

RESEARCH ARTICLE | *Control of Coordinated Movements*

Response preparation and execution during intentional bimanual pattern switching

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Maslovat D, Carter MJ, Carlsen AN. Response preparation and execution during intentional bimanual pattern switching. *J Neurophysiol* 118: 1720–1731, 2017. First published June 28, 2017; doi: 10.1152/jn.00323.2017.—During continuous bimanual coordination, in-phase (IP; 0° relative phase) and anti-phase (AP; 180° relative phase) patterns can be stably performed without practice. Paradigms in which participants are required to intentionally switch between these coordination patterns have been used to investigate the interaction between the performer's intentions and intrinsic dynamics of the body's preferred patterns. The current study examined the processes associated with switching preparation and execution through the use of a startling acoustic stimulus (SAS) as the switch stimulus. A SAS is known to involuntarily trigger preprogrammed responses at a shortened latency and, thus, can be used to probe advance preparation. Participants performed cyclical IP and AP bimanual elbow extension-flexion movements in which they were required to switch patterns in response to an auditory switch cue, which was either nonstartling (80 dB) or a SAS (120 dB). Results indicated that reaction time to the switch stimulus (i.e., switch onset) was significantly reduced on startle trials, indicative of advance preparation of the switch response. Similarly, switching time was reduced on startle trials, which was attributed to increased neural activation caused by the SAS. Switching time was also shorter for AP to IP trials, but only when the switching stimulus occurred at either the midpoint or reversal locations within the movement cycle, suggesting that the switch location may affect the intrinsic dynamics of the system.

NEW & NOTEWORTHY The current study provides novel information regarding preparation and execution of intentional switching between in-phase and anti-phase bimanual coordination patterns. Using a startling acoustic stimulus, we provide strong evidence that the switching response is prepared before the switch stimulus, and switch execution is accelerated by the startling stimulus. In addition, the time required to switch between patterns and relative limb contribution is dependent upon where in the movement cycle the switch stimulus occurred.

coordination dynamics; intentional switching; preparation; startle; transitions

HUMAN MOVEMENT often involves coordination between various limbs in a task-specific manner, requiring detailed temporal and spatial organization. While there are theoretically unlimited combinations of coordinated movements, certain patterns

are easily organized with little practice and are, thus, considered to be natural or intrinsic. Two such patterns involve “in-phase” (IP) movements in which the limbs are moved about a joint iso-directionally or with similar muscles and “anti-phase” (AP) movements in which the limbs are moved antidirectionally or with nonsimilar muscles. These patterns can be identified by their relative phasing, which is obtained by subtracting the phase angle of each limb's motion at any time, with IP resulting in a mean relative phase of 0° and AP resulting in a mean relative phase of 180° (see Kelso 1995, 2014; Swinnen 2002 for reviews). Although both IP and AP patterns are reasonably stable at lower oscillation frequencies, IP movement is found to be more accurate and stable (e.g., Carson 1995; Kelso 1984) and requires less attention than AP (Temprado et al. 1999). When AP coordination patterns are performed at increasing movement speeds, there is the tendency for a spontaneous phase transition from AP to IP, while the converse pattern of IP to AP does not occur, even at high frequencies (Kelso 1984, 1995). These findings have been described within a dynamical pattern theory, in which rhythmic movements are modeled as a system of coupled nonlinear oscillators (Haken et al. 1985; Schöner and Kelso 1988) and switching between patterns is governed by the relative stability of the pattern being produced before and following the phase transition.

While spontaneous transitions can occur from AP to IP, switches between patterns can also be made in response to an auditory or visual “switching stimulus,” providing insight into the relative time required to intentionally move between more and less stable patterns. Typically, this intentional switching time is significantly longer when required to switch from IP to AP as compared with a switch in the opposite direction, confirming that a faster transition occurs toward the pattern with greater stability (Carson et al. 1994; Kelso et al. 1988; Scholz and Kelso 1990). The use of an intentional switching paradigm has traditionally been examined through a coordination dynamics framework and has been useful to examine how the intentions of the performer can interact with the intrinsic dynamics of the body's preferred pattern generation. For example, Serrien and Swinnen (1999) investigated intentional switching between different effector combinations and found faster switching for homologous vs. nonhomologous muscles, consistent with the predictions derived from a dynamical the-

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ory approach. Similarly, Byblow et al. (2000) studied intentional switching in patients with Parkinson's disease, finding longer times to begin the switch between patterns as compared with healthy controls, indicative of impaired movement production.

