate participants performed the visual-haptic reaching condition. Before each block, participants received training to become familiar with the equipment and to ensure consistent right-handed reaching speed within and across participants. Following training, the eye tracker was calibrated, and participants were asked to keep their head in the chin and forehead rest throughout each block.

To correct for buffering delays in the display system, we corrected the time at which visual stimuli appeared to the participants. The delay between the time an event code was sent and the time visual stimuli appeared was on average 53 ms (range: 41-64 ms).

One-handed reaching experiment

In this experiment, two groups of participants perform the one-handed reaching task. Participants in the visual condition did not experience any forces when reaching. In contrast, participants in the visual-haptic condition experienced a force on the hand (via the handle of the robotic manipulandum) when the cursor, controlled by the hand, contacted the reach target. Specifically, as soon as the outer part of the cursor overlapped with the outer part of the reach target, the robot generated an elastic force (with a stiffness of 15 N/cm) that pulled the handle to the centre of the reach target, and held it there until the end of the trial.

In both conditions, participants used their right hand to move the robot handle (Fig. 2A). To initiate a trial, participants had to move the blue-coloured cursor (0.5 cm in diameter) inside the start position. Then, three grey hollow circles (0.8 cm in diameter), serving as saccade targets, and one pink-coloured hollow circle (0.8 cm in diameter), serving as the reach target, appeared. Participants were required to keep their gaze on the pink-coloured hand target and their hand at the start position for a randomly jittered time period of 1-1.5 seconds. After the fixation period, the pink-coloured hand target filled in, prompting participants to initiate a reaching movement from the start position to the hand target. The distance from the start position to the hand target was

15 cm. During this reaching movement, one of the three grey saccade targets filled in, prompting participants to move their gaze from the hand target to the cued saccade target as soon as possible. The horizontal saccade target was 10 cm away from the hand target, and upper and lower targets had a horizontal offset of 7 cm and a vertical offset of ± 4 cm (i.e., ± 52° from the horizontal). The saccade target was cued in every trial and could appear at one of three possible times during the reaching movement—when the hand had moved 2% (start of reach), 50% (during reach), or 95% (end of reach) of the distance from the start to the hand target (Fig. 1D)—inciting one of the grey circles to fill in. The position and time at which the eye target was cued was randomized between trials. The trial finished once the hand arrived at the hand target, and the cursor had to be within the hand target for 250 milliseconds for the trial to successfully finish. During the experiment, participants were notified if they moved their hand before the reaching movement was cued (pink target filled in), or moved their gaze before the saccade target was cued (one of three grey targets filled in). Trials in which participants moved their eyes or hands too early were immediately repeated.

Two-handed reaching experiment

In the two-handed visual condition, participants used both hands to move the robot handles (Fig. 2B). The hand start positions, hand target, and saccade targets were the same size as in one-handed reaching. The right start position was 15 cm to the right of the reach target and the left start position was 9 cm leftward of the right-hand reach target. At the start of each trial, participants moved the left and right robot handle to place the blue-coloured cursor at the left and right start position, respectively. Two grey hollow circles (the upper and lower saccade targets from the one-handed reaching condition) and one hollow, pink coloured right-hand target appeared. Participants were required to keep their gaze on the right-hand reach target and their two hands at the respective start positions for 1-1.5 seconds. After the fixation period, the right-hand pink target filled in, prompting participants to initiate a reaching movement from the right start position to the right-hand target. Next, one of the two combined saccade and left-hand targets was cued at the same cueing times as in the one-handed reach condition (start of reach, halfway through reach, end of reach). Once the combined saccade and left-hand target filled in, participants were instructed to move both their left hand and their eyes to the cued eye-hand target as soon as possible. Again, participants received immediate feedback, and trials were repeated if they moved their eyes or either of their hands before the respective cue.

