

Target Selection During Bimanual Reaching to Direct Cues Is Unaffected by the Perceptual Similarity of the Targets

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Investigations of bimanual movements have shed considerable insight on the constraints underlying our ability to perform coordinated actions. One prominent limitation is evident when people are required to produce reaching movements in which the two trajectories are of different amplitudes and/or directions. This effect, however, is only obtained when the movements are cued symbolically (e.g., letters indicate target locations); these planning costs are absent when the target locations are directly cued (J. Diedrichsen, E. Hazeltine, S. Kennerley, & R. B. Ivry, 2001). The present experiments test whether the absence of planning costs under the latter condition is due to the perceptual similarity of the direct cues. The results demonstrate that measures of response planning and execution do not depend on the perceptual similarity of the direct cues. Limitations in our ability to perform distinct actions with the two hands appear to reflect interactions related to response selection involving the translation of symbolic cues into their associated movements rather than arise from interactions associated with perception, motor programming, and motor execution.

Keywords: psychomotor performance, perceptual motor coordination, motor skills, coordination, reaction time

In many situations, the two hands operate with relative independence. We can simultaneously pick up different objects, such as keys and a wallet, as we rush out the door to work. The movements might be independently planned and controlled even if designed to accomplish a common immediate goal. For example, when shopping, we can use both hands simultaneously to pick apples from a bin, with each hand following a unique trajectory. In other situations, the gestures of the two hands must be coordinated. If we wish to purchase the entire bin of apples, both hands must be coordinated to lift the heavy object. In some cases, the movements will be very similar, as when we bend and lift the bin. In other cases, the movements can be very different, which would occur if the bin were at an oblique orientation with respect to the body.

Investigations of bimanual coordination over the past three decades have focused on limitations of the motor system. In a

seminal study, Kelso, Southard and Goodman (1979) demonstrated a strong preference for people to synchronize the initiation and termination of the hands when producing bimanual reaching movements, even when the movements of the two hands traverse different distances. This temporal coupling is remarkably robust, providing a powerful constraint on the coordination dynamics of repetitive movements (e.g., Franz, Eliassen, Ivry, & Gazzaniga, 1996; Klapp et al., 1985).

Coupling also exists in the spatial domain. When asked to simultaneously draw a circle with one hand and a line with the other, both hands are apt to produce elliptical trajectories (Franz, Zelaznik, & McCabe, 1991). To account for such findings, Heuer and colleagues (Heuer, 1993; Heuer, Spijkers, Kleinsorge, van der Loo, & Steglich, 1998; Spijkers & Heuer, 1995) proposed that motor programming processes for the two hands are susceptible to transient cross-talk during the specification of movement parameters. Thus, when planning bimanual reaching movements, parameters for the movement of one hand will influence either the planning and/or execution of the movement of the other hand. If the movements are symmetric, the cross-talk can reinforce planning and execution processes. However, if the movements are asymmetric, then the cross-talk can lead to substantial intermanual interference. For example, when attempting to simultaneously draw a line with one hand and a circle with the other hand, the cross-talk will result in pattern distortions of both trajectories (Franz et al., 1991).

A Challenge to Motor-Based Accounts

The hypothesis that constraints on bimanual movements reflect cross-talk associated with motor programming processes has re-

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cently been called into question. Mechsner, Kerzel, Knoblich and Prinz (2001) showed that the preferred patterns of bimanual coordination may be related to the manner in which the consequences of the movements are coded rather than result from constraints intrinsic to the motor system (e.g., preference to synchronize homologous muscles). In particular, they emphasized the stability of bimanual movements that result in perceptually symmetric actions. In one experiment, participants produced oscillating index finger movements. When both hands were oriented in the same direction, the movements were most stable when they involved the coactivation of homologous muscles (e.g., flexion together, extension together). However, when the orientation of one hand was rotated by 180°, the most stable pattern involved the coactivation of nonhomologous muscles (e.g., flexion of one index finger during extension of the other index finger). Hence, for both hand orientations, coordination was most stable when the resulting movements followed a spatially symmetric pattern.

A different line of evidence challenging the motor programming hypothesis comes from studies showing that intermanual cross-talk during reaching movements is strongly influenced by the manner in which the target locations are cued (Diedrichsen et al., 2001; Hazeltine, Diedrichsen, Kennerley, & Ivry, 2003). In these studies, there were two possible target locations for each hand. The critical manipulation involved the manner in which the targets for a particular trial were cued. For symbolic cues, centrally presented symbolic cues (e.g., letters, colors) indicated the target location for each hand. For direct cues, circles appeared at the target locations, directly specifying the endpoint locations for the movements. Compared with conditions in which the movements involved symmetric trajectories (congruent movements), participants were slower to initiate responses involving different directions or amplitudes (incongruent movements) with the symbolic cues, consistent with previous experiments (Spijkers, Heuer, Kleinsorge, & van der Loo, 1997). However, this reaction time (RT) cost was absent under direct cueing conditions; here, RTs were similar for congruent and incongruent movements and, in fact, essentially the same as when only a single reach was required (i.e., unimanual condition).

These results indicate that the costs associated with producing asymmetric reaching movements in the symbolic condition are not associated with motor programming or execution given the assumption that these processes should be similar for the symbolic and direct cueing conditions. Rather, the cross-talk must arise at a different stage of processing. One hypothesis is that response selection demands are greater for symbolically cued incongruent movements (Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003; Hazeltine et al., 2003). By response selection, we refer to central operations in which the stimulus is mapped onto its associated response (Pashler, 1984).

These operations are considered distinct from perceptual processes (McCann & Johnston, 1992; Pashler & Johnston, 1989). Rather, response selection encompasses the retrieval of the appropriate response, or action goal, and the ease with which response selection is completed is affected by a host of factors related to stimulus–response compatibility (Greenwald & Shulman, 1973; Kornblum, Hasbroucq, & Osman, 1990; McCann & Johnston, 1992). Consider a situation in which the letters *S* and *F* are used to indicate whether the movement should be sideways or forward. The translation of the symbolic cues to the appropriate responses

is slower when different cues are used to indicate the responses for the two hands (e.g., *S* and *F*) compared with when the same cue is used to indicate a common direction for the two hands (e.g., *S* and *S*). By the response selection hypothesis, two stimulus–response mapping rules must be retrieved in the incongruent condition, whereas the same mapping can suffice in the congruent condition. In contrast, the translation process is eliminated or minimized with direct cues, thus reducing demands on response selection operations (see Ivry, Diedrichsen, Spencer, Hazeltine, & Semjen, 2004).

