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Online Manual Movement Adjustments in Response to Target Position Changes and Apparent Target Motion

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This study set out to determine whether the fastest online hand movement corrections are only responses to changing judgments of the targets' position or whether they are also influenced by the apparent target motion. Introducing a gap between when a target disappears and when it reappears at a new position in a double-step paradigm disrupts the apparent motion, so we examined the influence of such a gap on the intensity of the response. We found that responses to target perturbations with disrupted apparent motion were less vigorous. The response latency was 10 ms shorter when there was a gap, which might be related to the *gap effect* that has previously been described for initiating eye and hand movements.

Keywords: visuomotor control, online control, response latency, gap effect, motion perception

When people aim for a target that disappears and reappears at a different position, they adjust their movement in accordance with the change in position (Soechting & Lacquaniti, 1983). Such a sequential presentation of two targets at different locations is perceived as a single target that moves from the first location to the second (Wertheimer, 1912; Zeeman & Roelofs, 1953). One might expect that the apparent motion is a prerequisite for the adjustment. However, if such a change in target position occurs during a saccade, this change is not perceived (no apparent motion; Bridgeman, Hendry, & Stark, 1975), but movement adjustments to the new target position are observed (Goodale, Pélisson, & Prablanc, 1986; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc & Martin, 1992). Moreover, Gritsenko, Yakovenko, and Kalaska (2009) did not find any effect of the perception of target displacement on response latency. A reason for this might be that motion sensing takes time (e.g., Smeets & Brenner, 1994), and the latency of a response will depend on the fastest input. Thus, the latency of online corrections may only depend on judgments of the new position, independent of judgments of motion.

However, there is some evidence suggesting that online movement adjustments do depend on motion information. In a task involving fast responses to changes in surface slant, van Mierlo, Louw, Smeets, and Brenner (2009) found less vigorous

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adjustments with a longer latency when subjects only perceived the initial and final slants than when they also perceived the transition between the two slants. They argued that the less vigorous adjustment and longer response latency might be caused by the removal of the response to perceived rotation. This effect of motion information may be specific for slant, or even monocularly defined slant, because the effects of removing motion information were not present when the change in slant was exclusively evident in the binocular information.

We investigated whether responses to changes in position are delayed and less vigorous when the apparent motion is disrupted. The vigor of online corrections is determined by the size of the required correction and the time left in which to make the correction (Gritsenko et al., 2009; Oostwoud Wijdenes, Brenner, & Smeets, 2011). Motion signals could provide information about the likely size of the required correction. The percept of apparent motion decreases if the time interval between two target presentations increases beyond about 50–100 ms (Baker & Braddick, 1985; Ekroll, Faul, & Golz, 2008; Georgeson & Harris, 1990; Roudaia, Bennett, Sekuler, & Pilz, 2010). We disrupted low-level apparent motion signals by introducing a 100 ms time gap between two successive target presentations. We assume that if apparent motion contributes to short latency movement adjustments, the response intensity will decrease when apparent motion is disrupted by introducing such a gap.

Method

Subjects

Sixteen right-handed subjects (five female; 18–39 years old) took part in this study after they gave their informed consent. They had normal or corrected to normal vision. This study is part of a program that was approved by the ethics committee of the faculty of Human Movement Sciences.

Experimental Setup

The experimental set-up was the same as we used in a previous study (Oostwoud Wijdenes et al., 2011). Stimuli were projected (InFocus DepthQ Projector; spatial resolution: 1024 × 768 pixels; screen refresh rate: 100 Hz) on a back-projection screen (Techplex 150, acrylic rear projection screen; width of projection: 120 cm; height: 90 cm; tilted backward by 30°). The position of the right fingertip was registered (500 Hz) with a single infrared marker and an Optotrak 3020 position sensor. The Psychophysics Toolbox (Brainard, 1997) and the Optotrak Toolbox (Franz, 2004) for MatLab were used to control the experiment. A small region at the top left of the projection was used to synchronize the Optotrak data with the images on the screen. Images presented there were not visible to the subject but stimulated a photodiode connected to the parallel port of the computer.

Experimental Design

A target appeared at its initial position a random interval (between 500 and 1500 ms) after the finger arrived at the starting position. A beep occurred 23 ms before the target appeared to stimulate short reaction times with a narrow distribution. A narrow distribution of reaction times and a fixed timing of target jumps makes averaging across trials more straightforward. Short reaction times will cause the subjects to start their movement before the direction to the target is completely processed.