To date, the intentional switching paradigm has been predominantly used within a dynamical systems approach to investigate how relative pattern stability affects the time required to switch between these intrinsic patterns. However, the paradigm also provides a unique opportunity to use a continuous bimanual coordination task to examine the processes associated with response preparation and execution. Within an information-processing framework, the time to prepare, initiate, and execute a movement are often quantified using a reaction time paradigm in which participants are asked to produce a response as quickly as possible following an imperative stimulus (Donders 1969). Typically, the time from stimulus presentation to movement onset (reaction time, RT) is considered to be a measure of response preparation and/or initiation time whereas the time from movement onset to completion (movement time; MT) is considered to be a measure of response execution. These measures can also be evaluated in an intentional switching task with the time between the switching stimulus and switch onset being analogous to RT and the transition/switch time being analogous to MT.

The purpose of the current experiment was to use the intentional switching paradigm to examine both the preparation and execution of switches between the relatively stable IP and AP coordination patterns. Typically, intentional switching studies are more concerned with the execution of the switching behavior, as this contributes to our understanding of coordination principles and their potential neural basis (Swinnen 2002). However, the intentional switching paradigm also allows for the examination of the preparation of the upcoming switch response to determine how the transition between coordination patterns is planned. From a dynamical systems approach, it is thought that following the switching stimulus, a change in the "intention" of the performer (Carson et al. 1996) causes an alteration of the coordination pattern (Kelso 2012). This change in intention, which is presumably mediated by neural structures, such as SMA, which are associated with limb coordination (Carter et al. 2017), results in a perturbation of the ongoing intrinsic dynamics to induce a shift in the coordination mode. Coupled oscillator models (e.g., HKB model; Haken et al. 1985) would suggest that more time would be required to intentionally switch from a more stable pattern (IP) to a less stable pattern (AP), yet these models make no predictions regarding the time to initiation of the switch. Indeed, it may be suggested that within these frameworks, no differences would be predicted in the time required to initiate a switch from one pattern to another, as in either case a "reactive" process involving the destabilization of ongoing neural patterns occurs following the switch stimulus.

An alternative, but untested, viewpoint would be that due to the knowledge that a pattern switch will be required, the performer prepares specific motor commands required to complete the switch response in advance and holds them in a state of readiness until the switch stimulus occurs. To date, the possibility of advance preparation of the switch response has not been examined, as previous switching studies have either not emphasized fast reactions to the switch stimulus (e.g.,

Byblow et al. 1999, 2000; de Poel et al. 2006) or have reported such long RT latencies (e.g., 500–700 ms; Leunissen et al. 2013) that it is unclear whether the switching behavior represents a preplanned action. Determination of whether the switching response is prepared in advance would provide novel information pertaining to the generation and initiation of rhythmic movements and how we are able to smoothly transition between coordination patterns. This is particularly noteworthy in an intentional switching task because, unlike a typical RT paradigm, the performer is engaged in a bimanual continuous movement when asked to react and execute a new response. Thus, the preprogramming and storage of the switch response would need to occur while motor commands are concurrently being executed, which provides an indication as to the flexibility and/or limitations associated with action organization.

To determine whether the motor commands associated with intentionally switching between patterns are prepared before the switch stimulus or whether the system acts in a more reactive manner to destabilize ongoing neural patterns (Kelso 2012), a loud acoustic stimulus, capable of eliciting a reflexive startle response was employed. When a startling acoustic stimulus (SAS) replaces the normal "go" stimulus in a RT task, responses that are preprogrammed and ready for execution can be triggered involuntarily, a phenomenon known as the "StartReact effect" (see Carlsen et al. 2012; Valls-Solé et al. 2008 for reviews). For example, Valls-Solé et al. (1999) used a simple RT paradigm to show that responses that are voluntarily initiated with a latency of 170 ms can be accelerated to latencies well below 100 ms when triggered by a SAS (see also Carlsen et al. 2004a). These results have been attributed to advance preparation and storage of the motor commands associated with the response, which are triggered by the SAS through the involvement of startle circuitry. Importantly for the current investigation, in situations where advance preparation cannot (or does not) occur, the SAS typically has little or no effect on response latency. For example, it has been shown that in choice RT tasks, where the required response is not known before the go-signal, the SAS does not result in early response triggering (Carlsen et al. 2004a; Maslovat et al. 2011a). Perhaps most relevant to the current study, a SAS has also been used to examine response preparation of a secondary task while performing a continuous primary task that was either motor or cognitive in nature (Maslovat et al. 2015b). In this previous dual-task experiment, the SAS caused a significant reduction in secondary task RT from latencies in the range of 200–300 ms on nonstartle trials to 130–190 ms on startle trials. Although response latencies were well above 100 ms, the authors considered the substantial decrease in RT as evidence for advance preparation of the secondary task, albeit at reduced levels of preparatory activation.

