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RESEARCH ARTICLE

Response biases: the influence of the contralateral limb and head position

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Abstract

Two experiments were designed to determine response biases resulting from production of force in the contralateral limb and head position. Participants were required to react with one limb while tracking a sinewave template by generating a pattern of force defined by the sinewave with the contralateral limb or watching a cursor move through the sinewave. In Experiment 1, participants had to react with their right or left limb while their head was in a neutral position. In Experiment 2, participants had to react with their left limb while their head was turned 60° to the left or right. A color change of the waveform signaled participants to produce an isometric contraction with the reacting limb. Reaction time was calculated as the time interval between the color change of the waveform and the initiation of the response. The results indicated mean reaction time for the left limb was significantly influenced by force production in the right limb. During left limb reactions, reaction time was faster for trials in which both limbs initiated force simultaneously as compared to trials in which the left limb initiated force while the right limb was producing force. Mean reaction time for the right limb was not influenced by force production in the contralateral limb. The results are consistent with the notion that crosstalk can influence the time required to react to stimuli but this influence occurs at the point of force initiation and is asymmetric in nature with the dominant limb exerting a stronger influence on the non-dominant limb than vice versa. However, we did not find a similar effect for head position via the tonic neck response.

Keywords Reaction time · Force control · Neural crosstalk · Bimanual coordination

Introduction

The ability to respond quickly to environmental stimuli has been implicated as a key factor in safeguarding health and independence. For example, reaction time (RT) has been associated with balance stability and risk of falls (e.g., Lajoie and Gallagher 2004 and Lord et al. 1993) as well as the fitness to drive automobiles (e.g., Andrews and Westerman 2012 and Christoforou et al. 2013). Therefore, understanding factors that may facilitate or interfere with an individuals' ability to react has both practical and theoretical importance. Recent research on RT has indicated that the ability to react with one limb is influenced by the activation of an ongoing movement by the contralateral limb (Kennedy et al. 2013). This influence was attributed to neural crosstalk.

Neural crosstalk is believed to result when a mirror image of the command(s) sent to one muscle group is also dispatched to the homologous muscles of the contralateral limb (e.g., Cattaert et al. 1999 and Swinnen 2002). This happens when both hemispheres send commands to the contralateral limb via the crossed corticospinal pathways while concurrently sending the same command to the ipsilateral limb via the uncrossed corticospinal pathways (Cardoso de Oliveira 2002; Cattaert et al. 1999). When the commands to both limbs are congruent (e.g., both limbs are producing the same action), interference is not likely to occur (Maki et al. 2008) and may even stabilize task performance when the contralateral and ipsilateral signals are integrated (e.g., Cardoso de Oliveira 2002 and Kagerer et al. 2003). However, tasks that require the limbs to produce disparate actions (e.g., different amplitudes, directions, forces, frequencies) may suffer ongoing interference believed to result from the conflicting

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information or partial intermingling of signals controlling the limbs (e.g., Cardoso de Oliveira 2002; Kagerer et al. 2003; Maki et al. 2008; Marteniuk et al. 1984).

Neural crosstalk may influence actions at both the execution and planning levels (e.g., Cardoso de Oliveira 2002; Heuer et al. 2001, 2002; Marteniuk et al. 1984; Spijkers et al. 1997). Interference at the execution level is associated with motor output from efferent motor commands whereas interference at the planning level is associated with the specification process prior to the execution of the task goal (Cardoso de Oliveira 2002; Heuer et al. 2001, 2002; Marteniuk et al. 1984; Spijkers et al. 1997). Reaction time tasks are commonly used as an indirect measure to examine influences at the planning level (e.g., Diedrichsen et al. 2001; Hazeltine et al. 2003; Hoyer and Bastian 2013; Obhi and Goodale 2005). Tasks requiring disparate relationships between the limbs should necessitate greater processing demands to inhibit and/or counter act the crosstalk from the contralateral limb than bimanual tasks that require the same action (Aramaki et al. 2010). This increased processing demand should result in increased RTs in tasks that require different patterns of activation for each limb. Indeed, in an experiment examining the effects of tasks demands (same or disparate actions for each limb) on motor planning (RT) while participants learned a novel bimanual isometric pinch force task, RT and errors increased when the task involved asymmetric forces compared to symmetric forces (Hoyer and Bastian 2013). Similarly, research has demonstrated increased RT in tasks that require the limbs to produce different amplitudes, directions, and frequencies compared to tasks that require the limbs to produce the same action (e.g., Daffertshofer et al. 2005; Hazeltine et al. 2003; Heuer et al. 2001, 2002; Spijkers et al. 1997). Note, however, that in many of these experiments, the participants were asked to initiate both left and right limb actions in response to stimuli.

Using an experimental design different from much of the previous research methods that examined how RT was influenced by bimanual discrete movements such as button pressing, sliding, or reaching movements (e.g., Diedrichsen et al. 2001, 2003; Hazeltine et al. 2003; Hoyer and Bastian 2013; Heuer et al. 2001; Obhi and Goodale 2005; Spijkers et al. 1997), Kennedy et al. (2013) used a RT task to determine whether the activation of a muscle group (flexors or extensors) used to produce an ongoing movement with the right limb influenced the RT and associated initiation of elbow flexion or extension movements of the left limb. The results indicated mean reaction of the left limb was significantly influenced by the concurrent type of movement (flexion/extension) of the right limb. Reaction times were shorter on trials in which both limbs were initiating movements with homologous muscles as compared to trials in which the limbs were initiating movement with non-homologous muscles. Interestingly, this influence only occurred at the point of muscle activation; no differences were detected when the stimuli were presented during the ballistic phase of the movement. This result is consistent with a series of experiments that have examined neural crosstalk at the execution level and demonstrated interference in one limb that could be associated with the initiation and release of force in the contralateral limb (Kennedy et al. 2015, 2016a, b). When the task involved the production of isometric forces produced by the homologous muscles of the two limbs, perturbations consistent with neural crosstalk were observed in the force and force velocity times series for the left limb that were coincident with the initiation and release of a force pulse by the right limb (Kennedy et al. 2015). It is important to note, however, that Kennedy et al. (2013) only examined the influence of right limb movement on left limb RT while the series of experiments investigating neural crosstalk at the execution level used continuous isometric forces.

