

Comparing limb proprioception and oculomotor signals during hand-guided saccades

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Abstract We previously showed that saccades tend to overshoot briefly flashed targets that were manually displaced in the dark (Ren et al. 2006). However it was not clear if the overshoot originated from a sensory error in measuring hand displacement or from a premotor error in saccade programming, because gaze and hand position started at the same central position. Here, we tested between these hypotheses by dissociating the initial eye and hand position. Five hand/target positions (center, far, near, right, left) on a frontally-placed horizontal surface were used in four paradigms: Center or Peripheral Eye-hand Association (CA or PA, both gaze and right hand started from the center or a same peripheral location) and Hand or Eye Dissociation (HD or ED, hand or gaze started from one of three non-target peripheral locations). Subjects never received any visual feedback about the final target location and the subjects' hand displacement. In the CA paradigm, subjects showed the same overshoot that we showed previously. However, changing both initial eye and hand positions relative to the final target (PA) affected the pattern, significantly altering the directions of overshoots. Changing only the initial position of hand (HD) did not have this effect, whereas changing only initial eye position (ED) had the same effect as the PA condition (CA \approx HD, PA \approx ED). Furthermore, multiple regression analysis showed that the

direction of the ideal saccade contributed significantly to the endpoint direction error, not the direction of the hand path. These results suggest that these errors do not primarily arise from misestimates of the hand trajectory, but rather from a process of comparing the initial eye position and the limb proprioceptive signal during saccade programming.

Keywords Saccade · Limb proprioception · Hand displacement · Update

Introduction

Eye-hand coordination is involved in many aspects of our lives, from simple reaching movements to more complex activities, such as driving, typing or manipulating multiple objects (Abrams et al. 1990; Flanagan and Johansson 2003; Helsen et al. 2000; Johansson et al. 2001; Neggers and Bekkering 2000, 2001). Many studies have looked at the mechanisms of visually or memory guided saccades (Colby et al. 1995; Henriques and Crawford 2001; White et al. 1994). However, few studies have examined another mechanism of eye-hand coordination—limb proprioceptively-guided saccades toward hand-held targets (Nanayakkara and Shadmehr 2003; Ren et al. 2006; Scheidt et al. 2005).

In a previous study (Ren et al. 2006), we showed that the saccade generator is able to use proprioceptive feedback from the limb to update target locations for saccades. However, limb proprioceptively-guided saccades were less well calibrated than visually-guided saccades. In particular, proprioception-related errors were different for different movement directions (being greater for hand movements along the axis of the forearm than the orthogonal axis), and the variability of hand-guided saccade endpoints was quite prominent, especially in the amplitude dimension.

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In our previous paper, we speculated that these changes in variability could be caused either by sensory noise in the internal estimate of the hand movement vector or by noise in the estimated difference between the initial eye position and the hand-held target. However, these two possibilities could not be disentangled in that experiment because both gaze and hand always started from the same central location. The purpose of the current study was to test between these two hypotheses by dissociating initial eye and hand positions in a task that was otherwise similar to the one used in our previous study (Ren et al. 2006).

In the current study we dissociated the initial positions of the eye and hand. In the illustrated example (Fig. 1), initial hand position (H_i) is on the right side of the display and initial eye position (E_i) is fixated on the center target. When the handheld target is shifted to the far location (H_f and E_f), what errors should occur in the final saccade positions? If saccade errors arise from sensory noise in the internal estimate of the magnitude of the hand movement vector, an overshoot along the hand movement path would be expected (the gray dashed arrow). On the other hand, if these errors are determined by a comparison between initial eye position and perceived final hand position, one would expect to see overshoot errors along the line between these

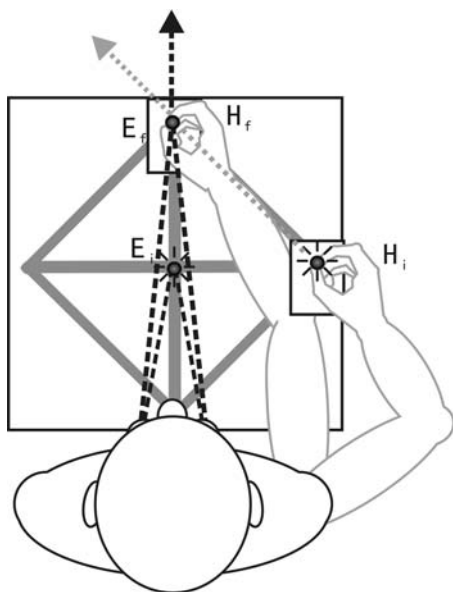


Fig. 1 Potential variability of saccade errors in table coordinates. When initial eye (E_i) and hand (H_i) positions are dissociated, the ideal directions of the eye (black dashed arrow) and hand (gray dashed arrow) trajectories are intersected at the same final location (E_f and H_f) with an angle of 45° . If the errors arise from sensory noise in the internal estimate of the hand movement vector, a direction error along the hand movement path would be expected (the gray dashed arrow). On the other hand, if the errors are determined by a comparison between initial eye position and perceived final hand position, one would expect to see the overshoot errors along the direction of eye movement (the black dashed arrow)

two positions (the black dashed arrow). As we shall see, it was the latter pattern that was consistently observed in our data.

