

Unified nature of bimanual movements revealed by separating the preparation of each arm

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Abstract Movement preparation of bimanual asymmetric movements is longer than bimanual symmetric movements in choice reaction time conditions, even when movements are cued directly by illuminating the targets (Blinch et al. in *Exp Brain Res* 232(3):947–955, 2014). This bimanual asymmetric cost may be caused by increased processing demands on response programming, but this requires further investigation. The present experiment tested the demands on response programming for bimanual movements by temporally separating the preparation of each arm. This was achieved by precuing the target of one arm before the imperative stimulus. We asked: What was prepared in advance when one arm was precued? The answer to this question would suggest which process causes the bimanual asymmetric cost. Advance movement preparation was examined by comparing reaction times with and without a precue for the left target and by occasionally replacing the imperative stimulus with a loud, startling tone (120 dB). A startle tone releases whatever movement is prepared in advance with a much shorter reaction time than control trials (Carlsen et al. in *Clin Neurophysiol* 123(1):21–33, 2012). Participants made bimanual symmetric and asymmetric reaching movements in simple and 2-choice reaction time conditions and a condition with a precue for the left target. We found a bimanual asymmetric cost in 2-choice conditions, and the asymmetric cost was significantly smaller when the left target was precued. These results, and the results from startle trials, suggest

(1) that the precued movement was not fully programmed but partially programmed before the imperative stimulus and (2) that the asymmetric cost was caused by increased processing demands on response programming. Overall, the results support the notion that bimanual movements are not the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit. When one target is precued, this critical unification likely occurs during response programming.

Keywords Bimanual symmetric and asymmetric movements · Start-react effect · Precue · Response programming

Introduction

It can be challenging to coordinate our two arms, especially when each arm requires different timing or spatial paths. Swinnen and Wenderoth (2004) aptly summarised this challenge as “two hands, one brain”, in their review on bimanual coordination research. We recently compared the movement preparation of asymmetric bimanual reaching movements with different target amplitudes to symmetric bimanual reaching movements with the same amplitudes (Blinch et al. 2014). An important distinction was that illuminating the targets cued these movements. These types of cues are referred to as direct or spatial cues, and they decrease the processing demands on movement preparation compared to symbolic cues (reviewed by Wenderoth and Weigelt 2009). Movement preparation occurs after the imperative stimulus in choice reaction time (RT) conditions, and its duration is reflected in the RT (Donders 1969; Klapp and Jagacinski 2011; Sternberg 1969). The movement preparation processes include imperative stimulus

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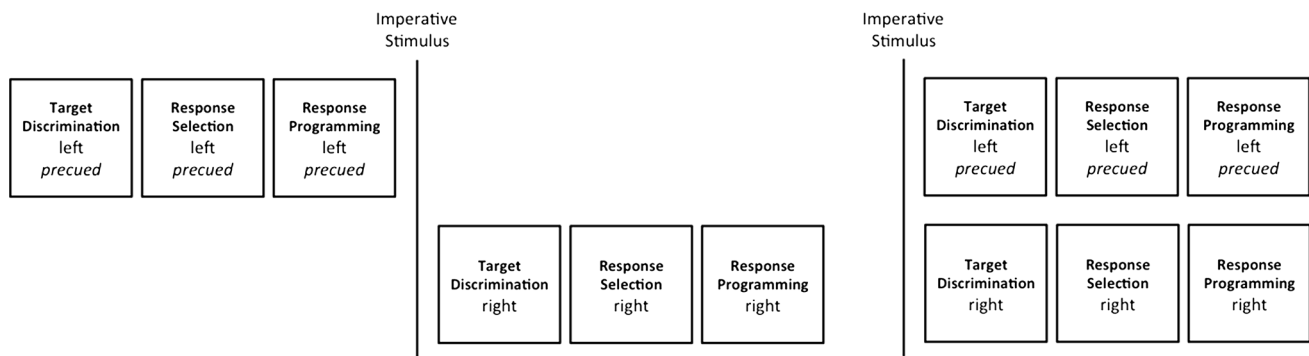


Fig. 1 Two possibilities for movement preparation when the left target is precued. The stages of information processing are target discrimination, response selection and response programming. In the first prediction (*left*), the precued arm and the other arm are fully pre-

pared at different times as two unimanual movements. In the second (*right*), a single, bimanual movement is prepared after the imperative stimulus when the targets for both arms have been cued

recognition, target discrimination, response selection, response programming and response initiation. Substantial movement preparation can occur before the imperative stimulus in simple RT conditions. This advanced preparation occurs before the imperative stimulus and causes a reduction in RT. The preparation after the imperative stimulus, which is measured by RT, includes imperative stimulus recognition and response initiation. The duration of movement preparation was comparable for symmetric and asymmetric movements in simple RT conditions. The lack of cost in simple RT suggested that the duration of imperative stimulus recognition and response initiation is comparable for symmetric and asymmetric movements. In choice RT conditions, the time for movement preparation of bimanual asymmetric movements was longer than bimanual symmetric movements (Blinch et al. 2014). The asymmetric cost in choice RT is likely caused by increased processing demands on one or more preparation processes unique to choice conditions (Donders 1969). These are target discrimination, response selection and response programming.¹ We argued that response programming was the most likely source of interference (Blinch et al. 2014), but this requires further investigation.

Preparing two different unimanual movements (i.e. a bimanual asymmetric movement) *at the same time* likely causes the bimanual asymmetric cost. Is it possible to prepare each arm of a bimanual movement *at different times*? This was tested in the present experiment by temporally separating the preparation of each arm by precuing the target of one arm before the imperative stimulus. We asked

the following question: what was prepared in advance when one arm was precued? The answer to this question would suggest which process is associated with the bimanual asymmetric cost and offer insight into the preparation of bimanual movements.

Our experimental predictions were related to how movement preparation may change when one target is precued (Fig. 1). We began with two predictions. The first prediction is that the precued arm is prepared before the imperative stimulus, and the other arm is prepared after the imperative stimulus (Fig. 1, left). This should *eliminate* the asymmetric cost, as the two unimanual movements are prepared at different times. As all preparation processes are temporally separated, an elimination is predicted regardless of which process causes the asymmetric cost. It may not, however, be possible to fully separate the preparation of each arm, and this leads to the second prediction (Fig. 1, right). This may be the case as bimanual movements are not simply the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit (Kelso et al. 1979; Swinnen and Wenderoth 2004). This could prevent the precued arm from being prepared before the other arm. Both targets must be discriminated and the movements selected before they can be programmed as a single, bimanual movement. Movement preparation in this prediction is the same as in choice RT conditions. Therefore, the size of the asymmetric cost in choice RT and with one precue should be comparable.

