

Unconstrained reaching modulates eye–hand coupling

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Abstract Eye–hand coordination is a crucial element of goal-directed movements. However, few studies have looked at the extent to which unconstrained movements of the eyes and hand made to targets influence each other. We studied human participants who moved either their eyes or both their eyes and hand to one of three static or flashed targets presented in 3D space. The eyes were directed, and hand was located at a common start position on either the right or left side of the body. We found that the velocity and scatter of memory-guided saccades (flashed targets) differed significantly when produced in combination with a reaching movement than when produced alone. Specifically, when accompanied by a reach,

peak saccadic velocities were lower than when the eye moved alone. Peak saccade velocities, as well as latencies, were also highly correlated with those for reaching movements, especially for the briefly flashed targets compared to the continuous visible target. The scatter of saccade endpoints was greater when the saccades were produced with the reaching movement than when produced without, and the size of the scatter for both saccades and reaches was weakly correlated. These findings suggest that the saccades and reaches made to 3D targets are weakly to moderately coupled both temporally and spatially and that this is partly the result of the arm movement influencing the eye movement. Taken together, this study provides further evidence that the oculomotor and arm motor systems interact above and beyond any common target representations shared by the two motor systems.

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Introduction

Eye–hand coordination is a common, if not essential, element of goal-directed movements. Throughout the course of a normal day, we make effortless eye and limb movements to objects in our environment in a coordinated fashion. When we move our hand toward an object, we usually direct our gaze to the same site. While the relative timing between the motion of the eyes, head, and arm has little influence on pointing accuracy, subjects perform more accurately when they have their eyes near the target when pointing (Fisk and Goodale 1985; Bock 1986; Abrams et al. 1990; Rossetti et al. 1994; Henriques et al. 1998).

Given that both the eyes and hand are ultimately driven by the same retinal image and that we tend to look at things we reach for simply to see them better, it is not surprising that eye–hand coordination studies have found that eye and limb kinematics are correlated in varying degrees depending on the task (van Donkelaar 1997, 1998; Sailer et al. 2000; Ariff et al. 2002; Gribble et al. 2002; Lünenburger and Hoffmann 2003).

Subjects may point more accurately toward a target that they are looking at because the brain has access to both foveal signals and eye-position signals to update the spatial representation of the fixated target. For example, subjects point with similar accuracy when they move their eyes onto a vanished target as onto a visible one (Fisk and Goodale 1985; Vercher et al. 1994). Thus, the eye-position signals may be sufficient to improve localization as visual-memory decays. Even when the eyes do not land on the target site, they can affect and possibly guide final hand position. Some studies have found that the size of the saccade influences the size of the hand movement, so that differences in saccade amplitude produce biases in open-loop pointing when the eye and arm movements are initiated from a common site, or at least move along the same single direction (Nemire and Bridgeman 1987; van Donkelaar 1997, 1998). In some cases, saccade adaptation can lead to a similar change in reach amplitude when they are combined with reaching movements to the same target (Kröller et al. 1999; Bruno and Morrone 2007; Cotti et al. 2007). Thus, in some cases, the positional signals of the eyes may be able to draw the hand to where the subject is looking, even leading the hand astray. However, in many other eye–hand coordination tasks, errors between gaze and the hand are not correlated (Sailer et al. 2000; Henriques et al. 2003), even when eyes and hand moved simultaneously (Sailer et al. 2000).

Some studies have found that the latency and velocity of simultaneously triggered goal-directed movements tend to be correlated. For instance, Sailer et al. (2000) found a correlation in the pattern of movement latencies of the eyes and hand across different eye–hand tasks, but found no correlation in their errors. Fisk and Goodale (1985) found that both saccade and reach latency varied with the location of the target such that both effectors had a shorter reaction time when they conjointly moved to targets that were on the same side of body as the arm used. The onset of electromyographic activity for the arm has been found to occur almost simultaneously with the start of (Biguer et al. 1982) or in advance of (Gribble et al. 2002) eye movements, suggesting that nerve signals driving the eyes, head, and hand may be derived concurrently. Gribble and colleagues also found a positive correlation between these eye and arm EMG onset latencies. Snyder et al. (2002) and Kattoulas et al. (2008) showed that for monkeys, saccades are faster when accompanied by a reach toward either a visible target

or a remembered target after a delay. Moreover, Snyder et al. (2002) found in macaques that reaction times were also shorter for the saccades made with the reach than when made without an arm movement (Snyder et al. 2002). This suggests that movements of the hand can also influence those of the eyes. The possibility that reaching movements can influence those of the eyes has also been demonstrated by Kattoulas et al. (2008). They found that for rhesus monkeys, saccade endpoints made immediately to a briefly flashed target, or after a short delay, were different from those produced when the monkey reached to the target at the same time, so that saccade errors were correlated with the systematic reach errors. Yet, while numerous studies have investigated the influence of eye movement or gaze direction on reaching in both human and nonhuman primates, only a few have investigated how eye kinematics may be affected by the absence or presence of an accompanying reaching movement.

Many of the results showing coupling between simultaneously triggered saccades and reaches are confounded by the fact that these effectors are moving toward a common target. Correlations in the timing and errors of these effectors could be merely due to processes involved in detecting and localizing the target itself, independent of any subsequent movement. For instance, trials where the subjects happen to notice or detect the target quicker will likely lead to both faster reaction times and velocities for both the eyes and hand than trials where it took longer to localize the target. Likewise, a target that is mislocalized to the left of its actual location may lead to both leftward reach and saccade errors. Thus, temporal and spatial correlates of movements of the eyes and hand may have nothing to do with any mutual influence of these two motor systems. The best way to test for coupling is to compare the absence and presence of one effector (e.g., reaches) on the movements of the other (e.g., saccades). Testing the effect of saccade on reaches, however, is problematic given the considerable evidence indicating that when gaze remains deviated (e.g., absence of eye movements), reaches to remembered targets systematically overshoot the targets for reasons that have little to do with eye–hand coupling (see Crawford et al. 2011 for examples and explanation). Also, given that the eyes arrive at the target well before reach onset (Sailer et al. 2000; Gribble et al. 2002), it would be also difficult to distinguish whether any effect of saccades on reaching is due to the influence of oculomotor system on arm motor system or to gaze position information (once the eyes arrive at the target site), providing guidance to the hand. However, these problems do not arise when testing the presence or absence of reaching movement on saccades. Eye movements occur all the time without the hand moving to the same location (while the opposite is far less the case), and even simultaneous movements of the eyes and hand usually involve

the eyes landing on the target site even before the reaching movement has begun. Thus, any effect of reaching on saccade (compared to saccade made alone) would have to be the result of arm motor programming.