It was hypothesized that if the motor commands to initiate a pattern switch were prepared in advance, then the switch RT would be significantly reduced by the SAS. On the other hand, if the central nervous system acts reactively to destabilize the ongoing coordination pattern, then a reduction in RT by the SAS would not be expected. Although intentional switch RT latencies are much longer than simple RT tasks (i.e., 500–700 ms vs. 150–200 ms), a significant RT reduction on startle trials would be viewed as evidence in support of a preprogrammed switch response (see Carlsen et al. 2012; Valls-Solé et al. 2008

for reviews). This result would provide new and compelling evidence that specific motor commands that produce a transition between coordination patterns can be prepared in advance and held in readiness, even while performing a continuous bimanual movement. In addition, the RT comparison between switching from AP to IP vs. IP to AP allowed for an examination if the preparation and initiation processes differed depending on the relative stability of the postswitch pattern.

To examine the execution processes associated with intentional switching, switching (transition) time was also analyzed. On the basis of previous findings, we expected that the time required to complete the switch from AP to IP would be faster than the converse; however, the predicted effects of the SAS on this variable were less obvious. Often, a SAS has little to no effect on the response output characteristics, providing evidence that the preplanned motor commands are involuntarily triggered by the SAS without modification (e.g., Carlsen et al. 2004b; Valls-Solé et al. 1999). However, some studies have shown that increased activation associated with the startle reflex can amplify or accelerate the timing between the motor commands, resulting in faster or larger movements (e.g., Fernandez-Del-Olmo et al. 2014; Maslovat et al. 2015c, 2011b). Given the requirement to switch between patterns as fast as possible following the switch stimulus, we predicted that the extra activation provided by the SAS would accelerate the execution process and, thus, reduce switching time for both switch directions. We also examined the processes involved in switching execution by determining the relative contributions of each limb during the transition period. Previous research has provided evidence that intentional switching is primarily mediated via phase adaptations of the nondominant limb (de Poel et al. 2006). We predicted a replication of this result and were also interested in whether limb contributions differed depending on the switch direction (AP to IP vs. IP to AP).

As a secondary objective, we were also interested in whether the switching behavior and the effects of the SAS were dependent upon the position in the movement cycle where the switch stimulus occurred. Previous intentional switching experiments have typically either provided the switch stimulus at a fixed point in the cycle, such as a reversal point (e.g., De Luca et al. 2010; Tallet et al. 2010) or randomly throughout the movement cycle (e.g., Byblow et al. 1999, 2000; de Poel et al. 2006). In the current experiment, we presented the switching stimulus at three different cycle positions to examine whether differences in preparation and execution occurred, depending on where in the coordinated movement the switching response was cued. If the switching behavior is affected by where in the cycle location the switch stimulus occurred, this would have important implications for future research involving the intentional switching paradigm.

To summarize, the use of a SAS in an intentional switching paradigm provided a novel method to determine whether specific motor commands are prepared in advance of a stimulus that signals the intentional switching between relatively stable coordination patterns. Analysis of switch RT allowed for investigation as to whether the switching response is prepared in advance and whether preparation differences occurred depending on the relative stability of the postswitch pattern. Conversely, analysis of switching time and relative limb contribution allowed for examination of response execution and determination of whether this process would be affected by an

increase in neural activation caused by the SAS. The investigation of intentional switching from an information processing approach rather than a dynamical systems perspective, may provide an important alternative but complementary viewpoint that could ultimately lead to a better understanding of behaviors associated with switching between various coordination patterns.

MATERIALS AND METHODS

Participants. Data were collected from 12 right-handed volunteers with no sensory or motor dysfunctions. To ensure participants exhibited a reliable startle reflex, sternocleidomastoid (SCM) activation was examined for the first 120 ms following the SAS on trials during a simple RT testing block that was performed at the conclusion of the experiment (see *Data reduction and Dependent measures* for details). Two participants showed SCM activation in less than three out of five simple RT SAS trials and were excluded from the data analysis (see Carlsen et al. 2011 for more details regarding recommended inclusion criteria); thus, data are presented from 10 participants (6 women, 4 men; age 23.2 ± 3.5 yr). All participants gave written, informed consent and were naïve to the hypotheses under investigation. This study was approved by the Research Ethics Board at the University of Ottawa and was conducted in accordance with the latest revision of the Declaration of Helsinki.