We also used a unique technique as a second measure of the relative amount of movement preparation that occurred in advance. The “go” tone was occasionally and unpredictably replaced with a loud, startling tone (120 dB). A startle tone can elicit two effects: the startle reflex and the start-react effect. The startle reflex consists of a stereotyped set of bilateral muscle contractions that is described as a generalised flexion response. A reliable indicator of the startle

¹ As imperative stimulus recognition and response initiation are unlikely to contribute to asymmetric costs in choice RT (Blinch et al. 2014), they have been excluded from subsequent discussion of the processes during movement preparation in choice RT.

reflex is activation of the sternocleidomastoid (SCM) muscles (Carlsen et al. 2011). The start-react effect consists of the release of a prepared movement with an RT much shorter than control trials (Carlsen et al. 2012; Valls-Solé et al. 1999).

The start-react effect has been explained by the hypothesis that a startling acoustic stimulus increases neural activation of a prepared response, raising it to the threshold to be released (reviewed by Carlsen et al. 2012). The increase in neural activation has distinct effects in simple and choice RT conditions, which allows the start-react effect to probe the relative level of movement preparation. In simple conditions, the required movement is fully prepared before the imperative stimulus. This advance preparation causes a high level of neural activation that is close to the threshold required to release the movement. A startle tone quickly increases this neural activation the small amount required to reach threshold, thus releasing the prepared movement with a much-reduced RT. It has also been shown that there is a high probability of a startle reflex (as indicated by activation of the SCM) in simple conditions (Maslovat et al. 2012). In choice RT conditions, the exact movement is unknown before the imperative stimulus and it cannot be fully prepared in advance. The result is a low level of neural activation that is far from threshold. A startle tone quickly increases the neural activation, but it takes longer to reach threshold. This delay affords an opportunity to finish movement preparation after the imperative stimulus, which can have two possible outcomes. For the majority of trials, the required response is prepared and initiated. For a minority of trials, movement preparation is disrupted by the loud, startling tone and a movement error is made (Carlsen et al. 2004, 2009; Forgaard et al. 2011; Maslovat et al. 2011). There is also a lower probability of a startle reflex in choice compared to simple conditions (Maslovat et al. 2012).

The predictions for startle trials depend on the possible effects of the precue on movement preparation. If the precued arm is fully prepared before the imperative stimulus and the other arm is prepared after the imperative stimulus (Fig. 1, left), the effects of the startle tone on the precued movement should be comparable to bimanual movements in simple RT conditions, with shorter RTs and a lower probability of a movement error. At the same time, the movements for the arm without the precue should be comparable to movements in choice conditions with longer RTs and a higher probability of a movement error compared to simple conditions. In other words, we predicted that the bimanual movement would be decomposed into two unimanual movements. Alternatively, if the bimanual movement is prepared after the imperative stimulus, the effects of the startle on the precued movement should be comparable to choice RT conditions, with shorter RTs than control

trials but longer RTs than startle trials in simple RT conditions. The two arms are prepared as a single, bimanual movement, and so, the arms should be initiated as synchronously on startle trials as control trials. The probability of a startle reflex should be lower than simple and comparable to choice conditions. Finally, the number of movement errors should be higher than in simple and comparable to choice conditions.

Methods

Participants

Twenty-three volunteer participants were tested from the university community. All participants reported being right-handed and had normal or corrected-to-normal vision. Data from only 18 participants (mean age of 24.7 ± 5.1 years, six female) were analysed [five participants lacked the startle reflex in simple RT conditions; see Carlsen et al. (2011) for detection and classification guidelines]. The research ethics board at the University of British Columbia approved the study, and participants gave informed written consent before participation.

Apparatus

Participants were seated at a table in a dark room, and each participant rested their head in a chin rest. On the surface of the table were two linear slides (Low Profile Redi-Rail, PBC Linear) that were perpendicular to the front edge of the table. The linear slides were 150 mm apart, and participants were seated so that their midsagittal plane was in the middle of the slides. Participants held the handles of the left and right slides with their left and right hands. The slides allowed forward and backward movements of the arms with minimal friction and prevented movements in other directions. There was an Optotrak marker at the top of each handle, and these were sampled at 750 Hz by an Optotrak system (3020; Northern Digital).

Virtual stimuli were projected on the surface of the table by an LCD monitor positioned over the table. Midway between the table and the monitor was a half-silvered mirror; it created the illusion that the stimuli appeared on the table. The stimuli created a three-row by two-column array of circle outlines (Fig. 2), and the two columns were aligned with the linear slides. The circles in the closest row to the participants were the two backward targets, and the two forward targets were the circles in the farthest row; the targets had a radius of 15.3 mm. The circles in the middle row were the home positions, and they had a radius of 3.4 mm. The distance from the centre of the home

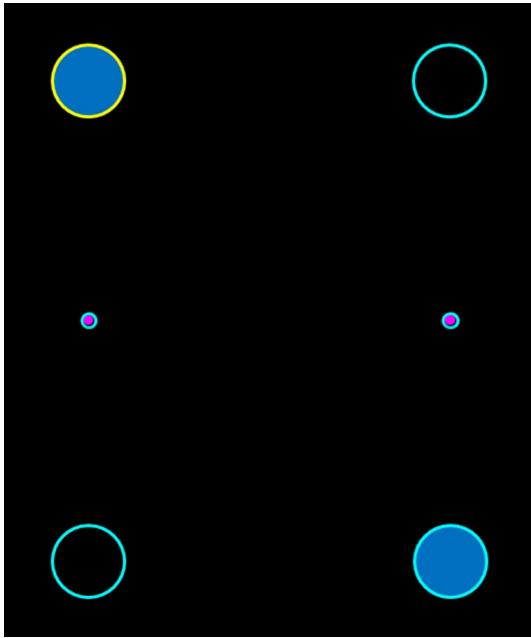


Fig. 2 Visual stimuli at the time of the imperative stimuli in the unilateral 2-choice condition. The left forward target was precued by changing the colour of the *outer circle* from *cyan* to *yellow* (colour figure online). In this example, the left forward target and the right backward target are illuminated as the imperative stimuli

positions to the centre of the forward or backward targets was 100 mm. Filling any of the circle outlines directly cued that target; this is subsequently referred to as illuminating a target.

Testing occurred in a dark room that prevented visual feedback of the participants' arms and the linear slides. The position of the handle for each slide was displayed on the surface of the table in real time as a magenta circle with a 1.7 mm radius. There was a 16.7 ms time lag between receiving the current positions of the Optotrak markers and displaying the feedback on the monitor that was determined by the 60 Hz refresh rate of the LCD monitor. To compensate for this lag, the positions of the markers in the next frame were predicted based on the current and previous positions.

Surface electrodes were used to collect electromyography (EMG) data bilaterally from the following three muscles: SCM (startle indicator), anterior deltoid (agonist for forward movements) and posterior deltoid (agonist for backward movements). The muscles on the left and right sides of the body were grounded to the left and right clavicles, respectively. The recording sites were scrubbed and cleansed to reduce electrical impedance. The EMG data were band-pass filtered between 30 and 1000 Hz, amplified (P511 AC Amplifier, Grass Technologies), sampled at 3000 Hz by an Optotrak Data Acquisition Unit (3020; Northern Digital), and then rectified.