It has been hypothesized that the effect of neural crosstalk is partially dependent on force, with higher forces resulting in stronger crosstalk effects and lower forces in weaker ones (Heuer et al. 2001). Indeed, perturbations such as those observed in the series of experiments investigating neural crosstalk at the execution level (Kennedy et al. 2015, 2016a, b) are typically not observed in similar tasks performed in near frictionless environments (e.g., Boyles et al. 2012; Kovacs et al. 2010a, b; Kovacs and Shea 2010, 2011). Although, isolated perturbations have been observed in a similar type of task in which participants were required to coordinate hand-held pendula (Sternad et al. 2007). Note, that the force requirements associated with coordinating hand-held pendula are greater than when the task is performed in near frictionless environments. As such, RT tasks that require the production of force rather than movement may provide additional insights on how actions in one limb influence responses in the contralateral limb.

In addition, it has been suggested that head position may facilitate or interfere with movement planning and/or execution (Heuer and Klein 1999; Klein and Heuer 1999). Research has indicated that the influence of head position on response biases is dependent on the direction in which the head is turned with respect to the involved flexors and extensors (Shea et al. 1995). Evidence suggest that the mechanism responsible is associated with the asymmetric tonic neck reflex (Hellebrandt et al. 1956; Shea et al. 1995). Asymmetric tonic neck responses are thought to reflexively heighten neural responsiveness of extensor muscles in the direction of head position and dampen the responsiveness of the contralateral extensor muscles (Easton 1972). The asymmetric tonic neck reflex is a primitive reflex found in newborn infants and is thought to integrate by 3 months of age (Gabbard, 2016). However, the asymmetric tonic neck response has been observed in children up to 9 years of age (Parr et al. 1974) and healthy adults in tasks which required participants to turn their head to the left or right (Bruijn et al. 2013; Heuer and Klein 1999). The asymmetric tonic neck response has also been observed in healthy adults in tasks that required the production of grip force (Berntson and Torello 1977) and tasks requiring force production with larger muscle groups (Deutsch et al. 1987; Hellebrandt et al. 1956).

Facilitation (interference) via the asymmetric tonic neck response may modify the muscular tone of flexors and extensors of the upper limbs (Shea et al. 1995). This could impact response initiation (reaction time) and response execution (duration). For example, in an experiment investigating the influence of head rotation on bimanual rotation of a steering device, Heuer and Klein (1999) reported shorter RTs for rotations (head and handle-bars) in the same directions. Similarly, Klein and Heuer (1999) investigated the influence of eccentric head position on bimanual rotation of a steering wheel and reported different kinematics associated with response execution (amplitude of response, duration of response) between right and left head positions. Our interest is on whether head position can also influence responses (reaction time, response duration) in one limb based on actions produced by the contralateral limb.

Experiment 1

Experiment 1 employed a RT task in which participants were required to produce an isometric force pulse with one limb while either generating a sinusoidal pattern of force by controlling a cursor to track a sinewave template with the contralateral limb (experimental task) or watching a cursor move through the sinewave pattern (control task). The purpose of the experiment was to determine whether the production of force with one limb influenced an individuals' ability to respond to a stimulus with the contralateral limb and if so, whether this influence was associated with the initiation and/or release of force in the contralateral limb. Faster RTs in trials that require both limbs to initiate force simultaneously using homologous muscles and slower RTs in trials that required a non-homologous pattern of muscle activation between the limbs would be consistent with the notion that neural crosstalk can influence the time required to react to a stimulus.

Methods

Participants

Eleven young adults (mean age 21.4, range 20–24 years; 8 females and 3 males) participated in the experiment. All participants were right limb dominant according to a standardized survey (Oldfield 1971; mean 87.5, STD 10.7, min = 74.4, max = 100). The Institutional Review Board at Texas A&M University approved the procedures, and participants provided written informed consent before participation in the study. The participants had no prior experience with the experimental task and were not aware of the specific purposes of the study.

Apparatus

The apparatus consisted of two static force measurement systems, each of which included a force transducer and an amplifier that converted the force exerted against the transducer into a voltage representing the instantaneous value of the applied force. One force transducer was attached to an adjustable metal frame mounted on the left side of a standard padded treatment table and the other force transducer was mounted on the right side (Fig. 1a). The voltages representing the applied forces were converted to digital values (16 bit) using an AD converter (DAS-16 Series Board, Keithley