Moreover, many of these studies on eye–hand coordination have involved constrained movements of the hand and eyes along a plane (such as a screen or tablet), and a very few have looked at the effect of the start positions of both effectors on the coordination of these movements. In our study, we had participants who make unconstrained movements of either their eyes or both their eyes and hand to one of three briefly presented targets from a common start position on either the right or left side of the body. This paradigm allowed us to investigate eye–hand coordination by measuring the extent by which programming a reaching movement influences saccades to the same target. Our hypothesis is that unconstrained movements of the arm should have a systematic effect on movements of the eyes compared to when the eyes move alone. In particular, given that reaching movements tend to have longer latencies, move slower, and are less precise than saccades, we predicted that the saccades produced in combination with a hand movement will also have longer latency and lower velocities than those saccades made alone. We further hypothesized that since the two sets of effectors are very different in terms of their dynamics, the influence of reaching movements on saccades, as well as correlations between these two effectors, will be greater in the temporal domain (latencies and velocities) than in the spatial domain (accuracy and precision).

Methods

Subjects

Fifteen subjects (between 20 and 41 years of age, ten males and five females) with no known neurological disorders participated in the study. All subjects were tested for hand dominance based on the Edinburgh Handedness Inventory (Oldfield 1971), and only right-handed subjects were selected. After detailed explanation of the procedures, all subjects signed a consent form approved by the institutional review board of the University of California, San Diego.

Apparatus and experimental setup

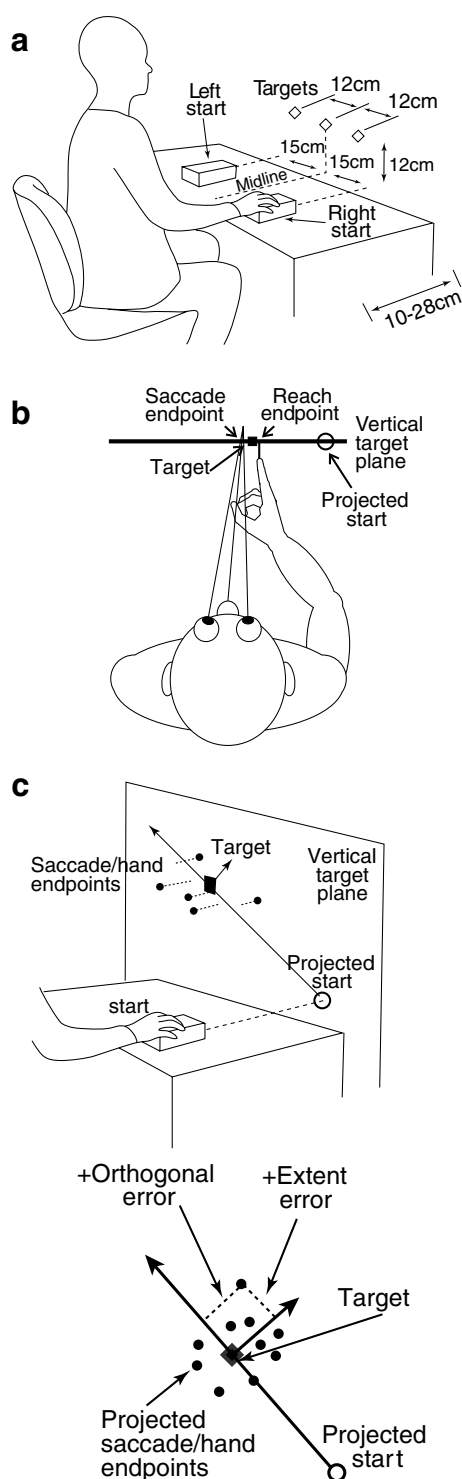
Subjects sat in front of a table where they rested their head on a height-adjustable chin rest to stabilize the head. Subjects placed their right hand over a computer mouse placed on the raised wooden block that rested on the table, (15 cm high for most subjects and 10 cm high for our shortest subject) positioned 15 cm either to the right or to left from

the body midline depending on the conditions, indicated as rectangular blocks in Fig. 1a. A five-degree of freedom (DOF) robot arm (Thermo Fischer Scientific Inc., Catalyst 5) randomly presented one of three target locations in a horizontal plane (diamonds in Fig. 1a). The targets were spaced 12 cm apart with the middle/center target positioned, so that it was aligned with the body midline and located 12 cm above the table that subjects sat on, and the chin rest was adjusted so that the eyes were roughly level with the height of the targets. Specifically, the relative coordinates of targets for the right start position are (lateral, vertical) = (−27, +12), (−15, +12), (−3, +12) cm and (+3, +12), (+15, 12), (+27, +12) for the left start position. The distance of the three targets was adjusted for each subject such that the farthest target was placed at a distance of the knuckles of each subject's clenched fist with the arm extended (between 10 and 28 cm away from the start position), so that subjects were able to reach to the targets comfortably without fully extending their arm. The subjects were never told how many targets would be presented or in which locations, or given feedback of their hand or gaze errors. Moreover, since the targets (flashed LEDs) were presented singly, subjects would not know the size or alignment of the overall target set. An LED was placed on the index fingertip, which served as the initial fixation point, and another LED was placed on the tip of the robot arm for target presentation.

Eye movements were recorded using an EyeLink II eye tracker (SR Research, Osgoode, ON, Canada) at 250 Hz sampling rate in pupil tracking with corneal reflection mode. The three-dimensional arm and fingertip movements were recorded at a 240 Hz sampling rate using the Polhemus Liberty (Polhemus, Colchester, VT) electromagnetic motion tracking system. Five Polhemus sensors (six DOFs) were placed on the fingertip, forearm, upper arm, neck, and head. One sensor on the head was used to compensate for any head movement in eye movement recording should any head movement occur although the head was stabilized on a chin rest. The head movement during the task was minimal, and the maximum deviation in any direction was on average 2.7 ± 1.9 mm. The MotionMonitor system (Innovative Sports Training, Chicago, IL) was used to control both EyeLink II and Polhemus recordings and to synchronize both data streams in time and space. The sampling rate after synchronization was 240 Hz.

Experimental procedures

There were three conditions: (1) eye-only-flashed target; (2) eye-and-hand-flashed target; and (3) eye-and-hand-static target. In all three conditions, the room was completely dark. Subjects were asked to place their right hand on the raised block at the start of each trial and come back to the same



position after the trial. Subjects were asked to make either a saccade only or to both saccade and reach to a briefly flashed target as soon as it appeared, and then keep their eyes and finger at the remembered target site for a short pause detailed below. Subjects maintained their eyes on the target until the hand completed the reach. They were also asked to minimize head movement and blinking during the task.