Procedure

Trials began with the outlines of the four potential targets and the two home positions appearing on the surface of the table. The home positions were illuminated as a cue for the participants to move the handles into the home positions. Participants could not see their arms or the handles for the entire trial. They could always see two small circles that were displayed on the table surface to represent the positions of the handles in real time. A 1-2s variable foreperiod began when the handles were in the home positions. During the foreperiod, a fixation cross appeared between the home positions, and participants were instructed to fixate on it while they awaited the imperative stimuli. In simple RT blocks, the outlines of the correct targets would change colour (from cyan to yellow) during the foreperiod to encourage movement preparation before the imperative stimulus. Preprogramming was also encouraged in the block where only one target was precued. We will refer to this block as the unilateral 2-choice block, and the left, forward target was always precued during the foreperiod. Importantly, the right target was not precued, so participants did not know whether the target for the right arm would be the forward or backward target until the imperative stimuli.

The imperative stimuli consisted of illuminating the targets (by filling the circles in with blue) and sounding a 1000 Hz tone for 40 ms. The tone was 85.7 ± 1.29 dB on practice, and control trials and startle trials were 120.2 ± 0.44 dB. Participants were instructed to “react and hit the targets as quickly as possible”. The positions of the handles at the end of the bimanual movement were displayed after the 2.0 s recording interval of the Optotrak. These endpoints and the correct targets were displayed in green for a target hit and red for a target miss. Participants were encouraged to use this feedback to help them with subsequent trials.

Each trial was labelled as “good” or “bad”, with bad trials being excluded from subsequent analyses. The types of bad trials were different for control and startle trials. For control trials, types of bad trials were anticipation (RT < 100 ms), inattention (RT or movement time >500 ms) and asynchronous movement initiation (>60 ms RT difference between the arms). For startle trials, the only type of bad trials was anticipation (RT < 50 ms). Movements with asynchronous initiation were included as the precued movement may be released by the startle tone and the other arm initiated later. In total, 1.51 % of all control trials and 0.52 % of all startle trials were excluded. If it was a bad trial, then a message explained the reason to the participant. Every trial ended with a blank screen for 1 s.

A “speed score” was given to participants after every six good trials. This score gave participants feedback

Table 1 Movements performed in each of the five blocks in the experiment

	Simple	2-Choice	Unilateral 2-choice
Symmetric	Forward–Forward	Forward–Forward Backward–Backward	Forward–Forward
Asymmetric	Forward–Backward	Forward–Backward Backward–Forward	Forward–Backward

Symmetric and asymmetric movements were tested in separate blocks in the simple and 2-choice conditions. Both of these types of movements were combined in one block in the unilateral 2-choice condition. The target for the left arm is indicated before the hyphen, and the right arm's target is indicated after the hyphen. Forward–Backward, for example, means a forward movement with the left arm and a backward movement with the right arm

on their total response time (RT + movement time) and was intended to motivate them to react and hit the targets as quickly as possible. It was calculated by comparing the mean total response time of the last six good trials to the previous six good trials. The per cent change was calculated and multiplied by ten; for example, if the total response time decreased from 300 to 270 ms (a 10 % change), then the speed score would be -100 [$-100 = 1000 \times (270/300 - 1)$]. A multiple of ten was used to make the small changes in total response time (typically <5 %) more salient to the participants.

Design

The experiment consisted of testing bimanual symmetric and asymmetric movements in simple, 2-choice and unilateral 2-choice RT conditions. There were two simple blocks (Forward–Forward, Forward–Backward), two 2-choice blocks (symmetric, asymmetric) and one unilateral 2-choice block (unilateral 2-choice), for a total of five blocks (Table 1). Note that symmetric and asymmetric movements were tested in different blocks in simple and 2-choice conditions, whereas they were tested in the same block in the unilateral 2-choice condition. The order of these blocks was counterbalanced by the type of RT (simple, 2-choice, unilateral 2-choice). The blocks that fell within this counterbalance were randomised; for example, the order of the two 2-choice blocks (symmetric, asymmetric) was randomised.

Each block consisted of practice trials followed by test trials. In simple RT, there were 16 practice trials and 32 test trials. Four of the test trials were randomly selected as startle trials with the stipulation that two startle trials never occurred in a row. The same randomisation of startle trials was used for each participant. The number of test trials was doubled in 2-choice and unilateral 2-choice RT (16 practice, 64 test trials). There were two potential movements in these blocks, so each type of movement was used on half the trials. The order of these movements was randomised in each block. Eight of the test trials were randomly selected as startle trials, with four startle trials for each movement.

The number of practice trials on the participant's first block was doubled to 32.

There were two important aspects of the experimental design. First, movements were either forwards or backwards. We have previously tested bimanual movements that were in the same direction to either short- or long-amplitude targets (Blinch et al. 2014). The problem with those movements is that default forward movements could be preprogrammed even in choice conditions, as all movements begin in the same direction (Forgaard et al. 2011). Forward and backward movements were used in this experiment to prevent preprogramming in 2-choice conditions and for the arm without a precue in unilateral 2-choice. Second, the requirement of ensuring safe noise exposure from startle trials prevented us from testing all possible precues in unilateral 2-choice. Any of the four targets could have been precued: left forward, left backward, right forward or right backward. Deciding to precue only the left, forward target reduced the number of startle trials in the entire experiment from 64 to 32 trials.

Analysis

The position data from the Optotrak were filtered with a dual-pass, second-order, low-pass Butterworth filter with a cut-off frequency of 10 Hz. When an Optotrak marker was missing for four frames or less, the position was linearly interpolated. Velocity and acceleration in the forward–backward direction were calculated with a three-point central difference method. A trajectory analysis of control and startle trials was performed with emphasis on detecting movement errors, and this is described in the Results.

RT for each arm was calculated as the time from the imperative stimuli until movement onset. The difference between left and right arm RTs was the delta RT, and a negative delta RT indicated that the left arm was initiated before the right arm. Movement onset was determined by finding the first time after the imperative stimuli that forward or backward displacement exceeded 5 mm from the starting location. This is a relatively late criterion for movement initiation; for example, displacement exceeded

5 mm about 30 ms after the velocity exceeded 50 mm/s. This conservative measure was used to prevent small movements related to the startle reflex as opposed to the true movement onset from exceeding the criteria. Movement offset was determined by finding the first time after peak velocity that the absolute value of velocity was <50 mm/s. The difference between movement offset of the left and right arms was the delta total response time, and a negative value indicated that the left arm was terminated before the right arm.

Significant SCM EMG was determined by calculating a 99.999 % confidence interval (4.4172 standard deviations) from the SCM activity for 100 ms before the startle tone. This confidence interval was then compared to the SCM activity from 30 ms after the imperative stimuli to either 120 ms or movement onset, whichever was first. If SCM activity was outside the confidence interval, then the startle reflex was deemed to be present. This algorithm was also checked by visual inspection of all startle trials.