There were three different conditions. In the *control condition* the target remained at the initial target position. In the *step condition* the target jumped up or down 200 ms after it appeared. In the *gap condition* the target disappeared 100 ms after it appeared and reappeared at a higher or lower position 100 ms after it disappeared (Figure 1). The starting position was at chest-height on the right side of the screen. There were two different initial target positions, located 72 cm to the left of the starting position and either 1.5 cm higher or lower. The radius of the target was 1.5 cm and the size of the upward or downward jump was 3 cm. Conditions were presented in 15 blocks of 12 trials. Each block consisted of 4 trials of each experimental condition (one upward and one downward displacement for each initial target position for the *step* and *gap* conditions), and 2 trials for each initial target position for the *control* condition. The order of the trials within each block was randomized. The large proportion of trials in which the target was displaced (2/3), and presenting such displacements early during large movements, was expected to allow us to precisely follow the online corrections. We do not expect the response intensity to decrease due to the high proportion of targets that are displaced, since it is relevant to correct for the target displacement.

Procedure

Subjects moved their index finger to the starting position and waited there for the beep and the appearance of the target. They were instructed to move as quickly and as accurately as possible to the target. They were allowed to lift their finger off the screen during the movement. There were no instructions about eye movements. Subjects received feedback after each movement. If they hit the target, it exploded in one of nine colors, indicating how quickly they had moved, and

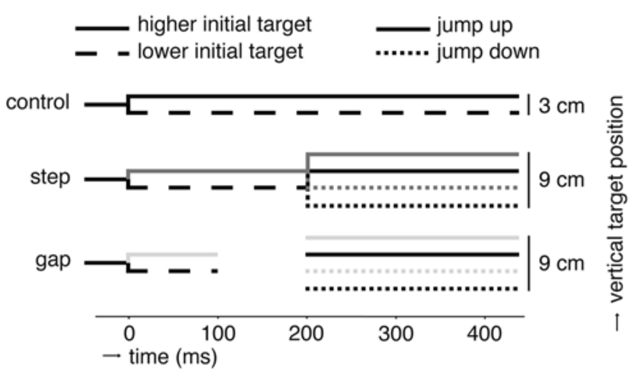

Figure 1 — Schematic representation of the three different conditions. At time = 0 the target not only jumped 1.5 cm up or down as shown but also jumped 72 cm to the left.

they received a number of points related to their movement time. If they missed the target, the target turned red and they did not receive points. Before the experiment, subjects performed 20 practice trials. After 90 trials there was a short break.

Data Analysis

In total there were 2880 trials (16 subjects, 180 trials each). Trials were excluded if the Optotrak marker was not visible throughout the movement (which was the case for 122 trials), if the movement was initiated before the target appeared (42 trials), if the movement was never within 10 cm of the target (4 trials), if the reaction time was larger than 450 ms (2 trials) and if the peak speed was lower than 2 m/s (1 trial). For the remaining 2709 trials, movement initiation was defined as the last moment before the first peak in velocity at which the tangential velocity was smaller than 0.02 m/s. Reaction time was defined as the time between initial target appearance and movement initiation. We used the multiple sources of information method (Schot, Brenner, & Smeets, 2010) to determine movement end. To do so, we multiplied a binary horizontal position probability function that was 1 if the finger was within 6 cm of the target center and 0 otherwise, a continuous speed function that was 1 when the finger's speed was zero and 0 at the maximal speed during that trial, and a linearly decreasing function of elapsed time (1 at target appearance and 0.9 800 ms thereafter) to determine the most likely end of the movement. Movement time was defined as the time between movement initiation and movement end. The correction fraction was defined as the part of the total target displacement that was corrected for, whereby a fraction of 1 indicates complete correction, and a fraction smaller than 1 indicates an undershoot in the direction of the target displacement.

The vertical acceleration was obtained by numerical double differentiation of the Optotrak position data and filtering of these time series with a 2nd order recursive bidirectional Butterworth filter at 50 Hz. Average vertical acceleration profiles (parallel to the slanted screen) were calculated for the different initial and final target positions within each of the conditions. These profiles were then averaged over the two initial target positions. The latencies of the responses to the perturbations were determined for each participant and each condition with the method described in detail in Oostwoud Wijdenes et al. (2011). The latency was based on fitting a line to the increasing difference in vertical acceleration between the averages of trials in which the target jumped up and down. We expressed how vigorous the response was in terms of response intensity: the peak of the difference in vertical acceleration. This variable is influenced by both the size and the duration of the correction.