An alternative account may be derived by reexamining these findings from the perspective that actions are coded in terms of their perceptual consequences and goals (Hommel, Musseler, Aschersleben, & Prinz, 2001). In the reaching studies of Diedrichsen and colleagues, the contrast between symbolic and direct cues was confounded with stimulus similarity. In symbolic cueing conditions, congruent movements were cued with identical stimuli and incongruent movements with nonidentical cues (e.g., Diedrichsen et al., 2001; Spijkers et al., 1997). In direct cueing conditions, the stimuli—the filling in of the target circles—were the same for the congruent and incongruent conditions. Thus, the lack of an RT difference between these conditions might be due to stimulus similarity. That is, with symbolic cues, the critical stimuli are the same when compatible movements are made and different when incompatible movements are made. With direct cues the critical stimuli are always the same regardless of the type of movement. In essence, the interaction between congruency and cue type might not be related to differential demands in response selection but are rather due to the costs associated with processing perceptually dissimilar cues when incongruent movements are cued symbolically.

The current experiments evaluate the stimulus similarity hypothesis. We focus on the absence of a congruency effect with direct cues. Specifically, we compared conditions in which the direct cues were perceptually identical (except for their spatial location) with conditions in which the cues were perceptually different (i.e., differently colored). If stimulus similarity influences the preparation of bimanual responses, we should observe RT costs for movements involving nonidentical stimuli for the two targets. These costs should be evident for both congruent and incongruent movements.

Experiment 1

To test the role of stimulus similarity in bimanual costs, we manipulated the colors of the direct cues. At the beginning of each trial, two possible target locations for each hand (a total of four target locations) were indicated by outlined, white circles, one to the side and one straight ahead of the initial hand positions. The actual target locations were then indicated by filling in two or one of these four circles for bimanual and unimanual trials, respectively. On bimanual trials, two variables were manipulated (see Figure 1). First, the required movements were either congruent, following a common directional path (e.g., both forward), or incongruent, following orthogonal paths (e.g., one forward, one sideways). Second, the direct cues were either the same color or different colors. According to the stimulus similarity hypothesis, RTs should be slower when different colors are used to indicate the target locations. This effect should be present for both congruent and incongruent trials, although the magnitude of the effect may

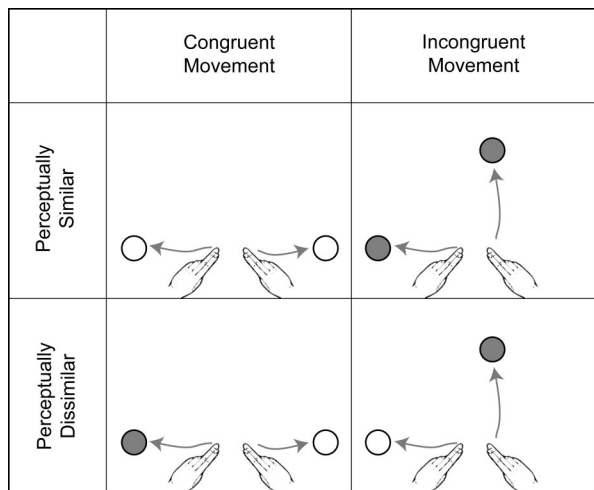


Figure 1. The conditions for Experiment 1. The movement of each hand was either sideways or forwards. The direct cues were red or green colored rings. All trials were cued by the synchronous onset of the two direct cues. Unimanual trials, not shown here, were cued by the appearance of a single colored ring.

differ between these conditions. In contrast, the response selection hypothesis assumes that the color of the targets will have no effect on performance. By this hypothesis, the direct cues specify two distinct target locations regardless of whether the movements are congruent or incongruent and independent of the similarity of the two stimuli. We included unimanual trials to provide a baseline from which to evaluate costs that arise during the planning of bimanual movements.

Method

Participants. Twenty right-handed undergraduates participated in this experiment to satisfy a research participation course requirement. Participants provided informed consent under a protocol approved by the Institutional Review Board of the University of California, Berkeley. The procedures complied with American Psychological Association ethical standards in the treatment of human participants.

Apparatus and stimuli. A two-dimensional virtual environment was used for stimulus presentation and online visual feedback (see Diedrichsen et al., 2001, Figure 1). Participants were seated at a table (110 × 77 × 75 cm) with their head position stabilized by a chin rest. A projection screen was mounted 48 cm above the table surface, and a reflecting mirror was mounted halfway between the table and screen. Stimuli were presented using a DLP projector (Texas Instruments; Dallas, TX) mounted 112 cm above the screen. By viewing the stimuli through the mirror, participants had the illusion that the stimuli were presented directly on the table surface. However, the mirror occluded vision of the hands.

All movements were produced on the table surface in a center-out fashion. A magnetic three-dimensional movement tracking system (mini-BIRD, Ascension Technologies; Burlington, VT) was used to record the position of the participants' hands. Two small transmitters (15 × 7 × 7 mm) were taped to the tip of the

participants' index fingers, and the x , y , and z positions were sampled at a rate of 140 Hz by a desktop computer. The output from the tracking system was used to provide the participants with veridical online feedback of the current position of each hand. This feedback was in the form of small white dots (2 mm in diameter) that appeared on the table surface.

Two white circles (3.6 cm in diameter), located 35 cm in front of the participant and separated by 20 cm, were used to indicate the starting positions. There were four possible target locations, two relevant to each hand. Two of these were 10 cm in front of the starting circles, and the other two were 10 cm lateral to each starting circle. The target location(s) on each trial were indicated by the appearance of a colored circle or circles (3.6 cm in diameter) at the selected target locations.