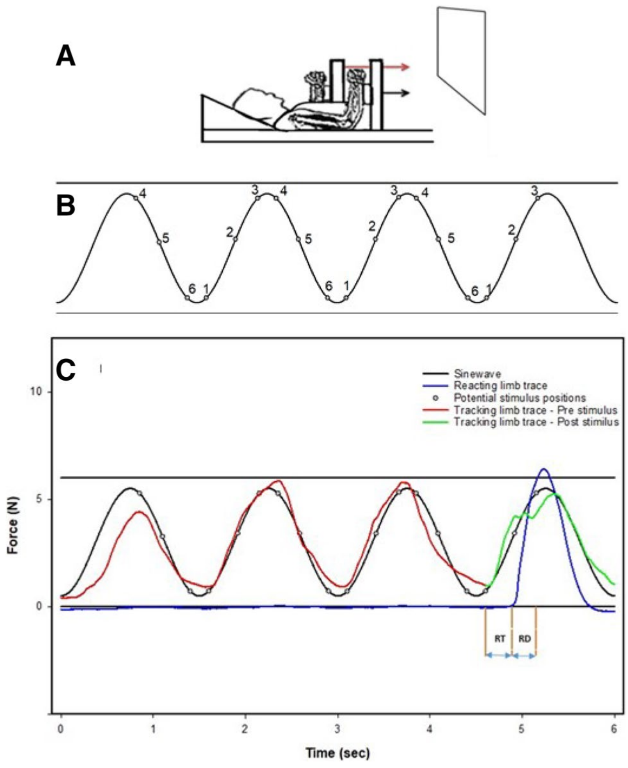

Fig. 1 Illustration depicting the experimental arrangement (**a**), the sinewave, the potential stimulus position on the sinewave task (**b**), and examples of the left and right limb force trace for one participant in the experimental task conditions (**c**). Note the RT stimulus was a change in color of the cursor moving along the sinewave and was presented at one of 6 locations on one the cycles of the sinewave form. RT was calculated as the time interval between the presentation of the stimulus (color change of the cursor) and the initiation of the response. RD was calculated as interval of time from the initiation of the response until the force waveform crossed the upper goal (6 N)

MegaByte Corp, MA, USA) installed on the computer. The computer was programmed to sample at 200 Hz. A goal template and a cursor representing the applied forces were displayed in a 1.64 × 1.23 m image projected on the wall in front of the participant.

Procedure

Prior to entering the testing area, participants were randomly assigned to an order in which they would to be tested under four conditions. The four conditions were comprised of the limb used to react (left or right) and whether the participant was required to track the sinewave template by generating a pattern of force (experimental condition) or simply watch the cursor move through the sinewave pattern (control condition). Participants were then placed in a supine position on a treatment table with their head slightly elevated with a pillow to view a projected image on the wall located 2 m in front of the participant (Fig. 1a). The force transducers were adjusted so that the participant's arm just below the wrist contacted the transducer so that they could produce isometric force utilizing left and/or right triceps. This position allows for isolation of force produced by the limbs without the effects of gravity and mechanical/elastic stretch properties of the muscles and tendons.

In both the left and right experimental task conditions, the target pattern of force for one limb was defined by a sinewave template in the display (Fig. 1b). The participants were asked to exert force with the designated limb so that the cursor projected on the wall in front of them moved along the path defined by the sinewave. The maximum force required to produce the pattern illustrated by the sinewave pattern was 5 N. The participant maintained the cursor for the contralateral limb below a horizontal line positioned below the sinewave display while they tracked the sinewave with their assigned limb (Fig. 1c). They were instructed to maintain the contralateral limb position until the cursor depicting the force exerted by the limb tracking the sinewave changed color. The color change was the stimulus to exert a rapid force pulse with the contralateral limb so that the cursor moved from the bottom to the top of the display as quickly as possible. The required force to move the cursor from the bottom to the top of the display was 6 N. In one experimental condition, the participant tracked the sinewave with their right limb and reacted to the change in cursor color with the left limb. In the other experimental condition, the participant tracked the sinewave with their left limb and reacted with their right limb. Participants were told that there were no accuracy requirements for the limb they were to react with other than to move the cursor from the bottom to the top of the display.

In the control conditions, participants were instructed to observe the cursor move through the sinewave pattern. Note that no tracking force was required. Participants were simply asked to monitor the cursor that moved along the sinewave path. Participants were asked to place their limb designated for reaction in the instructed position until the cursor moving along the sinewave changed color at which time they were instructed to exert force with that limb in an attempt to move the cursor from the bottom to the top of the sinewave display as quickly as possible.

Participants were given two trials to practice tracking the sinewave template by increasing and decreasing the force produced by the right or left limb, depending on condition. Participants were also given two trials to visually track the movement of the cursor through the sinewave in the control conditions. On Trials 3–22, participants were asked to complete 20 test trials of 6 s each. The RT stimulus (cursor color change) only occurred once in each trial. The position at which the cursor changed color was varied across trials with half of the color changes occurring while the cursor was moving up and half while the cursor was moving down. Stimulus positions 1–3 corresponded to the production of force and 4–6 corresponded to the release of force (see Fig. 1b). The cycle in which the stimulus occurred and the position within a cycle (Fig. 1b) was varied across trials. The stimuli occurred in the same positions in the sinewave for the experimental and control conditions although the order was changed across conditions.

Measures and data analysis

The force time series for the left and right limbs for all conditions were analyzed in the same manner. Prior to analysis, the force time series for the left and right limb were dual-passed filtered (Butterworth, 10 Hz). Reaction time (RT) was determined as the interval from the presentation of the stimuli (cursor color change) to the time when the limb initiated force. Response duration (RD) was calculated as the interval of time from the initiation of the response until the force waveform crossed the upper goal (6 N) (see Fig. 1b). The dependent variables of RT and RD were analyzed in separate Condition (experimental, control) × Reacting limb (left, right) × Stimulus position (1–6) analyses of variance (ANOVAs) with repeated measures on all factors.