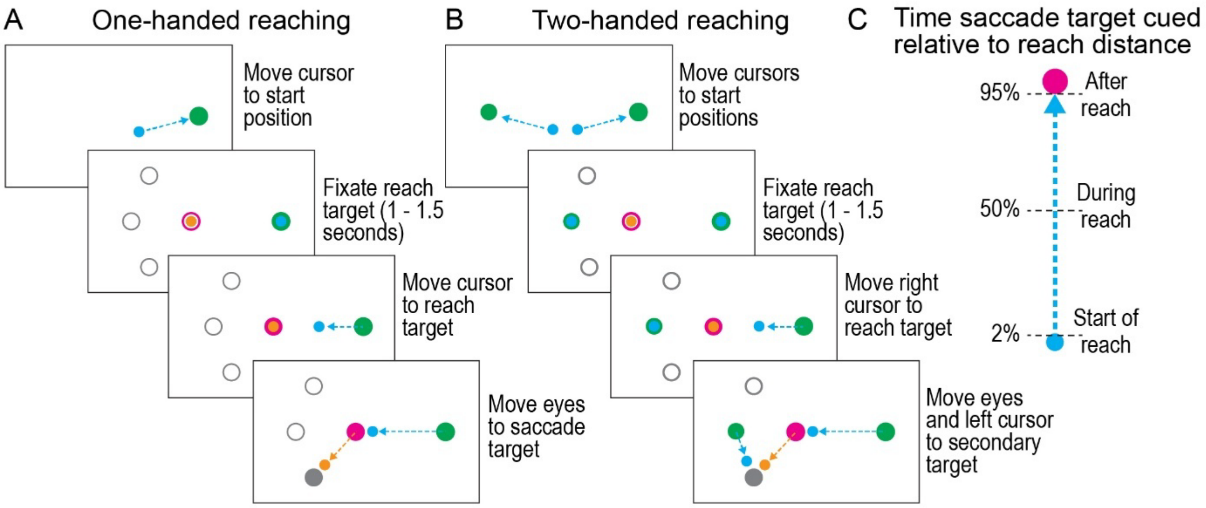

Figure 2. Experimental conditions and task procedure. (A) In the one-handed reaching task, participants moved the cursor corresponding to their right-hand position to the start location. Participants were instructed to fixate a hollow pink reach target and, once it filled in, to reach from the start to the reach target using their right hand. While reaching, one of three hollow grey saccade targets filled in, cueing the participant to move their eyes to the saccade target as soon as possible. (B) In the two-handed reaching task, participants moved both cursors, indicating their left and right hand, to the respective start locations. Participants were instructed to fixate a hollow pink reach target and keep their left hand at the left start location. Once the pink reach target filled in, participants moved their right hand to the reach target. While reaching, one of two hollow grey saccade targets filled in, cueing the participant to move their eyes and their left hand to the combined saccade and left-hand target as soon as possible. One group of 14 participants completed the one- and two-handed reaching tasks with visual targets, where 'contact' between cursor and reach target was visual only. A second group of 14 participants performed the one-handed task with visual-haptic targets with simulated contact forces between the cursor and reach target. (C) Saccade targets or combined saccade and left-hand targets were cued at the start, during, or after the right-handed reaching movement.

Eye and Hand movement recordings and analysis

To analyze eye and hand movement data, we created custom-made routines using MATLAB (version 2023b). For hand movement analyses, we analyzed the centred x and y positions of the robotic handles that were sampled at 1000 Hz. Position data were filtered using a third order 20 Hz Butterworth filter. For all reaching movements, we determined the start of the reach, the end of the directing phase—which coincided with the start of the guiding phase—and the end of the guiding phase (i.e., the end of the movement). The start and end of the reach were defined at the times at which the hand velocity first exceeded and subsequently dropped below 5% of the peak velocity of the current reach, respectively. To determine the time point at which the directing phase ended and the guiding phase started, we first selected all samples during which the hand decelerated. We then differentiated this hand deceleration and found the time at which the jerk peaked. In bimanual reaching trials, we further analyzed left-hand latency. Hand latency was defined as the difference between the time at which the combined left-hand and saccade target was cued and the start of the left-hand movement, defined as the time at which the left-hand velocity first exceeded 5% of the peak velocity of the current reach.

We recorded the x- and y-position of the right eye with a sampling rate of 500 Hz. Eye position signals were filtered using a second-order 15 Hz Butterworth low pass filter. Eye velocity was determined by differentiating the eye position signal. Eye velocity samples were labelled as saccades when five consecutive samples exceeded a fixed velocity criterion of 50 cm/s. To determine saccade onsets and offsets, we found the nearest reversal in the sign of the eye acceleration signal before eye velocity exceeded the fixed velocity threshold (saccade onset), and the nearest reversal in the sign of eye acceleration after eye velocity was back below the fixed velocity threshold (saccade offset). We then calculated saccade latency relative to the time of saccade cue, and saccade latency relative to the time at which the right hand first contacted the reach target.

Data exclusion

For both one- and two-handed reaching, one participant was excluded because they were unable to follow task instructions and moved their eyes away from the reach target before the reaching movement was cued in a majority of trials. One other participant was not included in the one-handed visual contact group because of an erroneous Kinarm calibration. For the remaining participants we excluded 717 out of 12636 trials (5.7%). Specifically, we excluded trials in which participants moved their eyes or left hand anticipatory to the cue (before the time of cue or within 100 ms of the cue, respectively; 1.6%), the eyes did not land on the cued target (1.5%), or fixation on the reach target was not maintained (2.6 %). Fixations on the reach target were not maintained due to blinks, saccades to the hand starting position(s), or to the visual scene.

Statistical Analysis

In the one-handed reaching task, one group of participants performed the task with only visual feedback, while another group of participants performed the task with visual-haptic feedback. To assess and compare gaze anchoring in these two conditions, we fit a piecewise regression equation—with an initial constant segment followed by a sloped segment—to predict saccadic reaction time (time from the cue to saccade onset) as a function of the remaining duration of the movement at the time of the cue (i.e., time from the cue to the end of the movement; see Fig. 3E). The model has 3 parameters:

$$y = b_0 \qquad if\ x < b_2 + b_3 D \tag{1}$$

$$y = b_0 + b_1 (x - P) \qquad if\ x > b_2 + b_3 D \tag{2}$$

where *D* is a dummy variable coding for condition (0 for visual, 1 for visual-haptic), b_0 is a constant value representing the minimum reaction time, b_1 is the slope for the for the visual and visual-haptic conditions, and b_2 and b_2+b_3 are the breakpoints between the segments for the visual and visual-haptic conditions. Importantly, this model allows the breakpoints to differ between conditions but forces a constant and a single slope. This allows us to assess whether saccades are anchored to different temporal events in the two conditions, with the assumption that the saccade reaction time is the same in the two conditions.

We used the same approach to compare saccadic reaction times in the one-handed and two-handed reaching tasks, with the dummy variable coding task. We also used the approach to compare saccadic and left-hand reaction times in the two-handed reaching task. However, in this case we included one additional parameter to allow for different constant values (i.e., minimum reaction times) for gaze and the left hand:

$$y = b_0 + b_1 D \qquad if\ x < b_3 + b_4 D \tag{3}$$

$$y = b_0 + b_1 D + b_2 (x - P) \qquad if\ x > b_3 + b_4 D \tag{4}$$

where b_0 and b_0+b_1 are the constant values for saccadic and left-hand reaction time, respectively.