Procedure. The start of each trial was denoted by the appearance of one or two of the starting circles. Only one circle appeared on the unimanual trials, and its location with respect to midline indicated the appropriate hand for these trials. The participant moved his or her hands into the starting circle(s) and was required to remain within the circle for 1 s. When this criterion was met, a "+" sign appeared at the vertical meridian, 40 cm from the participant. This served as a fixation point. After maintaining the starting position for an additional variable delay of 1–2 s, the target circle(s) appeared. The target(s) indicated the endpoint location for the reaching movement(s) and also served as an imperative signal. On bimanual trials, the required movements were either congruent (both forward or both sideways) or incongruent (one forward, one sideways), with each type occurring 50% of the time. The color of the target(s) was either green or red. On bimanual trials, the two colors were the same on 50% of the trials and different on 50% of the trials.

Participants were instructed to reach to the target locations as quickly as possible while maintaining accurate movements. They were required to lift their finger (and arm) when reaching, making contact with the table only at the onset and offset of the movement. At the end of each trial, a bonus score was projected on the table surface. This score was primarily based on RT,¹ with the criterion determined on an individual basis. The bonus was used to provide repeated motivation to the participants to move as quickly as possible. RT was defined at the moment the sensor velocity exceeded 2 cm/s following the presentation of the target circles, and movement time (MT) was the difference between the RT and when the hand velocity fell below 2 cm/s.

Participants began the experiment with a practice block of 24 trials. The mean RT for this block defined the initial criterion for the bonus point system. Following the practice block, participants completed six test blocks of 48 trials each. Within each block, there were six types of trials, two unimanual (left or right) and four bimanual. The four bimanual types were created by the factorial

¹ The bonus composite ($b = RT + MT/2$) was compared with mean performance on the previous block, *standard*. When $b < criterion - 50$, 7 points were awarded; 2 fewer points were awarded as bins increase by 50 ms, until just 1 point was awarded for being within 100 ms of the *criterion*. In Experiment 3, successful performance of a unimanual reach resulted in a doubling of the temporally based earned bonus score and 20 points were awarded for withholding both responses on a bimanual no-go trial. Twenty points were deducted for any no-go failure. For all experiments, failure to terminate movements in the target locations resulted in 0 points earned for that trial.

combination of movement congruency (same direction or different directions) and stimulus similarity (same color or different color). Each trial type occurred eight times in a block, with an equal number of all location and color combinations used across blocks.

At the end of each block, participants were provided feedback indicating mean RT and MT. They were repeatedly encouraged to initiate the movements as quickly as possible and to reach for the targets in a rapid, continuous manner. We did not provide accuracy feedback, given the simplicity of the task and the emphasis on speed. To further emphasize speed, we reset the speed criterion used to calculate the bonus following any block in which the mean time was faster than the criterion.

Results

RT and MT were highly correlated for the two hands ($r > 0.95$) on the bimanual trials. Given this, the analyses and graphs are based on the data obtained for the right hand (see the Appendix for data from each hand for each experiment). The pattern of results is essentially the same if the analyses were based on the left hand data or a composite measure of the two. Movements were defined as correct when the finger(s) touched the table within the target circle. Overall, accuracy was high (89%, $SE = 1.9\%$) and did not vary with movement congruency or color similarity (both $F_s < 1$). The RT and MT analyses were based on data from correct trials only.

RTs from bimanual trials were submitted to a two-way analysis of variance with color similarity and movement congruency as factors (see Figure 2). There were no reliable main effects or interactions involving perceptual similarity nor movement congruency, each $F(1, 19) < 1$. A similar pattern of results was observed for the MT data. Stimulus similarity did not affect MT, $F(1, 19) < 1$, and there was no evidence of an interaction, $F(1, 19) < 1$. There was a reliable effect of movement congruence in MT, $F(1, 19) =$

6.64, $p = .019$, with incongruent movements taking 29 ms longer to complete than congruent movements.

Unimanual trials were not included in the main analyses. However, they allow us to assess whether there is a cost associated with planning bimanual movements compared with unimanual movements with direct cues. Similar to what was shown previously (see Diedrichsen et al., 2001), RTs in unimanual trials were comparable to those observed during bimanual trials (339 ms vs. 343 ms). Although this null result further underscores the minimal demands placed on planning processes by direct cues, it is tangential to the stimulus similarity issue under investigation in the present study.

Given that the selection hypothesis predicts a null result with respect to color similarity, it is critical to estimate the power of the experimental design. Diedrichsen et al. (2003, Experiment 2) compared conditions in which the target colors were either the same or different. In that study, the target color for each hand was fixed for the entire experiment and distractor colors were presented at the nontarget locations. Under such conditions, an RT cost of 57 ms was observed when the targets were specified by different colors (Diedrichsen et al., 2003, Figure 7), with a variance of 24 ms. These values can be used to calculate the sample size required to show a significant result under the alternative hypothesis that stimulus similarity influences RT. Such a calculation indicates that a sample size of 9 participants would be sufficient to detect such a difference ($\beta > 0.999$ for $\alpha = .05$, one-tailed test). Given that we tested 20 participants, the sample size appears to be more than sufficient. Thus, it is unlikely that the lack of a stimulus similarity effect in the present experiment was due to a Type II error.

Discussion

The results of Experiment 1 suggest that the absence of a congruency effect during bimanual reaching to directly cued targets cannot be attributed to the perceptual similarity of the stimuli. Although this conclusion is based on a null result, the lack of an effect of color similarity was observed on measures of RT, MT, and accuracy. Thus, having stimulus displays that were perceptually identical in terms of color identity did not confer an advantage over trials in which the displays involved nonidentical colors.

Diedrichsen et al. (2003) required participants to reach to same or different colored targets, similar to what was done in the current experiment. However, they consistently found that RT was faster when the movements were made to same-colored targets compared with when reaches were made to differently colored targets. How can these seemingly contradictory results be reconciled? In the Diedrichsen et al. (2003) experiments, target selection demands were greater than in the current experiment. Critically, candidate locations were indicated by circles of varying colors, and participants had to select the targets based on a specified color. In contrast, in the present experiment, participants were required to identify the location of the colored target, but the color itself was irrelevant for the reaching action. We propose that because selection processes did not have to represent the colors of the targets, conflict during response selection did not occur. That is, responding to direct cues only requires the interpretation of location information, and color information is not associated with the responses.