Methods

Subjects

Six healthy volunteers (three males and three females) were recruited in this study, with ages ranging from 24 to 34 and a mean age equal to 29. All subjects were healthy with normal or corrected-to-normal vision and had no known history of sensory, perceptual or motor disorders. All subjects were naive to the purpose of the experiment. Signed informed consent was obtained prior to their participation in experiments, which were approved by the York University Human Participants Review Subcommittee.

Common apparatus

The main measure techniques, equipment and experimental setup have been described in detail in our previous experiment (Ren et al. 2006). In brief, subjects sat in a dark room with their head immobilized and tilted 45° downward by a personalized dental impression bar (Fig. 2a). Subjects were asked to look down at a horizontal board that was indented with linear grooves to guide hand movements. The center of the board was aligned to the subjects' midline, at a vertical distance of 30 cm and a horizontal distance of 20 cm from the center of the two eyes. The subject's right hand rested on a hand plate ($5 \times 10 \times 1$ cm) with a spring-loaded guide pin placed underneath so as to slide smoothly along the grooves of the target board. The top of the plate had a central vertical dowel (2 cm) which was held by subjects' right thumb and index finger. Subjects learned to recognize the central position by a deeper indentation for the guide pin. We used an Optotrak system to record the movement of the hand plate and a two-dimensional (2-D) eye-coil system to record the movement of subject's right eye (Henriques et al. 1998; Ren et al. 2006).

In this experiment, the board had four grooves along the four perpendicular directions on the cardinal X–Y axes respectively, with the eccentric positions placed 10 cm apart from the central indentation. And, four peripheral oblique grooves were placed between the adjacent ends of the four perpendicular grooves (Fig. 1b). Therefore, five start positions (S) for the saccade and/or hand movement were located at central (c), right (r), far (f), left (l) and near (n) locations, four of which (r, f, l, and n) also served as final target positions (T). In addition, five green LEDs were placed 4 cm above the horizontal surface of the hand-held red target LED, intersecting the gaze direction line between

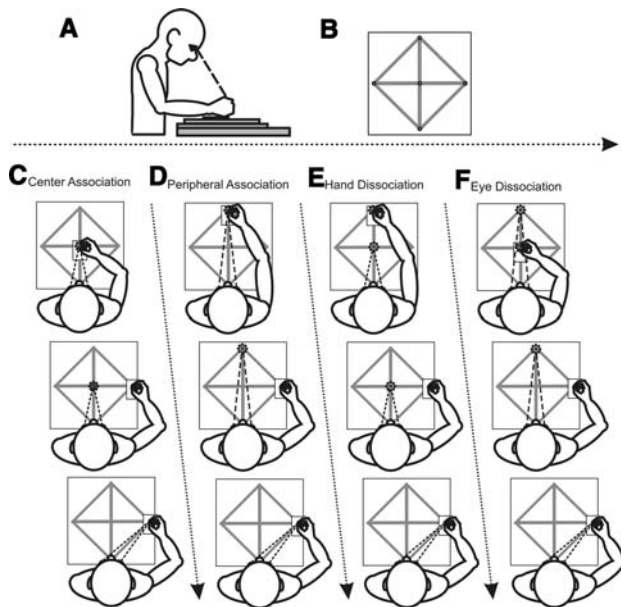


Fig. 2 Experimental setup and paradigms. **a** Subjects sat in a dark room in front of a horizontal table, with the head fixed (using a bite-bar) at a 45° downward orientation toward the table. Subjects held a short dowel topped by an LED between the right index finger and thumb, with the hand resting on a plate that could slide on a grooved board. **b** Five start locations (*circle*), including four peripheral target locations and eight grooves, viewed from above the table [10 cm from the center, at visual angles 8° (far target), 13° (near target), and 12° (left and right targets) relative to the center]. **c** Center Association (CA). *Top panel* subjects first fixated on the illuminated center LED and the hand-held target LED. *Middle panel* after the target LED was extinguished, subjects moved the hand-held target toward the end of one of the grooves. At the same time, they still fixated on the center LED. *Lower panel* subjects made a saccade toward the peripheral target after the central fixation LED was extinguished. **d** Peripheral Association (PA). This task was the same as in Fig. 2c with the exception that both eyes and hand started from one of three non-target peripheral locations. **e** Hand Dissociation (HD). In this paradigm, subjects' hands started from one of three non-target peripheral locations and eyes started from the center fixation LED. The remaining components were the same as in Fig. 2c. **f** Eye Dissociation (ED). This paradigm was nearly the same as in Fig. 2c, but this time, the saccades started from one of three non-target peripheral locations, and the hand started from the center

the subject's right eye and each central or peripheral location of the hand-held red LED. These five green LEDs served both as the initial gaze fixation positions in our four experimental paradigms, and the central and peripheral gaze fixation points for our fixation control condition.