The force time series for the limb producing the sinewave pattern in the experimental were filtered in the same manner as that for the reacting limb. The analysis involved calculating constant error (CE). CE for the tracking limb was defined as the difference between the force produced by the participant's tracking limb and the sinewave template at the time the stimulus was presented and was analyzed in a tracking Limb (right, left) × Stimulus position (1–6) ANOVA with repeated measures on both factors. Significant main effects were further analyzed with Duncan's new multiple range test and significant interactions were further analyzed with simple main effects. An $\alpha = 0.05$ was used for all tests.

Results

Figure 2 provides illustrations depicting the RT at each stimulus position on the sinewave for the left (a) and right (b) limbs in both the experimental and control conditions. In addition, mean CE for the tracking limb in the experimental condition at each of the positions where the stimulus to react was presented is provided for both the right (b) and left (d) limbs.

Reaction time (RT)

The analysis detected a main effect of condition, $F(1,10) = 35.98$, $p < .01$, as expected, with RT shorter for the control condition ($M = 388$ ms, STD 39 ms) than the experimental condition ($M = 492$ ms, STD 83 ms). The main effect of stimulus position, $F(5,50) = 4.78$, $p < .01$, was also significant. In addition, the Condition × Stimulus position, $F(5,50) = 2.78$, $p < .05$, and the Reacting limb × Condition × Stimulus position, $F(5,163) = 4.06$, $p < .05$, interactions were also significant. Simple main effects analysis for the left limb did not detect a difference between the control and experimental conditions at Stimulus position 1, while significant differences between the control and experimental conditions at Stimuli positions 2–6. Simple main effects

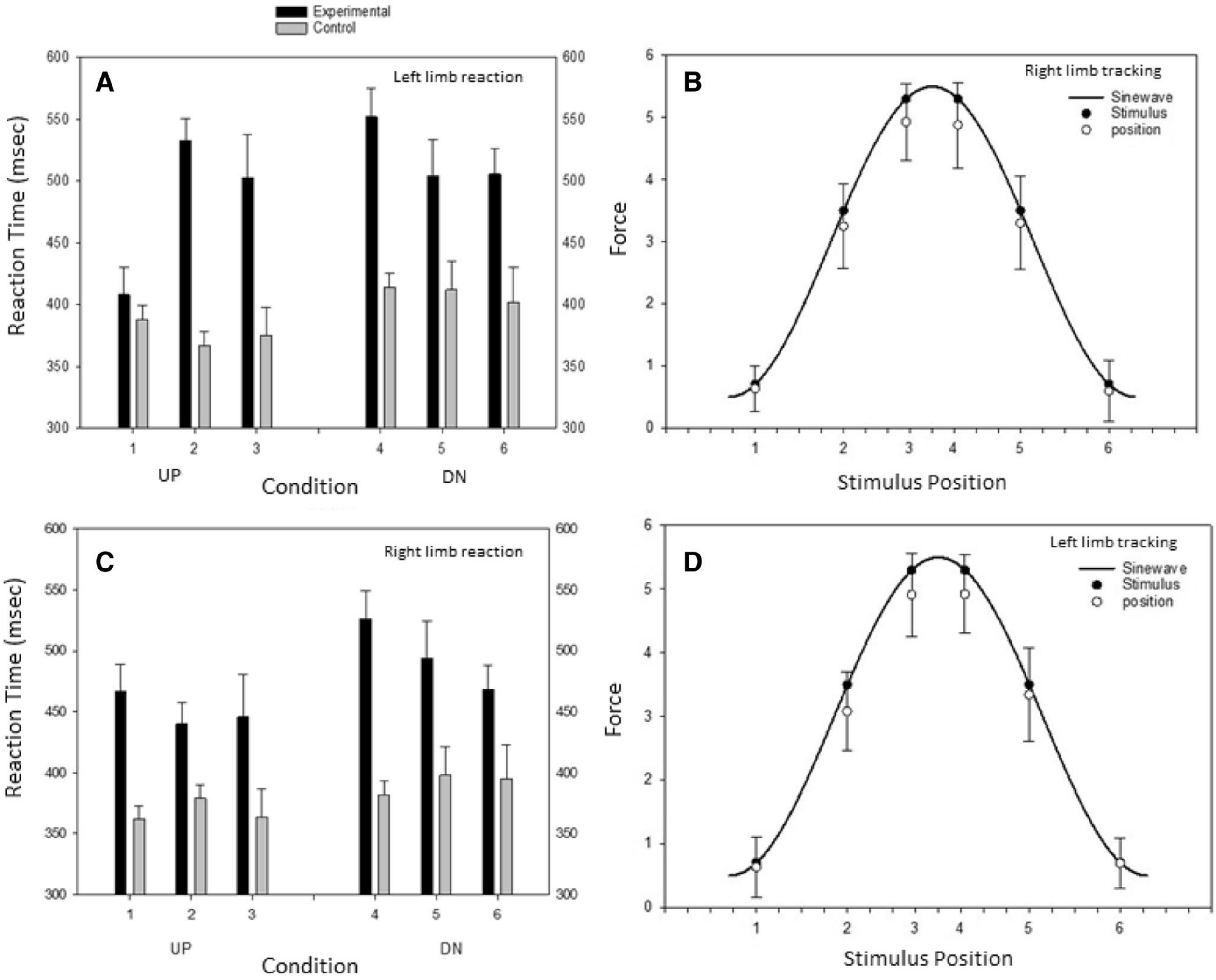

Fig. 2 Illustration depicting the mean left limb RT at each of the positions where the stimulus to react was presented for the experimental task and control conditions (**a**), the mean right limb force and the sinewave template at the time the stimulus was presented for the experimental condition (**b**), the mean right limb RT at each of the positions where the stimulus to react was presented for the experimental and control conditions (**c**), and the mean left limb force and the sinewave template at the time the stimulus was presented for the experimental condition (**d**)

analysis for the right limb detected RT differences between the control and experimental conditions at all stimuli positions (1–6).