To estimate confidence intervals for the model parameters, we used a nonparametric bootstrap procedure with 1,000 resamples. On each bootstrap iteration, we randomly sampled (with replacement) from the original dataset and re-estimated the model parameters by minimizing the sum of squared errors using constrained nonlinear optimization. The optimization was performed using the fmincon function in MATLAB. For each resampled dataset, we recorded the resulting parameter estimates. The 95% confidence intervals for each parameter were obtained by taking the 2.5th and 97.5th percentiles of their bootstrap distributions.

To assess the contribution of key model components, we performed a series of likelihood ratio tests (LRTs) comparing a full model (including the parameter of interest) to a reduced model (with that parameter constrained or removed), and evaluated the improvement in model fit using the LRT statistic:

$$\lambda = 2\left(\log L_{full} - \log L_{reduced}\right) \tag{5}$$

where *L* denotes the log-likelihood. The test statistic was compared to a chi-squared distribution with 1 degree of freedom.

When comparing saccadic and left-hand reaction times in the two-handed reaching task, the difference in breakpoints is not equivalent to the difference in intercepts of the sloped segments because of the difference in the height of the constant segment. To assess whether the intercepts of the sloped portions differed, we estimated 95% confidence intervals for the intercept difference using non-parametric bootstrapping (1,000 resamples), recomputing all model parameters on each bootstrap iteration. The difference was considered statistically significant if the resulting confidence interval did not include zero.

For the one-handed reaching experiment, we used mixed-factor repeated measures ANOVAs to test whether the durations of the directing and guiding phases of the reach varied with cue category (start of reach, halfway through the reach, end of reach) and feedback upon contact (visual vs. visual-haptic). A p value ≤ 0.05 was considered to be statistically significant.

Results

Gaze anchoring in one-handed reaching depends on sensorimotor feedback

In the one-handed reaching task, we aimed to link the timing of eye and hand movements to the functional demands of gaze. Participants performed right-handed reaches to move a cursor, controlled by the hand, to a stationary reach target. After, during, or at the start of the reach, a secondary saccade target filled in, cueing participants to shift their gaze from the fixated reach target to the saccade target as soon as possible. In the visual condition, participants only received visual feedback about contact (i.e., when the cursor “contacted” the target), whereas in the visual-haptic condition, participants also experienced a force upon contact.

Figures 3A and B show, for representative trials from the visual and visual-haptic conditions, eye and hand (i.e., cursor) paths and target positions in a screen-centred reference frame. Figures 3C and D show gaze and hand movement velocities as a function of time for the same trials. The time of the cue and the end times of the directing phase and movement are shown by vertical lines. In both of these trials, the top potential saccade target was cued as the saccade target just after movement start. Gaze shifted to the saccade target just after the end of the movement in the visual condition, and just after the end of the directing phase (and before the end of the movement) in the visual-haptic condition.

Depending on the position of the saccade target, the saccade to the saccade from the hand target to the saccade target required either a horizontal or an oblique eye movement. We found no difference in saccade latency between horizontal and oblique targets ($t(12) = 1.11$; $p = 0.29$) and thus averaged across saccade target locations.

We used a mixed-factor ANOVA to examine the effects of the between-subjects factor feedback (visual vs visual-haptic) and the within-subjects factor cue category (start, during or end of the reach movement) on the durations of the directing and guiding phases. The duration of the directing phase (M = 511 ms, SE = 21 ms) did not depend on feedback ($F(1,24) = 1.09$; $p = .31$), cue category ($F(2,48) = .92$; $p = .40$), or the interaction ($F(2,48) = .37$; $p = .69$). The duration of the guiding phase was greater ($F(1,24) = 7.58$; $p = .012$) in the visual condition (M = 175 ms, SE = 47 ms) than in the visual-haptic condition (M = 111 ms; SE = 30 ms), but did not depend on cue category ($F(2,48) = 1.01$; $p = .37$) or the interaction between feedback and cue position ($F(2,48) = 1.65$; $p = .20$). These results indicate that participants did not alter the way they reach depending on when the saccade target was cued. In addition, whereas the final guiding, or approach, phase of the reaching movement depended on contact feedback, the initial larger amplitude directing phase did not.

Figure 3E shows saccadic reaction time (time from the saccade target cue to saccade onset) as a function of the remaining duration of the movement at the time of the cue (i.e., time from the cue to the end of the movement). The data points represent medians for each combination of participant and cue category. Thus, each participant contributed three data points in either the visual or visual-haptic condition. Because the timing of the cues depended on hand position (5, 50 or 95% of the distance to the target), the actual time of the cue, relative to the end of the movement, varied considerably because overall speed of the movement, and the speed profile over time, varied across participants. Note that the time from the cue to movement end was negative if the ‘end’ of the movement—defined as the time at which hand velocity dropped below 5% of the peak velocity—occurred before the cue was delivered, which could occur when the cue was delivered when the hand reached 95% of the distance to the target. The black dashed line is the unity line; thus, saccades initiated at the end of the movement would fall on this line. The height difference between the unity line and the dashed-dotted line is 111 ms, which is the mean duration of the guiding phase in the visual-haptic condition. Thus, on average, saccades initiated at the end of the directing phase in the visual-haptic would fall on this line.