Paradigms

There were a total of four peripheral target locations. In each of the following paradigms, five trials were made to each of these target locations relative to a start position in computer-randomized order:

Paradigm 1: center association (CA)

This was the same condition used in our previous study (Ren et al. 2006), where the hand movement and gaze displacement were always associated. Initially, both the central green fixation LED and the hand-held red LED were turned on. The latter was extinguished after 500 ms. In the meantime, a computer-generated voice command (e.g. left, right, far or near) instructed the subject to slide the hand plate (as fast as possible) along one of the four cardinal directions to the end of the groove. Subjects were required to maintain fixation at the central green LED during the hand motion. Since all experiments were done in a completely dark room, and the hand-held target was only flashed at the initial positions, subjects received no visual feedback about their hand movements or the final handheld target positions. A total of 3,500 ms after the target LED was extinguished, an auditory 'beep' signaled subjects to saccade toward and fixate the proprioceptively perceived location of the hand-held target (specifically, the top of the dowel between the index finger and the thumb where the target LED was located). At the same time, the fixation LED was also extinguished. Another 1,000 ms later, a second beep signaled subjects to return the gaze and hand position back to the center location. Each trial lasted 7,000 ms (Fig. 2c).

Paradigm 2: peripheral association (PA)

This paradigm was like paradigm 1, but both the gaze and the right hand started at the same location of one of the three non-target peripheral locations. This meant, for each peripheral target, there were three different start positions for both eye and hand movements. For example, when the final target location was the end of the rightward groove (Tr), the start point for both eye and hand movements could be the far, near or left locations (Sf, Sn, or Sl). Therefore, there were a total of 12 different tasks with four target locations and three initial conditions. The temporal sequence of each trial was the same as in paradigm 1 (Fig. 2d).

Paradigm 3: hand dissociation (HD)

This condition was similar to paradigm 2, except that the right hand started from one of three non-target peripheral locations and the gaze started fixating on the central green fixation LED. Thus, the gaze trajectories were similar to paradigm 1 and the hand trajectories were similar to paradigm 2, hand and gaze trajectories being dissociated (Fig. 2e).

Paradigm 4: eye dissociation (ED)

This paradigm was similar to paradigm 2 except that the right hand always started from the central location and the

gaze started at one of the three non-target peripheral fixation points. As a result, the gaze trajectories were similar to paradigm 2 and the hand trajectories were similar to paradigm 1 (Fig. 2f).

Fixation control

Subjects fixated each of the five illuminated green fixation LEDs for 2 s, respectively. These fixation controls established the appropriate gaze directions for each target. This was used for calibration purposes, and to establish a reference point for saccade errors.

Subjects were provided with a short practice session one day before the experiment in order to familiarize themselves with the tasks and instructions (but received no feedback on their performance). The order of the four experimental paradigms was counter-balanced equally across subjects. A 30 s resting interval was provided between each paradigm. Subjects were provided with no visual feedback about their performance during the experiment.

Calibration and data analysis

Eye-coil signals were pre-calibrated using a method described by Tweed et al. (1990). The Optotrak system was

calibrated according to methods supplied by the manufacturer (Northern Digital). Off-line calibration of eye coil signals (using the visual fixation data) was the same as previously described (see Ren et al. 2006). In addition, we removed all trials where subjects did not move their eyes or hand, where they did not move their hand in the correct direction, or if the hand did not reach the stopper. For data analysis, saccade onset was defined to be the time at which the velocity of the primary saccade rose above $30^\circ/\text{s}$. Corrective saccades were observed in most tasks and in all subjects. Most of these occurred before 400 ms after the primary saccade. Therefore, the final saccade endpoint was defined as the eye position 400 ms after the primary saccade, no matter how many corrective saccades subjects made (typically 0 or 1). This selection criterion is consistent with the criteria used in our previous paper (Ren et al. 2006). Quantitative analysis of saccade accuracy and precision was performed on the final eye position (after corrective saccades) as defined above. We show all the data in “table coordinates” (Figs. 3, 4, 5), i.e., the intersections of the gaze line with the plane containing the hand-held target were converted so that the eye and hand data were in the same coordinate system (Ren et al. 2006).

We defined the *endpoint direction errors* in polar coordinates as the angles intersected by the positive horizontal

Fig. 3 Sample data from a typical subject: two-dimensional saccade (*black and colored traces*) and hand movement (*gray traces*) trajectories plotted in table coordinates. For each of the paradigms (**a–d**) five movements are shown toward a target to qualitatively show intra-individual variability and task-dependent saccade accuracy. **a** Center Association (CA). **b** Peripheral Association (PA). **c** Hand Dissociation (HD). **d** Eye Dissociation (ED). Legend: *colored dots* target locations or start positions; *big filled circle* center fixation location; *black and colored lines* saccade trajectories relative to the hand and/or eye start positions with the same color; *small filled circle* saccade endpoints; *gray lines* trajectories of hand movement