Whether there was a difference in response latency, intensity, and correction fraction between the step and the gap conditions was tested with paired samples *t* tests across subjects. The effect of the conditions on reaction time and movement time was tested with repeated-measures ANOVAs, with Huynh-Feldt correction if the Greenhouse-Geisser epsilon was larger than 0.75, and Greenhouse-Geisser correction if epsilon was smaller. Main effects were tested post hoc with *t* tests with a Bonferroni correction. The other tested differences were considered significant if $p < .05$. All mentioned differences differed significantly from zero.

Results

Averages of the vertical components of the movements are shown in Figure 2. The left panels show the complete movements. The right panels zoom in on the moment of the adjustments. The average reaction time with respect to the onset of the target was very short (136 ms), irrespective of the condition (Figure 3). This is probably because subjects responded to the tone that was presented 23 ms before the target appeared. The average movement time was significantly shorter for control trials (343 ms) than for step trials (350 ms), but there was no difference between gap trials (348 ms) and control or step trials. Responses to step perturbations resemble responses to perturbations after a gap, but close examination shows that responses in the gap condition are slightly earlier and less intense. This pattern was consistent across subjects. On average, responses in the gap condition were 10 ms earlier than in the step condition ($p = .003$; step: 99 ms, gap: 89 ms) and less intense than in the step condition ($p < .001$; step: 24 m/s^2; gap: 19 m/s^2). The correction fraction of the responses did not differ significantly between step and gap trials. On average, subjects had a correction fraction of 0.95 in step trials and 0.93 in gap trials, thus the corrections were almost complete.

Discussion

Adjustments were quicker but less intense in the gap condition, in which the apparent motion signals were disrupted. The effect on the response intensity is congruent with findings of van Mierlo et al. (2009), who found weaker responses when a change in slant could not be perceived due to a gap. This result raises the possibility that apparent motion normally contributes to adjusting movements at very short latency.

Previous research has shown that the intensity of the response depends on the magnitude of the perturbation and on the time left to make the correction; the intensity is larger for a larger perturbation (Gritsenko et al., 2009; Liu & Todorov, 2007; Veerman, Brenner, & Smeets, 2008) and if there is less time left to make the correction (Oostwoud Wijdenes et al., 2011). The decrease in response latency in the gap condition meant that there was 10 ms more time to make the correction (movement times were similar for the step and gap condition). However, the decrease in response intensity cannot be completely ascribed to an increase in time to correct if we assume that the correction can be described by a minimum jerk trajectory (Flash & Hogan, 1985; Oostwoud Wijdenes et al., 2011). The minimum jerk model predicts a response intensity decrease of 1.25 m/s^2 for a correction that lasts 10 ms longer for movement durations as in our experiment. The increase in time to correct can thus only explain a quarter of the difference of 5 m/s^2 in the average response intensity. Thus, apparent motion might indeed contribute directly to the intensity of the response.

The lower intensity of responses in the gap condition does not necessarily mean that responses in individual trials are less intense, but could also be due to a higher temporal variability of the responses, because we determined the response intensity from the average responses. However, even if this were the case, we would still be able to conclude that removing apparent motion by introducing a gap perturbs the online responses.

