RESEARCH ARTICLE

Comparing Online Adjustments to Distance and Direction in Fast Pointing Movements

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ABSTRACT. It has been suggested that movements are planned in terms of direction and distance. If so, online adjustments to changes in the direction and distance of the movements may also differ. The authors therefore investigated whether fast online movement adjustments are the same for perturbations of the direction and of the distance. While subjects made fast pointing movements, the authors perturbed either target direction or distance or both shortly after movement initiation. Both kinds of perturbations resulted in accurate online adjustments. The latency and intensity of corrections for distance and direction perturbations were quite similar. This suggests that there might be one mechanism controlling both distance and direction perturbations.

Keywords: latency, online control, perturbation, visuomotor control

hen writing an article, moving a finger to a key on the keyboard is a (preferably) frequently occurring event. Rosenbaum (1980) argued that before such a movement is executed, different parameters need to be specified in series: (1) the arm that will be moved, (2) the direction in which the finger has to move, and (3) the distance that the finger has to cover to land on a key is needed. Gordon, Ghilardi, and Ghez (1994) suggested that movements are planned in terms of direction and distance, and this hypothesis is supported by experimental evidence (Ghez et al., 1997; Krakauer, Pine, Ghilardi, & Ghez, 2000). In the extraordinary situation that while the finger approaches a key and the individual is looking at the keyboard, the individual accidentally pushes the keyboard to the side or further away, it is very likely that he or she will adjust the movement to end on the correct key. Fast movement corrections can be made if the target of a movement changes its position during the movement, both for changes that affect movement distance and movement direction (Gielen, van den Heuvel, & Denier van der Gon, 1984; Goodale, Pélisson, & Prablanc, 1986; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc & Martin, 1992; Soechting & Lacquaniti, 1983). However, some authors have argued that the online control may be different for distance than for direction. Based on studies in which vision of the hand was occluded either early or late during a movement, Paillard (1996) concluded that direction is controlled early during the movement, while the distance is only controlled during the last phase of the movement. To determine whether online movement adjustments are controlled in terms of distance and direction, we compared the spatial and temporal aspects of corrections to perturbations of movement distance and direction.

Spatial Aspects

We found hints in the literature that the endpoint accuracy, reflected by a systematic error in end position, is similar after fast corrections to perturbations of target distance and direction. When the target distance was perturbed around the time of movement initiation, Sarlegna et al. (2003) reported an incomplete correction for targets jumping closer: subjects corrected for about 62% of the target jump. Similarly, when the target direction was perturbed around the time of movement initiation, studies also report incomplete online corrections: subjects corrected for about 87% (Blouin, Bridgeman, Teasdale, Bard, & Fleury, 1995) or about 75% (Turrell, Bard, Fleury, Teasdale, & Martin, 1998) of the perturbations. Other studies did not find a difference between the endpoint errors for perturbed and unperturbed targets. Complete adjustments to the perturbations have also been reported for both perturbations of distance (Goodale et al., 1986; Hansen & Elliott, 2009; Komilis, Pélisson, & Prablanc, 1993; Pélisson et al., 1986; Sarlegna et al., 2003) and of direction (Liu & Todorov, 2007; Oostwoud Wijdenes, Brenner, & Smeets, 2011). Although the range of reported behavior is the same for both types of perturbations, we obviously cannot draw a definitive conclusion from this indirect comparison of results.

Temporal Aspects

When we look at reported movement durations we see that perturbations of direction and distance do not have the same effect. The duration of movements to targets that jumped further away is longer than that to targets that jumped closer by (Goodale et al., 1986; Heath, Hodges, Chua, & Elliott, 1998; Komilis et al., 1993; Pélisson et al., 1986; Sarlegna et al., 2003). Although Goodale et al. found similar movement times for movements to targets jumping further away and movements to unperturbed targets at the same position, other studies found that movement times were longer for both types of distance perturbations (positive and negative) than for unperturbed targets at the same position (Hansen & Elliott, 2009; Heath et al., 1998; Komilis et al., 1993). For direction perturbations, there was no difference in movement time between movements to targets that were perturbed in a clockwise direction and movements to targets

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that were perturbed in a counterclockwise direction (Liu & Todorov, 2007; Turrell et al., 1998). Other studies found no difference in movement time between movements to targets that were perturbed and movements to unperturbed targets (Blouin et al., 1995; Oostwoud Wijdenes et al., 2011). Although the effects of perturbations of distance and direction on movement duration were not compared directly, it seems that perturbations of distance affect movement duration, while perturbations of direction do not affect movement duration.

