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Problems in planning bimanually incongruent grasp postures relate to simultaneous response specification processes

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ABSTRACT

The purpose of the current experiments was to examine whether the problems associated with grasp posture planning during bimanually incongruent movements are due to crosstalk at the motor programming level. Participants performed a grasping and placing task in which they grasped two objects from a table and placed them onto a board to targets that required identical (congruent) or non-identical degrees of rotation (incongruent). The interval between the presentation of the first stimulus and the second stimulus (stimulus onset asynchrony: SOA) was manipulated. Results demonstrate that the problems associated with bimanually incongruent grasp posture planning are reduced at SOA durations longer than 1000 ms, indicating that the costs associated with bimanual incongruent movements arise from crosstalk at the motor programming level. In addition, reach-to-grasp times were shorter, and interlimb limb coupling was higher, for congruent, compared to incongruent, object end-orientation conditions in both Experiment 1 and 2. The bimanual interference observed during reach-to-grasp execution is postulated to arise from limitations in the visual motor system or from conceptual language representations. The present results emphasize that bimanual interference arises from constraints active at multiple levels of the neurobiological–cognitive system.

1. Introduction

Many of our everyday activities involve using our two hands in a coordinated fashion. In some bimanual tasks, such as breaststroke swimming, the limbs produce very similar motor outputs. However, in other tasks (such as buttoning a shirt, or striking a match), the limbs perform markedly different actions. Interlimb coupling is a predominant constraint in both the spatial and temporal domains (see Franz, 2003 for a review). During tasks in which the left and right hands perform different actions (incongruent, e.g., circles paired with lines, or circles paired with squares) each hand tends to take on some of the spatial characteristics of the other hand (Franz, 2003; Franz, Zelaznik, & Mccabe, 1991). Another robust observation is that the individuals generally take longer to initiate and execute bimanually incongruent, compared to congruent, actions (Bingham, Hughes, & Mon-Williams, 2008; Hughes & Franz, 2008; Kelso, Southard, & Goodman, 1979; Kunde & Weigelt, 2005).

Over the years, researchers have sought to identify the source of interference during bimanually incongruent movements. One of the earliest explanations was that the increased motor planning and execution costs associated with bimanually incongruent movements arise from cross-talk during the specification of two unequal parameter values (Heuer, Spijkers, Kleinsorge, van der Loo, & Steglich, 1998; Spijkers & Heuer, 1995; Spijkers, Heuer, Steglich, & Kleinsorge, 2000). Evidence in support of the transient nature of coupling (i.e., transient programming coupling hypothesis, Heuer, 1986, 1993) at the motor programming level of bimanually performed amplitudes was provided by Spijkers, Heuer, Kleinsorge, and van der Loo (1997). In that study participants performed bimanual reaching movements to targets of same (10–10 cm, 20–20 cm) or different (10–20 cm, 20–10 cm) amplitudes. In addition, the interval between the presentation of the movement goals (precue signal) and the imperative signal was varied (0, 250, 500 and 750 ms in Exp 1; 0, 125, 250, 375, 500, 750 and 1000 ms in Exp 2). Spijkers et al. (1997) hypothesized that short precueing intervals would not afford sufficient time for complete parameter

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programming. Thus, programming would occur during the reaction time interval, resulting in longer reaction times for different than for same amplitude movements. In contrast, programming of same or different amplitudes could be completed at long precueing intervals, and as such there should be no reaction time difference between these two conditions. Consistent with their hypothesis, Spijkers et al. (1997) found that the reaction time difference between movements of same and different amplitudes decreased as a function of the preparation interval, indicating that the costs associated with bimanual incongruent movements arise from crosstalk at the programming level.

This account of bimanual interference was, however, challenged by a series of studies that manipulated the manner in which the movement end-goals were cued (Diedrichsen, Hazeltine, Kennerley, & Ivry, 2001; Diedrichsen, Ivry, Hazeltine, Kennerley, & Cohen, 2003; Hazeltine, Diedrichsen, Kennerley, & Ivry, 2003). Replicating previous work (Heuer et al., 1998; Spijkers et al., 1997), responses were initiated much faster during congruent compared to incongruent conditions when the targets were symbolically cued (e.g., visual representation of movement amplitude). However, when the targets were cued directly (e.g., a circular light that appeared to the side of the target), the planning and movement costs associated with bimanually incongruent movements were reduced or even eliminated. The authors argued that the advantage observed during congruent movements relates to processes involved in processing symbolic cues (e.g., stimulus identification, response selection), rather than the concurrent programming of two different actions.

Motivated by this corpus of work, research from our laboratories has investigated whether limitations in bimanual grasp posture planning share similar underlying mechanisms as those observed during bimanual aiming movements. In general, examinations of bimanual grasp posture planning have shown that participants are sensitive to bimanual spatial coupling (i.e., grasping objects with identical postures) as well as comfortable final postures (i.e., end-state comfort) (Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; Hughes, Reissig, & Seegelke, 2011; Weigelt, Kunde, & Prinz, 2006). When the end-goals of both hands are congruent, participants will adopt grips that allow them to satisfy both end-state comfort and bimanual coupling (Hughes & Franz, 2008; Weigelt et al., 2006). However, when the end-goals for the two hands are incongruent, neither bimanual coupling constraint nor end-state comfort emerge as a predominant constraint (Hughes & Franz, 2008; Hughes, Haddad et al., 2011; Hughes, Reissig et al., 2011).