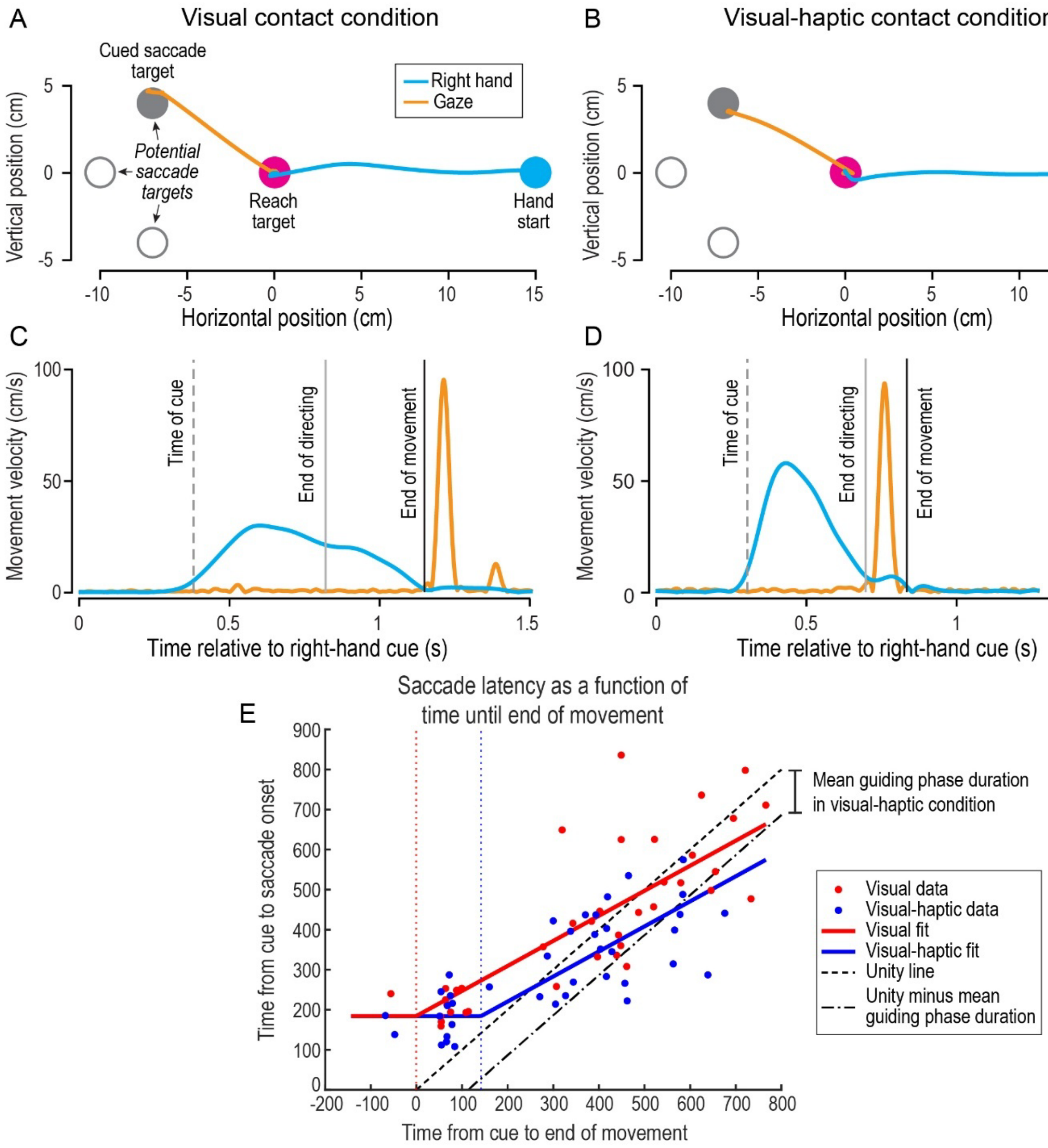

Figure 3. Results from the one-handed reaching task. (A, B) Gaze and hand (i.e., cursor) paths and target positions, in screen coordinates, from representative trials from the visual and visual-haptic conditions. Participants used their right hand to reach from the start position to the reach target and were instructed to shift their gaze from the reach target to cued saccade target, randomly selected from three potential saccade targets. (C, D) Gaze and hand tangential velocity profiles from the trials in A and B. The times of the cue and ends of the directing phase and movement are indicated by vertical lines. (E) Saccadic reaction time as a function of the remaining movement time at the time of the cue in the visual and visual-haptic conditions. Dots represent medians from individual participants. Solid lines show fits with the piecewise regression model with the vertical dotted line marking the boundary between the constant and sloped segments. Black dash line is the unity line and the height difference between the unity lines and the dash-dotted line is the mean duration of the guiding phase in the visual-haptic condition.

The piecewise linear regression revealed that the common height of the constant segment (184 ms) and the common slope (.63) were both significantly greater than zero ($p < .001$ in both cases). Importantly, the difference between conditions in the breakpoint (142 ms) was significant ($p < .001$). Note that the difference in breakpoints can also be expressed as the difference in the intercepts of the sloped segments for the visual and visual-haptic conditions, which was 89 ms. Thus, the height difference between the sloped segments of the two conditions was only a little less (23 ms) than the mean duration of the guiding phase in the visual-haptic condition (111 ms).

Overall, these results provide evidence that gaze anchoring is not only observed in the visual condition, as expected, but also in the visual-haptic. However, gaze appears to be anchored to different events in these conditions. Specifically, in the visual condition, gaze appears to be anchored to the end of the movement, whereas in the visual-haptic condition, gaze appears to be anchored more to the end of the directing phase.ms).