The participants were slower to complete bimanual movements that followed incongruent trajectories. The magnitude of this MT

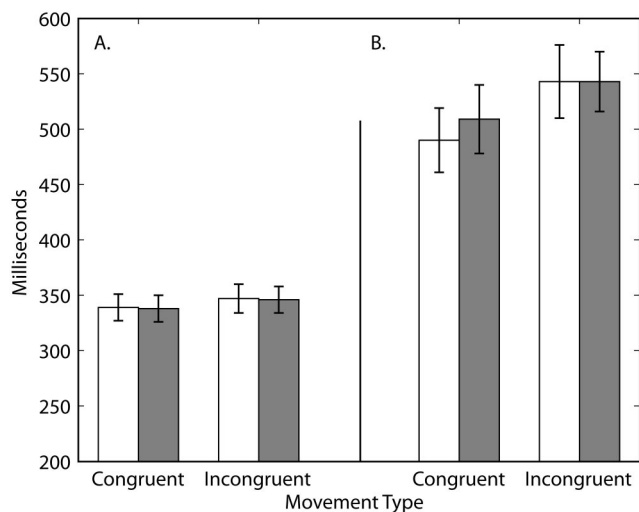


Figure 2. Results of Experiment 1: average reaction (A) and movement (B) times produced in response to direct cues. Data associated with perceptually similar cues are denoted by white bars and data associated with perceptually dissimilar cues are denoted by gray bars. Error bars indicate standard error of the mean.

effect was quite small (29 ms), especially compared with the effect of compatibility on RT when symbolic cues are used (see Diedrichsen et al., 2001; Hazeltine et al., 2003; Heuer & Klein, 2006). The MT cost may be due to cross-talk during motor execution as initially proposed by Heuer (1993; Heuer & Klein, 2006). Indeed, the effect persists even when both locations are precued (Diedrichsen et al., 2001), suggesting that it does not reflect deferred motor programming. With respect to the present study, the important point is that the magnitude of this effect was similar for the same and different color conditions. Thus, it was independent of stimulus similarity.

Experiment 2

The lack of an effect of stimulus similarity on the preparation of bimanual reaching movements in Experiment 1 may have been due to the fact that the cueing method required minimal perceptual analysis of the stimuli in order to select the responses. To be successful in the task, participants had to accurately identify the stimulus location. Because color information was irrelevant to task performance, participants may have ignored or even inhibited this information.

To explore this possibility, we added a secondary task in Experiment 2 that required the participants to report the color of the target circles on a subset of the trials. The color identification responses were obtained at the end of the trial, after the reaching movement(s) had been completed. We added two manipulations to ensure that participants attended to the colors. First, the colors were only briefly present. In this manner, we sought to force the participants to attend to the colors at the beginning of the trial, prior to movement onset. Second, the number of possible colors was increased to reduce the likelihood that participants would correctly report the target color(s) just by guessing.

Method

Participants. Twenty right-handed undergraduates participated in this experiment to satisfy a research participation course requirement.

Procedure. The procedure was similar to that employed in Experiment 1, with the addition of the color identification task. The target colors were selected at random from a palette of six colors: blue, green, teal, red, pink or brown. On same color trials, one color was selected at random and assigned to both target locations. On different color trials, two colors were selected at random without replacement. To force the participants to attend to the colors at stimulus onset, the targets appeared in their assigned color for only the first 100 ms of stimulus presentation. Following this, the target circles turned white. To increase the power to detect a difference between similarly and differently colored targets, we did not include unimanual trials in this experiment.

Color reports were required on only 25% of the trials, selected at random. This secondary task was performed after the participant had completed the reaching movements and was prompted by the appearance of a probe including the names of the six potential target colors. Color identifications for the left and right targets were made sequentially. The participant responded verbally, and an experimenter recorded the responses on the computer keyboard. Participants were informed that it was important to pay attention to the colors and that errors on the color identification task would

lead to a significant reduction in their bonus score. Feedback on this task was provided on the projection screen immediately after the response was recorded.

Participants began the experiment with a practice block of 24 trials. The mean RT for this block again defined the initial criterion for the bonus point system. Following the practice block, the participant completed six test blocks of 48 trials each. Within each block, there were four types of trials created by the factorial combination of movement congruency (same direction or different directions) and stimulus similarity (same color or different color). Each trial type occurred 12 times in a block, with an equal number of all location and color combinations used across blocks.

At the end of each block, summary feedback was provided regarding mean RT, mean MT, and accuracy on the primary reaching task and secondary color identification task. The experimenter emphasized that, although primary emphasis should be given to initiating and completing the reaching task as fast as possible, it was also important to maintain about 80% accuracy on each of the two tasks.

Results

All participants were able to maintain at least 75% accuracy on the color identification task. Participants reported both colors correctly on 90% of the trials ($SE = 1.3\%$), with no difference in accuracy on trials in which the two colors were the same or different ($p = .958$). Chance performance on the color identification tasks would be 20% on congruent trials and just 4% on incongruent trials assuming independent processing of each color.

The reaching movements terminated in the target location on 94% of the trials across participants ($SE = 1\%$). Reaching accuracy did not vary with movement congruency or color similarity.

For the RT data, neither the main effect of color similarity, $F(1, 19) = 2.51, p = .13$, movement congruency, $F(1, 19) = 4.17, p = .06$, or the interaction of these two factors, $F(1, 19) < 1$, was significant (see Figure 3). RTs were essentially identical (2 ms difference) on bimanual trials in which the initial color of the targets was the same or different. As in Experiment 1, the times to initiate congruent movements and incongruent movements were very similar, although there was a small effect (4 ms) for incongruent movements to be initiated more slowly, which in this case proved to be nearly significant.

The MT data also failed to reveal an effect of color similarity. MTs to different colored targets (414 ms) were similar to those to identically colored targets (405 ms), $F(1, 19) < 1$. MTs for incongruent movements were 19 ms slower than MTs for congruent movements, $F(1, 19) = 4.56, p = .046$.