Our initial foray into this line of work examined whether limitations in bimanual grasp posture planning are also due to goal-selection conflicts (Hughes, Seegelke, Reissig, & Schütz, 2012). Motivated by the work of Diedrichsen and colleagues (Diedrichsen et al., 2001, 2003; Hazeltine et al., 2003), we manipulated the manner in which the action end-goals were cued (symbolic cueing vs. direct cueing). In accordance with previous work we expected that cueing the movement goals in a symbolic fashion would result in conflicts related to the translation of symbolic cues into response codes during incongruent conditions, whereas interference in goal-selection would be minimized for directly cued movement goals. However, contrary to our initial expectations, there was no advantage in grasp posture planning for the direct cueing condition, indicating that limitations in bimanual grasp posture planning do not arise from stimulus identification or response selection conflicts associated with the translation of symbolic cues into action responses.

The purpose of the current experiments was hence to examine whether the problems associated with grasp posture planning during bimanually incongruent movements are due to crosstalk at the motor programming level (i.e., during the specification of two unequal parameter values), as previously found in bimanual reaching movements. In accordance with previous studies from our laboratory, the task required participants to perform a bimanual grasping and placing task in which they were to grasp two objects from a table and place them onto a board to targets that required identical (congruent) or non-identical (incongruent) degrees of rotation. Similar to Spijkers et al. (1997) we manipulated the interval between the presentation of the first and the second stimulus (stimulus onset asynchrony: SOA). We hypothesized that participants would be less able to satisfy grasp posture planning constraints (i.e., bimanual spatial coupling and/or end-state comfort, depending on condition) when the stimuli were presented simultaneously or separated by short time intervals, but that crosstalk (at the programming level) would be reduced or absent at longer SOA durations. If this hypothesis is correct, then the grasp posture planning congruency difference (i.e., between congruent and incongruent object end-orientation conditions) should decrease as a function of SOA duration. This finding would indicate that the costs associated with bimanual grasp posture planning arise from crosstalk at the programming level.

During our investigations into bimanual grasping and placing, we have repeatedly reported a reduction in hand interlimb coupling values during the reach-to-grasp and grasp-to-place phases for movements to incongruent, compared to congruent, object end-orientation conditions (Hughes, Haddad et al., 2011; Hughes, Reissig et al., 2011; Hughes et al., 2012). The manipulation of SOA duration employed in the current study afforded the possibility to examine whether limitations in bimanual execution arise from transient parametric coupling. Indeed, if the decrease in hand interlimb coupling during the execution of bimanually incongruent movements arises from interference between concurrent processes of parametric specification, it would be expected that SOA duration would have a strong effect on interlimb coupling. Specifically, short precueing intervals would not afford sufficient time for complete programming parametric specification of either bimanually congruent or incongruent movements, and as such the hands would be less coupled during incongruent than congruent object end-orientation conditions. In contrast, participants should be able to program the individual parameters for the two hands at long precueing intervals, and as such there should be no interlimb coupling difference between conditions with congruent and incongruent object end-orientations.

2. Experiment 1: Methods

2.1. Participants

Eighteen individuals were recruited to participate in the experiment. The dataset from three participants were removed prior to analysis because the participants were not able follow the instructions to move bimanually. This left us with a sample of fifteen right-handed participants (mean age = 25.07 years, SD = 4.57, SD = 6.45, 7 men and 8 women). Participants had normal or corrected to normal vision, and did not have any known neuromuscular disorders. The methodology and consent form for this study were approved by the Bielefeld University Institutional Review Board, and conformed to the declaration of Helsinki.

2.2. Apparatus

Participants stood in front of a custom built placement board (1.5 m × 0.4 m) that was braced by two legs (Fig. 1a). The placing board was adjusted to shoulder height, and the center of the board was oriented so that it coincided with the midline of the participants. On each side of the board were four white target circles

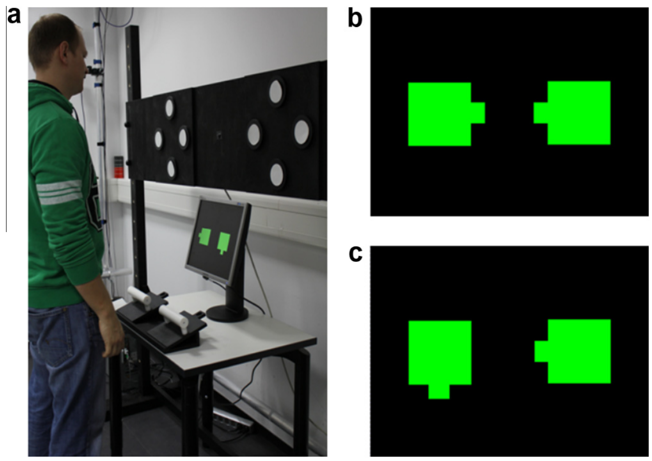

Fig. 1. (a) Side view of the experimental set up. Exemplar of the stimuli during (b) congruent and (c) incongruent conditions.