Independence of gaze and hand anchoring in two-handed reaching

In the two-handed reaching task, we asked how the timing of the gaze shift to the secondary target would be affected if participants were asked to also move their left hand to the secondary target. More specifically, we asked whether gaze anchoring would still be observed and, if so, whether the left hand would also exhibit anchoring. Participants used their right hand to reach to the fixated right-hand reach target, and received only visual feedback about target contact (just as in the visual condition in the one-handed reaching task). The secondary—combined saccade and left hand—target was cued when the right hand reached 5, 50, and 95% of the distance to the target, instructing participants to move both their gaze (from the fixated reach target) and their left hand (from the left hand start position) to this secondary target as soon as possible.

Figure 4A shows gaze, right hand, and left-hand paths and target positions for a representative trial in a screen-centred reference frame. Figure 4B shows gaze and hand velocities as a function of time for the same. The time of the cue and the end times of the directing phase and movement are shown by vertical lines. In this trial, the top potential saccade target was cued as the saccade target just after the right-hand movement started. Note that the left hand started moving towards the secondary target well before the right-hand movement ended, whereas gaze shifted to the secondary target at the end of the right-hand movement.

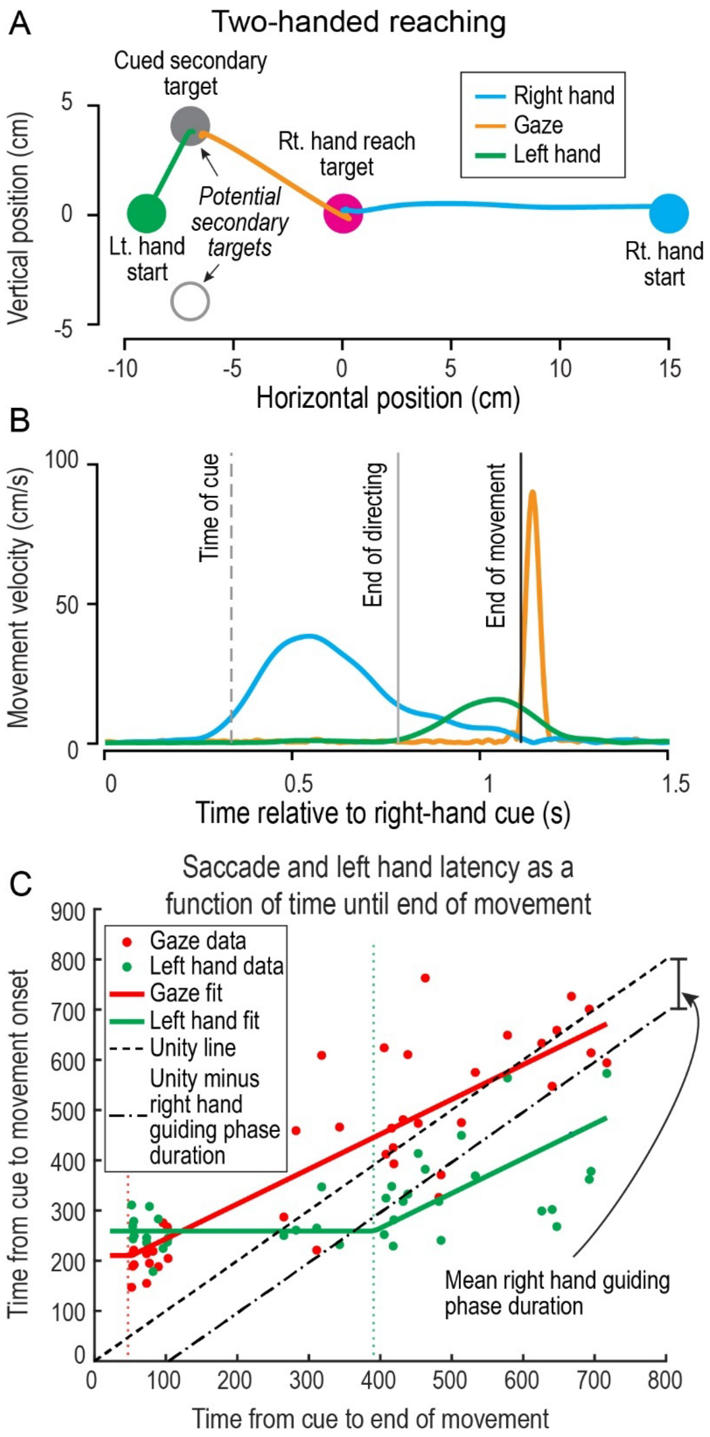

Figure 4. Results from the two-handed visually guided reaching task. (A) Gaze and left and right hand (i.e., cursor) paths and target positions, in screen coordinates, from a representative trial. Participants used their right hand to reach to the right-hand reach target, and were instructed to shift their gaze and move their left hand to the secondary target—randomly selected for two potential secondary targets—when it was cued during the right hand movement. (B) Gaze and left and right-hand tangential velocity profiles from the trial in A. The times of the cue and ends of the directing phase and movement are indicated by vertical lines. (C) Saccadic (red dots) and left hand (green dots) reaction time as a function of the remaining movement time at the time of the cue. Dots represent medians from individual participants. Solid lines show fits with the piecewise regression model, with the vertical dotted line marking the boundary between the constant and sloped segments. The black dashed line is the unity line. The height difference between the unity line and the black dashed-dotted line is the mean duration of the guiding phase of the right-hand movement.