Fig. 1 Experimental setup and error definition. **a** A subject is shown with the two starting positions (*rectangular blocks*) for reaching to any of the 3 targets (*diamonds*). The middle target was aligned with the subject's midline, and the other two targets were positioned 12 cm to the right and to the left of the midline. **b** An above view of the subject is shown with the vector (from the project start position to the target) that determined saccade and reach endpoint definition. **c** Both reach and saccade errors were calculated in the vertical target plane. The extent error was defined as the error along the line of the projected start position (*circle*) to target location (*square*). The orthogonal error was orthogonal to the projected start to target line (positive above the extent line)

Eye only: flashed target

Six subjects participated in this condition. Four of them also participated in the other conditions, three in the eye-and-hand-static target condition and one in the eye-and-hand-flashed target condition. Subjects began each trial looking at a fixation LED (lit for 1 s) located in starting blocks mentioned above (15 cm on either side of the body midline). One second after the fixation LED on the fingertip turned off, the robot arm moved to the one of the three target locations in pseudorandom order and the target LED was flashed for 100 ms. Subjects were instructed to look at the remembered location of the briefly flashed target. They were further asked not to make corrective saccades even if they thought that they missed the target. Subjects were instructed to look back at the initial position after gazing at this site for a brief pause. Their eyes stayed at the target for an average, $482 \text{ ms} \pm 251 \text{ SD}$ before returning to start position. Both left and right start positions were used for each subject. For each initial fixation position, three targets were presented fifteen times, for a total of 45 trials per start position. The order of left or right start position was counterbalanced across subjects.

Eye and hand: flashed target

Eight subjects participated in this condition. Two of them also participated in other conditions, one in the eye-only-flashed target condition, and one in the eye-and-hand-static target condition. In this condition, subjects began with both their reaching hand and eyes at the start block located 15 cm on either side of the body midline. An LED placed on the fingertip served as the fixation point and was lit for 1 s. As in the previous condition, 1 s after this fingertip/fixation LED was extinguished, one of the three targets was positioned by the robot and flashed for 100 ms. After the target LED flashed, the robot arm was retracted. Subjects were instructed to simultaneously look and reach at a comfortable speed to the location where the target LED had flashed. They were also instructed to make one smooth movement out, briefly pause, and return movement without correction. Subject's eyes stayed at the target for an

average of $986 \text{ ms} \pm 283 \text{ SD}$ before returning to the start position. Since the robot had been retracted right after the target presentation, they did not have any visual or tactile feedback about the reach. Both left and right start positions were used for each subject. The order of left or right start position was counterbalanced across subjects as well. The number of trials was the same as in the eye only condition and 45 for each start position.

Eye and hand: static target

Six subjects participated in this condition. Four of them also participated in the other conditions, one in the eye-and-hand-flashed target condition and three in eye-only-flashed target condition. As in the previous condition, the fixation/fingertip LED was on for 1 s and then off for another second before one of the three targets was positioned and turned on for 1.5 s. Subjects were instructed to simultaneously look and reach at a comfortable speed to the location as soon as they saw the target LED. Since the target was on the robot arm, subjects had full vision of the target and they were able to actually touch the target location. Since subjects touched the actual target, endpoint errors should be minimal. In this case, it should not matter which start position was used, so we ran this condition only with the left start position (start position did not have a significant effect on eye coupling in the briefly flash target condition). The number of trials was the same as in the other two conditions and 45 for the left start position. The purpose of this condition was to determine whether temporal aspects of eye–hand coordination differed when the target remains continuously visible compared to when it was removed.

Data processing

The eye and hand data were temporally aligned at target onset and spatially aligned by translating one coordinate system to the other and matching the two coordinate systems prior to exporting the data from the MotionMonitor system (Innovative Sports Training, Chicago, IL). This made both eye and hand data share common frame of reference for comparison. The data then were processed by custom developed MATLAB (The MathWorks, Natick, MA) codes. Hand kinematic data were first low-pass filtered at 10 Hz using a 4th-order Butterworth filter with a forward and reverse direction. The time course of the tangential velocity of the hand was calculated in order to determine the reaching movement onset and offset; these were defined as the hand's velocity exceeding or falling below 5 % of its peak value. Eye movement data were low-pass filtered at 25 Hz using the same Butterworth filter. We then took the location where the average gaze direction of the two eyes met the vertical target plan (Fig. 1b). Eye movement data

from this point on were confined to this target plane, and two-dimensional analyses performed. The two-dimensional tangential velocity of the eye was also calculated, and the saccade onset and offset were defined as gaze velocity exceeding or falling below 10 % of its peak value. Every trial was visually inspected and corrected if necessary. Trials in which subjects broke the fixation before the target LED light and which had latencies of less than 100 ms (anticipatory saccades) were removed. Trials that had unstable eye movement recording due to loss of corneal reflection were removed as well. Overall, 21 % of all trials were removed.

Data analysis

Latency was measured from the onset of the target LED to the detected onset of the eye and/or arm movement. Since gaze errors were only measured in the frontal-parallel target plane, in order to directly compare reach and gaze errors, both were calculated in the target plane. Two error measures, extent and orthogonal errors, were used (Fig. 1c). First, the initial position was marked on the frontal-parallel target plane by drawing the line orthogonal to the target plane that intersected with the initial position. The extent error was defined as the distance between the location reached by the eye (or the hand) and the location of the target along the line connecting the target and the projection of the start position of the effector on the target plane (projected start-target line). The error was positive when subjects overshot the target and negative when subjects undershot the target. The orthogonal error was orthogonal to the projected start to target line (thus in the direction indicated by the small vector in Fig. 1c) and was positive when the endpoint was above this projected start-target line and negative when it was below. To present endpoint distributions, 95 % confidence ellipses were computed per target and per subject. The averaged ellipse was computed by averaging the orientation angles and major/minor axes of the individual subject ellipses. In order to get an estimate of the overall saccade and reach variance for each target for each subject, we computed the sum of the eigen values of these covariance matrices. This method approximates an area of a confidence ellipse for relatively isotropic reaching endpoint distribution, and we will refer to this measure as the overall saccade or reach variance. We also calculated the orientation angle of these ellipses to approximate the direction of most of the scatter of the reach and saccade distributions.

Statistical analysis

We conducted several three-way mixed ANOVAs (between factors: task condition and start position; repeated factor: target location) to test whether three task conditions (eye-only-flashed target; eye-and-hand-flashed target; and

eye-and-hand-static target), three target positions (left, middle, and right), and two start positions (left and right) statistically affected movement latency, velocity, and duration. For these ANOVA's, start position was treated as a between-subjects factor because we tested only one start position for the eye-and-hand-static target condition. We ran similar three-way mixed ANOVAs to examine movement errors and scatter, but only for the two tasks with the flashed target; in this case, the start location was treated as a repeated factor since both left and right positions were used in these two tasks. To compare scatter of endpoints across the two effectors for the eye and hand task to flashed targets only, the three-way mixed ANOVA included the repeated factor, effector (eye, hand), as well as start position and target location. We used Bonferroni post hoc comparisons to compare across the three target positions when there was a significant effect of target. In cases in which sphericity was violated for this factor (it was the only factor with more than 2 levels), a Greenhouse–Geisser correction was used. All statistical tests and regression fits were conducted using the Statistical Package for Social Sciences (SPSS, IBM Corp.).