(10 cm in diameter), which required that the objects be rotated either 0°, 90° internally, 180°, or 90° externally.[1] The manipulated objects were two square wooden blocks (17.8 cm × 17.8 cm × 3.8 cm) that had a 3.8 cm square protruding from one of the sides. The objects had a handle affixed to the center of the main body that allowed participants to either use an underhand or overhand grip. The objects were placed on a small table (50 cm × 15 cm × 5 cm), 40 cm in front of the 43 cm computer display (SyncMaster 943T, Samsung) and positioned so that the protrusions always faced upwards.

Three-dimensional movement kinematics were recorded at 200 Hz using an optical motion capture system (VICON Motion System, Oxford, UK), consisting of ten Bonita cameras. Three reflective markers were placed on each object to obtain object motion, and a cluster of three markers was also placed on the wrist of each hand (the distal end of dorsal third metacarpal (MCP), the styloid process of ulna (WRP), and the styloid process of radius (WRT) to collect wrist motion. Each trial was recorded using a Sony DCR-HC36 digital video camera (synchronized with the VICON motion capture system) that was placed above the apparatus, providing a bird's eye view of the apparatus and the participant. The digital video camera was used to record grasping postures.

2.3. Procedure

Participants were instructed to lift the objects from the table and align them on the placement board so that the protrusion of each object was placed over the appropriate white target circle, as indicated by the stimuli (Fig. 1b and c). They were informed to grasp the left object with the left hand and place it to the left side of the board, and the right object with the right hand and place it to the right side of the board. In addition, participants were explicitly instructed to wait until both stimuli had been presented before grasping the objects, and to move both hands at the same time. Participants were told that final object end-orientation accuracy was of utmost importance, and were also instructed to perform the task as quickly as possible.

At the beginning of each trial, participants placed both hands by their sides. One thousand milliseconds later, the word German word for Attention ("Achtung") was displayed on the computer monitor. After a random interval (ranging from 1500 ms to 2500 ms) the first stimulus was presented. Depending on SOA condition, the second stimulus was either presented simultaneously (SOA = 0 ms), or after a 1000 ms or 2000 ms time delay. The order of the stimulus presentation was manipulated, with either the left stimuli presented first, followed by the right Stimuli or vice versa. After both stimuli were displayed, participants grasped and moved the objects to the instructed end-orientations on the placement board. The factor SOA was blocked and the order of blocks was randomized across participants. Within each block, the object end-orientation and SOA location were presented in a completely randomized fashion. Between each testing block, there was a rest period of 2 min.

Participants performed a total of 96 unique trials, consisting of 16 object end-orientations, 3 SOA's (0 ms, 1000 ms, 2000 ms) and 2 SOA locations (left stimulus first, right stimulus first). The entire testing session, including informed consent, lasted approximately 45 min.

2.4. Data and statistical analysis

In line with previous experiments using a similar experimental set up (Hughes, Haddad et al., 2011; Hughes, Reissig et al., 2011; Hughes et al., 2012) the data were first separated into congruent (objects required identical degrees of rotation) and incongruent (objects required different degrees of rotation) object end-orientation conditions. In addition, the 16 possible conditions were separated into two categories. The first constraint satisfaction category included the conditions where it was possible for the hands to (1) satisfy end-state comfort for one hand, (2) adopt identical initial grasp postures, or (3) adopt identical initial grasp postures and satisfy end-state comfort for both hands. The second constraint satisfaction category included the conditions where it was only possible to (1) adopt identical initial grasp postures or (2) satisfy end-state comfort for both hands. The first constraint satisfaction allows us to examine whether both bimanual coupling and end-state comfort are predominant motor planning constraints, whereas the second allows us to ascertain whether one constraint dominates the other (e.g., end-state comfort dominates bimanual coupling, or bimanual coupling dominates end-state comfort).

To examine the extent to which initial grasp behavior and hand kinematics were influenced by response specification processing, we combined SOA duration (0, 1000 ms, 2000 ms) and SOA location (left stimulus first, right stimulus first) into a single "SOA" variable. Trials in which the left stimulus appeared first were coded as minus values, while right stimulus first trials were coded as positive values. Thus, −2000 refers to trials in which the left stimulus preceded the right stimulus by 2000 ms, and −1000 refers to trials in which the left stimulus preceded the right stimulus by 1000 ms. Similarly, +2000 refers to trials in which the right stimulus preceded the left stimulus by 2000 ms, and +1000 refers to trials in which the right stimulus preceded the left stimulus by 1000 ms. Trials in which the stimuli appeared simultaneously were coded as 0 ms.

2.4.1. Grasp behavior

Initial grasp postures that satisfied end-state comfort were defined in accordance with recent studies in our laboratory using a similar experimental set up (Hughes, Haddad et al., 2011; Hughes, Reissig et al., 2011). Specifically, end-state comfort satisfaction was defined by initial underhand grasp postures for movements that required 90° internal rotation and 180° rotation, and by initial overhand grasp postures for movements that required 0° rotation and 90° external rotation. Bimanual coupling was defined by the adoption of identical initial grips (i.e., overhand or underhand for both hands), irrespective of whether the grips satisfied end-state comfort.

