Coordinated Flexibility: How Initial Gaze Position Modulates Eye-Hand Coordination and Reaching

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Reaching to targets in space requires the coordination of eye and hand movements. In two experiments, we recorded eye and hand kinematics to examine the role of gaze position at target onset on eye-hand coordination and reaching performance. Experiment 1 showed that with eyes and hand aligned on the same peripheral start location, time lags between eye and hand onsets were small and initiation times were substantially correlated, suggesting simultaneous control and tight eye-hand coupling. With eyes and hand departing from different start locations (gaze aligned with the center of the range of possible target positions), time lags between eye and hand onsets were large and initiation times were largely uncorrelated, suggesting independent control and decoupling of eye and hand movements. Furthermore, initial gaze position strongly mediated manual reaching performance indexed by increments in movement time as a function of target distance. Experiment 2 confirmed the impact of target foveation in modulating the effect of target distance on movement time. Our findings reveal the operation of an overarching, flexible neural control system that tunes the operation and cooperation of saccadic and manual control systems depending on where the eyes look at target onset.

Keywords: eye-hand coordination, saccade, reaching, limb motor control, oculomotor control, minimum variance model, optimal motor control

In two classic studies on how humans reach for targets, Fitts (1954; Fitts & Peterson, 1964) discovered that movement time (MT) is lawfully related to the difficulty of the movement, indexed by target distance and target width. In general, MT increases with increasing target distance and decreasing target size. Scores of studies have confirmed the robustness of Fitts' law in a variety of aiming tasks and populations (for a review, see Plamondon & Alimi, 1997). The prevailing explanation of Fitts' law is the minimum variance model (Harris & Wolpert, 1998) in which consecutive muscle activations are planned in order to keep the variance of the final hand position at a minimum (see also Todorov & Jordan, 2002). Because motor noise increases with increasing muscle activation, movements of large amplitude have endpoints that are more variable. In order to meet precision requirements with distant or small targets, MTs will increase to match the expected endpoint variance. While the dynamics of movement planning have been modeled in detail, few studies have investigated how initial gaze position affects reaching movements. Initial gaze position with respect to the target is likely to affect sensory noise because the spatial resolution of visual information depends on retinal eccentricity. The question is how sensory and motor noise are connected. It may be possible that reductions of sensory noise simply decrease motor noise and therefore reduce endpoint variability. Alternatively, effects of sensory noise on pointing may be mediated by different patterns of eye-hand coordination. To answer this question, we examine effects of gaze position at target onset on the temporal and spatial characteristics of reaching movements. In addition, we investigate effects of initial gaze position on the temporal coordination between eye and hand movements.

Hand movements to targets in space are usually preceded by eye movements (e.g., Abrams, Meyer, & Kornblum, 1990; Neggers & Bekkering, 2000). This eyes-first/hand-second strategy ensures the availability of fine-grained visual information delivered by the fovea to optimize the speed and accuracy of hand movements. Interestingly, so far, the influence of eye position on eye-hand coordination and reaching has not been examined. This is somewhat surprising given the large body of behavioral and neurophysiological evidence that demonstrates a strong interaction between ocular and manual motor systems during reaching (for reviews, see Bekkering & Sailer, 2002; Carey, Della Sala, & Ietswaart, 2002; Crawford, Medendorp, & Marotta, 2004; Desmurget, Pélisson, Rossetti, & Prablanc, 1998).

In Fitts and Peterson's (1964) discrete aiming experiments, targets were located at several distances to the right and left of a central starting point. At the start of a trial, the eyes were directed to a separate stimulus display in front of the participants that contained a fixation point midway between two signal lights. Depending on which light came on, the participants had to move a hand-held stylus to the left or right target as quickly as possible. Hence, in Fitts and Peterson's experiment, the position of the eyes and the position of the hand at stimulus onset did not coincide—they were directed at different spatial locations. Moreover, the signal light that specified which target to move to was physically different from the target. Later studies, which used more direct stimulus-response mappings, confirmed Fitts' law (e.g., Keulen, Adam, Fischer, Kuipers, & Jolles, 2002; Murata & Iwase, 2001; Smyrnis, Evdokimidis, Constantinidis, & Kastrinakis, 2000), but because eye behavior was not recorded, its effect on hand reaching dynamics is unknown.

Ample neurophysiological and behavioral evidence suggest that initial gaze position can influence the neural control of reaching movements. Single-unit recording studies in primates (e.g., Boussaoud, Jouffrais, & Bremmer, 1998) and functional imaging studies in humans (e.g., Bédard, Wu, & Sanes, in press; Beurze, de Lange, Toni, & Medendorp, 2009) have demonstrated that eye position modulates the activity of movement-related neurons in premotor and parietal areas. In a behavioral study, Van Donkelaar (1997) asked participants to make saccades and reaching movements to peripheral targets starting from independent initial positions. On two thirds of the trials, the saccades needed to cover a larger distance to reach the target than the hand movement and on the remaining trials not (i.e., eyes and hand started from the same start position). Results showed that when the saccade amplitude increased the accompanying hand movement covered a slightly larger distance too, suggesting a significant influence of the saccadic control system on the manual control system. Unfortunately, this study only reported the constant horizontal manual reaching error and did not systematically vary the distance of the reaching movement, so a more detailed and systematic investigation is needed to examine the influence of initial gaze position on reaching performance and eye-hand coordination.