The piecewise linear regression (Fig. 4C) revealed that the common slope of the sloped segments (.69) was significant ($p < .001$), and that the height of the constant segment was greater ($p < .001$) for the left hand (259 ms) than for gaze (210 ms), indicating that the minimum saccadic reaction time was ~50 ms less than the minimum left hand reaction time. The regression also revealed that the difference in breakpoints (340 ms) was significant (p < .001). We found that the difference between the intercepts of the sloped segments (187 ms) was significantly different from zero (i.e., the 95% confidence intervals [135 ms, 338 ms] did not include zero). Thus, it appears that gaze and the left hand are anchored to different time points linked to the right-hand movement. The saccadic reaction times were generally quite close to the unity line, suggesting that gaze was roughly anchored to the end of the movement. The mean duration of the guiding phase of the right-hand movement was 104 ms, which is shorter than the height difference (187 ms) between the sloped segments, suggesting that, on average, the left hand was anchored to a time point that occurred earlier than the end of the directing phase of the right hand. However, inspection of the left-hand reaction times indicates that little or no left-hand anchoring was observed in some participants. For the others, the left-hand reaction times are generally quite close to the dashed-dotted line, suggesting that the left hand was roughly anchored to the end of the directing phase of the right hand. In any event, what is clear is that the left hand is not ‘co-anchored’ with gaze.

Comparison of gaze anchoring in the one- and two-handed reaching task

We asked whether similar gaze anchoring occurred in the visual condition of the one-handed reaching tasks and the two-handed reaching tasks, in which only visual feedback about target contact was provided. Note that the same participants performed these two tasks. Figure 5A shows saccadic reaction time as a function of the remaining duration of the movement at the time of the cue for the two tasks. The data points represent medians for each combination of participant and cue category. The black dashed line is the unity line. The piecewise linear regression revealed that the common slope of the sloped segments (.69) was significant (p < .001) but that there was no significant difference in the breakpoints (p = .31), and hence the intercepts of the sloped segments. Thus, similar gaze anchoring, with gaze roughly anchored to the end of the right-hand movement, was observed in the two tasks. In other words, the instruction to move the left hand to the secondary target did not seem to have any effect on gaze anchoring.

We observed considerable variability, across participants, in terms of how long saccades were delayed relative to the end of the reaching movement. To test whether the magnitude of the delay was participant specific, we compared saccade latencies of the one- and two-handed reaching tasks. Figure 5B shows, for each combination of participant and cue category, saccadic latency in the two-handed task as a function of saccadic latency in the one-handed task. Note that for this analysis (and plot), we only used one-handed reaching trials in which the location of the secondary gaze target was in one of the two locations used in the two-hand reaching trials. In other words, we matched saccade directions. Linear regression revealed an R-squared value of 0.895 and a significant slope of .93 (t = 17.7; p < .001).

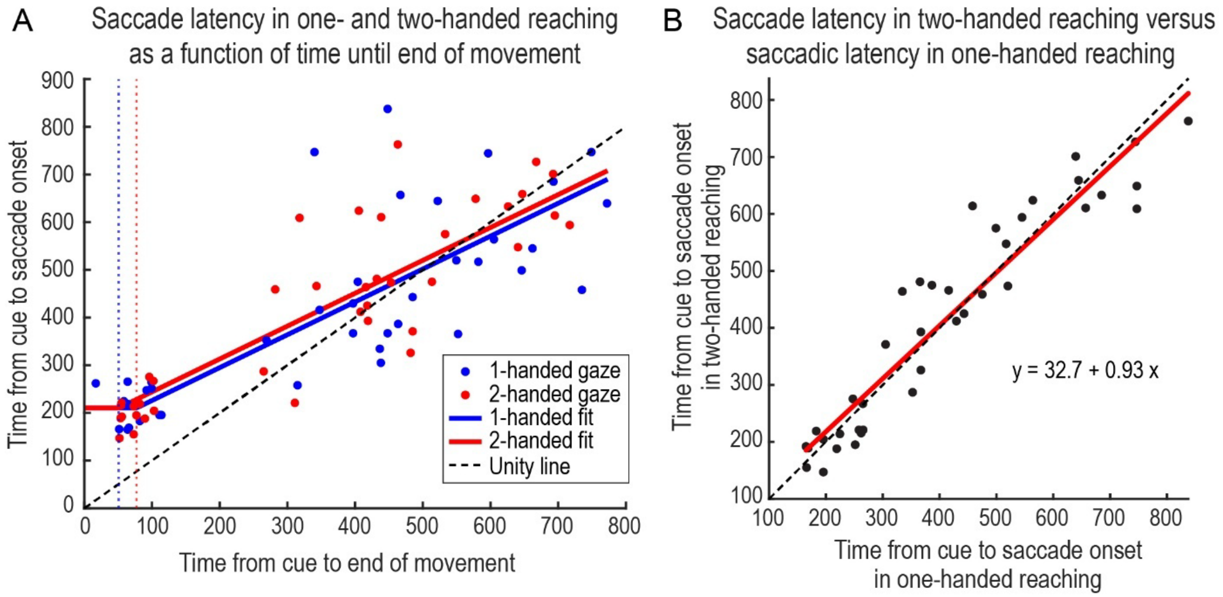

Figure 5. Comparison of gaze anchoring in the one- and two-handed reaching tasks. (A) Saccadic reaction time as a function of the remaining movement time at the time of the cue in the visual condition of the one-handed reaching task and the two-handed reaching task. In both cases, only visual feedback about target contact was provided. Dots represent medians from individual participants. Solid lines show fits with the piecewise regression model with the vertical dotted line marking the boundary between the constant and sloped segments. The black dash line is the unity line. (B) Correlation, across participants, of saccadic reaction times in the visual condition of the one-handed reaching task and the two-handed reaching task. The black dash line is the unity line.