[1] Viewed from the participant's perspective, these were: 12 o'clock for both hands, 3 o'clock for the left hand and 9 o'clock for the right hand, 6 o'clock for both hands, and 9 o'clock for the left hand and 3 o'clock for the right hand.

For the first constraint satisfaction category, the proportion of trials in which both bimanual spatial coupling and end-state comfort were satisfied was calculated for each participant. Similarly, for the second constraint satisfaction category, we calculated the proportion of trials in which end-state comfort was satisfied for each participant. For both categories, the data was normalized using an arcsine transformation prior to statistical analysis in order to meet the assumptions of parametric tests (i.e., homogeneity, normal distribution). Differences in grasp behavior were examined using separate repeated measures analyses of variance (RM ANOVAs) with the factors object end-orientation congruency (congruent, incongruent) and SOA (−2000, −1000, 0, +1000, +2000), separately for each constraint satisfaction category.

2.4.2. Hand kinematics

The 3D coordinates of the reflective markers were reconstructed and missing data were interpolated using a cubic spline. All kinematic variables were calculated using custom written MatLab programs (Mathworks, Version 7.0). The marker coordinates were low-pass filtered at a 5 Hz cut-off, using a second order Butterworth filter. The wrist joint center (WJC) was calculated as the midpoint between WRT and WRP.

For each trial, the reach-to-grasp phase was identified as the time period between when the hand (WJC) left the body to the time the hand (WJC) contacted the object. Reach-to-grasp onset was determined as the time of the sample in which the resultant velocity of the hand (WJC) exceeded 5% of peak velocity of the corresponding phase. Movement offset was determined as the time of the sample in which the WJC resultant velocity dropped and stayed below 5% of peak velocity of the corresponding phase. Reach-to-grasp time was defined as the time period between reach-to-grasp phase onset and reach-to-grasp phase offset.

To calculate interlimb coupling at the start and end of the reach-to-grasp phase we calculated the absolute asynchrony difference (Hughes & Franz, 2008; Hughes, Haddad et al., 2011; Hughes et al., 2012). The absolute asynchrony difference reveals the magnitude of difference between the hands regardless of which hand initiates (absolute onset) or completes (absolute offset) the movement first. Large values indicate that the performance of the two hands was not in close synchrony. In contrast, values less than 50 ms indicate a tight coupling between the two hands. Absolute onset asynchrony was determined by subtracting the movement onset of the left hand from the movement onset of the right hand. Absolute offset asynchrony was determined by subtracting the time of left-hand contact from the time of right-hand contact on the placement board. For both absolute onset and offset, the absolute difference for each trial was calculated, and these individual trials were then averaged to provide a mean value for each condition.

In addition, the strength of spatiotemporal coupling between movement onset and offset was examined by calculating the between-hands root-mean-squared (RMS) difference during the reach-to-grasp phase. RMS velocity difference provides information regarding magnitude differences between the movements of the two hands over time. Lower RMS velocity difference values (<50 mm/s) indicate similar spatial trajectories, whereas values larger than 50 mm/s indicate that the spatial trajectories of the two hands were dissimilar and not close in synchrony. Differences in reach-to-grasp time were examined using a 2 congruency (congruent, incongruent) × 2 hand (left, right) × 5 SOA (−2000, −1000, 0, +1000, +2000) RM ANOVA. Interlimb coupling during the reach-to-grasp was examined using separate RM ANOVAs on the variables absolute onset, absolute offset, and RMS velocity difference, using object end-orientation congruency (congruent, incongruent) and SOA (−2000, −1000, 0, +1000, +2000) as factors.

3. Results and discussion

Trials in which the object(s) were placed to the incorrect object end-orientation were counted as errors and not included in analysis. The total number of rejected trials due to errors was less than 3% of the data, and was equally distributed across conditions and participants. Given the low error rate, mean substitution was used to replace missing values.

3.1. Grasp posture planning

3.1.1. Composite grip behavior

The proportion of trials in which composite grip type satisfied end-state comfort for both hands *and* bimanual spatial coupling is illustrated in Fig. 2a. Analysis revealed that the proportions in which both end-state comfort and bimanual coupling were satisfied was higher during movements to congruent (90.9%), compared to incongruent conditions (73.9%), $F(1,14) = 36.090$, $p < 0.001$, $\eta_p^2 = 0.721$. The interaction between congruency and SOA was also significant, $F(1,14) = 3.575$, $p = 0.011$, $\eta_p^2 = 0.203$. Post hoc analysis revealed that the proportion of trials in which both constraints were satisfied was similar across SOA during congruent movements. There were, however, significant differences in grip behavior as a function of SOA for incongruent movements. The proportion of trials in which both constraints were satisfied was significantly lower when the stimulus was presented at the same time (0 ms = 60.0%), compared to all other SOA conditions, $p < 0.001$. In addition, the proportion of trials in which both constraints were satisfied was higher when the stimuli were separated by 2000 ms (left stimulus first = 86.7%, right stimulus first 81.7%), compared to when the stimuli were separated by 1000 ms (left stimulus first = 71.1%, right stimulus first 70.0%), all p's < 0.001.