Another temporal parameter is the latency of the corrections. The fastest reported response latencies in target jump experiments for direction perturbations are about 100 ms (Brenner & Smeets, 1997; Day & Brown, 2001; Gritsenko, Yakovenko, & Kalaska, 2009; Oostwoud Wijdenes et al., 2011; Prablanc & Martin, 1992; van Sonderen & Denier van der Gon, 1991; Veerman, Brenner, & Smeets, 2008). It is more difficult to determine the response latency for distance perturbations than for direction perturbations. As movement speed is higher in the direction between the start position and the target than perpendicular to this direction, relatively small differences in velocity profiles between trials mask corrections of movement distance.

Studies that determined the response latency to distance perturbations by means of EMG measurements of the biceps and triceps muscles report latencies of about 200 ms (Fautrelle, Barbieri, Ballay, & Bonnetblanc, 2011; Mutha, Boulinguez, & Sainburg, 2008), although latencies of 125 ms have been reported when muscles activate more intensely and longer to reach the new target (Gielen et al., 1984). Sarlegna et al. (2003) determined the response latencies to distance perturbations by means of statistical comparisons of the movement amplitudes in different conditions and report latencies of 320 ms. Given the large range of latencies reported in these studies, it is not really possible to directly compare response latencies to perturbations of target distance and direction.

Visual Perturbation of the Hand

Online corrections are not only observed in response to a target perturbation, but they can also be induced by a perturbation of the visual representation of the hand. Saunders and Knill (2005) and Sarlegna and Blouin (2010) perturbed the distance and direction of the visual representation of the hand with respect to its position along its path to a target to examine whether the resulting corrections were different. They both found similarly incomplete corrections for distance and direction perturbations, although the percentages of correction differed between the studies, 75% for Saunders and Knill and only 14-16% for Sarlegna and Blouin. Sarlegna and Blouin found longer movement durations when targets jumped further away and shorter durations when targets jumped closer by, while the movement duration was shorter when the direction changed than when the direction did not change. Saunders and Knill found a shorter latency for direction perturbations than for distance perturbations. However, they conclude that both distance and direction are controlled continuously and that the differences in latency are due to a higher resolution for detecting errors in direction than in distance. It is unknown whether findings for perturbations of the visual representation of the hand generalize to target perturbations.

Aim

Although the percentage of correction for target jumps during an ongoing movement seems to be similar for perturbations of direction and distance, the different effects on movement time suggest that the underlying mechanisms may differ. In this study we tried to examine more directly to what extent movement adjustments differ between these two kinds of target perturbation. During large, fast pointing movements we perturbed either the distance or the direction of the target position, or both, and measured the resulting movement corrections. In theory, subjects could use the same strategy to adjust for both kinds of perturbations. They could adjust the direction or speed of their movement in response to the perturbation in such a way that the new target is reached accurately and with the same movement time, as we previously observed for corrections of direction (Oostwoud Wijdenes et al., 2011).

Method

Subjects

Fifteen subjects (5 men) age 23–29 years old participated in the study. All subjects were right-handed, had normal or corrected-to-normal vision, and gave their informed consent. This study is part of a program that has been approved by the ethics committee of the Faculty of Human Movement Sciences.

Experimental Setup

We used the same experimental setup as in Oostwoud Wijdenes et al. (2011). In this setup a white background and colored targets were projected (InFocus DepthQ Projector, Portland, OR; resolution: 1024×768 pixels; screen refresh rate: 100 Hz) onto a 120×90 cm back-projection screen (Techplex 150, Herlev, Denmark, acrylic rear projection screen; tilted backward by 30°). Subjects stood in front of the screen. The position of a marker that was attached to the left side of the tip of their right index finger was registered by an Optotrak 3020 position sensor (Waterloo, Ontario, Canada; 500 Hz) that was located to the left of the screen. The coordinate system of the Optotrak was aligned with the screen in such a way that the positive horizontal axis pointed to the right on the screen, the positive vertical axis pointed upward along the screen and the z-axis was the distance from the screen.