In the present study, we addressed this issue by asking participants to make reaching movements to peripherally appearing targets using two different initial gaze positions. In the "fixate-start" (or "fixate-0-cm") condition, the eyes fixated the start position of the hand at the beginning of a trial. From this common start position, the eyes and the hand both moved to the target that appeared in 1 of 7 locations at a distance from 10 to 19 cm to the right of the start position (see Figure 1). Hence, in the fixate-start condition, eyes and hand started and finished at common locations, creating similar amplitude and direction requirements for both. This allows for a maximal cooperation between the eye and hand control systems. In the "fixate-center" (or "fixate-14.5-cm") condition, the position of eyes and hand at target onset were different. We achieved this by cuing the eyes, at the start of a trial, away from the hand start position to the center of the range of seven possible target locations, which was at a distance of 14.5 cm. Hence, in this condition, amplitude and sometimes direction (in trials with target distances smaller or equal 14.5 cm) metrics were different for eye and hand movements. This weakens their coupling. Comparing speed and precision of hand reaching move-
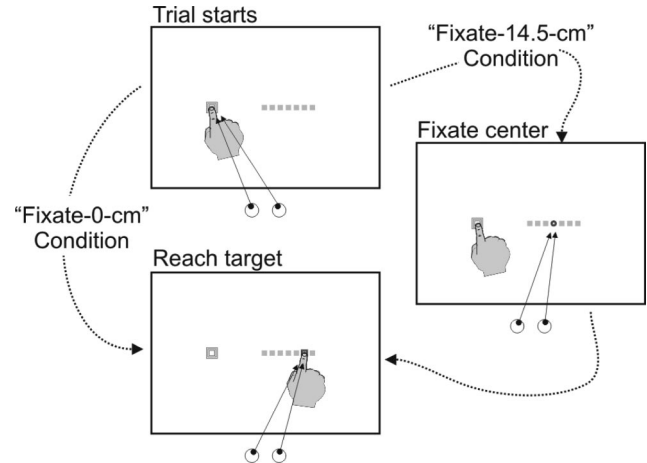

Figure 1. The experimental paradigm (drawn to scale). The main task was to reach from the start position on the left to the red target location on the right. The gray filled boxes were not visible in the actual experiment, but represent the seven possible target locations. In the "fixate-start" (or "fixate-0-cm") condition, participants had to look at the start position until the target appeared. In the "fixate-14.5-cm" condition, participants first looked at the start location and then at a bull's eye that appeared in the center of the range of target locations.

ments as a function of movement amplitude in the fixate-start and fixate-center conditions will reveal how differences in initial gaze position modulate the dynamics of reaching movements. We also recorded response latencies of eyes and hand to determine how gaze position influences their temporal coordination.

Experiment 1

Method

Participants. Sixteen university students (13 female, 15 right-handed) with a mean age of 20.7 years ($SD = 1.7$) participated in the experiment. All were naïve with respect to the purpose of the experiment and had normal or corrected-to-normal vision. The study was approved by the local ethics committee.

Apparatus and stimuli. An Eyelink II (Osgood, Ontario, Canada) eye tracker was used to record eye movements. The eye tracker was set to pupil only mode at 250 Hz sampling rate. Before each block, a horizontal, 3-point calibration procedure was performed. The X, Y, and Z coordinates of manual movements were recorded by an ultrasonic system (CMS20S, zebris Medical GmbH, Isny im Allgäu, Germany) at a sample frequency of 150 Hz by means of a marker positioned on the nail of the right index finger.

Hand movements were executed on a flat panel screen. The screen was placed in a frame and attached to the edge of a table, which allowed changing the inclination of the screen relative to the table. We chose an angle of about 38° between the screen and the table. The screen dimensions were 37.6 × 30.2 cm (width × height). One cm on the screen corresponded to approximately 1.4° of visual angle. The start location was marked by red, nested squares of 1-, 1.5-, and 2-cm width and was situated 10.2 cm to the left of the screen center (see Figure 1). The target for the reaching

movement was a 1×1-cm red outline square that appeared at a distance of 10, 11.5, 13, 14.5, 16, 17.5, or 19 cm to the right of the start location. Expressed in degrees of visual angles, these distances correspond to 14.3°, 16.5°, 18.6°, 20.8°, 22.9°, 25.1°, and 27.2°, respectively. All distances are center-to-center. In the "fixate-0-cm" condition, fixation was maintained on the start location. The fixation mark in the "fixate-14.5-cm" condition was a gray 1-cm bull's eye that appeared at the center of the range of target locations (i.e., at 14.5 cm from the start position). Note that "fixate-0-cm" and "fixate-14.5-cm" refers to the initial gaze fixation before target onset. Subjects were not required to maintain the initial fixation during the reaching movement, but typically made a saccade to the target before reaching to it.

Procedure. The experiment took place in a dimly lit room. Participants' eyes were at a distance of approximately 40 cm from the flat panel screen, and the head was restrained by a chin rest. A trial was initiated by placing the right index on the start location. Participants were instructed to maintain eye fixation on the finger's start location until another stimulus appeared. Once the finger had been on the start position for 350 ms, the trial started. In the "fixate-0-cm" condition, the red target square appeared and observers were instructed to move to and touch it with the index finger as rapidly and accurately as possible. Thus, eye fixation was on the start location of the finger when the reach target appeared. In the "fixate-14.5-cm" condition, a gray bull's eye appeared in the center of the target range for 600 ms and participants made a saccade to foveate it. Then, the red target square appeared and participants touched it with the index finger. Participants were free to move their eyes after target onset and typically made a saccade to the target before the hand started to move. In both gaze conditions, target onset was preceded by a random wait between 0 and 300 ms at the current fixation (start location or bull's eye). Participants received about 30 practice trials before the experiment started.

Design. The fixate-0-cm and fixate-14.5-cm conditions were blocked. One block was composed of 70 trials (7 target positions × 10 repetitions) preceded by seven warm-up trials that were not analyzed. Two blocks were completed for each condition. The two conditions alternated: Half of the participants started with the fixate-0-cm condition and the other half with the fixate-14.5-cm condition. Between blocks, participants rested and the eye tracker was calibrated before each block.

Analyses. During the experiment, we defined hand movement onset as the first sample exceeding a velocity of 5 cm/s with the constraint that the velocity stayed above this value for at least 100 ms. Movement offset was defined as the sample with a distance to the screen smaller than 0.4 cm. In our offline analysis, we corrected the on- and offsets to improve precision. First, we low-pass filtered the tangential velocity traces at 35 Hz (Butterworth filter, zero phase shift). Movement onset was defined as samples that were above 5.9 cm/s. Movement offset was the first velocity sample that was smaller than 20% of peak velocity. The relatively high threshold was motivated by observers' tendency to make a small submovement at the end of the reach. The first submovement brought the hand to the position of the target. Then, the movement almost ended at some distance from the screen. The second submovement brought the hand toward the screen surface without much displacement along the horizontal axis. An example is shown in Figure 2. It is also clear that there was some "rolling
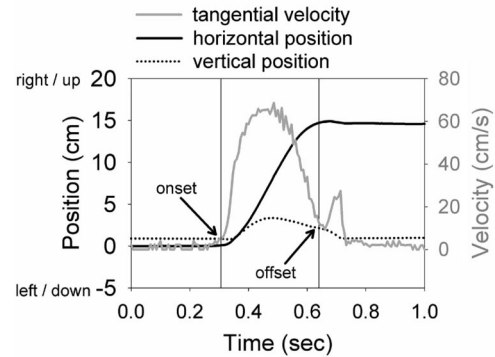
Figure 2. Sample trial. The left axis displays the horizontal and vertical position of the marker attached to the finger. Negative numbers indicate positions on the left or close to the screen surface. The tangential velocity (after low-pass filtering) is displayed on the right. The graph shows that the hand was lifted and moved to the right. At the end of the movement, the finger was lowered without any displacement along the horizontal axis. Movement offset was defined as 20% of maximal velocity to cut off the sub-movement at the end.