During forced-choice conditions (trials in which participants could satisfy end-state comfort *or* adopt identical initial grips), end-state comfort satisfaction was higher during congruent, compared to incongruent conditions (Fig. 2b; congruent = 92.9%, incongruent = 68.0%), $F(1,14) = 5.237$, $p = 0.038$, $\eta_p^2 = 0.272$. There was also a main effect of SOA (−2000 = 85.5%, −1000 = 75.2%, 0 = 67.6%, +1000 = 70.2%, +2000 = 82.2%), $F(4,56) = 3.161$, $p = 0.021$, $\eta_p^2 = 0.184$. Post hoc analysis indicated that end-state comfort satisfaction was lower when the stimuli appeared simultaneously (0 ms SOA condition), compared to the −2000, −1000, +1000 and +2000 conditions, all p's < 0.05.

3.2. Reach-to-grasp hand kinematics

Average reach-to-grasp time values were similar for the left (754 ms) and right hand (746 ms), $F(1,14) = 2{,}427$, $p = 0.142$, $\eta_p^2 = 0.148$. There was, however, a main effect of congruency, with movements to congruent end-orientation (698 ms) yielding shorter reach-to-grasp time values than movements to incongruent end-orientations (802 ms), $F(1,14) = 41.570$, $p < 0.001$, $\eta_p^2 = 0.748$. Mean interlimb coupling values during the reach-to-grasp movement segment are displayed in Table 1.

Analysis of absolute asynchrony difference indicated that the hands were more coupled during movements to congruent, compared to incongruent object end-orientations at both the start (congruent = 35 ms, incongruent = 52 ms) [$F(1,14) = 9.647$, $p = 0.008$, $\eta_p^2 = 0.408$], and the end of the movement (congruent = 32 ms, incongruent = 57 ms) [$F(1,14) = 25.241$, $p < 0.001$, $\eta_p^2 = 0.643$]. The effects of congruency were also observed throughout the reach-to-grasp phase (as indicated by the RMS velocity difference analysis), $F(1,14) = 36.174$, $p < 0.001$, $\eta_p^2 = 0.721$. As expected, the hands were more coupled during movements to congruent (76 mm/s) than to incongruent object

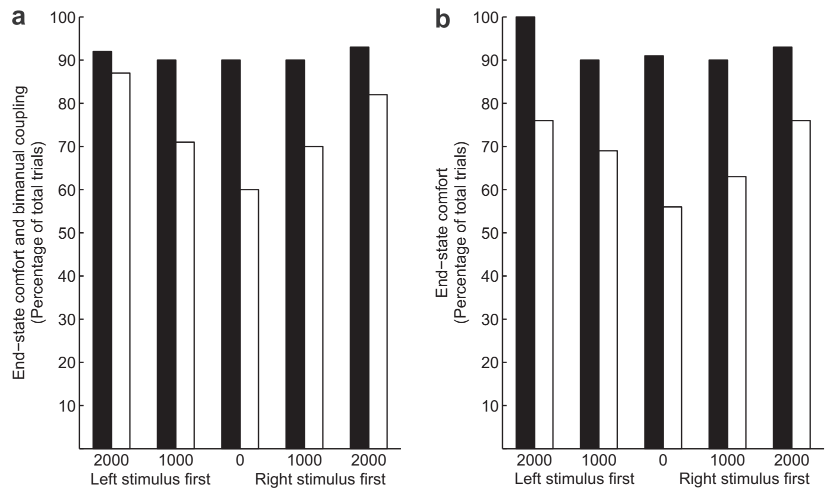

Fig. 2. Percentage of trials in which participants (a) satisfied end-state comfort and bimanual coupling, and (b) end-state comfort for both hands in Experiment 1. Black bars refer to congruent object end-orientation conditions. White bars refer to incongruent object end-orientation conditions.

Table 1
Mean interlimb coupling variables as a function of congruency and SOA during the reach-to-grasp and the grasp-to-place movement segments.

	Absolute onset	Absolute offset	RMS velocity difference
Congruent	33	30	76
0 ms	27	21	77
1000 ms	45	32	75
2000 ms	29	38	77
Incongruent	52	56	94
0 ms	49	65	97
1000 ms	60	48	94
2000 ms	48	56	92

end-orientation conditions (94 mm/s). Interlimb coupling was not influenced by SOA, all *F*'s < 1.0.

3.3. Summary

The results of Experiment 1 demonstrate clearly that the problems associated with grasp posture planning during bimanually incongruent movements can be reduced by increasing the time interval between the presentation of the first and the second stimulus. These findings are in accord with the research of Heuer and colleagues (1998; Spijkers & Heuer, 1995; Spijkers et al., 1997), indicating that the problems associated with grasp posture planning during bimanually incongruent movements are due to cross-talk at the motor programming level.