Discussion

The aim of this study was to investigate how quickly participants could initiate a visually-cued eye movement while engaging in manual reaching. In line with previous research, we found that saccades were delayed—relative to the cue—if the saccade was cued at the start or during the reach. However, the saccade delay depended on the availability of haptic feedback, with eye movements being initiated at the end of the reaching movement when feedback was only visual and at the end of the directing phase when participants received visual-haptic feedback upon contacting the reach target. We further tested the delay in movement initiation in a bimanual reaching task, in which the cued saccade target was also a left-hand reach target. Here, we found a similar saccade delay compared to one-handed reaching. However, the delay of the left-hand movement was much shorter than the saccade delay, indicating that the initiation of the left-hand reach was to some degree decoupled from gaze anchoring. Finally, we found that, in the visual condition, individual differences in how long saccades were delayed relative to the cue, were consistent across the one- and two-hand reaching tasks, suggesting that sensorimotor processing was similar in these two tasks.

Gaze anchoring depends on available sensory feedback

In natural action tasks, humans coordinate their eye and hand movements in stereotypical ways (de Brouwer et al. 2021; Land 2006). When reaching for and manipulating objects, gaze commonly fixates action-relevant objects before the hand arrives, and then shifts to the next location of interest around the time that the hand contacts the target object (Ballard et al. 1992; Bowman et al. 2009; Johansson et al. 2001). Fixating the action goal has been shown to increase endpoint accuracy both when reaching toward and placing objects (Bock 1986; Desmurget and Grafton 2000; Fisk and Goodale 1985; Luabeya et al. 2024). Moreover, maintaining fixation at the reach goal appears to be linked to hand movement control. When a saccade target is flashed during a reaching movement, saccades to the flashed target are delayed compared to saccades that are cued after reach completion (Neggers and Bekkering 2000). The duration of this delay depends on the time at which the secondary target is flashed relative to reach completion, with saccades being delayed longer if the secondary target is flashed early during the reach (Neggers and Bekkering 2001). These results suggest that gaze anchoring occurs, at least in part, to allow central vision to be used towards the end of the hand movement to guide the hand to the target. What is not clear is whether gaze anchoring also occurs to allow peripheral vision and gaze-related signals (e.g., gaze proprioception) to be used earlier during the hand movement to direct the hand towards the vicinity of the target.

Here, we extend previous findings by showing that gaze anchoring not only occurs in the visual condition, in which central vision is required to guide the hand to the target via slow visual feedback loops, but also in the haptic condition, in which central vision is not required for this purpose. These results indicate that gaze anchoring can arise from visuomotor demands during the directing phase when reaching to the target. During the directing phase, peripheral vision of the hand can be used continuously to monitor the position of the hand and to rapidly correct for potential reach errors (Brenner and Smeets 1997; de Brouwer et al. 2018; Paillard 1996; Sarlegna et al. 2003; Saunders and Knill 2003, 2004). Our results suggest that eliciting a saccade during the directing phase would disrupt ongoing visuomotor control. Such mechanisms of saccade inhibition might be mediated by releasing fixation-related neural firing (Paré and Munoz 1996; Yang et al. 2002; Zingale and Kowler 1987).

Previous work has described the role of visual feedback in visually-guided reaching and grasping (Janssen and Scherberger 2015; Sabes 2000). However, in real-world action tasks, humans not only rely on visual but also multisensory signals to guide reach-to-grasp movements (Betti et al. 2021). For example, when grasping an object, tactile information from the fingertips is used to rapidly adjust hand kinematics and the force exerted to grasp the object (Johansson and Flanagan 2009; Pruszynski et al. 2016, 2018). Moreover, whether and when an object is foveated prior to grasping depends on the availability of haptic feedback upon contacting the object. For example, whereas manipulating objects with fingertips can be guided by tactile feedback, observers prefer to foveate objects until they are grasped when performing the manipulation task with a tool (Fooken et al. 2024b). Our results indicate that as soon as haptic feedback became available to guide contact between the hand and reach target, ocular fixation was released. Thus, saccade inhibition during reaching is modulated by the sensory information available to control the reaching movement.

Inhibition of saccades in goal-directed hand movements does not only occur when reaching to stationary targets, but also when intercepting moving objects (Fooken et al. 2021). Typically, humans track moving objects with a combination of smooth pursuit and saccadic eye movements, but as the hand approaches the moving target, catch-up saccades are systematically suppressed (Goettker et al. 2019; Mrotek and Soechting 2007; Schroeger et al. 2024). The observation that objects are foveated shortly before the hand contacts the object raises the question of the functional role of gaze in goal-directed action (Illamperuma and Fooken 2024). How much visuomotor control is needed when reaching towards a foveated target depends on task demands, such as the precision requirements at the reach goal (Rand and Stelmach 2010; Sims et al. 2011), the time available to complete sequential reaches (Deconinck et al. 2011), or the reward structure of the task (Abekawa et al. 2021). Thus, the strength of gaze anchoring is generally modulated by the structure of the action task and the environment.

Dissociation between eye and hand movements in bimanual reaching

As highlighted in the previous section, the synergetic link between eye-and hand movement control can be modulated by visuomotor task demands (de Brouwer and Spering 2022; Coudiere and Danion 2024; Epelboim et al., 1995; Sailer et al. 2000). For example, rewarding fast-latency saccades to a saccade target that is cued during a reaching movement increases the occurrence of non-anchored saccades (Abekawa et al. 2021). Here, we tested whether making the saccade target an additional, left-handed movement target would affect gaze anchoring in any way. We found that in the two-handed reaching tasks, saccades were delayed as long as in the one-handed reaching task. However, the initiation of left-handed reaches was to some degree decoupled from gaze anchoring. These findings are in line with research showing that the latencies of eye-and hand movements are only weakly correlated when humans reactively point to visual targets or rapidly respond to sudden changes in target position (Fooken et al. 2024a; Prablanc et al. 1979). Thus, our results provide further evidence that whereas sensory information is shared between the eye and hand movement system, movement initiation and execution may be controlled in parallel.