Response duration (RD)

The analysis did not detect any main effects or interactions.

Constant error tracking (CE)

The analysis detected a main effect of stimulus position, $F(5,50) = 10.33$, $p < .01$. Duncan's new multiple range test indicated that CE at Stimulus positions 3 and 4 were more negative than that at the other positions that were not different from each other (see Fig. 2b, d). Note, that mean CE at all stimulus positions was less than ± 0.6 N from the sinewave template.

Discussion

Experiment 1 used a RT task to determine whether the initiation and/or release of force in one limb influenced an individuals' ability to respond to a stimulus with the contralateral limb at the planning level. We predicted shorter RTs when both limbs initiated a force pulse simultaneously and longer RTs when non-homologous muscles were activated. This prediction was based upon the notion that crosstalk would facilitate reactions when both limbs were activating homologous muscles due to the integration of contralateral and ipsilateral signals, whereas crosstalk would complicate processing when the reaction involved non-homologous muscles due to the conflicting information or a partial intermingling of the signals controlling the two limbs (Kagerer et al. 2003; Marteniuk et al. 1984). The results of Experiment 1 indicated that mean RT for the left limb was influenced by the initiation of force by the right limb. More specifically, the results indicated faster RTs for left limb reactions at Stimulus position 1, when both limbs initiated a force pulse simultaneously. Interestingly, we did not find a similar pattern of results with right limb reactions. Note, Kennedy et al. (2013) did not examine the influence of left limb movements on right limb reactions. However, the results of the current investigation are consistent with the serious of experiments using the continuous bimanual force tasks in which perturbations associated with neural crosstalk were observed in the force and force velocity times series for the left limb but not for the right limb (Kennedy et al. 2015, 2016a, b). Overall, these results are consistent with the notion that neural crosstalk is asymmetric in nature with the dominant limb exerting a stronger influence on the non-dominant limb than vice versa (e.g., Maki et al. 2008 and Stinear and Byblow 2004).

In addition, we predicted that RT would be longest at Stimulus position 4. This prediction was based on the results found by Kennedy et al. (2013), who used a similar experimental design to investigate the influence of movement, rather than isometric force, with the right limb on RT responses with the left limb. Kennedy et al. (2013) found that RTs were shorter on trials in which both limbs were initiating movements with homologous muscles (Stimulus position 1) and longer on trials in which the limbs were initiating movements with non-homologous muscles (Stimulus position 4). However, during the current investigation, the mean RT was no longer at Stimulus position 4 when compared to Stimulus positions 2, 3, 5, and 6. It is important to note the movement task used by Kennedy et al. (2013) required participants to initiate an extension movement and initiate a flexion movement to reverse direction whereas the task in the current investigation only required participants to initiate a force pulse. Taken together, the results of these two investigations suggest that the influence of the right limb on the left limb occurs during the initiation phase of the action.

Experiment 2

An asymmetric pattern of results was observed in Experiment 1. Left limb reactions were influenced by the initiation of force by the right limb, but mean RT for the right limb was not influenced by force production by the left limb. It has been suggested that head position may influence manual RT and contribute to RT asymmetries via asymmetric tonic neck reflexes (Barthélémy and Boulinguez 2002; Heuer and Klein 1999; Klein and Heuer 1999). Reflex effects could modulate the time needed to react to a stimulus (reaction time). In addition, the potential effects of head position may modify the muscular tone of flexors and extensors of the upper limbs (Shea et al. 1995), this could result in different kinematic characteristics (response duration) depending on whether the head is turned towards or away from the reacting limb. The purpose of Experiment 2 was to replicate the findings of the left limb reaction condition and to determine if head position also influenced reaction and/or response duration. Experiment 2 employed the same RT task as in Experiment 1, however, the head was turned 60° to the left or right.

Methods

Participants

Eighteen young adults (mean age 22.1, range 19–25 years; 9 females and 9 males) participated in the experiment. All participants were right limb dominant according to a standardized survey (Oldfield 1971; mean 88.1, STD 13.7, min = 60, max = 100). The Institutional Review Board at Texas A&M

University approved the procedures, and participants provided written informed consent before participation in the study. The participants had no prior experience with the experimental task and were not aware of the specific purposes of the study.

Apparatus

The same apparatus used in Experiment 1 was used in Experiment 2.

Procedure

The same general procedure used for Experiment 1 was used in Experiment 2 with participants tested under the same conditions (experimental and control) at the same 6 stimulus positions. However, participants were tested with different head positions (left and right). Note that the limb used to react was not manipulated. Participants were placed in a supine position on a treatment table with their head turned 60° to the left or right to view a projected image on the wall located 2 m to the side of the participant. All participants used their left limb to react to the stimuli and tracked the sinewave by generating a pattern of force (experimental condition) with their right limb or simply watched the cursor move through the sinewave pattern (control condition).