Apparatus, tasks, and experimental design. Participants sat facing a 24" full-HD LCD computer screen with both arms secured with Velcro to manipulanda that were mounted a custom frame attached to the chair on which the participant was seated. The Velcro were attached around the upper and lower forearm of each limb, such that the forearms were parallel to the floor and the palms facing inward with participants grasping a handle (12-cm length \times 2.5-cm diameter) in each hand. The manipulanda restricted movement to horizontal flexion and extension about the elbow axis, which was aligned with the axis of rotation. Participants were required to perform continuous IP or AP bimanual movements that consisted of a total range of 30° (i.e., $\pm 15^\circ$ toward and away from a neutral midpoint corresponding to the arms being parallel to the midline of the body; see Fig. 1, *top*). The movement and end-point targets were represented on the computer screen by presenting four small white rectangles (1.6 cm wide \times 0.65 cm high) aligned horizontally across the screen. The two left rectangles represented the "in" and "out" end points for the left limb, and the right two represented end points for the right limb. The position of each limb was indicated by a marker (0.3 cm wide \times 1.1 cm high) that moved horizontally between each set of two targets. The target centers were located 10.2 cm apart, so the movement was represented as 0.34 cm per degree on the computer screen (see Fig. 1, *bottom*). The movement patterns of IP (simultaneous flexion and extension of the forearms in a synchronous pattern) and AP (alternating flexion and extension of the forearms in a synchronous pattern) were explained to the participants. A speaker (MG Electronics M58H) was placed 30 cm behind the participant, in line with the vertical axis of the head.

Each trial began with the instructions presented on the screen for 1,000 ms to either "Begin in-phase" or "Begin anti-phase," followed by a tone (80 dB, 200 Hz, 100 ms) signifying the start of the trial. This was followed by a 1,000-ms blank screen, and then a visual metronome was presented involving the target rectangles flashing green at a rate of 1.5 Hz on the computer screen indicating when the participants' limbs should reach their respective end points. The cycling frequency was chosen to be comfortable for participants, yet below the critical frequency at which spontaneous transitions would be expected to occur (usually 2.0 Hz or greater). A single movement speed was chosen to limit participants' noise exposure to the SAS and because of previous results that have shown that cycling frequency has a limited impact on the switching process (Scholz and Kelso 1990). The relative locations of the left and right manipulanda were shown in real time, with the instructions to synchronize the end points

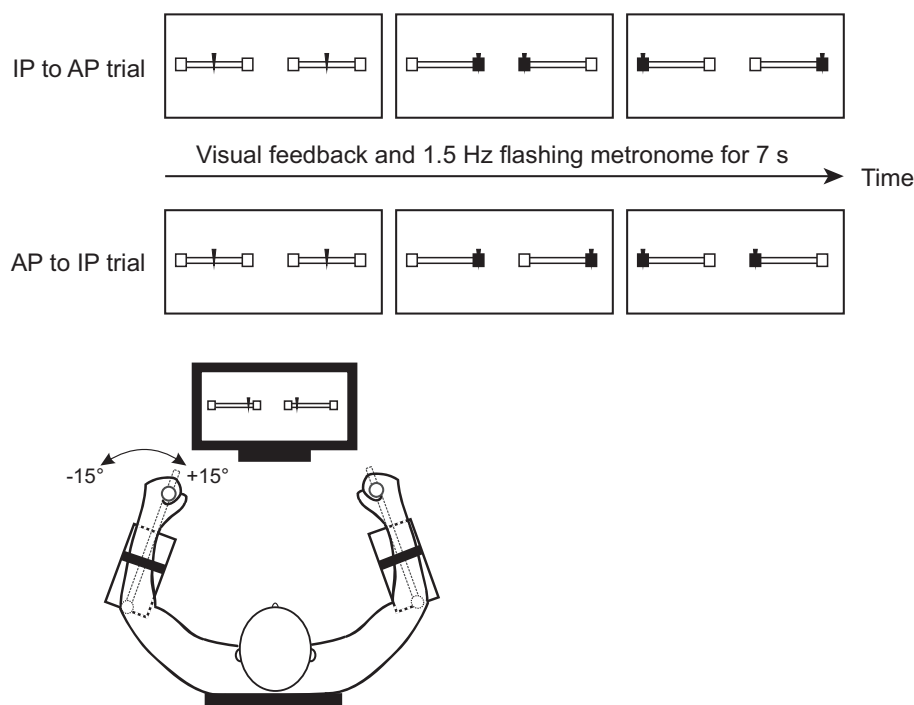


Fig. 1. A schematic representation of the requirement movements to be performed (*top*) and illustration of visual feedback provided to the participants (*bottom*). Participants began in either in-phase (IP) or anti-phase (AP) and switched patterns as soon as possible following an auditory switch stimulus.