The stimulus presentation and the Optotrak system were controlled in Matlab (The MathWorks, Natick, MA) with the Psychophysics Toolbox (Brainard, 1997) and the

Optotrak Toolbox (Franz, 2004). The presentation of the stimuli on the screen and the Optotrak recordings were synchronized by means of a photodiode and an Optotrak marker attached to the screen. When the diode registered a light in the upper left corner (presented together with the target), a custom-build electronic circuit deactivated the Optotrak marker on the screen. In this way, we could directly measure the timing of the stimuli in synchrony with the movements. The top 10 cm of the screen was covered to ensure that subjects were not distracted by the outline of the photodiode in the left corner.

Experimental Design

All trials had the same starting position (pink dot with radius of 1.5 cm) located 47.4 cm to the right of the screen center. All trials also had the same initial target position (pink dot with radius of 1 cm) located 43.3 cm to the left of the screen center (Figure 1). The initial distance to the target in our setup (90.7 cm) is larger than normally used. The large amplitude ensured that there was enough time to correct completely in response to the target perturbations while subjects were moving very fast. The large amplitude also ensured that the total distance to the target only increased by 1 mm when the direction was perturbed. In one out of nine trials, the target remained at its initial position. In the other eight trials, the target was shifted to a new location as soon as possible after movement onset, triggered on-line by a finger displacement of 0.1 mm in the direction of the target. Thus the percentage of perturbed trials was very high: 89%. As a result of this, subjects probably were very well prepared to correct their movements.

Offline analyses showed that the target appeared at its new position about 25 ms after movement initiation. The position at which the target appeared after the perturbation had a horizontal (left, center, or right) and a vertical component (up, middle, or down), whereby the center and middle positions

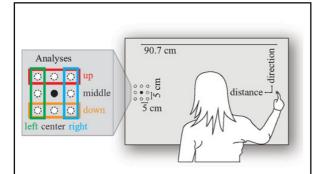


FIGURE 1. Schematic presentation of the setup. The inset explains how the final target positions are grouped for the analyses. The initial target appeared at the middle, center position. In perturbation trials the target jumped to one of the other positions. (Color figure available online).

are the same as before the perturbation. Each type of trial was repeated 20 times resulting in 180 trials. Trial order was randomized within blocks of nine different trials.

Procedure

Subjects made pointing movements with their right index finger from right to left and were instructed to move to the target as quickly and as accurately as possible. There were no instructions regarding head orientation or gaze direction. However, all subjects were already looking at the left side of the screen by the time the target appeared. The target appeared 2.5–3.5 s after subjects placed their finger at the starting position. A beep occurred about 23 ms before the target appeared. Movements were not restricted to the screen surface.

Subjects received 20 practice trials. Throughout the experiment, subjects received feedback about their performance on each trial. A hit was rewarded with a target explosion in one of nine colors (ranging from red for movements with a sum of reaction time and movement time of 750 ms, to green for movements with a sum of reaction time and movement time of 450 ms or less) and a number of points that was larger the faster the trial was completed (the slowest successful movements gave 12 points, the fastest 22 points). A miss was penalized with the target turning red and no points being awarded.

Data Analysis

The acceleration in both horizontal and vertical direction was determined by numerical double differentiation of the positions obtained with the Optotrak system and low-pass filtering of these time series with a second-order recursive, bidirectional Butterworth filter at 50 Hz. Movement initiation was defined as the last moment before the first peak in the speed (measured in three-dimensional space) at which the speed was lower than 0.02 m/s.

Trials were rejected if the marker did not remain visible, if movement initiation was too early (before the beep), or if the target jumped before subjects initiated their movement (i.e., a false alarm of our online movement detection algorithm). We employed these strict criteria of trial exclusion to ensure that the target jumped at about the same time with respect to the movement in all included trials. If more than 30% of a subject's trials were rejected, we excluded this subject from further analysis.