back" along the *x*-axis. This displacement may have been caused by an adjustment of the finger rotation at the end of the movement, which changed the horizontal position of the marker attached to the fingernail. Finally, we used the Eyelink II parser to detect the onset, offset, and amplitude of saccades.

Visual feedback about the following ocular and manual errors was given to participants: For all eye movement conditions, blinking during stimulus presentation and saccades before stimulus presentation were counted as errors. Manual latencies shorter than 100 ms and longer than 800 ms were anticipations and missed trials, respectively. Reaches that missed the target by more than 1.5 cm were considered erroneous. Also, loss of the ultrasonic signal was detected. To detect early saccades, we determined the size of the saccades made in a 600-ms window following the onset of the manual target or the bull's eye. If the amplitude of the saccade deviated by more than 3 cm from the expected amplitude, we assumed that the participant's gaze had deviated from the start location before the relevant stimulus was shown. These saccadic anticipations were frequent, which may be due to the predictive sequence of events.

The data from two participants were discarded because the error rate in at least one eye movement condition exceeded 40%. The total percentage of rejected trials was 11% and 16% with initial fixation on the 0 and 14.5-cm location, respectively. About half of these trials were rejected because of saccade errors (6% and 9% for fixation on 0 and 14.5 cm, respectively). Imprecise hand movements (deviation larger than 1.5 cm) led to the exclusion of 2% and 4% trials with initial fixation on 0 and 14.5 cm, respectively. Anticipations occurred at a rate of 2% and failures to lift the finger occurred in 2% of trials. Errors are not mutually exclusive.

Median saccadic RTs (RTs) and median manual RTs and movement times (MTs) were calculated for each condition and participant. All times are with reference to target appearance. Besides, we calculated the median amplitude and peak velocity of manual responses. We ran two-way, within-subject ANOVAs (2 initial gaze position × 7 target distance). Additionally, we evaluated

eye-hand coordination by correlating saccadic and manual reaction time (RT).

Results

Manual movement times. As shown in Figure 3A, MTs were shorter when participants initially fixated the position at 14.5 cm than when they initially fixated the start position (336 vs. 360 ms), $F(1, 13) = 130.16$, $p < .001$. MTs increased with the distance of the target position (from 324 to 371 ms), $F(6, 78) = 38.45$, $p < .001$. Importantly, the increase of MT with increasing distance was steeper for the fixate-start than the fixate-center condition, $F(6, 78) = 3.23$, $p = .007$. The differences between the smallest and greatest target distance are also shown separately for each eye fixation condition in Figure 5A. MTs did not differ between the two initial gaze positions at the shortest distance (7 ms), $t(13) = 1.51$, $p = .16$, whereas significant differences emerged at all other positions (19, 21, 29, 32, 33, 31 ms for distances from 11.5 to 19 cm, respectively), $ts(13) > 3.66$, $ps < .004$. Next, we ran linear regressions of MT on target distance, separately for each participant and gaze position. The average slope was greater with initial gaze at the start than at the 14.5-cm position (6.2 vs. 3.5 ms/cm), $t(13) = 3.52$, $p = .004$. These results indicate that initial gaze position significantly affected the slope of the function relating MT to target distance.

Manual endpoint variability. We calculated the standard deviation of the signed difference between the required and actual amplitude of the trajectory for each observer and condition. The

ANOVA on endpoint variability revealed a significant effect of target distance, $F(6, 78) = 6.93$, $p < .001$, but no interaction, $p = .667$. The mean variability was 0.40, 0.39, 0.43, 0.41, 0.47 0.48, and 0.49 cm from the shortest to the longest target distance, respectively.

Manual peak velocity. The peak velocity of the low-pass filtered velocity traces was determined between movement onset and offset. As shown in Figure 3B, velocity was higher in the fixate-14.5-cm than in the fixate-0-cm condition (74.6 vs. 69.7 cm/s), $F(1, 13) = 71.36$, $p < .001$. Peak velocity increased with increasing distance of the target (57.3, 61.7, 66.6, 72.5, 77.9, 82.3, 86.8 cm/s from shortest to longest distance, respectively), $F(6, 78) = 693.11$, $p < .001$. Importantly, there was a significant interaction between initial gaze position and target distance, $F(6, 78) = 13$, $p < .001$, showing that the increase of peak velocity with distance was stronger for initial gaze at the 14.5-cm position (from 57 to 90.9 cm/s) than for initial gaze at the start position (from 57.5 to 82.6 cm/s). The difference between the closest and farthest targets is shown in Figure 5C. The stronger increase of peak velocity with gaze at the 14.5-cm position corresponds with the smaller slope of the MT-distance function.

Manual reaction times. Figures 3C and 3D show manual and saccadic RTs, respectively. The ANOVA revealed a main effect of initial gaze position, $F(1, 13) = 8.06$, $p = .014$, indicating that manual RTs were shorter in the fixate-start than the fixate-center condition (265 vs. 310 ms). No other effects reached significance.

Saccadic reaction times. When observers fixated the 14.5-cm position, very few saccades occurred when the target appeared at the 14.5-cm position. In this and subsequent analyses, we entirely excluded the 14.5-cm target distance in the ANOVA to achieve a balanced design (2 initial gaze positions × 6 target distances). For correlations and t tests, we decided to keep the 14.5-cm target distance condition when fixation was on the start position. In contrast to manual RTs, saccadic RTs were longer in the fixate-start condition than in the fixate-center condition (224 vs. 168 ms), $F(1, 13) = 23.13$, $p < .001$. The main effect of target position, $F(5, 65) = 6.93$, $p < .001$, showed that saccadic RTs were longer toward the center position (186, 187, 198, 207, 206, and 195 ms from shortest to longest distance, respectively). The interaction between initial gaze and target position was significant, $F(5, 65) = 2.37$, $p = .049$, showing that the effect of target position was mainly driven by the fixate-center condition (see Figure 3D). This outcome accords with reports showing increased saccadic RTs for targets appearing very close to the fovea (e.g., Kalesnykas & Hallett, 1994).