of the movement with the flashing boxes (see Fig. 1, *bottom*). This visual feedback was provided for the first 7 s of each trial, after which participants were to maintain their current pattern until they heard the presentation of a switch stimulus, which could either be a nonstartling tone (80 dB, 1,000 Hz, 40 ms) or a SAS (120-dB white noise, 25 ms). Upon presentation of the switch stimulus, participants were instructed to intentionally change their movement pattern as quickly as possible and maintain the new pattern for the remainder of the trial (i.e., IP to AP or vice versa). The total trial length was 18 s, and the switch stimulus occurred on a random movement cycle occurring between 8 and 13 s, and always occurred at one of three kinematic locations of the right arm: 1) flexion midpoint, defined as the neutral 0° location as the right arm moved in the flexion direction; 2) flexion reversal, defined as the point at which the right arm changed direction from flexion to extension; and 3) flexion prereversal, defined as the half way point between the flexion midpoint and flexion reversal for the right arm (i.e., 7.5° inward from the neutral position). Only three locations were chosen to minimize the number of SAS trials, and the above kinematic markers were considered the most salient locations within in each cycle.

To familiarize participants with the experiment protocol, four nonstartle practice trials were conducted in a predetermined alternating order of IP to AP, AP to IP, IP to AP, AP to IP, and the switch stimulus always occurred at the flexion midpoint. This was followed by 64 testing trials, which consisted of an equal number of trials starting with IP and AP. Within each starting pattern, the 32 trials included 15 nonstartle trials (five switch stimuli presented at each of the three kinematic locations), 15 startle trials (five switch stimuli presented at each of the three kinematic locations), and two catch trials in which no switch stimulus was presented. The order of trials was pseudorandom with the only restriction being that the first two testing trials were nonstartle trials to ensure the participant was sufficiently comfortable with the testing protocol before being presented with a SAS.

Following the completion of all testing trials, participants performed a single block of simple RT trials involving a 20° right forearm extension movement from the midpoint position. Trials began with “Get Ready!!” displayed on the screen, followed by a 2,000–2,500 ms random foreperiod, and then the acoustic go-signal, which consisted of either a nonstartling or startling stimulus identical to that

provided on switching trials. Ten nonstartle practice trials were followed by 25 trials that included five SAS trials pseudorandomized, such that the first two trials could not be startle trials, nor could there be two consecutive startle trials. Following each trial, final location (displayed as degrees undershoot/overshoot of target) and displacement RT were provided on the screen for 3,500 ms, with points awarded for RTs below 140 ms to motivate advance preparation. This testing block was implemented to ensure participants exhibited consistent startle-related activation in the SCM during startle trials in a more traditional startle paradigm, as it was unclear how participants would respond to the SAS while engaged in a continuous bimanual task (see Maslovat et al. 2015b for a similar rationale). Those participants who exhibited SCM activation in less than three out of five of the SAS trials were excluded from the analyses as they were considered to be “low responders.”

Recording equipment. EMG activity was recorded using bipolar preamplified surface electrodes (Delsys, Bagnoli DE-2.1) connected via shielded cabling to an external amplifier system (Delsys, Bagnoli-8). Recording sites included the left sternocleidomastoid (SCM) as a startle indicator, as well as the right and left prime movers, which comprised the lateral head of the triceps brachii and the long head of the biceps brachii. A reference electrode was placed on the left lateral epicondyle. Recording sites were prepared and cleansed to decrease electrical impedance. The electrodes were oriented parallel to the muscle fibers and were attached to the skin using double-sided adhesive strips. Positional data for each limb were collected using a linear potentiometer powered by a 5-V direct current power supply attached to the central axis of each manipulandum. For switching trials, band-passed (20–450 Hz) EMG, as well as position data, from both manipulanda were digitally sampled at 1 kHz for the entire 18-s trial, whereas for simple RT trials, data were sampled at 4 kHz for 3 s, beginning 1 s before the go stimulus. All data collection was performed using a customized program written in LabView (National Instruments) and stored for offline analysis.

Data reduction and dependent measures. For switching trials, continuous relative phase (Φ) between the effectors was calculated for the final 16 s of each trial. The first 2 s were discarded to avoid any transient fluctuations in performance, as participants adjusted their movement to match the pace specified by the metronome. Relative phase of the left in relation to the right effector was calculated for each

sample after the velocity and position of the limbs were rescaled to the interval of $[-1, 1]$ using the formula: $\phi = \Theta_R - \Theta_L$, where Θ (phase) for each limb = $\tan^{-1}([dX/dt] / [dX])$ (Scholz and Kelso 1989). Because of the circular nature of the relative phase, whereby 0° is equal to 360° , calculations were constrained in a different manner depending on the required switch direction. For AP to IP switching, relative phase before the switch was constrained to a value between 0° and 360° and to a value between -180° and 180° after the switch. The opposite was done for IP to AP switching. On the basis of these calculations, relative phase was always converted to a value ranging between the expected pattern $\pm 180^\circ$ (see Carter et al. (2015, 2017) for similar methods).