Because we expect the perturbations to influence the speed profile near the end of the movement, determining endpoints by using a fixed velocity threshold could bias the results. Therefore, the multiple sources of information method of Schot, Brenner, and Smeets (2010) was applied to determine the end of the movement. The horizontal position, the speed, and the elapsed time were converted into probabilities of each point in time being the end of the movement. For the horizontal position a binary function was constructed, whereby the probability of being the end position was zero if the position was outside a range that extends for 10 cm to either side of the

initial target and 1 if the position was within this range. For the speed, the likelihood was 0 at maximum trial speed and 1 when the speed was zero, and scaled linearly for intermediate speeds. The probability distribution for the elapsed time was a linearly decreasing probability starting with a value of 1 at the target jump, and decreasing to 0.9 over 600 ms. This distribution ensured that we took the first moment in time after the hand stopped if subjects maintained their end position. Multiplication of the three distributions resulted in one overall probability distribution. We considered the time of the peak of this distribution to be the end of the movement. The movement time was defined as the difference in time between movement initiation and movement end. Travelled path was computed as the sum of the measured displacements between successive position measurements from movement initiation to movement end.

As the Optotrak marker was on the side of the finger, we had to translate its coordinates to match the tip of the finger. To do so, we assumed that the mean end position of the tip of the finger for all movements to the central target coincided with the actual location of this target for each subject. Response accuracy was defined with respect to the target positions by calculating the horizontal and vertical difference between the target position and the movement end position on each trial. For each subject we computed mean errors and standard deviations for each of the nine final target location distributions. For the unperturbed middle, center target the mean errors were zero by definition.

For each subject and each of the nine final target locations we computed the average acceleration profiles for both the horizontal and the vertical movement component. We considered upward along the direction of the screen to be the positive vertical movement component, and rightward along the screen to be the positive horizontal movement component. We did not consider movements perpendicular to the screen. In order to summarize the responses, we created two perpendicular sets of three target groups, one for each component of the perturbation. The profiles of the horizontal movement component were averaged over the three vertical targets at the same horizontal location (see Figure 1). This resulted in three horizontal movement profiles to respectively leftward jumping targets, targets that did not jump in horizontal direction and rightward jumping targets. The same procedure for the vertical movement component resulted in three vertical movement profiles to respectively upward jumping targets, targets that did not jump in vertical direction and downward jumping targets.

To determine the response latency and intensity, we computed the difference in average acceleration between the target groups that jumped with respect to the group that stayed at the middle level. For perturbations of target distance, we computed the difference in horizontal acceleration between target groups that jumped to the right or to the left and the target group that did not jump in horizontal direction.

For perturbations of target direction we computed the difference in vertical acceleration between target groups that

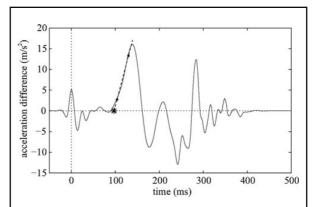


FIGURE 2. Illustration of the extrapolation method. The gray line represents the difference in vertical acceleration between movements to targets that did not change in vertical position (middle) and movements to targets that jumped down. Zero is the moment the target jumped and the black star indicates the determined latency. The acceleration difference around the moment of the target jump is an artifact of motion onset.

jumped up or down and the target group that did not jump in vertical direction. We defined the intensity of the response as the maximum of this difference in acceleration. We searched for the maximum between 100 and 290 ms after the perturbation. To determine the response latency, we applied the method of Oostwoud Wijdenes et al. (2011). We drew a line through the points at which the difference in acceleration reached 20% and 80% of the previously mentioned peak difference in acceleration, and defined response latency as the interval between the moment of the perturbation and the moment that this line crossed a difference value of zero (Figure 2).