Interval between saccadic and manual reaction times. Subjects moved the eyes before they moved the hand in 87% of the trials, and this tendency was more pronounced for the fixate-14.5-cm position than for the fixate-0-cm condition (96% vs. 77%), $t(13) = 4.35$, $p < .001$. Accordingly, the eye movement preceded the hand movement by a much greater interval with initial fixation on the 14.5-cm location than with initial fixation on the start location (140 vs. 38 ms), $t(13) = 7.16$, $p < .001$. Inspection of the lower panels in Figure 3 indicates that with initial fixation on the 14.5-cm position (unfilled circles), the hand movement occurred later (Figure 3C) and the saccade to the target occurred earlier (Figure 3D) than with gaze at the start (filled circles), resulting in more time to foveally inspect the target position before onset of the hand movement. That is, the lines with
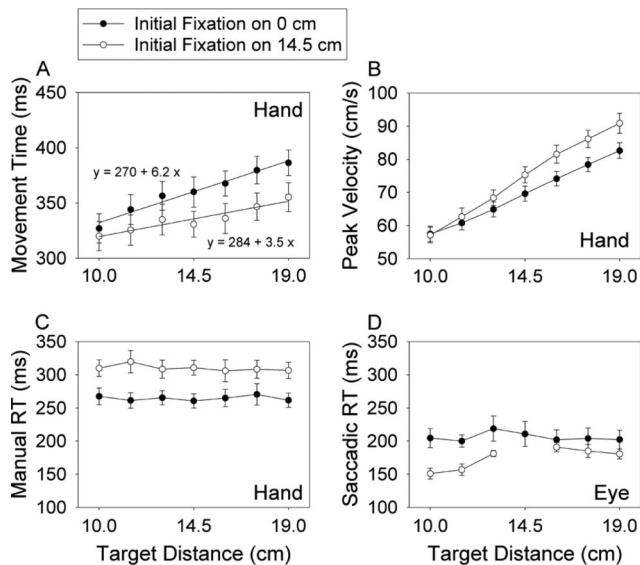
Figure 3. Results from Experiment 1. Initial fixation was either on the start position (0 cm) or on the position 14.5 cm away from the start position. Movement time and peak velocity are shown in panels A and B, respectively. Manual reaction times (RTs) and saccadic RTs are shown in panels C and D, respectively. Very few saccades (less than 1 on average) were made when the participants were looking at the bull's eye ("initial fixation on 14.5 cm") and the target appeared at the same position (at a distance of 14.5 cm). Therefore, there is a missing data point. Error bars denote the between-subjects standard error of the mean (of individual medians).

unfilled symbols (fixation on 14.5 cm) are further apart in Figures 3C and 3D than the lines with filled symbols (fixation on start). These findings reveal that gaze position at target onset significantly modulated the temporal coordination of eye and hand movements.

Temporal coupling between eye and hand movement. To further investigate eye-hand coupling, we correlated the saccadic and manual RTs. Before running t tests, correlations were transformed to Fisher's Z, but uncorrected means are reported. First, we calculated the correlation across single trials for each participant separately. With initial fixation on the start position, the correlation was positive and significant for 14 out of 14 participants ($ps < .003$). The mean correlation was .61, ranging from .26 to .80, and significantly different from zero, $t(13) = 11.1, p < .001$. With fixation on the 14.5-cm location, the correlation was positive and significant for 3 out of 14 subjects ($ps < .006$). The mean correlation was only .12, but significantly different from zero, $t(13) = 2.54, p = .025$. Because of the larger size of the correlation (.61 vs. .12), $t(13) = 8.94, p < .001$, and the higher number of significant individual correlations (14 vs. 3), we conclude that eye-hand coupling was much stronger when the eye was initially maintained at the start position than when it was initially directed at the center of the range of target locations.

Discussion

We investigated reaching movements to targets at different distances from the initial hand location. Consistent with Fitts' law, MTs increased with target distance. Relatedly, peak velocity increased for longer reaches. In contrast, manual RTs were hardly affected by target distance. Importantly, we observed that eye position before target onset changed the slope of the MT-distance function. When participants looked at the start location of the hand movement before target onset, the increase of MT with target distance was larger than when they looked at the center of the range of possible target positions. The greater increase in MT was accompanied by a smaller increase in (peak) velocity.

Because the biomechanical and precision constraints were the same in the two initial gaze conditions, the reason for the faster movement execution with initial fixation close to the endpoint has to be sought in the quality of the sensory signals. We suggest that sensory noise (or uncertainty) regarding target location was reduced with initial fixation at 14.5 cm because of the initially smaller retinal eccentricity (e.g., Adam, Ketelaars, Kingma, & Hoek, 1993; Prablanc, Echalier, Komilis, & Jeannerod, 1979; White, Levi, & Aitsebaomo, 1992). In the fixate-start condition, the targets appear at larger retinal eccentricities, which have a poor spatial resolution (e.g., Virsu & Rovamo, 1979). Hence, with the eyes and hand aligned at the start location, eyes and hand start to move in close temporal synchronicity to the target, which is visible in short eye-hand RT intervals (i.e., 38 ms) and a substantial correlation (.61) between eye and hand latencies. Because the eyes move much faster than the hand, the eyes still arrive on the target before the hand does (e.g., Bekkering, Adam, Van den Aarssen, Kingma, & Whiting, 1995; Prablanc et al., 1979). Furthermore, because of the initial inaccurate registration of the target's location on the peripheral retina, a relatively slow hand movement is planned and executed to allow sufficient time for online adjustments if necessary (e.g., Prablanc, Pelisson, & Goodale, 1986).