Mean RTs were calculated for each arm, and then, they were collapsed across arm. All dependent variables in 2-choice conditions were collapsed across the two symmetric movements (Forward–Forward, Backward–Backward), and they were collapsed across the two asymmetric movements (Forward–Backward, Backward–Forward). Probabilities were normalised with the arcsine square-root transformation before statistical analysis; the data reported are probabilities. Control and startle trials were analysed separately with three conditions (simple, unilateral 2-choice, 2-choice) by two symmetries (symmetric, asymmetric) repeated-measures ANOVAs. When local sphericity was violated (as indicated by Mauchly's test, $p < .10$), the Huynh–Feldt correction was used when the ϵ was greater than or equal to .75 and the Greenhouse–Geisser correction was used otherwise (Huynh and Feldt 1976). The uncorrected degrees of freedom and the ϵ values were reported (Huynh–Feldt ϵ_{HF} , Greenhouse–Geisser ϵ_{GG}).

Significant main effects were investigated with pairwise comparisons, and significant interactions were analysed with simple main effects on Symmetry. This post hoc analysis involved three paired-samples t tests that compared symmetric movements to asymmetric movements in the three conditions (simple, unilateral 2-choice, 2-choice). These tests allowed us to probe for asymmetric costs in simple, unilateral 2-choice and 2-choice conditions. The Sidak correction was used to control the familywise error rate of the analyses on main effects and interactions. The sizes of the bimanual asymmetric RT costs in unilateral 2-choice and 2-choice conditions were compared with a paired-samples t test. Effect size for paired-samples t tests are Cohen's d , calculated with the pooled standard deviation.

Reported values (unless otherwise noted) are means and 95 % within-participant confidence intervals (CIs; Cousineau 2005; Morey 2008).

Results

Smaller asymmetric cost in unilateral 2-choice than 2-choice

RTs on control trials had a significant main effect of Condition, $F(2,34) = 131$, $p < .001$, $\epsilon_{HF} = .76$, $\eta_p^2 = .89$. Simple RTs were shorter than 2-choice RTs ($p < .001$), and RTs in unilateral 2-choice and 2-choice conditions were comparable ($p = .987$; Fig. 3, left). Control RTs were also examined to determine which conditions had longer RTs for asymmetric movements compared to symmetric movements, or more specifically, a bimanual asymmetric RT cost. The interaction between Condition and Symmetry was investigated with simple main effects on Symmetry, $F(2,34) = 19$, $p < .001$, $\eta_p^2 = .53$. There was an asymmetric RT cost in 2-choice conditions (39.5 ms, CI [32.6,

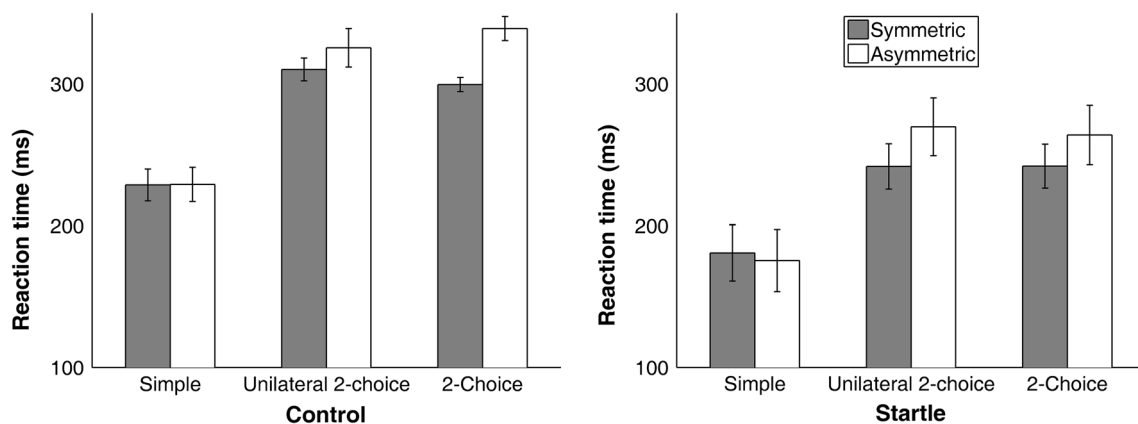


Fig. 3 Mean RTs for control trials (left) and startle trials (right). Error bars are 95 % within-participant CIs (Cousineau 2005; Morey 2008)

46.5], $p < .001$), and this cost was eliminated when the movements were prepared in advance in simple conditions (0.4 ms, CI [−10.0, 10.8], $p = .934$). Both of these findings have also been shown for movements with symmetric and asymmetric amplitudes (Blinch et al. 2014). The unique results were that there was an RT cost in unilateral 2-choice (15.3 ms, CI [4.6, 26.0], $p = .013$) and that this cost was smaller than in 2-choice, $t(17) = 4.3$, $p = .001$, $d = 1.20$.

Precued arm was initiated before the other arm on startle trials

The differences in movement onsets and offsets between the arms (delta RTs and delta total response times) were compared to determine whether the precued arm was initiated and terminated before the other arm in unilateral 2-choice. Delta RTs on control trials were relatively small (0.8 ms, 95 % between-participant CI [−1.2, 2.7]), and there were neither significant main effects nor interactions, $F_s < 3.1$, $p_s > .059$. Delta total response times on control trials were also relatively small (5.1 ms, 95 % between-participant CI [−1.2, 11.4]), and there were neither significant main effects nor interactions, $F_s < 0.9$, $p_s > .391$. These results suggested that bimanual movements were initiated and terminated relatively synchronously on control trials.

For delta RTs on startle trials, there was a significant main effect of Condition, $F(2,34) = 11$, $p < .001$, $\eta_p^2 = .39$. Bimanual movements in simple conditions were initiated relatively synchronously (−0.2 ms, CI [−2.5, 2.1]). The left arm was initiated 3.3 ms (CI [−6.8, 0.1]) before the right arm in 2-choice conditions, but the delta RTs were not significantly different from simple conditions ($p = .271$). In unilateral 2-choice, the left, precued arm was initiated 10.0 ms (CI [−13.6, −6.3]) before the right arm, and this was significantly different from simple conditions ($p < .001$) but not significantly different from 2-choice conditions ($p = .059$). We also noted a time difference between the precued arm and the other arm during movement execution. The precued arm arrived at all kinematics landmarks (first peak acceleration, peak velocity and second peak acceleration) approximately 20 ms before the other arm. For delta total response times, there was a significant main effect of Condition, $F(2,34) = 4.0$, $p = .038$, $\epsilon_{\text{HF}} = .82$, $\eta_p^2 = .19$. The left arm was terminated first by 4.3 ms (CI [−19.6, 10.9]) and 0.9 ms (CI [−10.0, 8.2]) in simple and 2-choice conditions, and the delta total response times in these conditions were not significantly different ($p = .960$). In unilateral 2-choice, the left, precued arm was terminated 24.9 ms (CI [−40.8, −9.0]) before the right arm, and this was significantly different from 2-choice conditions ($p = .026$) but not significantly different from simple conditions ($p = .252$).