In contrast to the influence of SOA on grasp posture planning, there were no observable effects of SOA on the reaching component (i.e., hand) of reach-to-grasp kinematics. There was, however, an effect of congruency on both movement time, and interlimb coupling during the hand reach-to-grasp phase. Replicating previous work (Hughes, Haddad et al., 2011; Hughes, Reissig et al., 2011; Hughes et al., 2012), hand reach-to-grasp and grasp-to-place times were longer for incongruent, compared to congruent, object end-orientation conditions. The congruency effects also extended to interlimb coupling, with a higher degree of coupling for congruent, than incongruent, object end-orientation conditions at the start, end, and throughout the reach-to-grasp and grasp-to-place movement phases. This latter finding is contrary to our original hypothesis that the hands would be more coupled for short SOAs, regardless of object end-orientation congruency. Taken together, these result suggest that the increased reach-to-grasp execution costs associated with bimanually incongruent movements (i.e., bimanual inference) do not arise from cross-talk during parametric specification, but from neuronal cross-talk in efferent pathways (Franz, Eliassen, Ivry, & Gazzaniga, 1996), or the selection of movement goals (Hazeltine et al., 2003). We will return to this issue in Section 7.

4. Experiment 2

Experiment 2 investigated if the SOA benefits on bimanual grasp planning found in Experiment 1 could also occur at shorter SOAs. Evidence for the transient coupling hypothesis would be obtained if the difference between congruent and incongruent object end-orientations was large at short SOA intervals and decreased as the SOA interval gets longer.

5. Methods

5.1. Participants

Ten right-handed individuals (mean age = 27.60, SD = 4.95, mean handedness = 1.0, SD = 0, 5 men and 5 women) participated in the second experiment. Participants had normal or corrected to normal vision, and did not have any known neuromuscular disorders. The methodology and consent form for this study were approved by the Bielefeld University Institutional Review Board, and conformed to the declaration of Helsinki.

5.2. Apparatus, procedure and data analysis

The apparatus, procedure and data analysis were similar to those of Experiment 1. There were four levels of SOA duration: 0 ms, 250 ms, 500 ms, and 750 ms. Participants performed a total of 128 unique trials, consisting of 16 object end-orientations, 4 SOA durations (0 ms, 250 ms, 500 ms, 750 ms) and 2 SOA locations (left stimulus first, right stimulus first). The entire testing session, including informed consent, lasted approximately 60 min.

6. Results and discussion

Trials in which the object(s) were placed to the incorrect object end-orientation were counted as errors and not included in analysis (1.10%), and were equally distributed across conditions and participants. Missing values were replaced using condition mean substitution.

6.1. Grasp posture planning

6.1.1. Composite grip behavior

During conditions in which both constraints could be satisfied (Fig. 3a), the proportions of trials in which grasp postures satisfied both end-state comfort and bimanual coupling was higher during movements to congruent (83.5%), compared to incongruent conditions (63.3%), $F(1,9) = 19.754$, $p = 0.002$, $\eta_p^2 = 0.687$. However, there was no difference in grasp posture as a function of SOA condition, nor was the interaction between congruency and SOA condition significant, both F's < 1.0. During forced-choice conditions (Fig. 3b), end-state comfort satisfaction was higher during movements to congruent (85.7%), compared to incongruent conditions (48.6%), $F(1,9) = 41.206$, $p < 0.001$, $\eta_p^2 = 0.821$. The main effect of SOA, and the interaction between congruency and SOA was non-significant, both F's < 1.0.

6.2. Reach-to-grasp hand kinematics

Average reach-to-grasp time values were significantly longer for incongruent (903 ms), compared to congruent end-orientation conditions(774 ms), $F(1,9) = 8.751$, $p = 0.016$, $\eta_p^2 = 0.493$. Reach-to-grasp times were similar for the left (837 ms) and right hand (840 ms), $p = 0.847$. The main effect of SOA condition was also non-significant, $p = 0.356$.

Mean interlimb coupling values during the reach-to-grasp movement segment are displayed in Table 2. Analysis of absolute asynchrony difference indicated that the hands were more coupled during movements to congruent, compared to incongruent object end-orientations at both the start (congruent = 59 ms, incongruent = 93 ms) [$F(1,9) = 5.789$, $p = 0.039$, $\eta_p^2 = 0.391$], and the end of the movement (congruent = 54 ms, incongruent = 104 ms) [$F(1,9) = 21.310$, $p < 0.001$, $\eta_p^2 = 0.703$]. The effects of congruency were also observed throughout the reach-to-grasp phase (as indicated by the RMS velocity difference analysis), $F(1,9) = 8.357$, $p = 0.018$, $\eta_p^2 = 0.482$. As expected, the hands were more coupled during movements to congruent (94 mm/s) than to incongruent object end-orientation conditions (107 mm/s). The manipulation of SOA was non-significant for all interlimb coupling variables, all F's < 1.0.

Table 2
Mean interlimb coupling variables as a function of congruency and SOA during the reach-to-grasp and the grasp-to-place movement segments.

	Absolute onset	Absolute offset	RMS velocity difference
Congruent	54	51	93
0 ms	27	34	81
250 ms	41	39	88
500 ms	68	51	100
750 ms	82	80	103
Incongruent	85	101	106
0 ms	58	103	108
250 ms	86	104	108
500 ms	94	98	106
750 ms	103	98	103

6.3. Summary

Experiment 2 was conducted to ascertain whether benefits in bimanual grasp planning during incongruent object end-orientation conditions are observable at shorter SOA durations. The results of the grasp posture analysis failed to indicate any noticeable benefits in bimanually incongruent grasp posture planning for SOA durations ranging from 250 ms to 750 ms. From this, and the results of Experiment 1, we conclude that problems associated with bimanually incongruent grasp posture planning are due to cross-talk during parametric specification (i.e. at the programming level), and that these planning difficulties are reduced when the action end-goals for the two hands are separated by a period greater than 1000 ms.