Discussion

Experiment 2 was designed to provide a stronger test of the hypothesis that stimulus similarity influences the preparation of bimanual reaching movements. The relatively high level of performance on the color identification task indicates that the participants attended to the colors. Nonetheless, the results indicate that stimulus similarity had no effect on either the time required to initiate the movements or the time required to complete the movements. Participants were just as fast to initiate and complete movements to targets that were initially presented in different

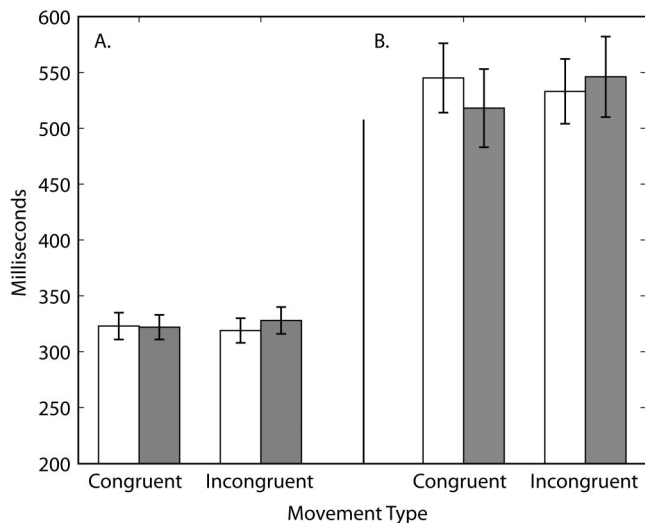


Figure 3. Results of Experiment 2: average reaction (A) and movement (B) times produced in response to direct cues. Data associated with perceptually similar cues are denoted by white bars and data associated with perceptually dissimilar cues are denoted by gray bars. Error bars indicate standard error of the mean.

colors compared with when the target colors were identical. These findings argue against the hypothesis that stimulus similarity is a viable source of constraint when the movements are selected on the bases of direct cues.

It is noteworthy that the inclusion of the color identification task had little effect on either movement variable. In terms of mean RT, participants initiated the movements more quickly under the dual-task conditions of Experiment 2 ($M = 320$ ms) compared with the single-task conditions of Experiment 1 ($M = 341$ ms). There were even greater reductions of MT in Experiment 2 ($M = 410$ ms) relative to Experiment 1 ($M = 568$ ms). Thus, participants were able to maintain their priority to respond quickly even while identifying the target colors. This suggests that color identification either occurred in Experiment 1, even though it was irrelevant to performance, or can occur in parallel without interference during the planning of bimanual reaching movements to directly defined targets.

Experiment 3

Experiments 1 and 2 both indicate that stimulus similarity does not affect the amount of time required to initiate bimanual reaching movements. Although the latter experiment imposed conditions that required participants to identify the color of both stimuli, it is possible that color identification might have been deferred until after reaching (see Lauwereyns, Wisnewski, Keown, & Govan, 2006). Even if identification was not deferred, determining the target locations did not require identifying the colors of the stimuli. Thus, perceiving the colors may have occurred independently of response selection for the reaching task. In Experiment 3, we modified the task such that color identification was relevant for target selection. As in Experiment 2, two circles were presented on each trial. There were five possible colors. The participants were instructed to reach to the target locations for four of the colors. For the fifth color, the participants were instructed to withhold the

reaching response; in essence, this created a go/no-go condition with four colors mapped to “go” responses and one color mapped to a “no-go” withheld response. In this manner, color was made relevant for the reaching task because the participant had to determine if the color of each target corresponded to a go or no-go signal prior to initiating a reaching movement.

Method

Participants. Twenty right-handed undergraduates participated in this experiment to satisfy a research participation course requirement.

Procedure. The color of each target circle could be one of five colors: blue, green, red, yellow, or brown. One color was assigned to be the no-go stimulus; participants were to not reach to the location of any circle presented in this color. The other four colors were designated go stimuli; participants were to reach to the locations of any circle presented in these colors. The no-go color was counterbalanced across participants. For each trial, two colors were selected at random. This resulted in the two colors being identical, or perceptually congruent, on 20% of the trials. The no-go color appeared on 80 of the 200 trials. For 8 of these trials, both circles were the no-go color and the participant should not have produced any reaching movement. For the other 72 of these trials, only one target was the no-go color. On these trials, the participants were to make a unimanual response, reaching to the other target. Bimanual responses were required for the remaining 128 trials, half of which required congruent movements and half of which required incongruent movements.

The participants were informed that it was important to pay attention to the colors and that errors on the color identification task (e.g., reaches to a no-go stimulus) would lead to significant reductions in their bonus scores. As in the previous experiments, the targets appeared in their assigned color for only the first 100 ms of stimulus presentation. Following this, the circles turned white. Feedback was provided after each trial with a bonus score (see Footnote 1).

The session began with two blocks of 50 trials each, which served as practice. The mean RT for the second was the initial criterion for the bonus system for the four test blocks and decreased between blocks commensurate with performance. There were four test blocks of 50 trials each. Within each block, there were seven conditions: four bimanual conditions created by the factorial combination of movement congruency (same direction or different directions) and stimulus similarity (same color or different color), unimanual left and unimanual right conditions (one no-go color), and the no response condition (two no-go colors). At the end of each block, summary feedback was provided regarding mean RT, mean MT, and accuracy. For the latter, the feedback indicated the percentage of reaches terminating at the target locations as well as the percentage of trials in which the response was correctly withheld to no-go targets.

Results

Bimanual trials. Reaching movements correctly terminated in the target circle on 89% of the trials ($SE = 0.9%$). Accuracy did not vary with movement congruency or color similarity. For trials with only one go stimulus, the percentage of correctly withheld

responses to the no-go target ranged from 79% to 100% ($M = 91%$, $SE = 1.2%$) across participants. For trials with two no-go stimuli, the mean percentage of correctly withheld responses dropped to 84.5% ($SE = 3.5%$). Note that there were only eight such trials per participant, and movement of either hand was considered a no-go failure.

RTs were longer when the movements were incongruent (427 ms) compared with when they were congruent (416 ms). Although small, the effect of movement congruency was significant, $F(1, 19) = 7.09$, $p = .014$. Most important, the effect of color similarity was not significant, $F(1, 19) = 1.03$, $p = .322$, nor was there any indication of an interaction of these two factors, $F(1, 19) < 1$ (see Figure 4). RTs were essentially identical (5 ms difference) on bimanual response trials in which the initial color of the targets was the same or different.