Startle RTs and the probabilities of a startle reflex in unilateral 2-choice were comparable to 2-choice and not simple conditions

RTs on startle trials in all conditions were expected to be shorter than control trials due to the start-react effect (compare Fig. 3 right to left). There was a significant main effect of Condition, $F(2,34) = 24$, $p < .001$, $\eta_p^2 = .59$, and RTs in simple conditions (178 ms, CI [156, 201]) were shorter than unilateral 2-choice (256 ms, CI [241, 271], $p = .002$) and 2-choice (253 ms, CI [234, 272], $p = .003$).² RTs were not significantly different in unilateral 2-choice and 2-choice conditions, $p = .989$. There was also a significant main effect of Symmetry, $F(1,17) = 11$, $p = .004$, $\eta_p^2 = .40$, and a significant Condition by Symmetry interaction, $F(2,34) = 4.7$, $p < .029$, $\epsilon_{\text{GG}} = .69$, $\eta_p^2 = .22$. The Condition by Symmetry was investigated with simple main effects on Symmetry. There was an asymmetric RT cost in 2-choice conditions (22.0 ms, CI [8.7, 35.3], $p < .005$), and this cost was eliminated when the movements were prepared in advance in simple conditions (−5.4 ms, CI [−20.2, 9.4], $p = .330$). There was also an asymmetric RT cost in unilateral 2-choice condition (28.0 ms, CI [5.7, 50.3], $p = .019$), and this cost was not significantly different than the cost in 2-choice, $t(17) = 0.5$, $p = .651$, $d = 0.16$. It is interesting that these costs were not significantly different on startle trials, whereas the cost in unilateral 2-choice was smaller than 2-choice on control trials. Unfortunately, it is difficult to compare movement preparation on startle trials with choice (2-choice and unilateral 2-choice) to the control trials. This is because movement preparation after the imperative stimulus was disrupted by the startle tone. The disruption caused an increase in movement errors, which are analysed below.

For the probabilities of a startle reflex on startle trials, there was a significant main effect of Condition, $F(2,34) = 3.5$, $p = .040$, $\eta_p^2 = .17$, but all pairwise comparisons were not significant. The main effect was likely caused

² Mean premotor RTs (interval from the imperative stimulus until EMG onset) on startle trials are typically less than 100 ms in simple conditions (Carlsen et al. 2011). Unfortunately, premotor RTs on startle trials could not be calculated in the present experiment. The challenge was that the startle reflex for some participants appeared in the deltoids and overlapped with the muscle activation for the movement. This made it difficult to determine whether the startle reflex or the motor command caused the EMG. Premotor RTs on startle trials were estimated by subtracting the motor RT (interval from EMG onset to initiation of the response) on control trials from the startle RTs (premotor RT = RT − motor RT). The motor RT on control trials was 83.8 ms, 95 % between-participant CI [78.9, 88.7]. The estimated premotor startle RTs were 94 ms in simple (94 = 178−84), 172 ms in unilateral 2-choice (172 = 256−84) and 169 ms in 2-choice (169 = 253−84). Therefore, the premotor startle RT in simple conditions was comparable to previous experiments.

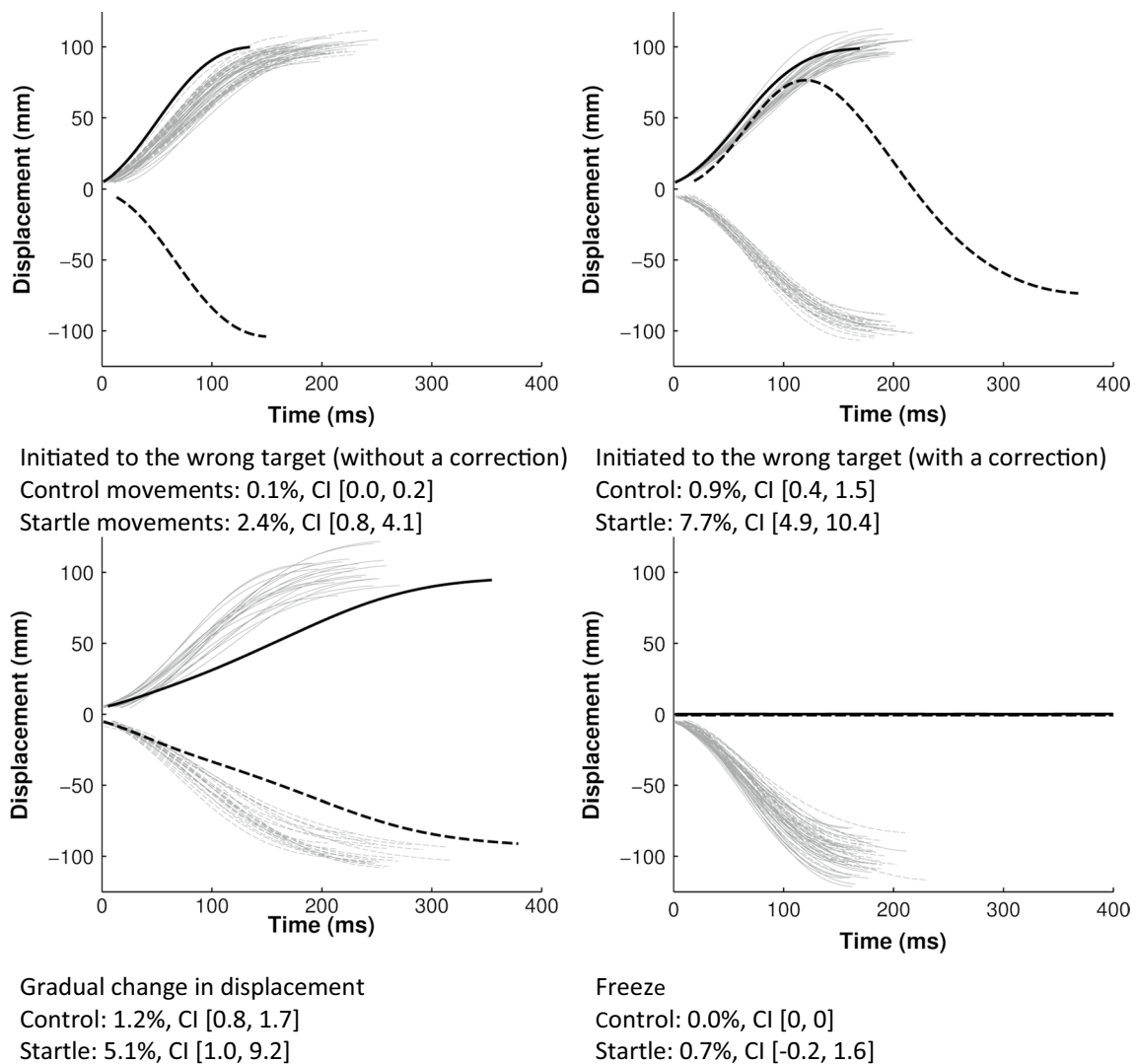


Fig. 4 Displacement by time plots of the four types of movement errors. In each plot, the left arm of a representative movement error on a startle trial is shown with a *black, solid line* and the right arm with a *black, dashed line*. The *grey trials* (left arm, *solid line*; right

arm, *dashed line*) are control trials without errors from the same movement, condition and participant. The percentages below each plot are the mean occurrences (and between-participant CIs) of that type of movement error for control and startle trials

by a greater probability of a startle reflex in simple (86.6 %, CI [75.6, 97.6]) compared to 2-choice (71.9 %, CI [63.0, 80.7]) and unilateral 2-choice conditions (72.9 %, CI [63.6, 82.3]). It has been shown that the probability of a startle reflex is initially comparable in simple and choice conditions. With exposure to more startle trials, however, the probability of a startle reflex in choice conditions decrease because of the inability to fully prepare movements in advance (Maslovat et al. 2012). It is possible that the startle reflex began to decrease in this experiment, in 2-choice and unilateral 2-choice, but not enough for the pairwise comparisons to be statistically significant. The probabilities of a startle reflex were not significantly different in unilateral 2-choice and 2-choice conditions, $p = .981$.