Although we did not replicate the effect of SOA on grasp posture planning, we did, however, replicate the effects of congruency on both the level of grasp posture planning and hand kinematics. As in Experiment 1, participants were better able to plan their grasp postures during movements to congruent, relative to incongruent, conditions. Moreover, we observed shorter movement times, and greater interlimb coupling for congruent, compared to incongruent, end-orientation conditions. We can thus be confident that the observed bimanual interference is not linked to cross-talk during parametric specification.

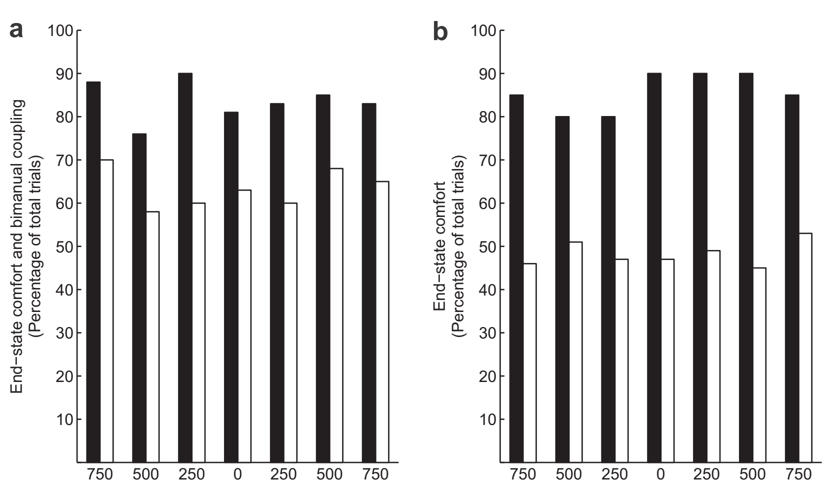

Fig. 3. Percentage of trials in which participants (a) satisfied end-state comfort and bimanual coupling, and (b) end-state comfort for both hands in Experiment 2. Black bars refer to congruent object end-orientation conditions. White bars refer to incongruent object end-orientation conditions.

7. General discussion

7.1. Grasp posture planning

The results of the two experiments presented here indicate that increasing the amount of time between the presentation of the first stimulus and the second stimulus by at least 1000 ms is able to reduce deficits in grasp posture planning during bimanually incongruent object end-orientation conditions. These findings, thus, support our original hypothesis that limitations in bimanually incongruent grasp posture planning are related to crosstalk at the motor programming level.

The results of the grasp posture planning data also add converging evidence to the transient programming coupling hypothesis (Heuer, 1986, 1993; Spijkers & Heuer, 1995). The three premises underlying this hypothesis are: (1) concurrent programming of bimanually incongruent movements takes longer to plan than bimanually congruent movements, (2) cross-talk occurs as long as the concurrent parameter specification processes are occurring, but does not occur once programming is finished, and (3) transient cross-talk at the motor programming level occurs due to the mutual inhibitory (between both motor [M1], premotor cortices [PMC] and/or between PMC and contralateral M1) influence of specification processes that each hand has on the other which slows the specification process for each hand, resulting in performance deficits (e.g., longer reaction times, reduction in end-state comfort) for incongruent, compared to congruent, actions.

It could also be argued that bimanual grasp posture planning is a form of dual-task performance, and thus, the observed interference is due (at least partially) to limited cognitive resources. Contemporary dual-task theories (Navon & Gopher, 1979; Wickens, 1980) suggest that, for concurrent tasks, performance on both may be maintained if the tasks are in separate processing stages, or involve different processing mechanisms (Wickens, Sandry, & Vidulich, 1983). In line with this theory, it is likely that the processing stages (e.g., stimulus perception, response selection) and mechanisms (e.g., working memory) needed to plan grasp postures are similar for the left and right hand. Because resources are limited, Task 1 (i.e., left hand) and Task 2 (i.e., right hand) must share the available processing capacity. Assuming that central processing of the two tasks needs approximately the same duration, a reasonable inference is that central processing of Task 1 and Task 2 overlap when the stimuli are presented simultaneously or separated by a short period, but that there is little overlap in central operations between the two tasks when the stimuli are separated by a long period of time. In the former situations, central processing of Task 1 and Task 2 overlap with Task 1 initially having full access to central stages and uses all available capacity. When the stimuli for Task 2 is presented, it gains access to some of the central capacity, and Task 1 and Task 2 must share the processing capacity (unless all capacity is allocated to either Task 1 or Task 2) until such a time as Task 1 has completed central processing. In contrast, central processing of Task 1 starts and finishes before Task 2 begins central processing at longer SOAs. The minimal overlap in processing, thus allows individuals to plan their grasp postures to achieve dominant action planning constraints (i.e., bimanual spatial coupling, end-state comfort).