The pattern of results observed for the MT data was comparable with that observed in the RT analyses. MTs for incongruent movements (310 ms) were slightly longer than those for congruent movements (293 ms), although this effect only approached significance, $F(1, 19) = 3.20$, $p = .090$. There was no effect of color similarity. In fact, movements to different colored targets (298 ms) were shorter than those to similarly colored targets (306 ms), although this effect did not approach significance, $F(1, 19) = 1.051$, $p = .392$.

Unimanual trials. On trials in which one of the targets was in the no-go color, the correct response required a unimanual movement. The mean RT on these unimanual trials was 457 ms, reliably longer than the mean RT of 424 ms on perceptually dissimilar bimanual trials, $F(1, 19) = 31.246$, $p < .001$. The slower RT for unimanual trials is likely due to the fact that inhibitory processes were engaged by the no-go stimulus and this led to a delay in initiating the single movement (see Band & van Boxtel, 1999 for review). Unimanual RTs were similar on trials in which the two circles appeared at congruent locations (469 ms) compared with incongruent locations (444 ms), paired-sample $t(19) = 1.599$, $p = .126$.

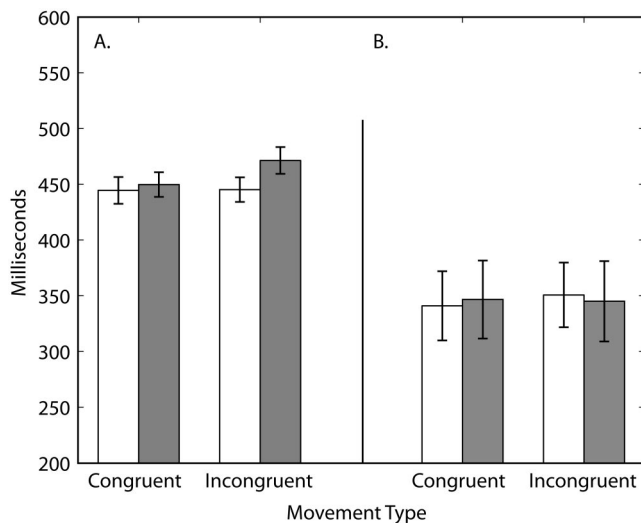


Figure 4. Results of Experiment 3: average reaction (A) and movement (B) times produced in response to direct cues. Data associated with perceptually similar cues are denoted by white bars and data associated with perceptually dissimilar cues are denoted by light gray bars. Error bars indicate standard error of the mean.

Discussion

Experiment 3 examined the influence of perceptual similarity in planning and executing bimanual reaching movements when the critical stimulus feature was relevant to response selection. The relatively high level of performance on the go/no-go task clearly indicates that the participants attended to the colors prior to the implementation of their response. Nonetheless, stimulus similarity had no effect on either the time required to initiate the bimanual movements or the time required to complete the movements. Participants were just as fast to initiate and complete movements to targets that were initially presented in different colors compared with when the target colors were identical. Thus, when responses are made to directly cued locations, color similarity is not a viable source of constraint even when color identification is relevant for determining whether or not a response is required.

In the latter two experiments we observed a small effect of movement congruency: RTs were slower on trials in which the responses followed orthogonal trajectories. In previous studies involving direct cues, the effect of movement congruency on RT has been inconsistent (Diedrichsen, Grafton, Albert, Hazeltine, & Ivry, 2006; Diedrichsen et al., 2001; Heuer & Klein, 2006). Even when reliable, the effect is on the order of 15 ms or less (see Heuer & Klein, 2006), considerably less than that observed with symbolic cues. The same effect at least approached significance for MT in each of the three experiments, although this has been observed quite regularly in previous experiments (Diedrichsen et al., 2001; Heuer & Klein, 2006). Again, these effects are still nearly an order of magnitude smaller than those commonly observed for symbolically cued reaching movements.

At a qualitative level, a few cross-experiment observations are noteworthy. The mean RTs were considerably slower in Experiment 3 compared with Experiments 1 and 2. This slowing is to be expected given that the participants had to identify the colors in order to determine which responses to make and which to withhold. As a post hoc account of this observation, we suggest that the longer RTs in Experiment 3 occurred because the no-go stimuli increased the duration of movement planning for all targets because the colors must be processed to determine if one or both are no-go stimuli. Alterations to voluntary reaching movements have been shown to occur more slowly when cued by color information compared with location information (Pisella, Arzi, & Rossetti, 1998). Extended planning should allow for more refined motor programming and execution and, therefore, result in fewer endpoint corrections (see Meyer, Kornblum, Abrams, Wright, & Smith, 1988). Interestingly, MTs were faster in Experiment 3 compared with Experiments 1 and 2.

General Discussion

The study of bimanual coordination has proven to be a fertile ground for exploring limitations in how people plan and execute complex actions. This literature is grounded in the observation that people exhibit a preference for certain forms of spatiotemporal coupling. Theoretical accounts of these effects have focused on factors related to movement planning and execution. For example, accounts derived from a dynamical systems perspective have conceptualized the moving limbs as spatiotemporal oscillators, with the coupling between the oscillators leading to a preference in which the movements are frequency locked and most stable when they follow symmetric trajectories. Such tendencies have been postulated to arise at various levels of the motor system, including

intrinsic biases to activate homologous muscles in a synchronized manner (Heuer, 1993; Swinnen et al., 1998).

Recent findings, however, suggest that processes associated with movement planning and execution are not the primary source of constraint on bimanual coordination, at least with respect to the spatial features of the movements. As confirmed in the present investigations, people show little cost in producing movements that follow orthogonal trajectories compared with movements that follow parallel trajectories when direct cues are used to specify the target locations. Indeed, from our everyday experience, it does not appear any more difficult to reach for an object when the hands follow nonparallel trajectories compared with when the object is positioned such that the two hands move in parallel. This last observation suggests that the manner in which action goals are represented imposes a fundamental constraint on bimanual coordination and action planning more generally.

One variant of this idea is articulated in Hommel and Prinz's theory of event coding (Hommel et al., 2001), with the central idea that actions are planned in terms of their perceptual consequences. Although this theory was formulated with respect to unimanual movements, it also provides a parsimonious account of the finding that people are more facile in producing symmetric bimanual movements regardless of whether the movements are produced by homologous or nonhomologous fingers (Mechsner et al., 2001). Rather than focus on motoric aspects, this theory suggests that the ease with which bimanual coordination is achieved will reflect the simplicity of the resulting perceptual consequences (Mechsner & Knoblich, 2004).