Movement errors on startle trials in 2-choice and for the arm without the precue in unilateral 2-choice

Trajectories on control and startle trials for the left and right arms were visually examined to identify movement errors. We identified four types of movement errors after looking at the trajectories for each trial: (1) primary sub-movements (Khan et al. 2006) that were initiated to the wrong target without a subsequent correction, (2) movements that were initiated to the wrong target with a correction, (3) movements with a gradual change in displacement and (4) freezes where no movement was made. Examples of movement errors and their occurrence in startle trials are shown in Fig. 4. The probability of a movement error was

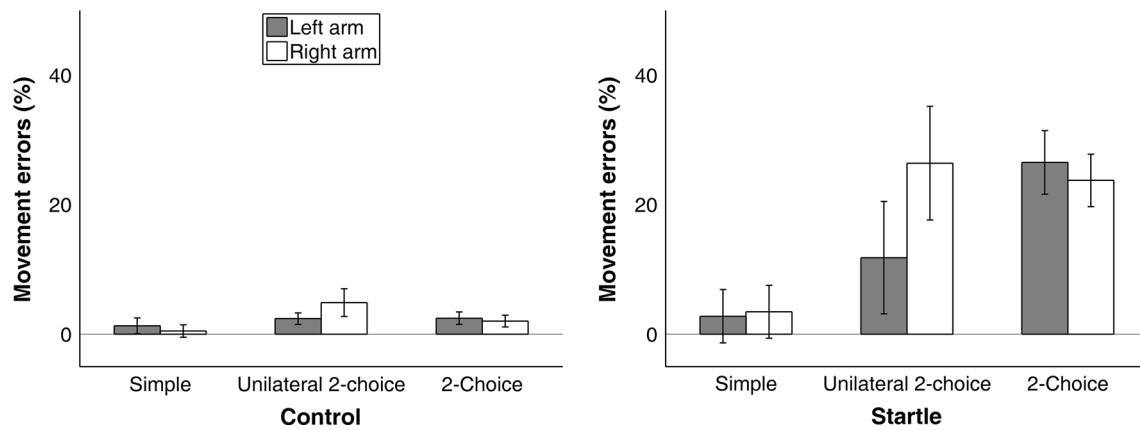


Fig. 5 Mean percentages of movement errors for control trials (left) and startle trials (right). Error bars are 95 % within-participant CIs (Cousineau 2005; Morey 2008)

calculated for each condition, movement and arm. These were normalised with the arcsine square-root transformation before statistical analysis. Control and startle trials were analysed separately with Condition (simple, unilateral 2-choice, 2-choice) by Symmetry (symmetric, asymmetric) by Arm (left, right) repeated-measures ANOVAs. The values reported are percentages.

On control trials, there were relatively few movement errors (Fig. 5, left). There was a significant main effect of Symmetry, $F(1,17) = 11$, $p = .004$, $\eta_p^2 = .40$, that showed there were more movement errors on asymmetric control trials (2.9 %, CI [2.4, 3.4]) than symmetric control trials (1.6 %, CI [1.1, 2.1]). There was also a significant Condition by Arm interaction, $F(2,34) = 14$, $p < .001$, $\eta_p^2 = .45$, that was analysed with simple main effects on Condition. This post hoc analysis involved three paired-samples t tests that compared the movement errors of the left arm in the three conditions (simple, unilateral 2-choice, 2-choice) and another three t tests that compared the right arm in the three conditions. The probabilities of movement errors for the left arm were not significantly different in simple, unilateral 2-choice and 2-choice conditions ($ps > .216$). For the right arm, simple conditions had the fewest movement errors (0.5 %, CI [−0.5, 1.5]); there were significantly more in 2-choice (2.0 %, CI [1.1, 2.9], $p = .016$) and significantly more than that in unilateral 2-choice (4.9 %, CI [2.7, 7.0], $p = .011$). Despite these small but significant differences, there were relatively few movement errors on control trials; the grand mean was 2.3, 95 % between-participant CI [1.3, 3.2].

For startle trials (Fig. 5, right), there was a significant Condition by Arm interaction, $F(2,34) = 5.1$, $p = .029$, $\varepsilon_{GG} = .62$, $\eta_p^2 = .23$, that was investigated with simple main effects on Condition. Both the left and right arms had low probabilities of movement errors in simple conditions (2.8 %, CI [−1.4, 6.9]; 3.5 %, CI [−0.6, 7.6]) and

significantly higher probabilities in 2-choice (26.5 %, CI [21.6, 31.4], $p < .001$; 23.7 %, CI [19.7, 31.4], $p < .001$). In the unilateral 2-choice condition, the left, precued arm had a probability of a movement error (11.8 %, CI [3.1, 20.5]) that was significantly lower than 2-choice conditions, $p = .006$, and not significantly different than simple conditions, $p = .052$. The right arm had a probability of a movement error (26.4 %, CI [17.6, 35.2]) that was significantly higher than simple, $p = .001$, and not significantly different than 2-choice, $p = .998$.

Discussion

Movement preparation was longer for bimanual asymmetric movements than bimanual symmetric movements in 2-choice RT conditions. This bimanual asymmetric cost was eliminated in simple RT conditions. Both of these results replicated previous findings for bimanual movements in simple and choice conditions (Blinch et al. 2014). A vital condition in the present experiment was unilateral 2-choice, in which one target was precued. The asymmetric cost was smaller with a unilateral precue than in 2-choice conditions. This attenuation was presumably caused by the precue that encouraged movement preparation before the imperative stimulus. The question of interest was: What was prepared before the imperative stimulus when one target was precued?

Temporal separation of movement preparation

We began with two predictions of how movement preparation may change when one arm is precued (Fig. 1). One prediction involved movement preparation of the precued arm *before* the imperative stimulus and preparation of the other arm *after* the imperative stimulus (Fig. 1, left).