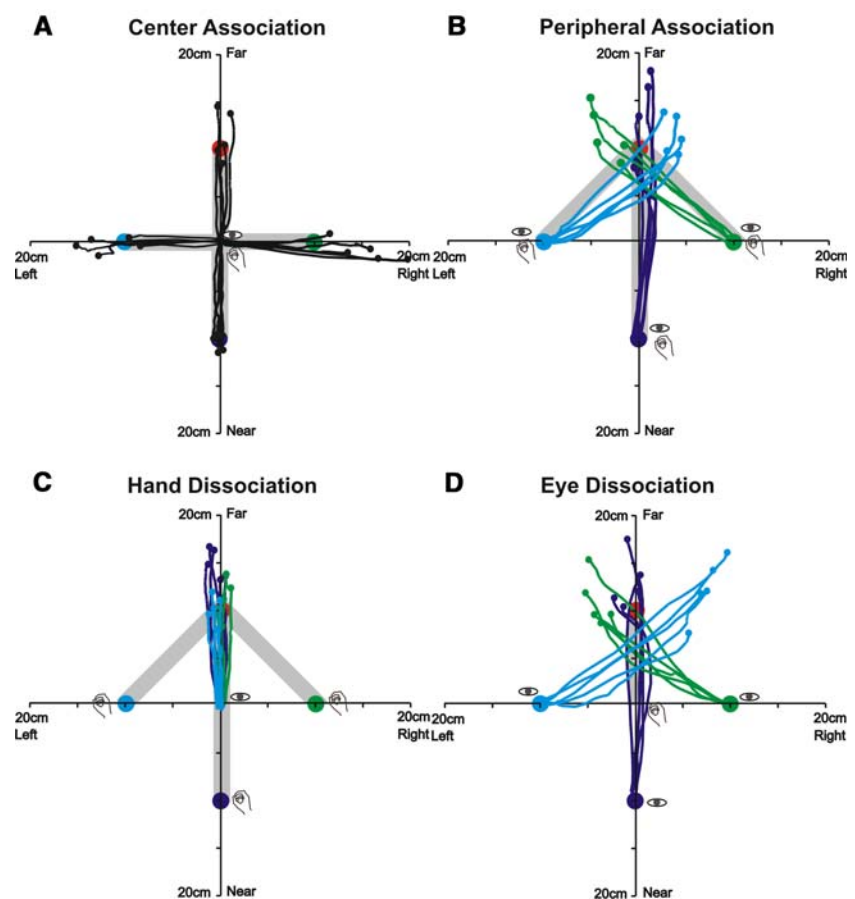
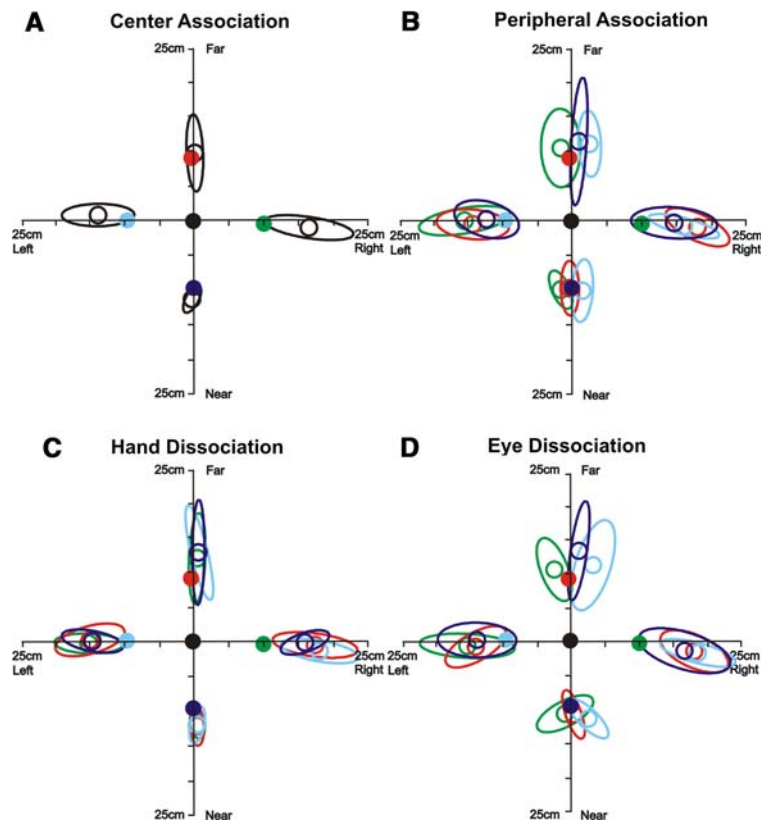


Fig. 4 Error distributions of saccades within subjects. The distribution ellipse relative to each target location was fit to each subject's saccade endpoints in table coordinates, then these ellipse parameters were averaged across the six subjects to provide the ellipses plotted here. **a** Center Association (CA). **b** Peripheral Association (PA). **c** Hand Dissociation (HD). **d** Eye Dissociation (ED). Legend: *colored dots* target locations or start positions; *filled circle* center fixation locations; *open circle* mean saccade endpoint; *black and colored unfilled ellipses* error distribution with 95% confidence intervals of intra-subject variability, averaged across subjects and colored corresponding to the color of the hand and/or eye start positions