Results

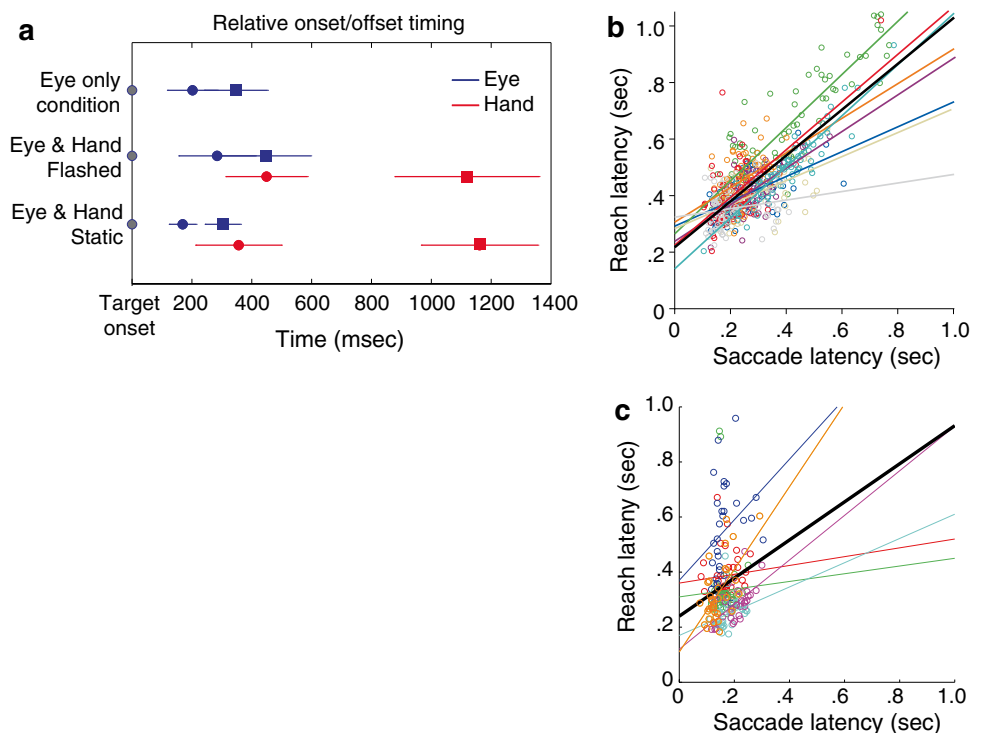
Latency and relative onset/offset timing

Figure 2a shows relative onset (colored dot) and offset (colored square) timing of both the saccade (blue) and

reach movement (red) aligned at target LED onset for the three conditions, averaged across trials and subjects. Eye movement led the hand movement even though subjects were instructed to reach at the same time, with reaching onset occurring near the end of the saccade, both when the target was continuously presented (static) and when just briefly flashed. We found a significant difference in eye latency ($F(2,29) = 4.69$, $p < .05$) across task conditions. Eye latency (blue dots) was significantly longer ($p < 0.05$; Bonferroni-corrected comparison) in the eye-and-hand-flashed target condition (283 ± 124 SD ms) than in the eye-and-hand-static target condition (186 ± 44 SD ms). Eye latency for the eye-only-flashed target condition (202 ± 88 SD ms) fell between these two conditions, but did not quite reach significant difference ($p = 0.08$; Bonferroni-corrected comparison) when comparing the two conditions to the flashed target. Reach latency (red dots) for movement to flashed targets (446 ± 129 ms) tended to take longer to initiate than those to static targets (353 ± 143 ms), but this did not reach significance ($F(1,19) = 3.41$, $p = 0.081$). However, target position and start position did not influence either saccade latency nor reach latency in any of the conditions ($p > 0.05$).

Saccade latency and reach latency were also linearly related for all eight subjects reaching to the flashed target, as illustrated in Fig. 2b, with an averaged slope across subjects of 0.62 ± 0.27 and overall r^2 of 0.58 across subjects (mean r^2 of 0.43 ± 0.28). Yet, when the target was visible (Fig. 2c), this relationship between the effectors was

Fig. 2 Relative onset/offset timing and movement latencies. **a** Relative onset and offset timing of the eyes (blue) and hands (red) aligned at target LED onset. The *dot* is the onset, and the *square* is the offset, and these are based on averages across subjects and targets for the three conditions. The *bar* is the standard deviation of onset and offset, respectively. **b, c** Reach latencies are plotted as a function of saccade latencies for movements to the flashed target (**b**) and for movements to the static target (**c**) for all trials for all subjects. *Colored points and lines* are individual data points and regression lines, respectively. *Black line* is the averaged regression line (color figure online)



diminished, with a mean r^2 of 0.14 ± 0.15 and only significant slopes for 2 of the 6 subjects.

Movement duration

The duration of the saccade (the difference between the dot and square in Fig. 2a) varied significantly across the three conditions ($F(2,29) = 4.91$, $p < 0.05$), with longer saccades for eye-and-hand-flashed target condition (162 ± 48 ms) than when the target was visible (eye-and-hand-static target condition, 130 ± 32 ms, $p < 0.05$ Bonferroni post hoc comparison), although no significant difference was between the two flashed target conditions ($p = 0.18$). Not surprisingly, reaches made to a visible target tended to take longer than those made to a briefly flashed target, although this trend did not reach significance ($F(1,19) = 3.71$, $p = .069$).

Peak velocity

Figure 3a shows saccade peak velocity per target location for all task conditions, averaged across subjects. Peak saccade velocity was significantly different across conditions ($F(2,29) = 5.66$, $p < 0.01$), with higher velocities in the eye-only-flashed target condition (on average, 4.7 ± 1.8 SD m/s; red dots) when compared to those in the eye-and-hand-flashed target condition (average 3.4 ± 1.4 SD m/s; blue dots, $p < 0.05$), but not when compared to the eye and hand static target condition (average 3.9 ± 1.5 SD m/s; green dots); not surprisingly, peak saccade velocity was higher for the farther target locations compared to nearer targets ($F(2,58) = 15.59$, $p < .001$, Greenhouse–Geisser corrected), but did not vary with the start position ($F(1,29) = 0.70$, $p > 0.05$). Likewise, peak velocities of reaching movements were also higher for farther target locations ($F(2,38) = 103.70$, $p < .001$) as illustrated in Fig. 3b, but did not differ as a function of start location, nor with target visibility ($p > 0.05$).