Statistics

To determine whether there was a difference between corrections of movement distance and direction in terms of response latency and intensity we performed two one-way repeated measures analyses of variance (ANOVAs), each with the single within-subject factor perturbation (values: left, right, up, and down). To determine whether the final target location influenced the reaction time and the movement time, we performed repeated measures ANOVAs on the average reaction times and movement times. We used a 3×3 design so that the horizontal final target position (left, center, and right) and vertical final target position (up, middle, and down) are treated as separate within-subject factors. To determine whether there was a difference in movement duration when the perturbation was in one dimension (only distance or direction) compared with two dimensions (both distance and direction), we performed a paired samples t test on the average movement times of movements to only distance or direction perturbed targets and movement times of

movements to targets of which both the distance and the direction were perturbed. To determine whether there was a difference in response accuracy, we performed a $2 \times 3 \times 3$ repeated measures ANOVA on the mean errors in horizontal and vertical direction with within-subject factors errorcomponent (horizontal and vertical), horizontal target position (left, center, and right) and vertical target position (up, middle, and down). To determine whether there was a difference in response accuracy when the perturbation was in one dimension (only distance or direction) compared with two dimensions (both distance and direction), we performed paired samples t tests on the average errors in horizontal and vertical direction of movements to only distance or direction perturbed targets and movement times of movements to targets of which both the distance and the direction were perturbed. For all ANOVAs, we applied a Huynh-Feldt correction if the Greenhouse-Geisser epsilon was larger than 0.75, otherwise a Greenhouse-Geisser correction was applied. We evaluated significant main and interaction effects post hoc with paired samples t tests with a Bonferroni correction. The other tested differences were considered significant if p < .05.

Results

Due to an error in file saving, data of one subject was lost. Two more subjects were excluded from further analysis because too many trials were rejected. Of the remaining 2160 trials (12 subjects; 180 trials each) 327 were excluded (15.1%), either because the marker did not remain visible (115 trials), because movement initiation was too early (4 trials), or because the target jumped before movement initiation (208 trials). The large number of trials excluded for the latter reason is probably a consequence of our very low threshold for triggering the target jump (a displacement of 0.1 mm). The excluded trials were distributed over the subjects, ranging from 5% to 25% excluded trials per subject. The excluded trials were also equally distributed over conditions. For one condition of one subject more than half of the trials were excluded (14 of 20 trials). We checked that removing this subject from the analyses does not change the trends in the data, and because it does not we decided to include this subject in the reported analyses.

Response Latency and Intensity

Figure 3 illustrates the average horizontal and vertical movement components to the different targets. On average, the finger's maximum distance perpendicular to the screen during the movement was 11 cm. Figure 4 shows the response latencies and intensities for the different kinds of perturbation. There was only a trend towards a significant effect of perturbation type on the response latency (p = .092). There was a significant main effect of perturbation type on the response intensity, F(2.2, 23.7) = 9.0, p = .001. Paired-samples t tests with Bonferroni correction ($\alpha = .0083$) revealed that the response intensity to downward perturbations

was larger than the response intensity to leftward and upward perturbations.

Movement Time and Reaction Time

The average reaction time was 176 ms and there was no significant effect of final target position on reaction time, as we expected because the target jumped after movement initiation. On average, it took subjects 409 ms to move from the starting position to the final target position (average horizontal distance between start and target was 90.7 cm). In general, movement times increased with the travelled distance (Figure 5). There were significant main effects on the movement time of both the horizontal final target position, F(1.9, 21.0) = 84.2, p < .001, and the vertical final target position, F(2, 22) = 19.0, p < .001. Paired samples t tests with Bonferroni correction ($\alpha = .0167$) revealed that the movement times were significantly different for the three horizontal positions (left: 427 ms; center: 410 ms; right: 396 ms). For the three vertical positions movement durations were significantly shorter after downward (407 ms) than after upward jumps (418 ms). Movements toward the middle targets (407 ms) were significantly faster than ones after upward jumps. There was no significant difference in movement duration between movements perturbed in one dimension (i.e., either distance or direction), and movements perturbed in two dimensions (i.e., distance and direction).

Response Accuracy

As illustrated in Figure 6, most corrections were adequate. The only significant effect on the endpoint errors was a three-way interaction between error component (horizontal or vertical shift), horizontal target position and vertical target position, F(2.2, 24.3) = 5.6, p = .008. Closer examination revealed that movements to targets that jumped to the left and either up or down ended too far to the right and that movements to targets that jumped up and either to the left or to the right ended too high (in all cases by about 3 mm). Although the interaction effect seems to reflect larger endpoint errors for movements to targets that jumped in two dimensions, we did not find significant differences in horizontal or vertical endpoint errors between movements perturbed in one dimension and movements perturbed in two dimensions.