In sum, the observed results of the two experiments reported here build on our previous investigations into grasp posture planning that have repeatedly demonstrated that individuals have problems achieving dominant action planning constraints during bimanually incongruent grasp postures (Hughes & Franz, 2008; Hughes, Haddad et al., 2011; Hughes et al., 2012), and indicate that difficulties in bimanual grasp posture planning can be mitigated by reducing any overlap in central processes.

7.2. Reach-to-grasp hand kinematics

A corollary purpose of the present study was to examine the effects of SOA duration on hand kinematics. In contrast to our original hypothesis that interlimb coupling would be influenced by SOA duration, we found that increasing the duration between the presentation of the first and the second stimulus had no effect on reach-to-grasp interlimb coupling. The observation that the hands are less coupled during movements to incongruent object end-orientations, regardless of SOA duration, suggest that limitations in bimanual execution are not due to cross-talk during parametric specification (Heuer et al., 1998), but are likely due to constraints that act on another level of the neurobiological–cognitive system (Franz, 2010; Obhi & Goodale, 2005).

In the following paragraphs we delineate possible foci of the observed interference, which although presently separately, are not mutually exclusive. One possibility is that bimanual interference during reach-to-grasp execution is attributable to limitations in the visual motor system (Meyer & Kieras, 1997; Meyer et al., 1995). In Hughes, Reissig et al. (2011) we argued that the decrease in interlimb coupling during incongruent movements arises from the inability to visually attend to more than one object or hand at a time (Bingham et al., 2008; Mason & Bruyn, 2009; Riek, Tresilian, Mon-Williams, Coppard, & Carson, 2003). Accordingly, participants employ a sequential gaze strategy in order to ensure accurate and successful motor performance when objects or targets are located outside a single foveal span, which results in larger congruency costs during reach-to-grasp execution.

It is also possible that the observed bimanual interference may have arisen from constraints that act on a conceptual level (Franz, 2010; Franz & McCormick, 2010; Franz, Zelaznik, Swinnen, & Walter, 2001; Kunde & Weigelt, 2005; Mechsner, Kerzel, Knoblich, & Prinz, 2001). Evidence for conceptual constraints comes from studies demonstrating that bimanual movements in which the action end-goals (Franz et al., 2001) or task instructions evoke a unified representation (Franz & McCormick, 2010), or can be conceptualized as having similar end goals (Kunde, Krauss, & Weigelt, 2009; Kunde & Weigelt, 2005) exhibit less interference than those bimanual movements that cannot be conceptualized as having a common goal. For example, Franz and McCormick (2010) recently demonstrated that participants were able to conceptualize a bimanual reaction task as a single unified action when the task instructions evoked a unified representation (as measured by shorter RTs), but that interference was large when the task instructions implied two separate action plans (leading to longer RTs). The task instructions used in the present study (as well as our past studies on bimanual grasp posture planning; e.g., Hughes & Franz, 2008; Hughes, Haddad et al., 2011; Hughes, Reissig et al., 2011b), specified that participants should "grasp the left object with the left hand and place it to the left side of the board, and the right object with the right hand and place it to the right side of the board." It is, therefore, possible that the instructions used in the present study did not afford the possibility to conceptualize the task in a unified fashion. To investigate whether the observed bimanual interference arises from limitations in the visual motor system and/or from conceptual language representations, future work should manipulate both task instructions (i.e., constraints in conceptual language representations) and the spatial separation between the two objects (inter-object distance) and the two targets (inter-target distance) (i.e., visuomotor constraints).

Although there was no effect of SOA condition on the reach or transport component, it is plausible that the manipulation of SOA may have affected parameters related to the grasp component (i.e., finger adjustments).[2] Previous work has shown that transport and

[2] We thank two anonymous reviewers for suggesting this possibility.

grasp components are differently influenced by task constraints (Dohle, Ostermann, Hefter, & Freund, 2000; Jackson, German, & Peacock, 2002; Jackson, Jackson, & Kritikos, 1999; Mason, 2007; Mason & Bruyn, 2009). For example, Dohle et al. (2000) examined the coordination of the upper limbs during bimanual reach-to-grasp movements to objects of identical or different size. That study reported high between-hand correlations for the reach component (i.e., hand displacement for both hands) regardless of object size. In contrast, correlations for the grasp component (i.e., grip aperture of both hands) were consistently lower than for the reach component and were significantly influenced by object size. The authors argued that modifications in the grasp component can be implemented into the motor plan independently of kinematic parameterization of the reach component, and suggest that bimanual coupling of arm movements is "hardwired," whereas coupling of grasp aperture is flexibly modulated by task constraints. Given these findings, future examinations should include grasp components (e.g., maximum grip aperture, time to maximum grip aperture) as these measurements may provide greater insight into the mechanisms underlying bimanual object manipulation.

8. Conclusion

The studies reported here demonstrate that motor planning cross-talk can account for bimanual interference at the level of grasp posture planning, but not at the level of (reach-to-grasp) execution. As such, the present results complement contemporary theories (e.g., Franz, 2010; Franz & McCormick, 2010; Franz et al., 2001; Obhi & Goodale, 2005) emphasizing that interference effects in bimanual movements are not a result of constraints acting at a single level of the neurobiological–cognitive system (e.g., sensorimotor, conceptual), but arise from constraints active at multiple levels of representation.

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