In the fixate-center condition, targets fall much closer to the fovea, which facilitates their localization and speeds up saccadic RTs. Moreover, in this condition, eye and hand movement metrics are different, precluding a close cooperation between the two effector systems. Apparently, in this situation, participants use a different visuomotor control strategy: They foveate the target longer and plan a faster hand movement. Thus, with the gaze directed at the center of the range of possible target locations, time lags between eye and hand onsets were large (140 ms) and initiation times were largely uncorrelated, reflecting independent control and decoupling of eye and hand movements.

Endpoint variability increased with target distance, but was not affected by eye position. This finding seems at odds with the minimum variance model (Harris & Wolpert, 1998), because fixating at the 14.5-cm location produced shorter MTs and, hence, stronger muscle activations without incurring larger endpoint variability. Therefore, it does not seem the case that a reduction of sensory noise resulted in a reduction of motor noise and therefore endpoint variability. As outlined above, our analyses of the temporal properties of eye and hand movements suggest that differences in the pattern of eye-hand coordination underlie changes in the MT-distance functions rather than reductions in motor noise.

Two further observations are relevant. First, MTs to targets at 10 cm were similar in both fixation conditions. Nevertheless, they were preceded by different patterns of eye-hand RTs. Apparently, similar MTs can be generated with different eye-hand coordination strategies (tight vs. loose eye-hand coupling).

Second, there is something special about moving the hand to an already foveated target. The pattern of MTs in the fixate-center condition depicted in Figure 3A shows that there was very little change in MT around the foveated 14.5-cm location. In fact, with the gaze directed at the 14.5-cm location, MT to the 14.5-cm location was slightly (but not significantly) shorter than that to the 13.0-cm location. The advantage of foveated targets may not have reached significance because foveated targets were much less frequent than nonfoveated targets. Participants may therefore have prepared for a nonfoveated target and this may have cancelled the advantage of foveated targets.

Experiment 2

In Experiment 2, we aimed at evaluating the contribution of foveated position by extending the number and range of initial gaze fixations. Experiment 1 suggested that MTs to a fixated target may be shorter, but strong converging evidence is needed. Overall, we included four initial gaze conditions: initial gaze on the start, on 10 cm (the shortest target distance), on 14.5 cm (which is the same as in the previous experiment), or on 19 cm (the longest target distance). To keep the number of trials in a reasonable range, we only included the shortest and longest target distance of 10 and 19 cm, respectively. Thus, the target was presented in the fovea on 50% of the trials with initial gaze at 10 and 19 cm, but never with initial gaze at 14.5 cm or with initial gaze at 0 cm.

Method

The methods were as in Experiment 1 with the following exceptions. Only target distances of 10 cm and 19 cm were presented. There were four different eye fixation conditions. In the

fixate-start condition, participants were instructed to look at their finger at the start position until the target appeared. This condition was run in a block of 36 trials. In a different block of 90 trials, the fixation mark was either presented at 10, 14.5, or 19 cm, randomly intermixed. Participants completed two blocks of each trial type for a total of 2x(36 + 90) = 252 trials. Note that the fixate-start and the fixate-14.5-cm condition replicate the fixation conditions of Experiment 1. Fifteen new students (14 female, 15 right-handed) with a mean age of 22.2 years ($SD = 3.9$) from the same subject pool as in Experiment 1 participated.

Treatment of the raw data was as in Experiment 1. The first six trials of each block were considered practice and not analyzed. We ran two-way, within-subjects ANOVAs (4 initial gaze position × 2 target distance). The percentage of rejected trials was 9% with initial gaze on the start location, and 16%, 13%, and 20% with initial gaze on the 10-cm, 14.5-cm, and 19-cm position, respectively. About half of these errors were due to saccade errors. The percentage of trials excluded due to eye movement errors (not exclusive to hand errors) were 5%, 7%, 7%, and 12% for initial fixation on 0, 10, 14.5, and 19 cm, respectively. The proportions of imprecise hand movements were 2%, 5%, 3%, and 3%, respectively. Anticipations accounted for 2% of errors and failures to lift the hand for another 3%. The data of one participant were removed because she showed longer MTs for closer targets, which is a violation of Fitts' law. The data are graphed in Figures 4 and 5.
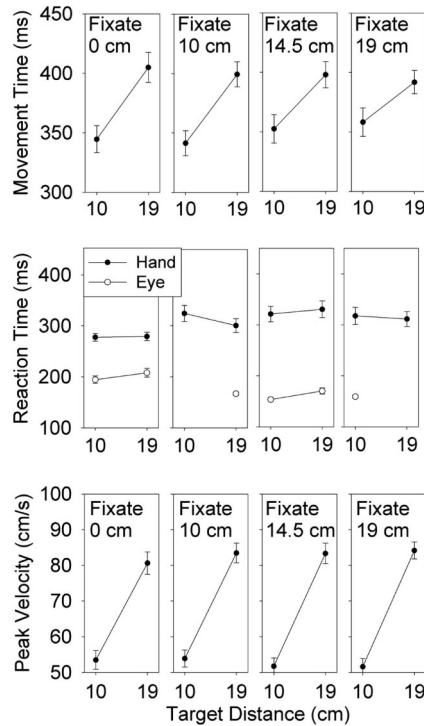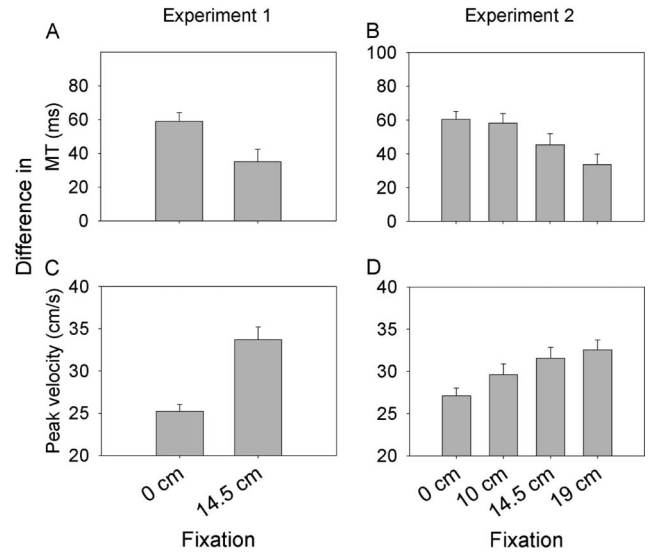

Figure 5. Summary of the results of Experiments 1 and 2. We calculated the difference in movement time (MT, panels A and B) and peak velocity (panels C and D) between the 10-cm and 19-cm targets. The difference scores are shown for the two fixation conditions in Experiment 1 (panels A and C), and for the four fixation conditions in Experiment 2 (panels B and D).