X-axis on the table surface and the lines between the target locations and final saccade endpoints. Also, we fitted 95% confidence interval ellipses to the saccade endpoints of each task from each subject (see “Results”) and defined the *variability direction errors* as the directions (in degrees) of the major axes of these fitted ellipses in polar coordinates. The polar coordinate system was based on a counterclockwise rotation from -90° to 360° . In this way, we defined the right (r), far (f), left (l), near (n) target locations (T) as 0° , 90° , 180° , 270° , respectively. In order to compare the data relative to different start positions (S), the ranges of the directions of the 95% confidence ellipses and the saccade endpoints were converted to lie within the following intervals: for the right target (Tr, 0°), the direction range was from -90° to 90° ; for the far target (Tf, 90°), the direction range was from 0° to 180° ; for the left target (Tl, 180°), the direction range was from 90° to 270° ; and for the near target (Tn, 270°), the direction range was from 180° to 360° . The basic variability ellipse fitting algorithm and the calculation of the endpoint direction error only provided the above directions between 0° and 180° . In order to correct for target locations according to the above limitation, we added 180° or 360° to the final corresponding variability direction error and endpoint direction error.

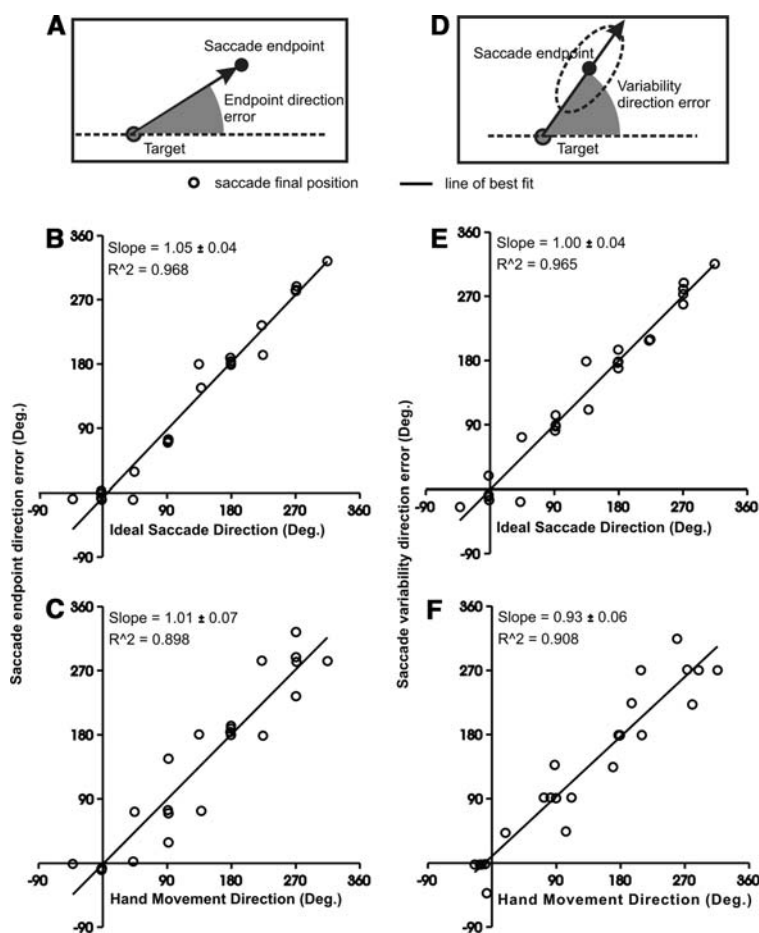
Results

Saccade and hand trajectories

Figure 3 illustrates examples of two-dimensional (2D) saccade trajectories (thin colored lines) and hand movement trajectories (thick gray lines) from one subject in “table coordinates”: a Cartesian coordinate system aligned with the far-near and transverse axes of the target board. In the CA paradigm (Fig. 3a), the subject's saccades showed an overshooting pattern past the peripheral targets (four colored dots). Figure 3b shows an example from the same subject and with the far target (red dot) in the PA paradigm. Here the pattern of the final saccade endpoints changed relative to different gaze start positions. For example, when both the gaze and hand started from the right position (green dot), the saccade endpoints tended to overshoot toward the left of final target location along the direction of the eye and hand movement. Also, the variability of the saccade endpoints increased. However, in these two paradigms, the gaze and hand trajectories were associated, so one cannot tell whether this effect was due to a change in the start positions of the saccade and/or hand movement.