Our main dependent measures for switching trials included RT and switching time. RT was defined as the time interval between presentation of the switching stimulus to the point at which the relative phase first deviated from its mean previous mode. Switching time was defined as the time interval from the point at which the relative phase first deviated from its mean previous mode until the new pattern was achieved. The criterion for achievement of the new mode of coordination was $\pm 40^\circ$ of the intended pattern (i.e., 0° or 180°) for at least three consecutive movement cycles. Determination of these two measures was performed offline using an interactive display of the individual displacement trajectories and the relative phase time series for each trial (similar to Serrien and Swinnen 1999; see Fig. 2).

To determine the relative limb contribution during the transition period, we determined an index of coupling (IC) for each switching trial (see de Poel et al. 2006 for more details). In brief, individual phase velocity of each limb was calculated using the rate of change of phase angle and were normalized with respect to the five seconds before the switch stimulus. The change in phasing for each limb was then determined by summing the difference in preswitch velocity from each velocity data point during the transition period (i.e., switch onset to switch completion). This provided a phasing change for each limb (A_L and A_R) and the relative contribution of the left limb to the pattern change was expressed by:

$$IC = \frac{|A_L|}{|A_L| + |A_R|}$$

Thus, the IC calculates a value between 0 and 1, which indicates the degree to which the switch was mediated by adaptations of each

limb. An IC equal to 0.5 would represent an equal contribution from each limb, whereas IC greater than 0.5 would indicate a larger adaptation of the left limb, and IC less than 0.5 would indicate a larger adaptation of the right limb.

For simple RT trials, our only dependent measure was premotor RT, which was calculated as the time from the auditory cue to onset of EMG activity in the triceps (agonist muscle for arm extension movement). EMG onset was defined as the first point where the rectified and filtered (25 Hz low pass elliptical filter) EMG activity first reached a value of two standard deviations above baseline levels (mean EMG activity in a 100-ms interval starting 1,000 ms before the stimulus) and was maintained for a minimum of 20 ms. EMG onset points were first determined using a custom LabView (National Instruments) program and then were visually confirmed and manually adjusted (if necessary) to compensate for any errors due to the strictness of the algorithm. For all startle trials (both switching and simple RT), SCM onset was determined in a similar fashion, with reflex activation deemed to be present if onset occurred within 120 ms of the SAS (i.e., SCM+ trials; see Carlsen et al. 2011).

Practice and catch trials were excluded from analysis, as were trials in which an error occurred. Intentional switching error trials included those in which participants either failed to switch patterns, switched before the stimulus, or did not accurately maintain the new pattern (37 trials). Simple RT error trials included those in which participants anticipated the go stimulus (two trials) or were unusually slow to respond (RT > 500 ms; four trials). Trials were also discarded if there was a lack of SCM activation on SAS trials (i.e., SCM trials), which was infrequent during simple RT trials (four trials or 8%) but occurred at a higher rate during intentional switching trials (87 trials or 30%). The increased proportion of SCM trials during switching trials is consistent with previous research involving a SAS presented during a continuous task and has been attributed to decreased attentional resources available for preparation of an upcoming response (Maslovat et al. 2015b). Overall, the inclusion rate was 79% for switching trials (476/600 trials) and 96% for simple RT trials (240/250 trials).

Statistical analysis. To confirm the typical effects of the SAS triggering, a prepared response at short latency, premotor RT for the simple RT condition was analyzed via a paired samples *t*-test comparing performance on startle vs. nonstartle trials. For switching trials, RT and switching time were independently analyzed via a 2 Direction