This should eliminate the asymmetric cost, as the asymmetric movements are prepared at different times. The other prediction involved the preparation of both arms after the imperative stimulus (Fig. 1, right). This is similar to 2-choice RT conditions, and so, the asymmetric cost should be comparable in unilateral 2-choice and 2-choice conditions. The results in the unilateral 2-choice condition showed a significant asymmetric cost that was smaller than the cost in the 2-choice conditions. Therefore, the degree of movement preparation in the unilateral 2-choice condition was somewhere in between the possibilities we initially proposed. The asymmetric cost was not eliminated, suggesting that the precued arm was not fully prepared in advance. The cost, however, was smaller than the cost in the 2-choice condition and suggests that there must have been partial preparation of the stage that caused the asymmetric cost before the imperative stimulus.

Probing movement preparation

The attenuation of the asymmetric cost in the unilateral 2-choice condition suggested that the precued arm was partially prepared before the imperative stimulus. The pattern of movement errors on startle trials offered insight into how movement preparation was split before and after the imperative stimulus in the unilateral 2-choice condition. First off, there were relatively few movement errors on startle trials in simple conditions. The required movement was likely fully prepared in advance and then released by the startle tone. In 2-choice conditions, there were a higher percentage of movement errors. This was likely because the movements were selected after the imperative stimulus and the startle tone disrupted response selection during this time. The critical results are the movement errors on startle trials in unilateral 2-choice. In unilateral 2-choice, the arm without the precue had significantly more movement errors than the same arm in simple conditions. Therefore, the movement for the arm without the precue was likely selected after the imperative stimulus, and this preparation was disrupted by the startle tone. Interestingly, there were fewer movement errors for the precued arm compared to the same arm in 2-choice conditions. This suggests that the movement for the precued arm was selected before the imperative stimulus and avoided the disruption by the startle tone. If the precued movement was selected in advance, then the precued target must have also been discriminated before the imperative stimulus. The target for the other arm was discriminated, and the movement was selected after the imperative stimulus.

The pattern of movement errors, therefore, suggests that target discrimination and response selection of each arm were temporally separated before and after the imperative stimulus. If the asymmetric cost was caused

by either target discrimination or response selection, then the cost should have been eliminated in the unilateral 2-choice condition. As the asymmetric cost was not eliminated, it was likely caused by the remaining preparation processes—those related to response programming. Furthermore, the attenuation of the asymmetric cost suggests that response programming was partially divided before and after the imperative stimulus. The precued movement was partially prepared before the imperative stimulus, and this partial preprogramming decreased the asymmetric cost. It may not have been possible to fully preprogram the precued movement because of the constraint of bimanual movements. That is, bimanual movements are not simply the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit (Kelso et al. 1979; Swinnen and Wenderoth 2004). Therefore, both arms needed to be programmed into a single, bimanual movement after the imperative stimulus when the movement for each arm had been selected. Programming two different unimanual movements into a bimanual asymmetric movement caused the asymmetric cost. The cost in the unilateral 2-choice condition was decreased by the partial preprogramming of the precued arm.

The difference in movement initiation between the two arms on startle trials provides further evidence that the precued arm was partially programmed before the imperative stimulus. If the precued arm was fully preprogrammed (Fig. 1, left), then the precued arm should have been initiated with startle RTs comparable to simple conditions and the other arm should have been initiated with longer startle RTs, comparable to 2-choice conditions. The mean difference in startle RTs between simple and 2-choice conditions was 75 ms. In comparison, the precued arm was initiated only 10 ms before the other arm. This small inter-limb difference reaction time can be explained by partial preprogramming of the precued arm. The partial preprogramming provided a slight advantage for the precued arm, and even though it needed to be programmed into an integrated movement with the other, it was ready to be initiated slightly before the other arm.

One result of preparing bimanual movements as a unified structure is that movement initiation and termination of each arm occur relatively synchronously (Kelso et al. 1979; Marteniuk et al. 1984). This requirement for temporal coupling may be another reason that the precued arm was partially preprogrammed; programming of a temporally coupled bimanual movement could only be finished after the imperative stimulus when both targets were known. Movements with the left and right arms on control trials were temporally coupled, as they were initiated and terminated relatively synchronously. This was the case even though participants were not explicitly instructed on

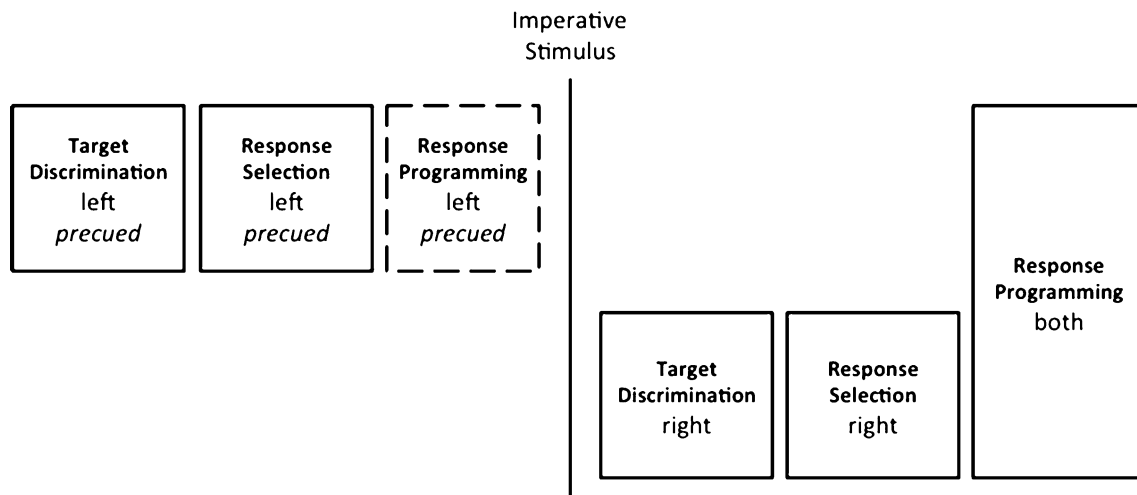


Fig. 6 Movement preparation in the unilateral 2-choice condition when the left target is precued. The stages of information processing are target discrimination, response selection and response programming. The precued movement is partially programmed before the

imperative stimulus (distinguished by the *dotted box*). The two unimanual movements are then programmed as a single, bimanual movement after the imperative stimulus. This is shown as a large box to emphasise that a single bimanual movement is programmed

how to coordinate the movements with their left and right arms; they were simply told to “react and hit the targets as quickly as possible”. Participants were told to initiate their movements more synchronously when the difference in movement initiation on control trials was larger than 60 ms. This, however, occurred on only 13 out of 4,032 control, test trials for all participants. Kelso et al. (1979) found that bimanual reaching movements were initiated relatively synchronously whether or not participants were instructed to start the movements simultaneously. It is possible to make asynchronous bimanual movements (e.g. Maslovat et al. 2009; Shea et al. 2012), but temporal coupling seems to be a default characteristic of bimanual coordination.