Discussion

We set out to determine the differences between movement adjustments in response to perturbations of target distance and direction. The response latencies for distance and direction perturbations were not significantly different. This might indicate that the same mechanism is controlling distance and direction adjustments. However, the response latencies for corrections to targets that jumped against the movement direction (i.e., to the right) tended to be higher than

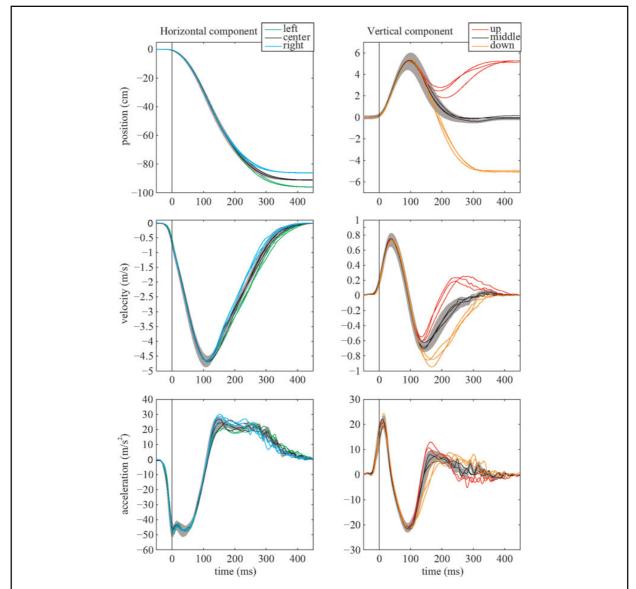


FIGURE 3. Position, velocity and acceleration profiles for each of the nine final target positions averaged over the 12 subjects. The target appeared at the final location at time = 0. The left column shows the horizontal movement component and the right column shows the vertical movement component (targets color-coded accordingly). Please notice that the scales of the two columns differ. The gray area represents the standard error of the mean between subjects for the no-perturbation condition. (Color figure available online).

the response latencies for other corrections. This cannot be explained by the fact that opposing jumps were represented in different visual hemifields, assuming that subjects were fixating the initial central target, because this would predict faster response times with the right hand to information in the right visual hemifield (Marzi, Bisiacchi, & Nicoletti, 1991; Poffenberger, 1912). Possibly the trend towards longer response latencies for corrections to targets that jumped against the movement direction occurs as a result of characteristics of

the effector system, instead of the control mechanism. This idea will be explained in the next paragraph.

We did not record muscle activation patterns in our study, because to identify the adjustment in the EMG the size of the perturbation would have to be much larger (Leonard, Gritsenko, Ouckama, & Stapley, 2011). Thus, we do not know what muscles were active at the moment of the adjustment. Gielen et al. (1984) showed that muscles' response latencies depend on whether they are active at the moment

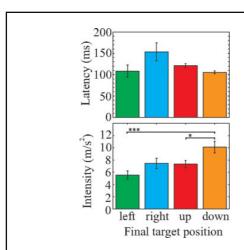


FIGURE 4. Response latency and intensity for target perturbations to the left, right, up, and down. Error bars represent the standard error of the mean between subjects. *p = .030. ***p = .001. (Color figure available online).

of the earliest response to the perturbation. This could lead to differences in the latency of the hand's response for corrections in different directions, because the latency would dependent on the timing of the target jump. When the agonist was active at the moment of the earliest response to the perturbation, Gielen et al. found faster responses when the target jumped further in the direction in which the hand was moving than when the target jumped closer by. When the agonist was not active at the moment of the earliest response to the perturbation they found a faster response when the target jumped closer by than when the target jumped further away. So, if in our study the muscles concerned with increasing the movement path were active at the moment of the earliest response to the perturbation, then this may explain why the latency tends to be shorter in conditions in which the path length was increased than in the condition for which the total path that the finger travelled decreased.

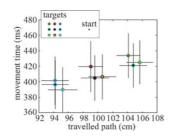


FIGURE 5. Average movement times plotted as a function of average travelled distances for movements to the different final target positions. Error bars represent the averaged standard deviation within subjects. (Color figure available online).