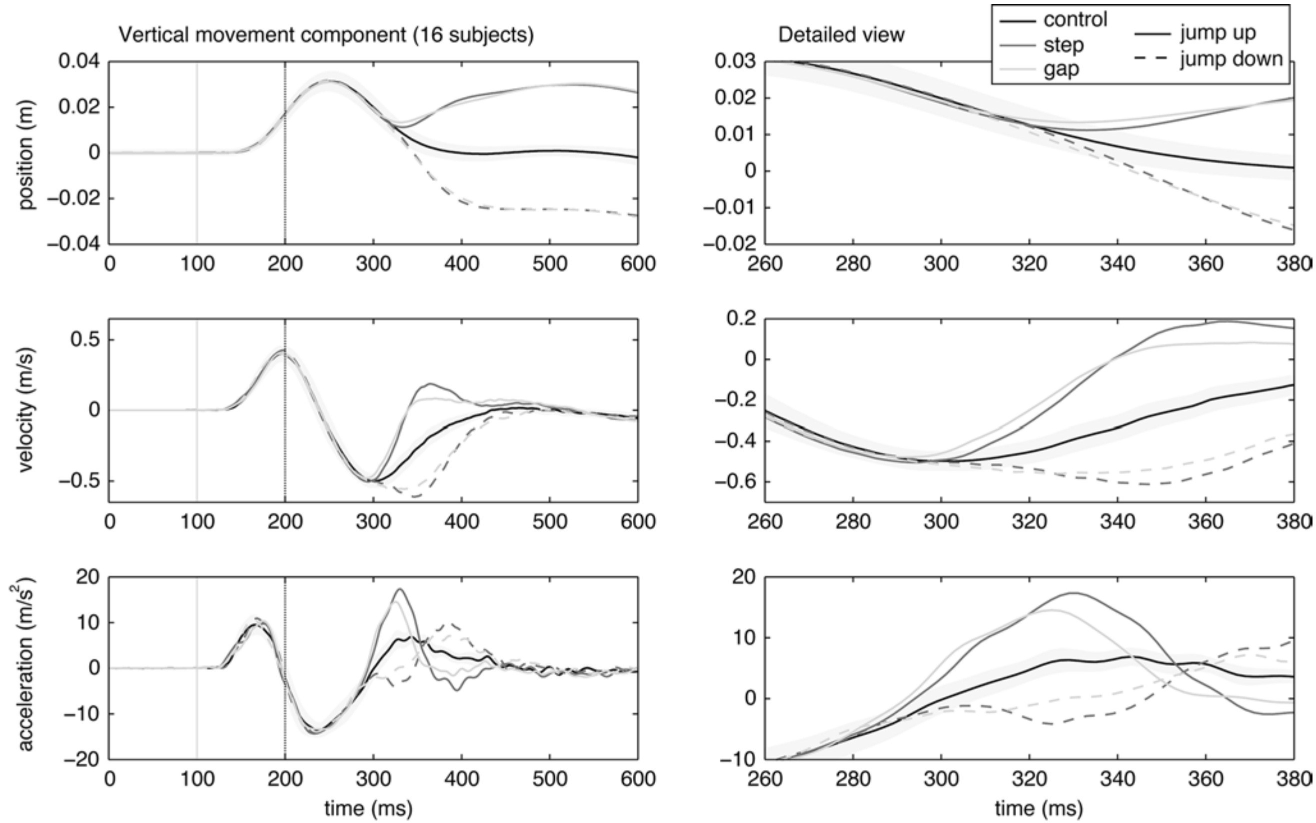

Figure 2 — Mean vertical position, velocity, and acceleration for the three different conditions, averaged over the two initial target positions and all subjects. The vertical solid light gray line indicates the moment the target disappeared in the gap condition. The vertical dotted line indicates the moment the target appeared at the final target position in the step and the gap conditions. The gray area around the curve for the control condition is the standard error when averaging across the subjects' mean values. The right panels give a more detailed view of the response.

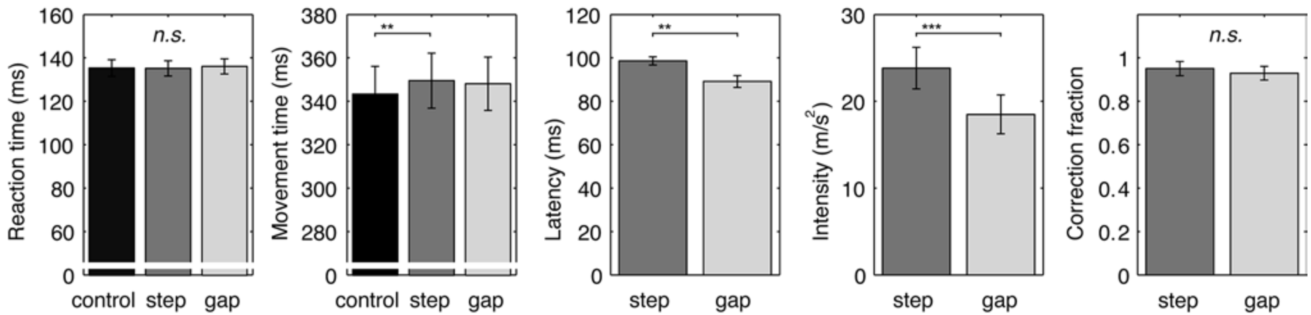

Figure 3 — Mean of the 16 subjects' reaction times, movement times, response latencies, intensities, and correction fractions (with the standard error of the mean). ** $p \leq .005$; *** $p < .001$.