Figure 3c shows the same subject's performance in the HD paradigm. When the hand started from one of three

Fig. 5 Single linear regression in dissociation paradigms. The independent variable was the ideal saccade direction or the hand movement direction, respectively. The dependent variable was the averaged saccade endpoint direction error or the averaged variability direction error across six subjects relative to each start position task. **a** The definition of endpoint direction error. **b** The linear regression between the averaged saccade endpoint direction error and the ideal saccade direction. **c** The linear regression between the averaged saccade endpoint direction error and the hand movement direction. **d** The definition of the saccade variability direction error. **e** The linear regression between the variability direction error and the ideal saccade direction. **f** The linear regression between the variability direction error and the hand movement direction. Legend in Fig. 5b, c, e and f: *open circle* paired points relative to each independent variable and its relative dependent variable; *black lines* the linear regressions



peripheral locations toward the far target location (red dot), there was still overshooting, but the direction of the errors did not depend on the direction of the hand displacement, instead, it depended on the direction of the saccade. Similarly, in the Eye Dissociation paradigm (ED, Fig. 3d), where the hand always started from the center location, the directions of the saccade endpoints tended to be hypermetric along the lines of the saccade movements, i.e., saccades tended to overshoot toward left side of the far target when starting from the right start position (green dot), toward right side of the far target when starting from the left start position (light blue dot).

These examples suggest that it is not the direction of the hand displacement that determines the errors in these tasks, but rather the saccade vector itself. We confirm and document this quantitatively in the following sections.

Saccade accuracy and precision

In order to quantify the pattern of the saccade errors (accuracy) relative to different saccade and hand start positions and illustrate the intra-individual variability (precision) of the saccades, we fitted 95% confidence interval ellipses to the saccade endpoints of each task from each subject, and

then averaged the parameters of these ellipses across subjects, including the center location of the ellipse, the length of the major and minor axes and the direction of the major axis (Fig. 4). We calculated and converted the *endpoint direction error* and the *variability direction error* in polar coordinates according to the definitions provided in the “Methods” section.

In the Center Association paradigm (CA, Fig. 4a), absolute errors of saccades were significantly hypermetric for the left [$T(5) = 2.76$, $P < 0.05$] and right targets [$T(5) = 3.48$, $P < 0.05$], respectively, which is consistent with our previous results (Ren et al. 2006). However, the absolute errors of saccades were not significantly hypermetric for far [$T(5) = 0.34$, $P = 0.75$] and near [$T(5) = 0.91$, $P = 0.41$] targets, although there was a trend to hypermetria.

In the PA paradigm where the eye and hand both started from the peripheral start positions (PA, Fig. 4b), we observed the same basic overshooting pattern as seen in the CA paradigm (Fig. 4a). However, in the PA paradigm, there was a difference in the endpoint direction errors for one target location as a function of initial eye position. This initial position dependence was significant for both the far target [$F(2,5) = 8.42$, $P < 0.01$] or the near target [$F(2,5) = 6.89$, $P < 0.05$]. For example, for the far target location

(Tf, red dot), the averaged saccade (green circle) landed on the left side of the far target when the saccade and hand started from the right start position (Sr, green dot), and in this case, the endpoint direction error (in polar coordinates) across subjects was $98.88^\circ \pm 9.55^\circ$ [mean \pm standard deviation (SD)]. When the saccade and hand started from the left start position (Sl, light blue dot), the saccade (light blue circle) ended on the right side of the far target, and the endpoint direction error was $76.34^\circ \pm 12.49^\circ$. Finally, between the left and right starting positions, when the saccade and hand movement started from the near start position (Sn) and ended at the far target location (Tf), the endpoint direction error was intermediate ($83.76^\circ \pm 4.54^\circ$). In other words, the saccade overshoot along the line of the saccade and hand movement direction.

There was no significant difference in the variability direction errors among the three different start positions for the near [$F(2,5) = 0.08$, $P = 0.92$] and far [$F(2,5) = 0.90$, $P = 0.44$] target locations, respectively. Also, there were no significant differences in the endpoint direction errors and the variability direction errors among the three different initial positions (Sr, Sf and Sn or Sf, Sl and Sn) for either the left or right target locations (Tl or Tr).

When comparing the CA paradigm with the PA paradigm, there was a significant difference in endpoint direction errors among different initial positions for the far [$F(3,5) = 4.96$, $P < 0.05$] and near targets [$F(3,5) = 6.31$, $P < 0.01$], but not for the left [$F(3,5) = 0.32$, $P = 0.81$] or right [$F(3,5) = 0.13$, $P = 0.94$] target. And, there was no significant difference in the variability direction errors among different initial positions for all targets (all $P > 0.05$) between the CA and PA paradigms.

Did these direction changes in the saccade endpoints in the PA paradigm come from the change in the hand start positions or from the change in the initial gaze positions? In order to answer this question, we looked at the HD and the ED paradigms. We found that unlike the PA paradigm, only changing the initial position of the hand (HD, Fig. 4c) did not produce direction error changes in the saccade endpoints, i.e., there was no significant difference in the endpoint direction errors among three different initial positions of the hand for any of the target locations (Tr, Tf, Tl and Tn) across subjects [$F(2,5) = 4.06$, 1.10, 0.68 and 0.03, $P = 0.06$, 0.37, 0.53 and 0.97]. When comparing the CA paradigm with the HD paradigms, there was no significant difference in both endpoint direction error and variability direction error as a function of different initial hand position for all of the four targets (all $P > 0.05$).

However, changing the initial eye position relative to the final target location (ED, Fig. 4d) did alter the direction of the overshooting pattern on the two vertical targets: the endpoint direction errors tended to align with the directions of the saccades (see next section for further analysis).