Measures and data analysis

The same measures used in Experiment 1 were used in Experiment 2. The dependent variables of RT and RD were analyzed in separate Condition (experimental, control) × Head position (left, right) × Stimulus position (1–6) ANOVAs with repeated measures on all factors. CE for the tracking limb in the experimental condition was analyzed in a Head position (right, left) × Stimulus position (1–6) ANOVA with repeated measures on both factors. Significant main effects were further analyzed with Duncan's new multiple range test and significant interactions were further analyzed with simple main effects. An $\alpha = 0.05$ was used for all tests.

Results

Figure 3 provides illustrations depicting the RT at each stimulus position on the sinewave for the left (A) and right (B) head positions in both the experimental and control conditions. In addition, mean CE for the tracking limb in the experimental condition is presented for each of the stimulus positions is provided for both the right (B) and left (D) limbs.

Reaction time (RT)

The analysis detected a main effects of condition, $F(1,17) = 66.99$, $p < .01$, with RT shorter for the control condition ($M = 398$ ms, STD 39 ms) than the experimental condition ($M = 483$ ms, STD 83 ms) and stimulus position, $(5,85) = 8.49$, $p < .01$. The Condition × Stimulus position, $F(5,85) = 3.07$, $p < .01$, interaction was also significant. Simple main effects analysis for stimulus positions across conditions did not detect a difference between the control and experimental conditions at Stimulus position 1, while significant differences between the control and experimental conditions was found at all stimulus positions. Simple main effects analysis for conditions across stimulus position did not detect differences across positions for the control condition. However, RT was lower for Stimulus position 1 than for all other stimulus position for the experimental condition.

Response duration (RD)

The analysis did not detect any main effects or interactions.

Constant error tracking (CE)

The analysis detected a main effect of stimulus position, $F(5,85) = 10.33$, $p < .01$. Duncan's new multiple range test indicated that CE at Stimulus positions 3 and 4 were more negative than that at the other positions that were not different from each other (see Fig. 3b, d). Note, that mean CE at all stimulus positions were less than ±0.6 N (see Fig. 3b, d).

Discussion

Experiment 2 used a RT task with the head turned 60° to the left or right to determine whether head position also influenced left limb RT. We predicted that we would replicate the pattern of results observed in Experiment 1 with left limb reactions. More specifically, we predicted that mean RTs would be faster when the stimulus was presented at Position 1 and longer at all other stimuli positions. We also predicted differences in mean RT and mean RD for all stimuli positions (in both control and experimental conditions) when the head was positioned to the left side of the body. This prediction was based upon the literature examining response biases associated with the asymmetric tonic neck response (Heuer and Klein 1999; Klein and Heuer 1999; Shea et al. 1995). Turning the head towards the limb producing the action (left, right) is thought to enhance extension while turning the head away from the limb producing the action is thought to diminish extension (e.g., Hellebrandt et al. 1956 and Shea et al. 1995). Although the results of Experiment 2 replicated the findings of Experiment 1 with faster RTs observed at Stimulus Position 1, there were no differences