Hand peak velocity and saccade peak velocity were slightly but significantly linearly related when the target was flashed for six out of the eight subjects as illustrated in Fig. 3c, with a mean slope of 0.06 ± 0.06 and r^2 of 0.10 ± 0.11 , when the target was visible for four out of six subjects, with a mean slope of 0.05 ± 0.04 and r^2 of 0.11 ± 0.11 (not illustrated). This is not merely an artifact of the target distance (i.e., velocity being higher for farther targets), at least for the briefly flashed targets, since the linear relationship between saccade and hand velocity was the same within each target, as it was across targets. Specifically, these significant slopes were 0.13, 0.18, and 0.15 for the near, middle, and far briefly flashed targets (r^2 of 0.29, 0.34, 0.23, respectively). For the static target, however, the linear relationship broke down when separated by the target location.

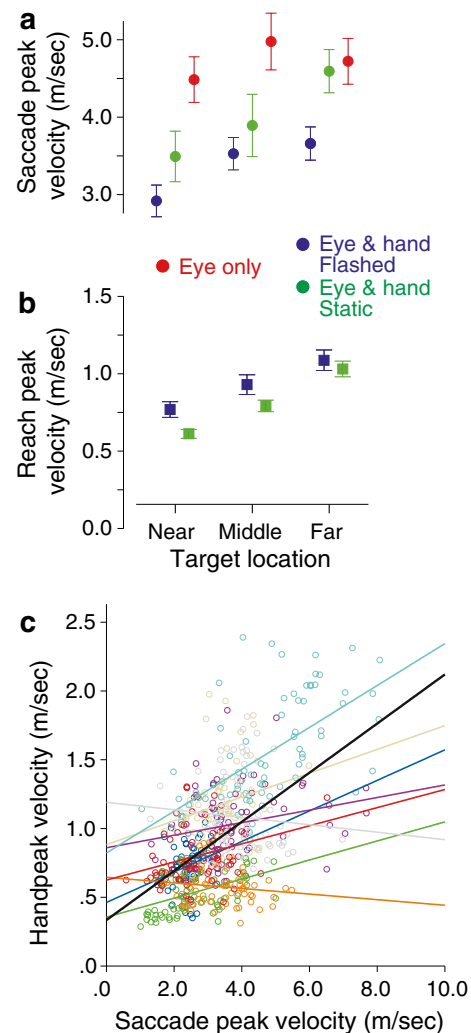
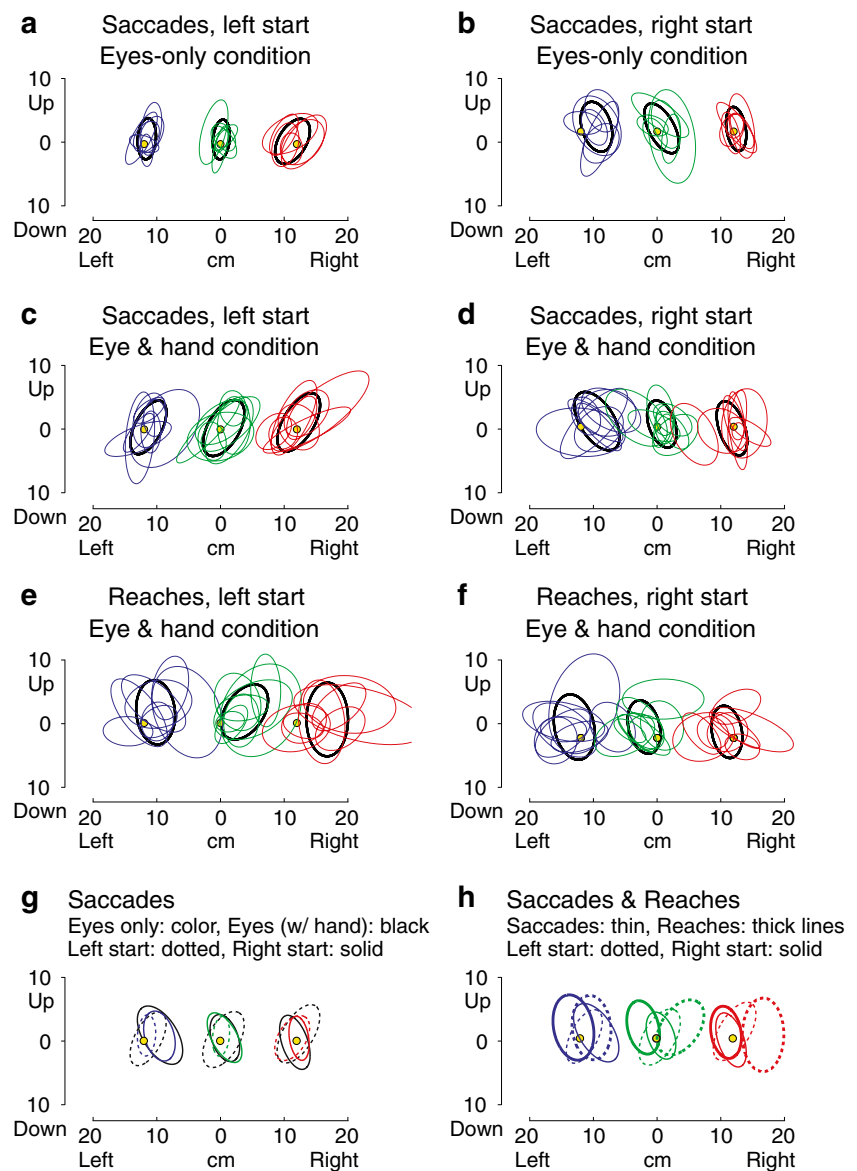


Fig. 3 Movement velocities. **a**, **b** Peak velocity for saccades (**a**) and reaching movements (**b**), averaged across subjects, is plotted as a function of target distance (near, middle, and far) for all three conditions. Error bars are SD. **c** Peak velocities of the hand plotted as a function of saccade peak velocities for movements to flashed targets for all trials for all subjects. Colored points and lines are individual data points and regression lines, respectively. Black line is the averaged regression line (color figure online)

Endpoint ellipses and error components

Figure 4a–f shows the individual subjects' 95 % confidence ellipses in color and averaged ellipses in thick black for endpoints for movements of the eyes and hand for the two flashed target conditions as a function of the effector and start position. (We do not show those for the static target since with visual and tactile feedback, the errors were minimal.) Qualitatively, the orientation of major axes was aligned with the desired movement directions especially for the eye (a–d). This is highlighted by the difference in the orientations of the ellipses for the two start positions