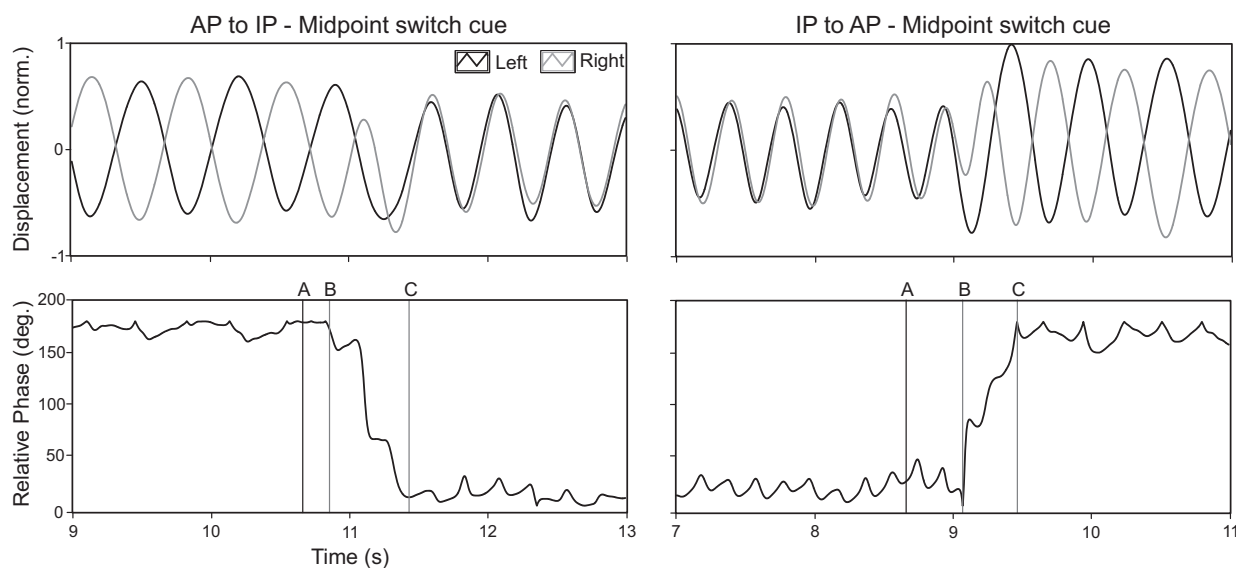


Fig. 2. Sample data from an AP to IP (left) and IP to AP (right) switching trial. Determination of reaction time and switching time were completed using an interactive display, showing individual displacement trajectories (top, black and gray lines, respectively; scaled to arbitrary units ± 1) and the calculated relative phase (bottom). The presentation of the switching stimulus is shown at marker A (in this case, the switch stimulus was presented at the midpoint marker), with marker B, indicating the onset of the switch and marker C, indicating the termination of the switch. The time period between marker A and B represents reaction time, whereas the time period between marker B and C represents switching time.

(IP to AP, AP to IP) \times 3 Location (midpoint, reversal, prereversal) \times 2 Stimulus (nonstartle, startle) repeated-measures ANOVA.

Because it was expected that a decrease in both RT and switching time would be observed for startle switch trials, it was important to confirm that any reduction effects of the SAS were due to engagement of the reflexive startle circuitry rather than stimulus intensity effects (Woodworth 1938). Although only SCM+ trials were included in the analyses detailed above, this distinction can be achieved by the comparison between SCM+ and SCM- trials. If the decreased RT in startle trials is due to the more intense stimulus only, there should be no difference between SCM+ and SCM- trials, as both involve a stimulus of equal intensity (Carlsen et al. 2009a; Honeycutt et al. 2013). Conversely, if the decrease on startle trials is caused by engagement of the reflexive startle circuitry, differences would be expected between SCM+ and SCM- trials, as has been previously reported (Carlsen et al. 2007; Honeycutt et al. 2015; Maslovat et al. 2015b, 2015d). In this manner, although only the SCM+ trials were considered indicative of those in which reflexive startle activation has been observed (and thus included in the main analyses), the SCM- trials acted as a control condition for the effect of stimulus intensity. Both RT and switching time on startle switch trials were independently analyzed via a 2 SCM Presence (SCM+, SCM-) \times 2 Direction (IP to AP, AP to IP) repeated-measures ANOVA. As not all participants exhibited both SCM+ and SCM- trials for both switch directions, this analysis was limited to 8 of the 10 participants. Simple RT startle trials were not subjected to this analysis due to the lack of SCM- trials for most participants.

Two separate analyses were performed on the index of coupling (IC) measure. First, mean IC values were collapsed by switch location and determined for each participant for the four main experimental conditions of IP to AP (nonstartle), AP to IP (nonstartle), IP to AP (startle), and AP to IP (startle). These mean IC values were compared with IC = 0.5 using individual one sample *t*-tests to determine whether each condition was significantly different to a value representing equal involvement of each limb in the transition behavior. Mean IC was also analyzed via a 2 Direction (IP to AP, AP to IP) \times 3 Location (midpoint, reversal, prereversal) \times 2 Stimulus (nonstartle, startle) RM ANOVA to examine any possible difference in switching behavior in the various experimental conditions.