Again, as in the PA paradigm, there was a significant difference in the endpoint direction errors among the three different start positions (Sr, Sl and Sn or Sr, Sf and Sl) for the far target [Tf: $F(2,5) = 19$, $P < 0.001$] and near target [Tn: $F(2,5) = 12.9$, $P < 0.005$]. In addition, there was a significant difference in the variability direction errors among three different start positions for the far target [Tf: $F(2,5) = 5.87$, $P < 0.05$] and the near target [Tn: $F(2,5) = 21.3$, $P < 0.001$]. When comparing the CA paradigm with the ED paradigms, there was significant difference in both the endpoint direction error and the variability direction error as a function of different initial eye positions for the far target [$F(3,5) = 4.86$, $P < 0.05$] and the near target [$F(3,5) = 11.2$, $P < 0.001$], but not for the left or right target (both $P > 0.05$).

Thus, it was obvious that the start positions of the saccades and hand movements had different effects on the hand-guided saccade endpoints, especially their directional component.

Multiple linear regression in dissociation paradigms

In order to statistically describe the relationship between the saccade direction errors and the ideal saccade or hand movement directions, we performed a linear regression analysis within subjects on the averaged data from the two dissociation paradigms (ED + HD) (Fig. 5). If the above saccade direction errors came from the noise in the internal estimate of the hand movement vector, we should be able to see a strong correlation between the saccade direction errors and the hand movement directions in these two dissociation paradigms. Alternatively, if the above saccade direction errors came from the estimate of the difference between the initial eye position and the hand-held target location during the saccade programming, one should see a strong correlation between the saccade direction errors and the ideal saccade directions (from initial position of the target) in these two dissociation paradigms.

Figure 5a and d provided the definitions of the endpoint direction errors and the variability direction errors. The linear regression slopes between the endpoint direction errors and both the ideal saccade directions (Fig. 5b) and the hand movement directions (Fig. 5c) were significantly different from 0 [$F(1,22) = 676$ and 195, both $P < 0.001$], with R^2 being 0.968 (the former) and 0.898 (the latter). The same trend was observed between the variability direction errors and the ideal saccade directions or the hand movement directions (for both, $P < 0.001$) (Fig. 5e, f), and R^2 were 0.965 and 0.908, respectively.

However, there could be an interaction effect in addition to the single linear regressions because the eye and hand had moved in the roughly same direction and extent along one axis of the table coordinates in each dissociation task (HD or ED paradigm). We therefore performed stepwise multiple linear regression analysis to see which variable

contributed more to the actual endpoint direction errors (Table 1): the ideal saccade direction or the hand movement direction. In this multiple linear regression, the two independent variables were the ideal saccade direction and the hand movement direction, and the dependent variables were the endpoint direction errors and the variability direction errors. The ideal saccade direction was the only independent variable in model 1. Model 2 had the hand movement direction as the independent variable. Model 3 has two independent variables: the ideal saccade direction and the hand movement direction. As shown in Table 1, although there were significant R^2 changes when adding the hand movement direction into the equation with both dependent variables, the actual values of R^2 changes between model 3 and model 1 were quite small for both the endpoint direction errors (0.006) and the variability direction errors (0.009). In contrast, when adding the ideal saccade direction into the equation, the R^2 changes between model 3 and model 2 were 0.076 for the endpoint direction errors and 0.065 for the variability direction errors, which were about 13 and 7 times bigger than the R^2 changes between model 3 and model 1, respectively. Therefore, the ideal saccade directions strongly contributed to the direction errors of the hand-guided saccade endpoints and the direction errors of the saccade variability ellipses, and there was only a very weak contribution from the hand movement directions.

Discussion

The current results confirm and extend our previous findings regarding the characteristics of the accuracy and precision of saccades toward hand-displaced targets. In general, the overshooting patterns obtained from our original experiment (Ren et al. 2006) and from the CA paradigm in this experiment are in excellent agreement. However, the new finding in this experiment is that the direction errors of both variability and accuracy of saccades toward hand-displaced targets are affected much more by initial eye positions with respect to the target itself, than the hand trajectory. In particular, the direction of the ideal saccade path (initial hand

position–initial eye position) contributed much more to the average direction and variability of saccades to handheld targets than did the direction of the hand movement itself. Here, we will consider the implications of these findings for sensorimotor integration and neurophysiology.

Accuracy and precision of limb proprioceptively guided saccades

From this experiment, one can see that there was a trend toward hypermetria in all directions, but in the CA condition (Fig. 4a), saccades toward the near and far targets were not as hypermetric as those toward the left and right targets. The same pattern was observed in the other three conditions (Fig. 4b–d). In our previous study, we tested more directions and found that the axis of greatest hypermetria roughly aligned with the orientation of the forearm (Ren et al. 2006). There, we proposed that this anisotropy occurs because the saccade generator does not completely compensate for anisotropic limb mechanics after receiving the efference copy signal of hand movement. For example, limb inertia (one aspect of limb mechanics) is anisotropic, and its maximum is thought to align approximately along the extension–flexion axis of forearm (Hogan 1985; Sabes et al. 1998; Soechting et al. 1995). Vercher et al. (1995) have speculated that similar factors lead to transient gain errors in ocular pursuit when subjects track a hand-moved target in the dark.