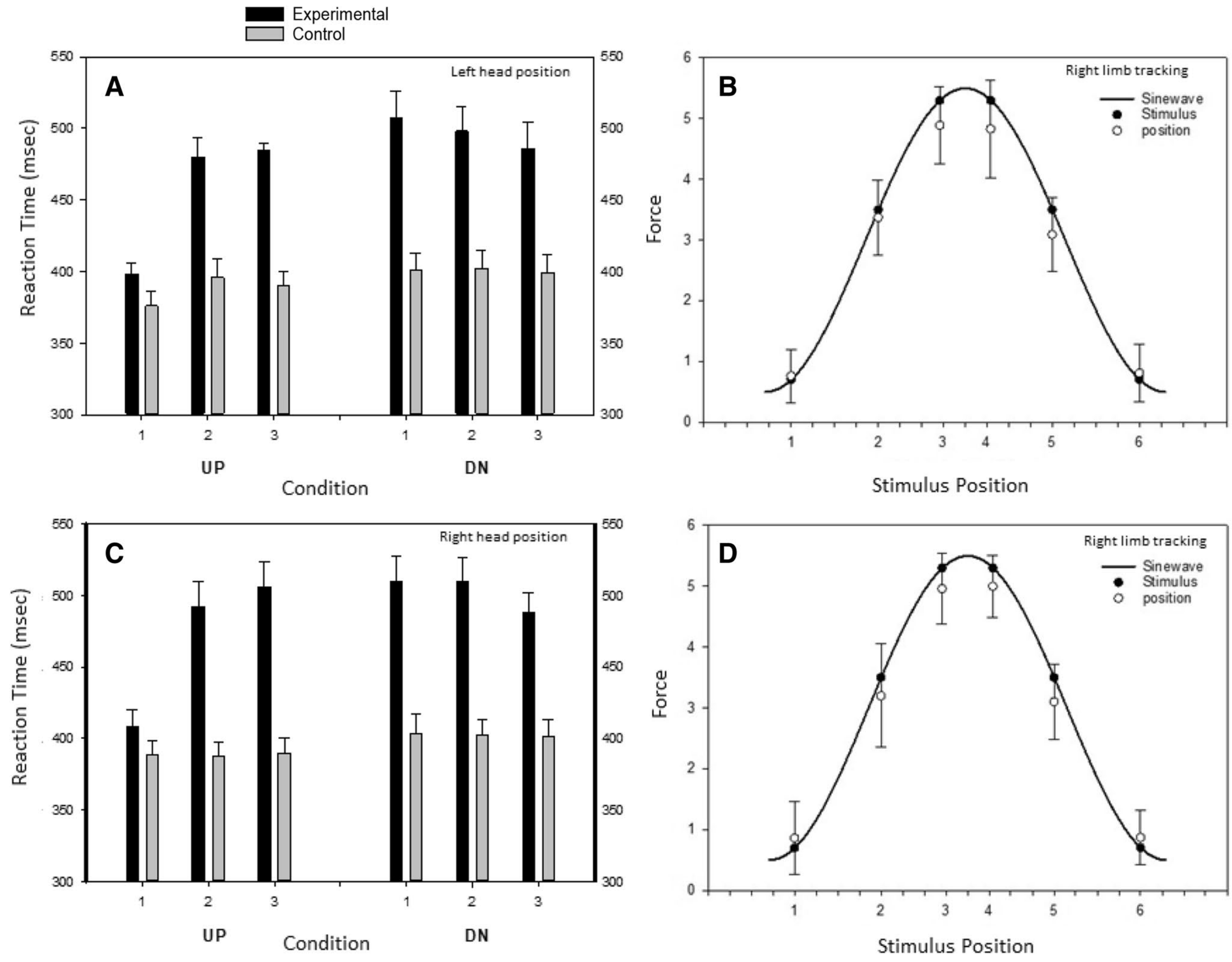

Fig. 3 Illustration depicting the mean left limb RT with the head turned 60° to the left for the experimental and control conditions at each of the positions where the stimulus to react was presented (**a**), the mean right limb force and the sinewave template at the time the stimulus was presented for the experimental condition (**b**), the mean left limb RT when the head was turned 60° to the right for the experimental and control conditions at each of the positions where the stimulus to react was presented (**c**), and the mean right limb force and the sinewave template at the time the stimulus was presented for the experimental condition when the head was positioned 60° to the right (**d**)

between mean RT for head position. In addition, there were no differences between RD for head position.

General discussion

Two experiments were designed to determine response biases resulting from the production of force in the contralateral limb and head position. The results of both experiments indicated mean RT for the left limb was significantly influenced by force production in the right limb. During left limb reactions, RT was faster for trials in which both limbs initiated force simultaneously as compared to trials in which the left limb initiated force while the right limb was producing or releasing force, regardless of head position (Experiment 2). Mean RT for the right limb was not influenced by force production in the contralateral limb (Experiment 1).

Left limb reactions

The results indicated mean RT for the left limb was significantly faster when the right limb was initiating force. Faster RTs at stimulus position 1 is consistent with a number of investigation that have demonstrated faster RT when both limbs produced the same (symmetric) action compared to tasks that require disparate (asymmetric) actions (e.g. Daffertshofer et al. 2005; Hoyer and Bastian 2013; Spijkers et al. 1997). Symmetric bimanual actions, which activate homologous muscles simultaneously, may be facilitated when the contralateral and ipsilateral signals are integrated.

Indeed, previous investigations have indicated that participants are faster, more accurate, and more stable during bimanual tasks when homologous muscles are activated compared to when non-homologous muscles are activated (e.g., Carson et al. 2000; Li et al. 2004; Salter et al. 2004).

It has been debated whether the differences between the activation of symmetric and asymmetric actions are related to the increased processing demands associated with the inhibition of neural crosstalk when non-homologous muscles are activated or with a cost-effective benefit when the same information is available to both limbs during homologous muscle activation (e.g., Aramaki et al. 2010). While the current investigation cannot directly answer this question, the results indicated that participants were able to respond significantly faster during trials that required symmetric activation of homologous muscles (Stimulus Position 1) compared to asymmetric activation patterns (all other stimulus positions) during left limb RTs. This result indicates that the processing demands associated with symmetric bimanual actions are less demanding than asymmetric bimanual actions. This finding is consistent with those found by Aramaki et al. (2010) who compared neural activity during bimanual symmetric and asymmetric movements with the sum of the activity during unimanual movement. Their results indicated that during symmetric movements, the neural substrates of bimanual movements demonstrated a cost-effective benefit due to the sharing of information to both limbs whereas a greater effort to keep the non-dominant limb stable was associated with asymmetric movements.

During the unimanual control condition in the current investigation, a program-controlled cursor moved in the pattern defined by the sinewave template and as with the experimental condition a change in the color of the cursor was the stimulus to produce a force pulse. Numerous investigations have demonstrated longer RTs in bimanual compared to unimanual tasks (see Klapp 2010 for review). As such, we predicted that RTs would be faster at all stimuli positions for the unimanual control task when compared to the experimental task. Interestingly, however, there were no significant differences between the unimanual and bimanual RTs at Stimulus position 1 for the left limb reactions. This result indicates that symmetric bimanual actions require no extra processing demands when compared with unimanual actions. This result supports the notion that neural crosstalk may facilitate the performance of symmetric bimanual actions by reducing the processing costs associated with the task when the same information is available to both limbs (Aramaki et al. 2010).

Right limb reactions

An asymmetric pattern of results was observed in Experiment 1. A number of investigations have indicated that interference between the limbs is asymmetric in that one limb is more affected by the interference than the other limb (e.g., Aramaki et al. 2005; Cattaert et al. 1999; de Poel et al. 2007; Kennedy et al. 2015, 2016b; Kagerer et al. 2003; Maki et al. 2008; Peters 1985; Semjen et al. 1995). Research has pointed to issues related to hand dominance as the source of the asymmetry (e.g., Treffner and Turvey 1995). Performance differences between the dominant and non-dominant limbs can be observed in many motor tasks. For example, individuals are more stable and accurate with the dominant limb than with the non-dominant limb during finger tapping tasks (e.g., Peters 1981, 1985), they are more accurate at producing the spatial and temporal goals of a task with the dominant limb than with the non-dominant limb (e.g., Carson et al. 1997; Gooijers et al. 2013; Semjen et al. 1995; Swinnen et al. 1997), and trajectory distortions and direction reversals most often occur in the non-dominant limb (Byblow et al. 1994; Semjen et al. 1995).