Fig. 4 95 % confidence ellipses of saccades and reach endpoints to flashed targets for both the eye only (**a, b**) and eye and hand (**c–f**) conditions. **a–f** Individual ellipses are shown in *color*, whereas averaged ellipses in *thick black*. **g** Averaged eye ellipses of eye only condition in *color* and eye and hand condition in *black*. **h** Averaged eye (*thin lines*) and hand (*thick lines*) ellipses. Left start is *dotted lines*, and right start is *solid lines* for both **g** and **h** (color figure online)



in Fig. 4g where we plotted averaged saccade ellipses for both conditions in one figure. The overall scatter of saccade endpoints was on average 30 % larger in the eye-and-hand-flashed target condition (black-outlined ellipses in Fig. 4g) than those in the eye-only-flashed target condition (colored-outlined ellipses) ($F(1,12) = 5.53$, $p = 0.037$). This is also shown in Fig. 5a, where the saccade variance, averaged across subjects, is plotted per target location for both task conditions. In this figure, the saccade variance increased over target distance ($F(2,24) = 5.34$, $p = 0.019$, Greenhouse–Geisser corrected), and this target effect did not differ between the two conditions ($F(2,24) = 0.21$, $p > 0.05$, no interaction). In contrast, the scatter of reach endpoints did not vary with target distance ($F(2,14) = 2.32$, $p > 0.05$).

The scatter of reach endpoints (thick-line ellipses in Fig. 4h) was 11 % larger than those for saccade endpoints (thin-line ellipses) although this trend did not reach significance ($F(1,7) = 1.65$, $p > 0.05$). Nonetheless, the amount of scatter of reach endpoints showed a weak but significant linear relationship to that of the saccade endpoints (slope = 0.38 and $r^2 = 0.10$, $t(46) = 2.26$, $p = 0.028$). When the scatter of one effector became larger, the scatter of the other tended to also become larger. This linear relationship held for both near and middle targets separately; however, there was no significant relationship for scatter between these effectors for the far target (only significant slopes are shown in Fig. 5b).

To find out whether errors in saccades and errors in reaching to briefly flashed targets are systematically related

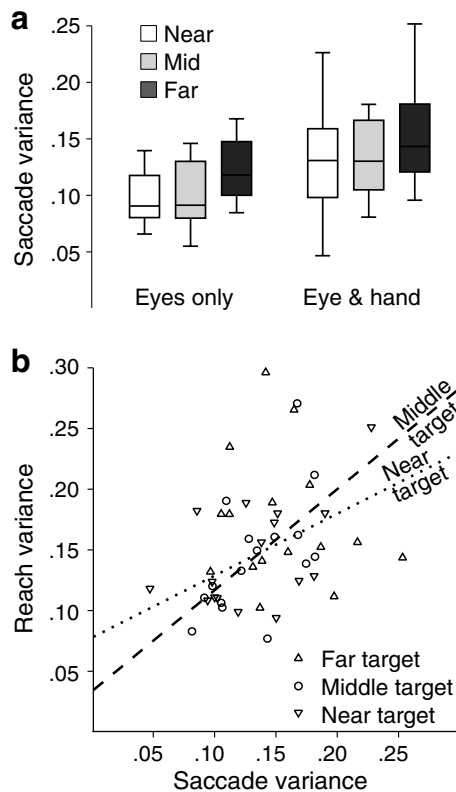


Fig. 5 Endpoint precision. **a** Variance of the saccade endpoints per target location for eye only condition (*left*) and eye and hand condition (*right*). **b** Reach variance is plotted as a function of saccade variance for each target for each subject. Those for the near and far targets are shown as *inverted triangles* and *regular triangles*, with those for the middle target are *circles*. Significant regression lines are shown for the near target (*dotted*) and middle target (*dashed*)

(to assess whether a spatial coupling exists between the effectors), we divided the error component into two, one in the direction of the desired movement (extent error) and the other one orthogonal to that line (directional error). We found that there is a small but significant linear relationship between the saccade and reach for both extent (Fig. 6a) and orthogonal errors (Fig. 6b), with average slopes of 0.27 ± 0.42 and 0.27 ± 0.54 , and mean r^2 of 0.15 and 0.13, respectively. Six of the eight subjects showed positive slopes for both types of directional errors.

Start position or movement direction had a significant systematic effect on the pattern of extent errors for saccades ($F(1, 24) = 12.08$, $p < .01$), but not for directional errors ($F(1, 24) = 2.00$, $p > 0.05$). Subjects overshoot the target with their eyes when they started from the left (white bars in Fig. 6c), but undershot when they started from the right (gray bars in Fig. 6c). Start position, however, did not affect the extent nor direction in reaching movement ($F(1, 7) = 1.22$, $p > 0.05$; $F(1, 7) = 2.96$, $p > 0.05$). The target position did have a significant effect on reaching extent ($F(2, 6) = 6.74$, $p < 0.05$), although not direction

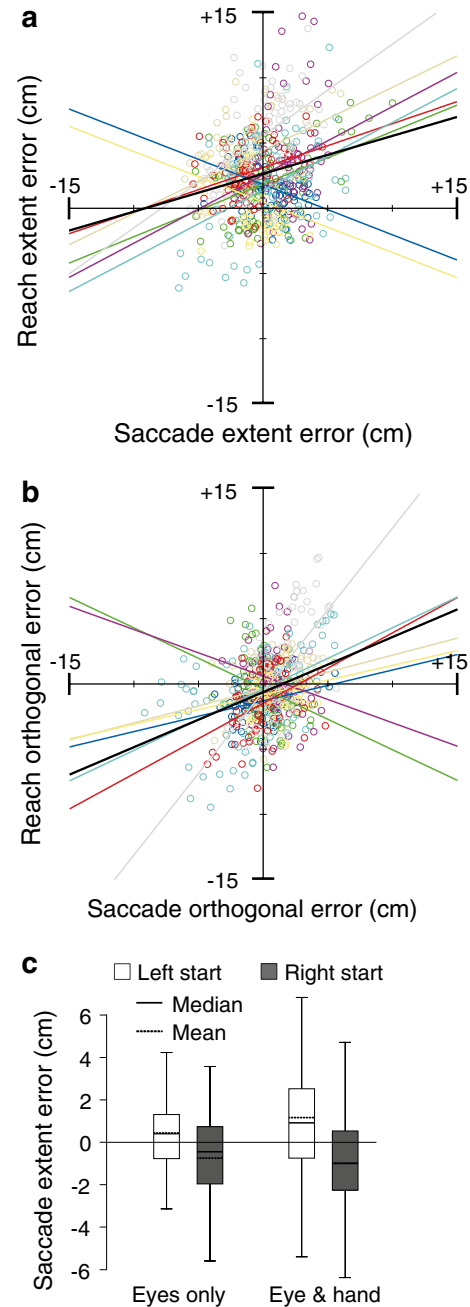


Fig. 6 Endpoint errors. **a** Reach extent errors are plotted as a function of saccade extent errors to flashed target for all targets and subjects. **b** The same as in **a** except for orthogonal error (tangential to the movement direction). **a, b** Colored circles and lines are for individual data points and regression lines, respectively. Black line is the averaged regression line. **c** Saccade extent error from left start (white bars) and right start (gray bars) positions, averaged across subjects and targets for the eye only condition (*left*) and eye and hand conditions (*right*). The mean across subjects are indicated by a dotted line, while the median is indicated by a solid line within these box plots (color figure online)