This hypothesis suggested a novel account of the lack of a congruency effect for directly cued bimanual reaching movements. In previous studies, such movements had always involved perceptually identical cues (e.g., white circles of identical brightness, shape, size). Perhaps the lack of cross-talk for incongruent movements was due to the high degree of stimulus similarity with such cues, at least in comparison to the different stimuli used in studies with symbolic cues. However, the present results fail to support the perceptual symmetry hypothesis. Stimulus similarity did not have any effect on performance when the movement targets were directly cued.

Although the current experiments were designed to contrast performance when reaching to identically and differently colored targets, numerous post hoc analyses were performed along color continuums that existed in the current data. For example, red and green are both principal colors of the visual system, via excitation of L and M cones (De Valois & De Valois, 1975). Brown is a combination of red and green, and as such it should be more similar to red and green than red and green are to each other. Thus, a similarity based effect should be most pronounced within this set of three colors. In Experiment 3, RTs to red–green pairs (433 ms) and red–brown pairs (454 ms) are in the opposite direction of the proposed effects of perceptual similarity, although not significantly, $t(11) = 0.699$, $p = .5$. This contrast could not include all subjects as not all subjects completed reaches to each of these colors due to the assignment of a no-go color in this experiment. Similar post hoc within-subjects analyses were conducted for plausible continuums of similarity, but none proved to generate a reliable effect.

It is, of course, possible that target color is not relevant in terms of the coding of the perceptual consequences of the reaching movements. Rather than code the actions in terms of “reach to the red target,” participants may simply code the actions as “reach for the illuminated circle.” Although this is a reasonable hypothesis,

the results of Experiment 3 show that even when color identification is essential for response selection, this stimulus property fails to influence performance on the reaching task.

Other perceptual features also fail to account for the lack of a congruency effect for directly cued movements. For example, one might imagine that a configural aspect of the display would be relevant in terms of perceptual coding. In particular, congruent movements to direct cues involve displays that entail symmetry about the y-axis compared with displays requiring incongruent movements. The lack of a congruency effect in the studies of Diedrichsen et al. (2001) and Hazeltine et al. (2003), however, already suggests that this form of perceptual simplicity is not relevant. Here we add to the argument against a perception-based account by looking at perceptual simplicity in terms of a property of the stimulus elements (e.g., color).

An alternative interpretation of the limitations observed in many bimanual tasks is that these costs reflect cross-talk at processing stages associated with response selection (Hazeltine et al., 2003). With symbolic cues, a translation process must occur between the stimulus and its associated response. When there are two, distinct stimuli, cross-talk can arise in the assignment of each stimulus to its respective response. Even when the movements are not specified by explicit symbolic cues, the representation of the task goals may be in terms of abstract, spatial goals. For example, the challenge when trying to rub your belly while patting your head arises because of the difficulty in sorting out the assignment of the two gestures to their respective hands. Along these lines, Hazeltine (2005) showed that cross-talk between bimanual keypress responses was largely conceptual rather than linked to particular stimulus or response properties. Thus, the cross-talk presumably occurred at a central stage of processing, such as response selection, in which the representations are likely to be abstract. By emphasizing a limitation in response selection, the constraints observed in bimanual coordination tasks are viewed from the same perspective as that which has proven useful in cognitive psychology for understanding dual-task performance (see Ivry et al., 2004). Much of what we call bimanual coordination is really best conceptualized as a study of dual task performance.

These dual-task costs are absent when the movement targets are directly cued. As shown in Experiment 1 of the present study, RTs were not only similar on congruent and incongruent trials, but the participants were just as fast to initiate movements with both hands compared with when only a single movement was required (see also Diedrichsen et al., 2001). We have hypothesized that the demands on response selection are minimal for direct cues because of the minimal requirements for translation between the stimulus and the response. Neuropsychological studies also indicate that direct reaching may entail processes relatively divorced from the cognitive machinery involved in stimulus identification and selection. The widely described patient studied by Milner and Goodale (1995) is able to reach and grasp for objects, even though she is unable to indicate knowledge of the object's orientation when responding in a more abstract, indirect manner (see also Goodale, Milner, Jakobson, & Carey, 1991).

The manner in which the action goals are coded may differ between conditions involving symbolic and direct cues (Ivry et al., 2004). For symbolic cues, the goals may be coded in terms of trajectories (e.g., “reach for the target to the side”). Such spatial representations are abstract in the sense that they code directional

information in a body-centered coordinate reference frame. In bimanual conditions, such spatial codes must be assigned to arms, entailing compatibility effects not only between the directional codes but also effectors (e.g., left or right hand that is moving to left or right side). For direct cues, the goals may be coded in terms of target locations (e.g., “reach to location *X*”). Our experience is of a world containing multiple objects at distinct locations. Under certain conditions, perceptual errors may arise when location codes become noisy (Ashby, Prinzmetal, Ivry, & Maddox, 1996; Prinzmetal, 2005). However, this requires situations in which the objects are closely spaced and the viewing conditions are taxing. For the most part, we are remarkably adept in representing and interacting with objects at multiple locations. The current experiments add to the evidence indicating that our ability to reach to two distinct locations appears to manifest few constraints—in terms of motor execution, planning, and response selection, as well as perceptual coding.