Neurophysiological studies have shown that the posterior parietal cortex plays a crucial role in coordinating eye and hand movements in visually-guided reaching (Andersen et al. 1997; Battaglia-Mayer et al. 2015; Buneo and Andersen 2006; Dean et al. 2012; Passarelli et al. 2021; Snyder et al. 2000). During reaching movements, neural firing in the lateral intraparietal area (LIP), an area associated with saccade and attentional control (Andersen et al. 1992; Barash et al. 1991; Bisley and Mirpour 2019), is systematically modulated by neural activity in the parietal reach region (PRR; Hagan et al. 2012; Hagan and Pesaran 2022). Specifically, saccades are transiently suppressed through a ‘reach-to-saccade communication channel’. One possibility is that whereas the reach target is represented in a common (oculomotor) reference frame (Batista et al. 1999; Carey 2000; Vesia and Crawford 2012), PRR and LIP operate in parallel to plan and control movement execution (Kang et al. 2024). Overall communication between PRR and LIP may be functionally organized such that the suppression of saccades during reaching supports goal-directed behaviour.

Individual differences in saccade latency

The tendency to inhibit saccades shortly before action-relevant events has not only been described in laboratory studies but also in the wild. Expert performance in many targeted action tasks, such as golf putting or basketball free throw, is characterized by a systematic suppression of saccades before the action is executed, a phenomenon known as ‘quiet eye’ (Vickers 1992, 1996). Maintaining steady fixation of the action goal is thought to facilitate information and attentional processing and aid motor preparation (Gonzalez et al. 2017; Vickers 2007). Yet, more dynamic action tasks require a disengagement of the fixation to make gaze available to gather new visual information and support ongoing action control. We observed that how long saccades were delayed during the ongoing reach greatly varied between individuals, reiterating the observation that eye movement behaviour systematically differs between individuals (Bargary et al. 2017; Castelhano and Henderson 2008; de Haas et al. 2019). Interindividual eye movement differences even persist across different tasks, if similar sensorimotor demands are required (Goettker and Gegenfurtner 2024). We observed that the delay in saccade latency to the visually cued target was consistent within individuals irrespective of whether participants performed the one- or two-handed reaching task. Taken together, these results suggest that the tradeoff between perceptual and motor processing is a balance that is tailored to each individual's sensorimotor ability. Although these sensorimotor traits may to some degree be hardwired (Kennedy et al. 2017), the fact that eye movement patterns in visual and motor experts are similar between individuals suggest that visuomotor experience also plays a role (Reingold and Sheridan 2011; Vickers 2007).

Conclusion

The current study investigates mechanisms of gaze anchoring, a phenomenon that describes the inability to move the eyes away from the reach goal to a visually cued target while the reaching movement is ongoing. We found that how long saccades were delayed—relative to the time of saccade cue—depended on the type of feedback participants received upon contacting the reach target. Specifically, whereas gaze anchoring was linked to the end of the reaching movement when the target was only visual, gaze anchoring was linked to the end of the directing phase when haptic information was available upon contact between the hand and the reach target. We further found that gaze anchoring did not depend on whether the cued target was only a saccade target or a combined saccade and left-hand target, and gaze anchoring was not systematically related to the initiation of a simultaneous left-handed movement. Effects of gaze anchoring were highly consistent within individuals and correlated across tasks. Taken together, our results suggest that visual feedback is continuously used to support goal-directed action until other sensory feedback is available or the action goal is attained. However, while the eyes are anchored to the reach target, a secondary goal-directed movement can be planned and initiated in parallel. The timing of these interacting visuomotor control mechanisms appears to be individual-specific and may indicate differences in trading off perceptual and sensorimotor processes.

Citation diversity statement

Recent work in several fields of science has identified a bias in citation practices such that papers from women and other minority scholars are under-cited relative to the number of such papers in the field (Bertolero et al. 2020; Caplar et al. 2017; Chatterjee and Werner 2021; Dion et al. 2018;

Dworkin et al. 2020; Fulvio et al. 2021; Maliniak et al. 2013; Mitchell et al. 2013; Wang et al. 2021). Here we sought to proactively consider choosing references that reflect the diversity of the field in thought, form of contribution, gender, race, ethnicity, and other factors. First, we obtained the predicted gender of the first and last author of each reference by using databases that store the probability of a first name being carried by a woman (Dworkin et al. 2020; Zhou et al. 2020). By this measure (and excluding self-citations to the first and last authors of our current paper), our references contain 15.28% woman(first)/woman(last), 10.27% man/woman, 19.44% woman/man, and 55.01% man/man. This method is limited in that a) names, pronouns, and social media profiles used to construct the databases may not, in every case, be indicative of gender identity and b) it cannot account for intersex, non-binary, or transgender people. Second, we obtained the predicted racial/ethnic category of the first and last author of each reference by databases that store the probability of a first and last name being carried by an author of colour (Ambekar et al. 2009; Chintalapati et al. 2023). By this measure (and excluding self-citations), our references contain 4.62% author of colour (first)/author of colour(last), 17.34% white author/author of colour, 18.30% author of colour/white author, and 59.74% white author/white author. This method is limited in that a) names and Florida Voter Data to make the predictions may not be indicative of racial/ethnic identity, and b) it cannot account for Indigenous and mixed-race authors, or those who may face differential biases due to the ambiguous racialization or ethnicization of their names. We look forward to future work that could help us to better understand how to support equitable practices in science.

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