It has been suggested that hand dominance affects bimanual coordination via an asymmetry in the strength of neural crosstalk with the dominant hemisphere exerting a stronger influence on the non-dominant limb than vice versa (Aramaki et al. 2005; Cattaert et al. 1999; Kagerer et al. 2003; Maki et al. 2008). Indeed, Cattaert et al. (1999) successfully developed a neural crosstalk model for bimanual interference based on the left limb receiving an attenuated mirror image of the commands sent to the right limb. The simulation reproduced characteristics observed with asymmetric bimanual circle drawing such as, increasing movement frequencies, decline of circular trajectories, and weakening of the phase coupling between the limbs (Cattaert et al. 1999). The results from the current investigation were consistent with the model produced by Cattaert et al. (1999). That is, neural crosstalk was asymmetric with force production with the dominant limb influencing the RT in the non-dominant limb whereas force production with the non-dominant limb did not influence RT in the dominant limb.

Head position

Previous investigations have indicated that lateral head position can influence motor performance of upper body tasks (e.g., Shea et al. 1995). Asymmetric tonic neck responses are thought to reflexively heighten neural responsiveness of extensor muscles in the direction of head position and dampen the responsiveness of the contralateral extensor muscles (Easton 1972). Given that participants were required to react with their left limb by producing an isometric contraction with the extensor muscle of the elbow joint (triceps), while their head was turned 60° to the left or right (Experiment 2) we predicted faster RT and RD when the head was positioned towards the left side of the body and slower RT and RD when the head was positioned to the right side of the body in both the control and experimental conditions. However, head position did not influence reaction time or response duration in the current investigation. This result is partially consistent with an experiment by Klein and Heuer (1999), who investigated the interactions between eccentric head positions on bimanual rotation of a steering device. They found differences in the response execution with eccentric head position but not for response initiation. This result indicated that head position effects response execution, but not movement planning.

Facilitation (interference) via the asymmetric tonic neck response should affect force production resulting in additional (weaker) forces depending on the direction in which the head is turned with respect to the flexors and extensors involved in the task (Shea et al. 1995). As such, kinematic variables related to force production (e.g., response duration and amplitude of response) should be impacted by head position. Indeed, movement reversal time and the amplitude of the response were affected by head position in the experiments by Heuer and Klein (1999) and Klein and Heuer (1999). However, head position did not influence the execution of the response (RD) in the current investigation (see Fig. 3) in either the control or experimental conditions. One possibility for these results may be related to the force requirements of our task. Shea and colleagues, for example, found that the magnitude of the effect of head position on a learned force task tended to increase as the force of the contraction increased. This is consistent with a number of investigations that have indicated tonic neck responses in healthy adults are associated with increased force requirements (e.g., Hellebrandt et al. 1956; Heuer and Klein 2001; Ikai 1950). The force requirements for the RT task in the current investigation was minimal (i.e. 6 N). Perhaps if the force requirements for the RT response were greater, we may have seen an influence of head position.

In addition, head position did not influence RT in the current investigation (see Fig. 3). This result is similar to those reported by Klein and Heuer (1999) with no effect of eccentric head position on RT. However, Heuer and Klein (1999) did find an effect of head rotation with shorter RTs for handle-bar rotations in the same direction (Experiment 2). Given that eccentric head position did not influence RT while head rotation did we have to consider the difference between the two types of head positions. The eccentric head position used by Heuer et al., similar to the current investigation, required participants to position their head laterally (left or right) during a block of trials whereas participants were required to rotate their head laterally (left and right) during a trial. It is possible that rotating the head while concurrently planning a movement response in same direction facilitated RT while turning the head in the opposite direction interfered with movement planning. Interesting, Heuer and Klein (2001) also found a bias in the random generation of leftward and rightward handle-rotation in the same direction as eccentric head position. Taken together, these results point more towards directional constraints associated with movement specification of the head and limbs in the same vs. different direction than modulation of force production via the tonic neck response.

Indeed, Heuer et al. attributed their results to neural crosstalk occurring at different levels of action control (Heuer et al. 2001). Execution level neural crosstalk was responsible for differences in response amplitude while programming level neural crosstalk was responsible for differences in RT when the head and handle-bar rotation occurred in the same direction compared to trials when the head and handle-bar rotation occurred in opposite directions. While our results are consistent with the notion that neural crosstalk can influence the time to respond to a stimulus (Experiment 1), we do not find a similar effect for head position via the tonic neck response (Experiment 2). It is possible, however, that neural crosstalk may facilitate or inhibit movement planning depending on whether the same or different head/limb directions are concurrently specified.

Conclusion

A RT task was used to determine response biases resulting from the production of force in the contralateral limb and head position. The results indicated that mean RT for the left limb was influenced by the initiation of force by the right limb, regardless of head position. However, mean RT for the right limb was not influenced by force production by the left limb. The results are consistent with the notion that neural crosstalk can influence the time required to react to a stimulus but this influence is associated with the initiation of force in the contralateral limb and is asymmetric in nature with the dominant limb exerting a stronger influence on the non-dominant limb than vice versa. However, we did not find a similar effect for head position via the tonic neck response.

Compliance with ethical standards

Conflict of interest The authors have not received any financial support in this study and declare no conflict of interest.

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