Results

Manual movement time. As shown in the upper row of Figure 4 and the upper right panel in Figure 5, the difference in MT between close and far targets decreased when initial gaze approached the far target position. MTs did not vary as a function of gaze position, $F(3, 39) = .44$, $p = .727$, but were significantly faster when the target distance was short than when it was long (349 vs. 399 ms for target distances of 10 vs. 19 cm, respectively), $F(1, 13) = 95.96$, $p < .001$. Most importantly, the interaction between gaze position and target distance was significant, $F(3, 39) = 12.45$, $p < .001$. The differences between far and close targets were 60, 58, 45, and 34 ms for initial fixation at 0, 10, 14.5, and 19 cm, respectively.

Next, we evaluated whether foveated targets produced shorter MTs. To this end, we compared MTs to the 10-cm and 19.5-cm targets when either the 10-cm or 19.5-cm positions were fixated. We only analyzed these two fixation conditions because they had equal chances of containing the reach target. MTs to the 10-cm target position were 17 ms shorter when this position was initially looked at than when the 19-cm position was initially looked at (341 vs. 358 ms), $t(13) = 4.18$, $p = .001$. Similarly, MTs to the 19-cm target position were 7 ms shorter with initial fixation on this position than with initial fixation on the 10-cm position (392 vs. 399 ms), $t(13) = 3.43$, $p = .004$. Thus, MTs were significantly shorter when the target position was foveated before onset of the reach.

Endpoint variability. The ANOVA on the standard deviation of the signed endpoint error showed a main effect of target distance, $F(1, 13) = 79.9$, $p < .001$. The variability was 0.38 and 0.45 cm for close and far targets, respectively. The interaction between target distance and initial gaze position was not signifi-

Figure 4. Results of Experiment 2. Movement time, reaction time, and peak velocity are shown in separate rows from top to bottom, respectively. The four fixation conditions (initial fixation on 0, 10, 14.5, and 19 cm) are shown in columns. Error bars represent the between-subject standard error.

cant, $p = .141$. Moreover, similar to the MT analysis, we examined whether foveation affected endpoint variability. This was not the case: Endpoint variability for the 10-cm target position was the same whether it was initially looked at or whether the 19-cm position was initially looked at (0.39 vs. 0.38), $p = .506$. Similarly, there was no difference for the 19-cm target position when the initial gaze was at this position or at 10 cm (0.44 vs. 0.42), $p = .272$.

Manual peak velocity. As shown in the bottom row of Figure 4, peak velocity was larger for far than for close targets (83 vs. 52.7 cm/s, respectively), $F(1, 13) = 1022.76$, $p < .001$. There was an interaction between gaze position and target distance, $F(3, 39) = 9.41$, $p < .001$, showing that the difference between far and close target positions increased when gaze was moved to the far target position. The differences between close and far target positions are plotted in Figure 5D. The pattern mirrors the MT data, suggesting that differences in movement dynamics cause the modulation in MT.

Manual reaction time. As can be seen in the middle row of Figure 4, manual RTs were shortest with initial gaze on the start position (278 ms) and longer with initial gaze on the 10-, 14.5-, and 19-cm positions (312, 315, and 326 ms, respectively), $F(3, 39) = 7.98$, $p < .001$. The interaction of initial gaze position and target distance, $F(3, 39) = 4.81$, $p = .006$, showed that when participants fixated at 10 cm, RTs were longer for targets at 10 cm than for targets at 19 cm (325 vs. 301 ms), $t(13) = 4.2$, $p = .001$, whereas no substantial RT difference occurred for the other fixation conditions (smaller than 10 ms, $ps > .268$, see Figure 4, middle row).

Saccadic reaction time. When participants were looking at the position of the reach target (i.e., initial gaze at 10 cm with 10-cm target distance, or initial gaze at 19 cm with 19-cm target distance), there were only very few refixations and no saccadic RTs were calculated. Therefore, we first compared the condition with initial gaze on the start to the condition with initial gaze at 14.5 cm, which provide data for both target distances because the target was not fixated prior to the reaching movement. Saccadic RTs were longer when observers initially looked at the start position than when they initially looked at the 14.5-cm position (201 vs. 162 ms), $F(1, 13) = 19.23$, $p < .001$. Further, saccades to the 19-cm target were slower than saccades toward the 10-cm position (189 vs. 174 ms), $F(1, 13) = 34.79$, $p < .001$.

In addition, we compared saccadic RTs when observers were initially fixating the start position to saccades with comparable amplitude (about 9–10 cm) when observers were initially looking at either the 10- or 19-cm positions. Saccades from the start location to the 10-cm target were initiated later than saccades from the 10-cm position to the 19-cm position (194 vs. 167 ms), $t(13) = 3.13$, $p = .008$, or saccades from the 19-cm position to the 10-cm position (194 vs. 159 ms), $t(13) = 4.19$, $p = .001$. These results suggest that when gaze was directed at the start position of the hand (fixate-0-cm), initiation of the eye movement was tied to the execution of the hand movement, which lengthened saccadic RTs. With gaze directed at distant locations from the hand, the coupling was weaker and saccades were initiated earlier.

Interval between saccadic and manual reaction times. Only the fixate-0-cm and the fixate-14.5-cm conditions were analyzed because saccadic RTs were not available for the foveated target in the fixate-10-cm and fixate-19-cm conditions. Subjects

moved the eyes before they moved the hand in 95% of the trials, and this tendency was more pronounced with initial fixation on the 14.5-cm position than with initial fixation on the start position (98% vs. 92%), $t(13) = 2.29$, $p = .039$. The eye movement preceded the hand movement by a greater interval with initial fixation on the 14.5-cm location than with initial fixation on the start location (150 vs. 75 ms), $t(13) = 4.52$, $p = .001$.