The movement times were shorter to targets that jumped closer by (to the right) than to targets that jumped further away (to the left). However, there was no difference in response intensity between these two conditions. Because movement time and acceleration are inherently coupled for responses in the main movement direction, it is impossible to determine from behavioral data whether subjects primarily adjusted their movement time or the additional acceleration in response to the perturbations.

Experiments on the effect of target distance or direction on movement duration revealed that the total movement duration was affected by distance, but not by direction (Smyrnis, Evdokimidis, Constantinidis, & Kastrinakis, 2000). However, the kinematics of the first peak in the velocity profile were affected by the direction of the target. Experiments on the effect of online changes in target distance or direction discussed in the introduction suggest that the movement duration was affected by distance perturbations, but not by direction perturbations. We did not measure single step movements to the perturbed target positions. As a result, we do not know whether the movement times in the perturbed conditions changed more than the amount of change expected due to the difference in final target position. However, by means of Fitts's law we were able to make predictions for the expected increase and decrease for single-step movements to the distance perturbed target positions (Fitts & Peterson, 1964). Based on the index of difficulty to accurately reach the target, Fitts's law would predict a 5-ms change in movement time for the targets located 5 cm to the left or the right of the initial target. We found a 24-ms increase in movement time for targets jumping away and a 7-ms decrease for targets jumping closer by. Thus the movement time appears to be larger in the presence of online corrections than one would expect for the distance after the correction if the distance increased. This is consistent with the graphical representation in Figure 5 and congruent with the results of Sarlegna et al. (2003).

Movement times were longer when moving to targets jumping up than to targets jumping down, and congruently the intensity of the response to targets jumping down was higher than that to targets jumping up. The longer movement duration for targets that jumped up might be related to the plane in which the perturbations took place. There are reports of similar durations for movements to targets perturbed in opposite directions when subjects made movements away from their body and the direction perturbations were in the transverse plane (Liu & Todorov, 2007; Turrell et al., 1998). In our setup, subjects made right-left movements and the direction perturbations were up and down in the plane of the screen (tilted backwards by 30°). We used this setup before with smaller (2 cm) target jumps, but did not analyze whether the movement times were different between upward and downward corrections in that study (Oostwoud Wijdenes et al., 2011). Additional analyses of the movement times in that experiment showed that movements to upward jumping targets were slightly (8 ms) longer than movements to

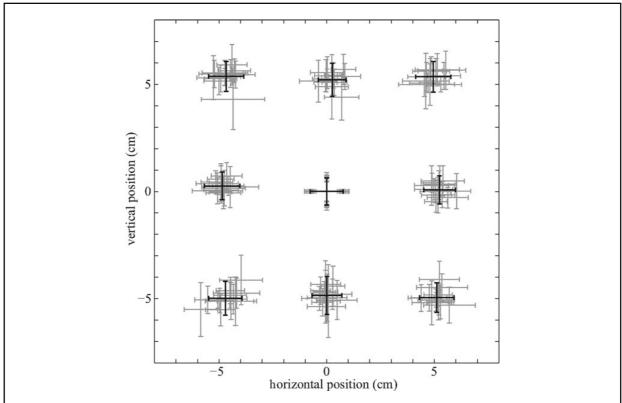


FIGURE 6. Means and standard deviations of the endpoint distributions of all 12 subjects for the nine different final target positions (in gray) and the mean and standard deviation across subjects for each of the target positions (in black).

downward jumping targets. Thus, the effect of jump direction on movement time seems to be a consequence of the plane of movement in our setup.

The shorter movement times for targets that jumped down in our setup is not related to the distance travelled by the finger, because the path to targets that jumped down was slightly longer than the path to targets that jumped up (Figure 5). It may be related to the opposite gravitational effect of our direction perturbations, because movements to downward jumping targets were faster compared to movements to upward jumping targets. The shorter movement durations to targets jumping down could also be related to the muscles involved in the correction. For downward corrections the arm needed to flex, because the target was lower and a bit closer to the body, while for upward corrections more extension was needed, as the target was higher and further away from the body. Possibly movements to the lower targets were faster because in general flexors can produce more force than extensors (Stoll, Huber, Seifert, Michel, & Stucki, 2000).