To review, our hypothesis for movement preparation in the unilateral 2-choice condition is detailed in Fig. 6. The precued target is discriminated, and the movement is selected and partially programmed before the imperative stimulus. After the imperative stimulus, the target for the other arm is discriminated and the movement is selected. A single, bimanual movement is then programmed. It takes longer to program two different movements into a bimanual asymmetric movement than two of the same movements into a bimanual symmetric movement. Thus, the asymmetric cost is caused by increased processing demands on response programming.

Other investigators have provided neurophysiological evidence of partial preparation before the imperative stimulus when a unimanual movement is partially precued (Cisek and Kalaska 2005; Leuthold et al. 1996; Ulrich et al. 1998). Leuthold et al. and Ulrich et al. investigated the cause of the decrease in RTs with the precuing of movement parameters [known as the precue effect (Rosenbaum

1980, 1983)]. They used the lateralised readiness potential to measure the duration of response programming to determine whether precuing some of the movement parameters caused motor preparation before the imperative stimulus. Both studies found that precuing the hand that would make the unimanual movement allowed some motor preparation before the imperative stimulus. They, therefore, argued that at least some of the precue effect occurred during motor preparation. In the present study, we refer to beginning motor preparation before the imperative stimulus as partial preprogramming. It is still unclear exactly what processing occurs during partial preprogramming; however, Leuthold et al. and Ulrich et al. argued that it involves muscle-specific preparation of the forthcoming response. Cisek and Kalaska showed that when primates were precued with two potential targets for one arm, neurons in the dorsal premotor cortex simultaneously represented the directions of both targets.

Another study that should be compared to our results was by Diedrichsen et al. (2001). They examined the asymmetric costs for symbolically and directly cued movements with and without one precue. Their experiments can also offer insight into movement preparation before the imperative stimulus. Similar to our logic, they reasoned that a decrease in a bimanual asymmetric cost with one precue would reveal interference during movement preparation of asymmetric movements. Diedrichsen et al. found a large asymmetric cost with symbolic cues (55 ms, Experiment 1) that was eliminated with one precue. They argued that the cost was caused by symbolic cues that placed increased processing demands on response selection, which has been confirmed by several studies (reviewed by Wenderoth and

Weigelt 2009). Precuing one target likely temporally separated the response selection of each arm. The movement for the precued arm was selected before the imperative stimulus, and the movement for the other arm was selected after. This avoided the bimanual interference during RT and eliminated the asymmetric cost. In the present study, we also argue that there was preselection of the precued arm. With direct cues, Diedrichsen et al. (2001) found a 6 ms bimanual asymmetric cost that was not significant (Experiment 1). RTs were also not significantly different with or without one precue. Later studies, including one by Diedrichsen and colleagues, found that there is a small asymmetric cost (15–20 ms) with direct cues (Blinch et al. 2014; Diedrichsen et al. 2006; Heuer and Klein 2006, Experiment 2). These studies, unfortunately, did not include a condition with one precue.

Unification of bimanual movements

Previous research has argued that asymmetric movements place increased processing demands on response programming (Blinch et al. 2014; Heuer 1986; Heuer and Klein 2006; Stelmach et al. 1988). The explanations of how asymmetric movements are programmed have differed; for example, Heuer and colleagues argued that there is crosstalk between concurrent processes of parameter specification of asymmetric movements that cause transient interference (Heuer 1986; Heuer and Klein 2006). It seems that the challenge with bimanual asymmetric movements comes down to programming two different movements at the same time. The results from the present experiment support that the asymmetric cost was caused by increased demands on response programming, but they also offer insight into how bimanual movements are programmed. We attempted to temporally separate the movement preparation of each arm by precuing one target. This allowed the precued movement to be selected before the imperative stimulus, but the precued movement was not fully programmed before the imperative stimulus. Complete programming of the precued movement waited until after the imperative stimulus when the response for the other arm was selected. Selecting the movements for each arm allowed them to be programmed as a single, bimanual movement. This reinforces the notion that bimanual movements are not simply the sum of two unimanual movements. Our results argue that the critical unification of a bimanual movement occurred during response programming in the unilateral 2-choice condition. Responses for each arm could be selected at different time, but the movements could not be fully programmed separately. Response programming of a bimanual movement necessitates that the movement of each arm is combined into a single response rather than two independent ones.

The results in the unilateral 2-choice condition suggested that the bimanual movement was unified during response programming and not during response selection. Precuing the left target encouraged the left movement to be selected before the imperative stimulus and the right movement to be selected after the imperative stimulus. In most experiments, however, the movements for each arm of a bimanual movement are cued at the same time (e.g. Blinch et al. 2014; Heuer and Klein 2006; Kelso et al. 1979). Therefore, the two movements are likely selected at the same time. The atypical movement preparation with a precue in the present study may have caused the bimanual unification to occur during response programming instead of response selection. When the two targets of a bimanual movement are selected at the same time, as in the 2-choice conditions, the unification of the bimanual movement could occur during response selection or response programming. Our protocol and results cannot determine exactly when the bimanual unification occurred in the 2-choice conditions; this remains a fascinating area of investigation for future studies.

Regardless of when the bimanual integration occurs, the results suggest that there is a cost to unify two different unimanual movements into a bimanual asymmetric movement compared to two identical movements into a bimanual symmetric movement. Other studies have shown that changing how bimanual movements are conceptualised can eliminate various forms of bimanual asymmetric costs (reviewed by Swinnen and Wenderoth 2004). This has been done by having a single goal for both arms (Franz et al. 2001) or by having a single stimulus that represents the positions of each arm. The latter has been shown for continuous (e.g. Kovacs et al. 2009; Swinnen et al. 1997) as well as discrete bimanual movements (e.g. Franz and McCormick 2010; Shea et al. 2012; White and Diedrichsen 2010). Franz and McCormick suggested that unified conceptualisations can release attentional control from lower levels of the sensorimotor system and prevent interference from those levels. Shea et al. reasoned that unified conceptualisations decrease or eliminate the interference caused by attentional and visual-perceptual factors.

It is possible that a unified conceptualisation might decrease the asymmetric cost in the present experiment. The asymmetric cost was caused by the need to unify two different unimanual movements into a bimanual asymmetric movement. The processing with a unified conceptualisation may always be on a single representation of the bimanual movement. This would bypass the unification of two unimanual movements into one bimanual movement and the asymmetric cost. Overall, changes in when bimanual unification occurs or whether bimanual unification is needed suggest that the preparation of bimanual movements is malleable.

In summary, the bimanual asymmetric cost was smaller in the unilateral 2-choice than the 2-choice conditions. This suggests that the precued movement was partially prepared before the imperative stimulus. Startle trials were included to determine what was prepared before the imperative stimulus in unilateral 2-choice. The probabilities of movement errors on startle trials suggested that the precued arm was selected before the imperative stimulus. The results from control and startle trials suggest that the precued movement was partially preprogrammed and that the partial preprogramming decreased the size of the asymmetric cost. This also implies that the asymmetric cost was caused by increased processing demands on response programming. Overall, the results support the notion that bimanual movements are not the sum of two unimanual movements; instead, the two arms of a bimanual movement are unified into a functional unit. When one target is precued, this critical unification likely occurs during response programming.

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