Temporal coupling between eye and hand movement. The correlation between saccadic and manual latency was positive and significant ($ps < .019$) in 11 out of 14 observers when the start location was initially fixated (range $-.07$ to .84), confirming close eye-hand coupling in this condition. The mean correlation in this condition was .45 and significantly different from zero, $t(13) = 5.32$, $p < .001$. When the 10-, 14.5-, or 19-cm locations were fixated, the correlations were weaker both at the group and at the individual level. For the fixate-10-cm and fixate-19-cm conditions, only the nonfoveated target position was analyzed. The mean correlations were .09, .12, and .17 for the fixate 10-, 14.5-, and 19-cm conditions, respectively. Correlations across subjects were significantly different from zero in the fixate 14.5-cm, $t(13) = 2.31$, $p = .038$, and fixate 19-cm conditions, $t(13) = 2.17$, $p = .049$. Note that after Bonferroni correction for post hoc testing, the latter t tests would no longer be significant (at critical $p = .05/4 = .0125$). Also, only 4 and 3 observers in the fixate-14.5-cm and fixate 19-cm conditions, respectively, showed significant correlations at the individual level ($ps < .022$). Overall, correlations were significantly smaller when the starting position of the hand was not fixated at the beginning of a trial, $ts(13) > 3.21$, $ps < .007$.

Discussion

We replicated the main findings of Experiment 1. With initial gaze directed at the center of the range of target positions (fixation at 14.5 cm), the increase in MT for farther targets was smaller than with initial gaze directed at the start position. Accordingly, the difference in (peak) velocity was larger with initial gaze on the 14.5-cm position than with initial gaze on the start position. Endpoint variability increased with target distance, but was again not modulated by initial gaze position. As in Experiment 1, this change in the slope of the MT-distance function was associated with a temporal de-coupling of eye and hand movements that allowed for longer inspection times and faster reaching movements.

We also observed modulations of the MT-distance function for initial gaze positions in the range of target positions (fixation at 10, 14.5, and 19 cm). Figure 5B shows that the difference in MT decreased as initial gaze was moved to the right. That is, when the 10-cm position was looked at before target appearance, the difference in MT between close and far targets was larger than when the 19-cm position was looked at (58 vs. 34 ms, respectively). Larger differences of peak velocity accounted for the smaller differences in MT (see Figure 5D). Importantly, we also confirmed that MTs to targets appearing at already foveated positions were significantly shorter than MTs to targets appearing at nonfoveated positions, without affecting endpoint variability.

General Discussion

Our study provided three novel, interrelated contributions that advance our understanding of how eye and hand movement sys-

tems work together during reaching toward targets in space. First, initial eye position modulated the temporal synergies between eyes and hand. Second, initial eye position modulated the function relating MT to target distance. Third, reaching was faster toward target locations that were already foveated when the target appeared than to initially nonfoveated targets. We discuss these findings and their theoretical implications in more detail below.

Temporal Eye-Hand Coordination

The temporal coordination of eye and hand movements in goal-directed behavior has been investigated extensively in motor neuroscience. Weak, modest, and strong correlations between saccadic and manual RTs have been documented (for a review see: Bekkering & Sailer, 2002), but it seems fair to state that the majority of the studies reported a modest to strong correlation varying between .50 and .70 (e.g., Bekkering et al., 1995; Binsted & Elliott, 1999; Prablanc et al., 1979; Rand & Stelmach, 2010). Interestingly, all of these studies required participants to align the eyes and hand at the same start position. This procedure is identical to the present fixate-start condition, which also showed a significant correlation between eye and hand movement onset (0.61 in Experiment 1; 0.45 in Experiment 2). This strong temporal coupling when eyes and hand share start and finish locations is usually interpreted as reflecting a common control mechanism that links eye and hand systems (e.g., Soechting, Engel, & Flanders, 2001).

In the fixate-start condition, the target appears on the peripheral retina, which has a poor spatial resolution. Hence, the hand movement is planned and executed on the basis of relatively coarse target position information provided by the peripheral retina. However, once the much faster saccade brings the fovea at or near the target location, an updated sample with more accurate spatial target information becomes available, allowing precise online adjustment of the hand movement. Thus, in the fixate-start condition, a relatively slow hand movement is generated to allow sufficient time to amend the movement en route to the target based on high resolution (foveal) target location information (e.g., Prablanc et al., 1986; Vercher, Magenes, Prablanc, & Gauthier, 1994).

In the fixate-center condition, the targets fall on average much closer to the fovea, allowing for a speedier initiation of the saccadic eye movement toward the target. In this condition, however, motor metrics for eye and hand movements are different, which hampers a close cooperation between the two effector systems. Indeed, in the fixate-center condition of Experiment 1 and the fixate 10-, 14.5-, and 19-cm conditions of Experiment 2, saccadic and manual RTs were poorly correlated and separated by a relatively large time interval, suggesting independent control. Furthermore, in these conditions, participants generated faster hand movements with greater peak velocities, reflecting a stronger reliance on feed-forward control.

Our conclusion that initial gaze position affects not only the temporal interplay between eyes and hand but also how the hand movement is planned and executed accords with recent cognitive and computational models of skilled limb control that posit a great degree of flexibility in visuomotor control strategies depending on task demands and movement types (e.g., Diedrichsen, Shadmehr, & Ivry, 2010; Elliott, Hansen, Grierson, Lyons, Bennett, & Hayes, 2010; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; Todorov & Jordan, 2002; Trommershäuser, Maloney, & Landy, 2008).

According to optimal feedback control theory, motor coordination does not so much rely on structural, rigid neural constraints, but rather is based on a flexible motor control strategy that incorporates tasks requirements and environmental details to optimize performance (e.g., Diedrichsen et al., 2010; Liu & Todorov, 2007; Shadmehr, Smith, & Krakauer, 2010; Todorov & Jordan, 2002). In this view, the motor control strategy contains both open-loop and closed-loop components, with no conceptual difference between feed-forward and feedback control; the control policy governs both (Diedrichsen et al., 2010). In other words, feed-forward and feedback control reflect a continuum that depends on the relative contribution of internal prediction and sensory feedback. An internal (forward) model predicts the sensory consequences of the motor commands, which are combined with actual sensory feedback information (e.g., Desmurget & Grafton, 2000). Furthermore, a weight is applied to each stream of information depending on its reliability. Hence, motor action depends on a continuous, weighted combination of internal predictions and sensory observations, with a higher weight for the more reliable source of information (e.g., Izawa & Shadmehr, 2008).