We did not find a difference in movement time and endpoint accuracy between conditions in which the target was perturbed in one dimension, either distance or direction, and conditions in which both the direction and distance of the target was perturbed. This suggests that adjusting both direction and distance did not result in longer movement times or bigger endpoint errors than adjusting only direction or distance. Because we were unable to determine the response latency for each individual target perturbation, we do not know whether the number of dimensions that had to be adjusted affected the response latency. In our analysis we grouped the responses in two perpendicular sets of three perturbations and compared the positive and negative direction and distance perturbations with the middle and center group. A precise determination of response latency requires more trials than determination of movement time or endpoint. Our main question was whether there are differences between distance and direction adjustments, and the analysis we employed could most reliably answer this question.

Our results are not completely congruent with the results of studies that perturbed the visual representation of the hand. As we did, Saunders and Knill (2005) found that the endpoint errors were of similar size for direction and distance corrections, although they did not find complete corrections. The latter may be explained by the mismatch between visual and proprioceptive information in their experiment. They found that the latency for distance perturbations was longer compared to direction perturbations, while we found only a trend towards longer latencies when the distance to the target

decreased. To determine the latency, they assumed that the same function could explain both positive and negative distance perturbations. Their analysis could not identify different latencies for perturbations in opposite directions within the same dimension. Probably the longer latency for distance perturbations they found was only caused by trials in which the distance between the hand and the target decreased. Sarlegna and Blouin (2010), on the other hand, found an interaction between direction and distance adjustments. When subjects had to stop their movement on the target, the percentage direction correction depended on whether they also had to adjust their movement distance. However, they did not find a similar interaction effect for the movement duration. We did not find an interaction effect of distance and direction on either endpoint corrections or movement duration. Sarlegna and Blouin perturbed the target distance and direction by 5 cm, while the total distance to the target was 40 cm and they found a peak velocity of 2.8 m/s. Our subjects moved about twice as fast, but also over about two times the distance, while the size of the target perturbation was the same: 5 cm. Probably there was not enough time to correct completely in the experiment of Sarlegna and Blouin, as they also found that the percentage of correction increased with movement duration.

A considerable number of trials (15.1%) were removed from the analyses, due to the very strict exclusion criteria we exploited. The criterion of online movement detection was very sensitive, because we wanted the target to jump as fast as possible after movement initiation. In 9.6% of the trials this resulted in false-positive online movement initiation detection and a target jump before the subject actually started moving. We excluded these trials because we are looking for subtle differences between the trajectories and want to make sure the differences we analyze are due to the target jump and not to variability in the timing of movement initiation. Moreover, we cannot detect a response if the hand is not moving. Another 5.3% of the trials were removed because the marker was not visible for short time intervals. We did not interpolate the data because this might interfere with detecting the corrections. Finally, 0.2% of the trials were excluded because subjects actually initiated their movement before the beep, as they were eager to respond very fast.

Obviously, objects do not switch location instantaneously in daily life. Instead, for example, balls move along trajectories. Studies on table tennis and cricket suggest that people are also able to adjust ongoing movements in response to perturbations of ball trajectories with very short latencies (Bootsma & van Wieringen, 1990; McLeod, 1987). However, the findings of Bootsma and van Wieringen (1990) could also be attributed to the dynamics of the effector system instead of to the continuous control of the movement (van Soest et al., 2010). Brenner and Smeets (1997) showed that the latency of responses to target jumps was about the same as the latency to respond to a target that starts moving (110 and 120 ms, respectively). It is unclear whether the same system is controlling responses to target jumps and responses to moving targets.

In conclusion, movement corrections to distance and direction perturbations are initiated with the same latency. Both the movement trajectory and duration were adjusted in response to distance and direction perturbations. The endpoint accuracy was the same for distance and direction perturbations. We did not find interaction effects on movement duration or endpoint accuracy when both distance and direction were adjusted. The results show that adjustments to the control of direction and distance are quite similar. We found no direct evidence that movement direction and distance adjustments are controlled by different mechanisms.

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