We realize that we do not completely remove all apparent motion by inserting a gap. However, we think that there is no clean way to eliminate the apparent motion when investigating fast responses. Other ways to influence the motion percept are by having the jump occur during the period of saccadic suppression (Bridgeman et al., 1975), by changing the target contrast in synchrony with the jump (Smith & Ledgeway, 2001), or by masking the relevant motion signal through motion in the background (Brenner & Smeets, 2010). A disadvantage of using saccadic suppression to mask the apparent motion is that it is difficult to determine when precisely the new target position becomes available, making it impossible to accurately determine the response latency (Prablanc & Martin, 1992). Veerman et al. (2008) showed that the target's luminance contrast influences the intensity of the response, so varying the contrast to affect apparent motion would also not be a clean manipulation. Using background motion to disrupt motion perception would probably make it more difficult to detect the target, which could lead to longer latencies. Moreover, background motion itself also induces a response (Brenner & Smeets, 1997; Gomi, Abekawa, & Nishida, 2006).

In general, the latencies of responses to changes during the movement were very short. Presumably subjects initiated their movement in response to the auditory warning and specified their movement direction when the target appeared. This, and the high probability of a target jump, probably made subjects prone to adjust their movement. The very short response latencies were even shorter if the apparent motion was disrupted by a gap. Gritsenko et al. (2009) found that the latency of online movement adjustments was not affected by the conscious perception of a target displacement. An important difference between the studies is that Gritsenko et al. (2009) disrupted apparent motion by having the jump occur during the period of saccadic suppression, while we did so by having a gap in time during which no target was presented. We cannot be sure whether the different results are due to the gap rather than to it not being possible to correct precisely for the duration of saccadic suppression.

A gap has previously been found to reduce the latency for initiating eye movements by 38–65 ms, in tasks that take about 260 ms without a gap, and to reduce the latency for initiating hand movements by 15–50 ms, for tasks that take between 215–359 ms to initiate without a gap (Bekkering, Pratt, & Abrams, 1996; Machado-Pinheiro, Gawryszewski, & Ribeiro-do-Valle, 1998; Pratt, Bekkering, Abrams, & Adam, 1999; Saslow, 1967). In those cases one finds faster response initiation to targets appearing some time after the starting position disappears than to targets that appear as soon as the starting position disappears. We here show that if the target position changes during the movement, we find faster online response adjustments when the target disappears sometime before it appears at the new position. Latencies of online response adjustments are faster than and show no correlation with response initiation latencies, and are therefore thought to be controlled by a different mechanism (Veerman et al., 2008). However, both seem to be influenced by a gap in a similar manner.

For eye movements, two components of the stimulus can give rise to faster movement initiation: a warning component that provides information about the timing of the appearance of the target and a fixation-offset component that consists of a release from the present fixation and thereby an increase in response readiness (Dorris & Munoz, 1995; Kingstone & Klein, 1993; Meeter, Van der Stigchel,

& Theeuwes, 2010; Reuter-Lorenz, Oonk, Barnes, & Hughes, 1995). Munoz and Wurtz (1992) showed that in monkeys the superior colliculus is involved in the release of fixation that is necessary for fast eye movements and Werner (1993) showed that the superior colliculus is also involved in goal directed arm movements. Bekkering et al. (1996) combined these findings to argue that the fixation-offset component may not only influence eye movements, but also movements of the hand.

In our setup, a warning component might have contributed to the decrease in response latency. Although the timing of the target appearance at the new position could be anticipated in both the step and the gap condition (it occurred 200 ms after the target appeared at the initial position), the target never reappeared at the initial position after a gap. Thus the presence of a gap could have resulted in a higher response readiness because when the gap appeared the target would always change its position. However, the direction of the target displacement after the gap could not be anticipated; this information was available at the same time as in the step condition. Moreover, Cameron et al. (2013) presented data that indicated that nondirectional information about an upcoming target jump did not affect the response latency. Release from fixation of the hand in the gap condition is unlikely to explain the difference, because in our set-up the hand had already left the starting position when the target appeared at its final position. On the other hand, release from fixation of the eye in the gap condition might facilitate movement adjustments via the superior colliculus (Bekkering et al., 1996).

Boulinguez, Blouin, and Nougier (2001) investigated eye and hand movement adjustments in a similar double-step paradigm with a gap condition, but they found longer latencies for responses in the gap condition. Overall, their latencies were considerably longer for both the step (172 ms) and the gap condition (222 ms). The effect and the size of the latencies they found resemble the data of van Mierlo et al. (2009). Possibly the gap only enhances the fastest online adjustments.

In sum, the vigor of online movement adjustments in a normal double-step paradigm seems to be the result of a response to the new target position and a response to the apparent motion percept. The gap effect might not only increase the response readiness for initiating eye and hand movements, but also decrease the latency of the online control of hand movements.

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