According to this theoretical framework, the faster hand movements in the eyes-at-center condition may reflect a greater confidence in the feedforward component, which is driven by an accurate initial registration of the target's location and allows for stronger motor signals without compromising endpoint precision. Conversely, the slower hand movements in the eyes-at-start condition may reflect a greater reliance on the feedback component, which may be prompted by the relative coarseness of the initial target's registration. Similarly, a cognitive model of motor control developed by Elliott et al. (2010) underscores the flexibility and sophistication of visuomotor control that tunes and refines the relative contributions of feed-forward and feedback control processes depending on tasks constraints, including advance knowledge about the sensory information available for planning and online control. These recent models seem more appropriate for understanding hand movements to targets appearing in uncertain locations than computational models that are purely feedforward in nature, such as the minimum variance model (Harris & Wolpert, 1998) and the minimum torque-change model (Uno, Kawato, & Suzuki, 1989).

Together, our findings reveal the operation of a flexible, overarching neural control system that tailors the degree of cooperation between eye and hand movement systems depending on where the eyes look at target onset. This conclusion is consistent with recent neurophysiological evidence showing that neurons (in the dorsal premotor cortex) directly encode the relative position of gaze, hand, and target (Pesaran, Nelson, & Andersen, 2006). Relative position codes are evidence of cross-coupling between oculomotor and manual representations, allowing direct visual-motor transformations between gaze- and hand-centered vectors (Buneo & Andersen, 2006), which makes them extremely useful for coordinating eye and hand movements (Pesaran, Nelson, & Andersen, 2010). Our conclusion is also consistent with Bekkering and Sailer's (2002) review, who contended that the organization of eyehand coordination is inherently flexible and task-dependent. It also agrees with work by Land, Mennie, and Rusted (1999), who demonstrated a strong flexibility of eye-hand latencies and coordination in activities of daily living. According to Prado, Clavagnier, Otzenberger, Scheiber, and Perenin (2005), this flexibility is

mediated by distinct areas in the cortex (medial occipito-parietal junction and dorsal premotor cortex), which play crucial roles in decoupling eye and hand movements. The present findings corroborate and extend these reports by demonstrating the critical impact of gaze position at target onset in determining how eye and hand movement systems cooperate during reaching toward a target.

Foveated Targets

Both Experiments 1 and 2 showed movement time advantages for targets appearing at locations, which were already fixated before the target appeared (Experiment 1: initial fixation on 14.5 cm; Experiment 2: initial fixation on 10 cm and 19 cm). This phenomenon goes beyond the well-known finding that reaching is more accurate to targets in foveal vision than to targets in peripheral vision, that is, when foveation of the target is not permitted (e.g., Abrams et al., 1990; Neggers & Bekkering, 1999).

Researchers have identified several factors that may contribute to this latter advantage. First, the better spatial resolution of the central retina improves the accuracy of target location information, which may facilitate both initial planning and later online modification of the hand movement (e.g., Vercher et al., 1994). Second, fixating the target position provides extraretinal information about eye position, which also may facilitate the planning and execution of hand movements (e.g., Soechting et al., 2001). Third, foveating the target location aligns gaze with a future contact location and contact event, allowing the sensorimotor system to establish and maintain correlations between retinal, extraretinal and other sensory signals, including those provided by tactile receptors at target contact (e.g., Johansson, Westling, Backstrom, & Flanagan, 2001). Fourth, reaching in peripheral vision and reaching in central vision are mediated by distinct cortical systems in the parietal cortex (e.g., Clavagnier, Prado, Kennedy, & Perenin, 2007).

It is relevant to note, however, that in the present study eye movements to the targets were always permitted (albeit from different start positions), so we can assume that most, if not all, targets were foveally "captured" prior to the hand movement. This removes, or at least reduces, the facilitative impact of the above mentioned factors as determinants of the movement time advantage toward our "already foveated targets." The crucial factor then appears to be that no concurrent eye movement was needed, as we observed very few, if any, saccades in these conditions. Thus, the movement time advantage of the hand response to "already foveated targets" may reflect an overhead or dual-task cost for coordinating eye and hand movements toward nonfoveated targets. A similar dual-task cost has been demonstrated for saccadic RTs (e.g., Bekkering et al., 1995).

Remapping

Finally, our paradigm bears some resemblance to studies on remapping of visual space (see for reviews: Crawford, Henriques, & Medendorp, 2011; Medendorp, 2011; Thompson & Henriques, 2011). In a typical remapping study, a reach target is presented before the fixation location changes. The question is whether the change of fixation location will influence the reach to the target compared to stationary eyes. If the position of the target were coded in head-centered coordinates, there would be no effect of the intervening change in fixation location. If, however, the current gaze position affected the remembered target location, this would be evidence for gaze-dependent coding. Often, effects of the current gaze position on the spatial errors of the reach are reported. Similar to studies on remapping, we manipulated gaze position before a reaching moving was initiated. Unlike studies on remapping, however, the task was not performed in darkness and the target was visible during the reach. Thus, it comes as no surprise that we did not find large effects in spatial parameters of the reach (i.e., endpoint precision), but rather in temporal parameters. Nonetheless, we cannot exclude that changes in reference frames may have contributed to our results. In the fixate-start condition, the gaze-centered reference frame was aligned with the hand at target onset. The subsequent saccade eliminated the alignment and often engendered larger changes in reference frame than when gaze was already in the vicinity of the target. Smaller perturbations of the gaze-centered reference frame may therefore also contribute to the faster movements we observed in the fixate-center condition.

Conclusion

Our results demonstrate fundamentally different eye-hand control strategies during goal-directed reaching depending on where the eyes look at target onset. When the eyes and hand are aligned at the same start position and the target appears in peripheral vision, eyes and hand start to move almost simultaneously toward the target location, revealing a close cooperation between the two effector systems. However, when eyes and hand start from independent start locations and the target appears in central vision, participants switch to a different control strategy, characterized by accelerated eye onsets, delayed hand onsets, and longer foveal inspection times of the target. In this situation, target-directed hand movements show greater peak velocities and shorter MTs, reflecting a stronger reliance on feed-forward control. Consistent with recent computational models, these findings emphasize the flexibility with which the brain can weigh predictive and reactive control mechanisms contingent on the available sensory information. Our empirical and theoretical contributions link largely separate fields of study (eye-hand coordination and reaching), thereby providing a more integrated, deeper understanding of the flexibility and sophistication of eye-hand coordination and how it affects goal-directed reaching.

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