References

- Ashby, F. G., Prinzmetal, W., Ivry, R., & Maddox, W. T. (1996). A formal theory of feature binding in object perception. *Psychological Review*, *103*, 165–192.
- Band, G. P. H., & van Boxtel, G. J. M. (1999). Inhibitory motor control in stop paradigms: Review and reinterpretation of neural mechanisms. *Acta Psychologica*, *101*, 179–211.
- De Valois, R. L., & De Valois, K. K. (1975). Neural coding of color. In E. C. Carrette & M. P. Friedman (Eds.), *Handbook of Perception* (Vol. 5, pp. 117–166). New York: Academic Press.
- Diedrichsen, J., Grafton, S., Albert, N., Hazeltine, E., & Ivry, R. B. (2006). Goal-selection and movement-related conflict during bimanual reaching movements. *Cerebral Cortex*, *16*, 1729–1738.
- Diedrichsen, J., Hazeltine, E., Kennerley, S., & Ivry, R. B. (2001). Moving to directly cued locations abolishes spatial interference during bimanual actions. *Psychological Science*, *12*, 493–498.
- Diedrichsen, J., Ivry, R. B., Hazeltine, E., Kennerley, S., & Cohen, A. (2003). Bimanual interference associated with the selection of target locations. *Journal of Experimental Psychology: Human Perception & Performance*, *29*, 64–77.
- Franz, E. A., Eliassen, J. C., Ivry, R. B., & Gazzaniga, M. S. (1996). Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. *Psychological Science*, *7*, 306–310.
- Franz, E. A., Zelaznik, H. N., & McCabe, G. (1991). Spatial topological constraints in a bimanual task. *Acta Psychologica*, *77*, 137–151.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991, January 10). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*, 154–156.
- Greenwald, A. G., & Shulman, H. G. (1973). On doing two things at once: II. Elimination of the psychological refractory period effect. *Journal of Experimental Psychology*, *101*, 70–76.
- Hazeltine, E. (2005). Response-response compatibility during bimanual movements: Evidence for the conceptual coding of action. *Psychonomic Bulletin & Review*, *12*, 682–688.
- Hazeltine, E., Diedrichsen, J., Kennerley, S. W., & Ivry, R. B. (2003). Bimanual cross-talk during reaching movements is primarily related to response selection, not the specification of motor parameters. *Psychological Research*, *67*, 56–70.
- Heuer, H. (1993). Structural constraints on bimanual movements. *Psychological Research*, *55*, 83–98.
- Heuer, H., & Klein, W. (2006). The influence of movement cues on intermanual interactions. *Psychological Research*, *70*, 229–244.
- Heuer, H., Spijkers, W., Kleinsorge, T., van der Loo, H., & Steglich, C. (1998). The time course of cross-talk during the simultaneous specification of bimanual movement amplitudes. *Experimental Brain Research*, *118*, 381–392.
- Hommel, B., Musseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral & Brain Sciences*, *24*, 849–878; discussion 878–937.
- Ivry, R. B., Diedrichsen, J., Spencer, R. M., Hazeltine, E., & Semjen, A. (2004). A cognitive neuroscience perspective on bimanual coordination and interference. In S. P. Swinnen & J. Duysens (Eds.), *Interlimb Coordination* (pp. 259–295). Boston: Kluwer Academic.
- Kelso, J. S., Southard, D. L., & Goodman, A. (1979). On the coordination of two-handed movements. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 229–238.
- Klapp, S. T., Hill, M. D., Tyler, J. G., Martin, Z. E., Jagacinski, R. J., & Jones, M. R. (1985). On marching to two different drummers: Perceptual aspects of the difficulties. *Journal of Experimental Psychology: Human Perception and Performance*, *11*, 814–827.
- Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitive basis for stimulus-response compatibility—A model and taxonomy. *Psychological Review*, *97*, 253–270.
- Lauwereyns, J., Wisniewski, R., Keown, K., & Govan, S. (2006). Crosstalk between on-line and off-line processing of visual features. *Psychological Research*, *70*, 170–179.
- McCann, R. S., & Johnston, J. C. (1992). Locus of the single-channel bottleneck in dual-task interference. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 471–484.
- Mechsner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001, November 1). Perceptual basis of bimanual coordination. *Nature*, *414*, 69–73.
- Mechsner, F., & Knoblich, G. (2004). Do muscles matter for coordinated action? *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 490–503.
- Meyer, D. E., Kornblum, S., Abrams, R. A., Wright, C. E., & Smith, J. E. K. (1988). Optimality in human motor performance: Ideal control of rapid aimed movements. *Psychological Review*, *95*, 340–370.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action* (Vol. 27). Oxford, England: Oxford University Press.
- Pashler, H. (1984). Processing stages in overlapping tasks: Evidence for a central bottleneck. *Journal of Experimental Psychology: Human Perception and Performance*, *10*, 358–377.
- Pashler, H., & Johnston, J. C. (1989). Chronometric evidence for central postponement in temporally overlapping tasks. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *41*, 19–45.
- Pisella, L., Arzi, M., & Rossetti, Y. (1998). The timing of color and location processing in the motor context. *Experimental Brain Research*, *121*, 270–276.
- Prinzmetal, W. (2005). Location perception: The X-Files parable. *Perception & Psychophysics*, *67*, 48–71.
- Spijkers, W., & Heuer, H. (1995). Structural constraints on the performance of symmetrical bimanual movements with different amplitudes. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *48A*, 716–740.
- Spijkers, W., Heuer, H., Kleinsorge, T., & van der Loo, H. (1997). Preparation of bimanual movements with same and different amplitudes: Specification interference as revealed by reaction time. *Acta Psychologica*, *96*, 207–227.
- Swinnen, S. P., Jardin, K., Verschueren, S., Meulenbroek, R., Franz, L., Dounskaia, N., et al. (1998). Exploring interlimb constraints during bimanual graphic performance: Effects of muscle grouping and direction. *Behavioural Brain Research*, *90*, 79–87.

Appendix

Means of Reaction Times (RTs) and Movement Times (MTs) of the Left and Right Hands Across All Three Experiments

Task and measure	Congruent movement				Incongruent movement			
	Perceptually similar		Perceptually different		Perceptually similar		Perceptually different	
	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>
Experiment 1								
Left Hand								
RT	340	14	349	16	336	11	340	14
MT	559	42	569	43	566	46	546	45
Right Hand								
RT	334	12	338	16	342	12	343	13
MT*	549	37	557	38	582	42	583	38
Experiment 2								
Left Hand								
RT	331	9	331	10	333	10	333	10
MT*	430	32	419	26	444	27	462	30
Right Hand								
RT	319	8	317	8	323	9	321	9
MT*	406	26	403	24	397	21	431	25
Experiment 3								
Left Hand								
RT*	415	12	418	15	430	15	434	16
MT	301	15	314	16	318	24	307	15
Right Hand								
RT*	414	13	419	15	424	16	430	16
MT	294	12	293	15	318	22	302	12

Note. Conditions in which the effect of movement congruency was significant are marked with an asterisk. The effect of perceptual similarity was never significant for either RT or MT in all three experiments.

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