($F(2, 6) = .40$, $p > 0.05$), with smaller overshoots for near targets compared to the other two targets ($p < 0.05$, Bonferroni post hoc comparisons).

Discussion

We studied eye movements and the coordination between eye and hand movements when participants moved either their eyes or both their eyes and hand to one of three briefly presented targets from a common start position on either the right or left side of the body. Our main goal was to measure the extent to which eye movements were affected by accompanying movements of the hand to briefly presented targets. We found that combining these unconstrained reaching movements led to lower saccade peak velocities, and a trend toward longer saccade latencies compared to when the eyes moved alone. Likewise, although the effect was small, combined movements of the eyes and hand produced greater scatter of saccade endpoints than when the eyes moved alone, and the magnitude of the scatter increased with increasing magnitudes of scatter of reach endpoints. We also found a high correlation between eye and hand latency for movements to flashed targets (Fig. 2b), as well as a moderate correlation between eye and hand velocity (Fig. 3c). The variability of reach and saccade endpoints (Fig. 6), like the overall extent of variability (magnitude of scatter, Fig. 5b), was weakly but significantly correlated. This suggests that while there is a significant coupling between saccade and reaching movements, such that reaching movements have an appreciable effect on saccades made to the same target, the movements of the eyes and hand were more correlated on temporal than spatial measures. It is likely that the difference between temporal coupling and spatial coupling reflects the different dynamics of these two effectors, and thus other independent factors that contribute to endpoint variance that are independent in these two effectors.

Temporal coupling of eye and hand movements

As found in previous studies (e.g., Prablanc et al. 1979; Biguer et al. 1984; Bekkering et al. 1995; Helsen et al. 2000), saccade latencies were shorter than reach latencies, with gaze arriving at the target site even before reach onset (Fig. 2a). This is not surprising given the greater inertia to overcome when moving the hand compared to the eye (Gribble et al. 2002). However, we found that saccade latencies also trended toward being longer (near-significance) when accompanied by a simultaneous reach compared to when the eyes moved alone for movements that were made to a briefly flashed target, but not when made to a static target (Fig. 2a). Since we did not include an eyes-only condition to static targets in this study, it is possible the same pattern of slightly shorter eye latencies in the absence of reach movements compared to when accompanied by a reach would also occur for static targets. Our results are consistent with the results of Bekkering et al. (1995) who

also showed that saccade reaction times were longer when accompanied by a reaching movement if the target location was unknown prior to the movement onset, as in the current study. In other words, if the target was presented for some time and thus well localized prior to triggering the eye and hand movements, saccade latency did not differ when the effectors move alone or together (Bekkering et al. 1995). These results are different from those of Lünenburger et al. (2000) and Snyder et al. (2002) who found that saccades had shorter reaction times when produced with a reach than when produced alone, whether made to visible targets (human participants; Lünenburger et al. 2000), or to either visible targets or to remembered targets after a delay (monkeys, Snyder et al. 2002). Yet, when Kattoulas et al. (2008) had monkeys saccade to targets either immediately after the target disappeared, or after a 3-s memory delay and either accompanied with a reach or not, they found no differences in saccade latencies across the 4 conditions. While it is not clear why saccade latencies are sometimes facilitated, sometimes delayed, and other times not affected at all by a simultaneously triggered reach, these results suggest that in many cases, combined movements of the hand affect saccade latency. However, neither the location of the target nor the start position affected the latencies of either effector, made separately or together.

Consistent with the suggestion that reaches affect saccadic behavior and vice versa, we, like others (Bekkering et al. 1994, 1995; Helsen et al. 2000; Sailer et al. 2000), found a high correlation between the latencies of the eyes and hand, especially when the target was only briefly flashed (Fig. 2b). Now, while the high correlation between saccade and reach latencies could be merely due to how quickly the target is detected and located, since this would generally impact all effectors, the results showing that the presence of a reaching movement tended to increase (near-significance) saccade latencies suggest that this cannot explain the high correlation entirely. The correlation was weak for combined movements made to a static target (Fig. 2c), suggesting that for continuously visible targets (and thus more salient targets), the influence of reaching movements on saccade was weaker, or did not have an effect at all. Note that the range of saccade latencies to the static target was small and tended to cluster closer to 200 ms, with very few saccades having latencies over 250 ms and covarying with the reach latency. Given the greater uncertainty of location when targets are only visible for 100 ms and movements are made immediately to its remembered location, it may be that the movement onset is delayed and more susceptible to other factors such as motor planning of other effectors to the same location.

Saccade peak velocity overall was higher when the eyes moved without the hand, again suggesting that programming a combined reach influences saccade speed. Peak

velocities of the saccade and reaching movements were also correlated, although not as strongly nor as consistently across subjects as they were for latencies. At least for the briefly flashed target, this correlation could not be accounted for by the fact that peak velocity was also greater for both effectors when moving to farther targets than to nearer targets, since the linear relationship was similar for each target separately. Our results for both latency and peak velocity were somewhat inconsistent with those of Fisk and Goodale (1985) who found that reaches and saccades to targets on the left side of the body (and contralateral to the reaching hand) were initiated and moved slower than those on the right (ipsilateral) side. Again, we did not see any difference in latencies for either effector as a function of target nor start position. And while peak velocity of both combined saccades and reaches did vary with target location, they did so only as a function of the distance of the target with respect to the start position, and thus the required movement amplitude, and not with its location with respect to the body. Fisk and Goodale (1985) only had one central start hand position (saccade start positions were either central or directly left or right of the targets). Thus, given that the consistent relationship between the speed and the amplitude of a movement (larger movements involve higher peak velocities for both eyes and head) (Gordon et al. 1994b; Harris and Wolpert 1998; Messier and Kalaska 1999), it is possible that the large effect of movement amplitude on peak velocity washed out any possible effect of target location with respect to the body midline.