In terms of saccade precision, we observed that the variability of saccade errors was much smaller for the near target location than for the other three target locations in all four conditions (Fig. 4). This difference may arise from the limb somatosensory inflow signals used to drive the saccade generator. Van Beers et al. (1998) have observed that hand positions that were held closer to the shoulder were localized more precisely (by pointing with the other hand) than positions further away from the shoulder. Other studies (Clark 1992; Clark et al. 1995; Scott and Loeb 1994) have shown similar results supporting the idea that the different precision of proprioceptive localization for different arm postures can be predicted from the geometry of the arm.

Table 1 Stepwise multiple linear regression

Direction error	Model 1 (R^2 , P)	Model 2 (R^2 , P)	Pearson correlation (between IVs)	Model 3			R^2 change (M3–M1) (P)
				R^2	Slope 1	Slope 2	
Endpoint direction error	0.968 (*)	0.898 (*)	0.938	0.974	0.789	0.208	0.006 (*)
Variability direction error	0.964 (*)	0.908 (*)	0.938	0.973	0.734	0.264	0.009 (*)

M1: independent variable (IV) is ideal saccade direction, M2: independent variable (IV) is hand movement direction, M3: IVs are ideal saccade direction and hand movement direction

* $P < 0.05$

Origin of errors in proprioceptively guided saccades

In our previous study (Ren et al. 2006), the reliance on somatosensory input produced larger systematic saccade errors compared with the errors in visually-guided or visual memory-guided saccades: saccades were significantly hypermetric in all directions. Moreover, the variability of hand-guided saccades were prominently and equally increased on both amplitude and direction components, with amplitude always greater than direction. Previous studies have demonstrated that the endpoints of visually-guided saccades aimed at targets of a given meridional direction scatter predominantly along the vector pointing from the initial fixation point to the target position (eccentricity scatter) and less in the transverse direction (meridional scatter) (Deubel 1987; van Opstal and van Gisbergen 1990). The same trends were evident in our previous and current study, but the endpoint errors and variability magnitudes observed in hand-guided saccades are much larger than those in visually-guided or visual memory-guided saccades (Ren et al. 2006).

Therefore, the errors observed here do not arise primarily from an imprecision in the knowledge of eye position itself. The errors are specific to saccades directed to hand-held targets without vision, and specific to certain arm configurations (Ren et al. 2006). Moreover, we have shown here that the errors do not arise from a misestimate of the hand trajectory. This suggests that the oculomotor system makes an error in defining saccade vectors when comparing the initial eye position and a limb proprioceptively defined target location. In particular, the data suggest that the oculomotor system overestimates the distance aspect between current and desired gaze direction when the latter is derived from the somatosensory system.

Although this was the main source of error—the estimated difference between the initial eye position and the hand-guided target—hand displacement still had a weak effect on the errors in hand-guided saccades. Moreover, when comparing the ED paradigm with the PA paradigm, one can see that the direction errors of variability of saccades within subjects changes. This also suggests that initial hand position (or hand path) has a weak effect on hand-guided saccades.

How might error arise in comparing gaze and hand position? Some studies have suggested that there is a common short-term working memory for target storage and updating which is in an eye-centered coordinate system (Andersen and Buneo 2002; Batista et al. 1999). In our experiment, the gaze-centered visuospatial memory can receive and synthesize information from (1) the visual system itself; (2) the oculomotor system to update targets in eye-centered coordinates; and (3) the somatosensory updating system (Ren et al. 2006) several reference frame transformations are

required during somatosensory updating to correctly transform proprioceptive signals from limb-based coordinates into gaze-centered coordinates (Buneo et al. 2002). In our previous paper, we suggested that the errors arise from a failure to compensate for limb mechanics in this process.

This could implicate a number of possible cortical and subcortical saccade areas as the targets of proprioceptive updating for saccades, including the superior colliculus (Nakamura and Colby 2002), the later intraparietal area (LIP) (Duhamel et al. 1992; Medendorp et al. 2003) and the frontal eye fields (Heide et al. 2001). Some studies have demonstrated that LIP preferentially encodes targets for upcoming eye movements but also possesses responses related to limb movements (Dickinson et al. 2003; Snyder et al. 1997). Therefore, we speculate that the reference frame transformations, required for proprioceptive-oculomotor updating, take place through a mechanism similar to that proposed by Buneo et al. (2002) for arm movements, but targeting specifically the saccade-related network, including LIP (Dickinson et al. 2003; Duhamel et al. 1992).

In conclusion, the saccades toward the hand-held and displaced targets are hypermetric along the saccade movement directions. We have shown that the changes in the saccade endpoint direction errors and the saccade variability direction errors are caused mainly by the noise in the estimate of the difference between the initial eye position and the hand-displaced target location during saccade vector programming.

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