Spatial coupling of eye and hand movements

Saccades to briefly flashed targets were more precise than the reaches to the same targets, as has been found by others (e.g., Sailer et al. 2000), and saccades made without the hand were even more precise (a third less variable) than saccades that are combined with the reaching movements. The magnitude and pattern of variability of simultaneously triggered reaches and saccades were weakly but significantly correlated. This correlation could not be accounted for by the fact that variance was also greater for both effectors when moving to farther targets than to nearer targets. And while it is possible that the correlation may be higher if we were able to measure errors in both gaze and reaching in the depth dimension. Henriques et al. (2003) were able to measure the depth of the gaze point (the point where the two converge) and found no correlation ($r^2 = 0.02$) between gaze fixation and reach errors to targets whose location varied in depth.

The correlation between the variability of saccades and reach endpoints may simply be because both motor systems are relying on a common spatial representation that may be relatively noisy, given that the target was only briefly

flashed (100 ms) in an otherwise dark room. Yet, the fact that precision was greater when the eyes moved alone suggests that the greater variance in saccade endpoints when accompanied by a reaching movement may be due partly to the influence of arm motor programming on saccades. Thus, the correlation in the reach and saccade endpoints is unlikely to be simply due to the fact that the two effectors have a common goal. This is also supported by the research that shows that distracters have different effects on target-directed saccade and reach endpoints (Sailer et al. 2002).

The overall orientation of the elliptic fits for saccades tended to be in the direction of the movement, i.e., elongated along the vertical, but tilted left when movements started from the left and tilted right for movements starting from the right. This was not the case for reaches. The elliptical fits were elongated mainly along the vertical direction, suggesting that variance was somewhat greater along the direction of the movement, given that the start positions were also below the target locations. This is partly consistent with previous studies that suggest that scatter of endpoints is larger along the direction of movement (Gordon et al. 1994a, b; McIntyre et al. 1997; Messier and Kalaska 1997; Vindras et al. 2005; Ren et al. 2006). However, there was no systematic tilt in the major axes as a function of the start location across subjects.

Given that the size and orientation of the scatter of the endpoints for the two effectors were different, it is not too surprising that their respective errors in extent and direction were also only weakly (but positively) correlated. Others have found similar positive correlations between reach and saccade amplitude when the two effectors start simultaneously from a common site and move along the same one-dimensional direction (Nemire and Bridgeman 1987; van Donkelaar 1997, 1998), while some have found no correlation at all (Sailer et al. 2000; Henriques et al. 2003). However, task parameters in these different studies could explain the presence and absence of spatial coupling. In the studies showing significant correlations in saccade and reach errors, the eyes and hand move simultaneously along the same single direction to the target. The correlated errors also were along this direction (i.e., movement amplitude). Those studies showing little or no correlation involved subjects reaching forward toward distal targets that were displayed on a vertical screen (Sailer et al. 2000) or to 3D targets in depth (Henriques et al. 2003), with very different starting positions (or aiming directions) of the hand and gaze. Moreover, in these studies, the effectors did not always move simultaneously; in Henriques et al. (2003), the eyes landed on the visible target prior to the reaching movement being initiated (triggered when the target disappeared). In the current study, we combine elements of both a common start position of the hand and gaze, but to targets that required moving the effectors in 3D without constraint.

This may explain why the correlations for errors in extent (and in the orthogonal direction) of the eyes and hand were not as strong as those studies that had the eyes and hand move in the same single direction and/or were constrained, but not so weak as that produced in studies when the effectors moved from different locations and also in 3D. Overall, our results suggest that when the start position, and thus the required movement (or movement direction), of the two effectors are the same, gaze endpoints may provide some weak guidance for aiming the hand, but less so than when the movements are confined to a planar 1D movement direction. Moreover, because our findings indicate that saccade endpoint scatter was greater when produced with reach movements, this suggests that the weak correlation between the two effectors may not be merely due to a common, but independent, effect of movement direction on the scatter of endpoints along this direction.

Saccades with and without reaching

As discussed above, saccades made with the hand moved more slowly overall than saccades made alone tended to take longer to initiate, and the resulting endpoints were also less precise. As far as we know, there is only one other study that has also compared saccadic endpoints made to flashed targets when moving alone or with the hand that of Kattoulas et al. (2008). Kattoulas et al. (2008) found in monkeys that saccade endpoints made to radial (center-out) targets on a 2D surface were significantly different when the saccades were made jointly with hand movements, compared to those made without. Like in our study, they also found that these saccade errors were weakly but significantly correlated with the reaching errors. These spatial differences along with our temporal differences for the two tasks can be attributed to an influence of the arm movement system on the saccadic behavior. This suggests that the neural circuitry involved in programming saccade movements interacts with those responsible for programming movements of the arm.

The idea that arm movements can influence eye movements is supported by the results in different tasks as well. van Donkelaar et al. (2004) showed that the force used by the arm to compensate for an assistive or resistive load during reaches influenced saccade amplitudes to the same targets. The temporal characteristic of oculomotor tracking and sequential movements also seem to be influenced by actions of the hand (Epelboim et al. 1997; Engel and Soechting 2003).

Eye–hand coordination to flashed versus static targets

In the current study, we were particularly interested in investigating saccade and reaching movements to briefly

flashed targets, so we could assess both spatial and temporal eye–hand coordination. Most studies of eye–hand coordination have investigated the latter; thus, it is not very clear how simultaneous movements of eyes and hand influence the precision and accuracy of their movements. van Donkelaar and Staub (2000) made a comparison between eye–hand coordination to visible versus remembered targets along a single horizontal direction (with an additional 1–4-s delay before movement onset). While they do not report nor compare saccade reaction times for saccades to visual versus remembered targets, they found the reaction times of visually guided reaches were longer than those made to remembered targets after a 1–4-s memory delay. We found the reverse for the immediate (non-delayed) reaches in our study; reaches (like saccades that accompanied reaching) were initiated faster for static targets than for the briefly flashed target. The difference in our results may have been due to the fact that van Donkelaar and Staub (2000) imposed a delay for the memory-guided movements, or perhaps due to the predictability of the direction of the hand (and gaze) movement in their study. Targets in their study were always to the right, just at different distances. In summary, when comparing the timing of eye-and-hand movements to briefly flashed targets and to that for static targets, the latencies for both effectors in the former condition tended to be longer than the latter condition, but the relationship between the latencies of the two effectors was somewhat stronger. The arm moved slower and took longer when reaching to a static target. The longer duration is consistent with the fact that people decelerate their hand for a longer time in order to use the visual feedback of the target to guide their hand, although surprisingly van Donkelaar and Staub (2000) did not find this difference in their study on this topic.

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Conflict of interest The authors declare that they have no conflict of interest.

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