For all analyses, Greenhouse-Geisser corrected *P* values are reported where the assumption of sphericity was violated. Partial eta squared (η_p^2) and Cohen's *d* values are reported as an estimate of

effect size, and differences with a probability of less than 0.05 were considered significant. Post hoc analyses were performed using Bonferroni-corrected pairwise comparisons, where appropriate, to determine the locus of any significant differences.

RESULTS

Simple RT. Analysis of premotor RT for the simple RT condition confirmed the typical effects of the SAS, whereby trials were performed at a significantly shorter RT on startle trials ($M = 96$ ms, $SD = 52$ ms), as compared with nonstartle trials ($M = 139$ ms, $SD = 19$ ms), $t(9) = 3.53$, $P = 0.006$, $d = 1.10$.

Switch RT. Reaction time for switching trials is presented in Fig. 3. Similar to the simple RT task, analysis of switch task RT also confirmed that switches were initiated at significantly shorter latencies during startle trials ($M = 257$ ms, $SD = 47$ ms) compared with nonstartle trials ($M = 395$ ms, $SD = 70$ ms), $F(1, 9) = 128.27$, $P < 0.001$, $\eta_p^2 = 0.93$. No main effects were found for switch direction, $F(1, 9) = 0.25$, $P = 0.628$, $\eta_p^2 = 0.03$, or stimulus location, $F(2, 18) = 0.93$, $P = 0.414$, $\eta_p^2 = 0.09$, and no significant interaction effects were found, suggesting that the SAS reduced RT to a similar degree for all conditions.

Switching (transition) time. Time to complete the switch (switching time) is presented in Fig. 4. Similar to the RT results, analysis of switch time showed a main effect for stimulus, $F(1, 9) = 17.46$, $P = 0.002$, $\eta_p^2 = 0.66$, due to significantly faster transition between patterns on startle trials ($M = 506$ ms, $SD = 110$ ms), as compared with nonstartle trials ($M = 588$ ms, $SD = 131$ ms). Switching time also revealed a main effect for direction, $F(1, 9) = 16.71$, $P = 0.003$, $\eta_p^2 = 0.65$, which was superseded by a significant Direction \times Location interaction, $F(2, 18) = 6.98$, $P = 0.006$, $\eta_p^2 = 0.44$. Post hoc analysis of this interaction confirmed that the locus of this effect was due to a significantly shorter switch time from AP to IP vs. IP to AP for the midpoint and reversal locations, but no difference in switch time between patterns for the prereversal location.

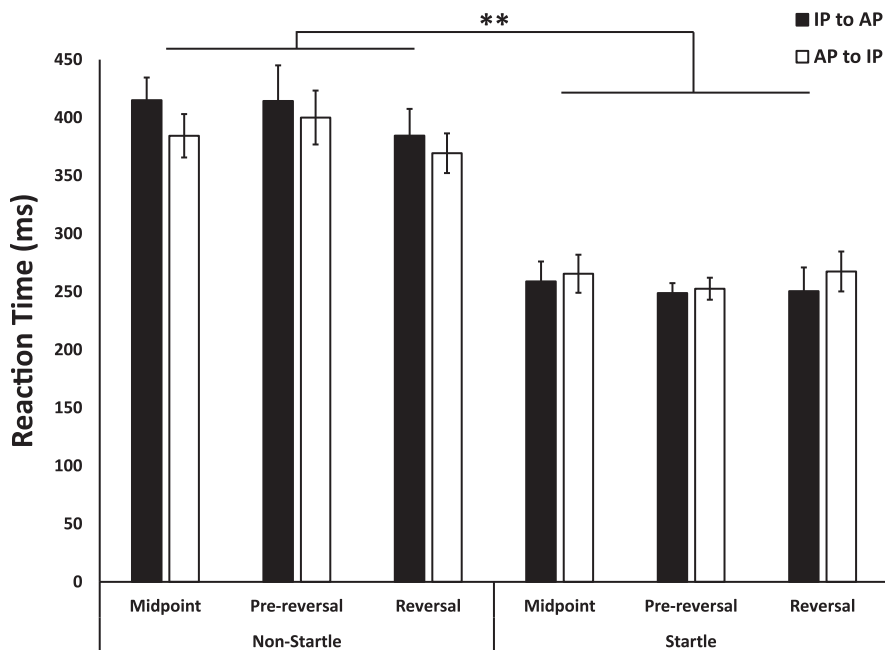


Fig. 3. Reaction time data for switching trials showing mean values with standard error bars, separated by stimulus type (nonstartle, startle) and stimulus location (midpoint, prereversal, reversal). Reaction time from IP to AP is shown in black bars, whereas AP to IP is shown in white bars. **Significant main effect of stimulus type, $P < 0.01$.

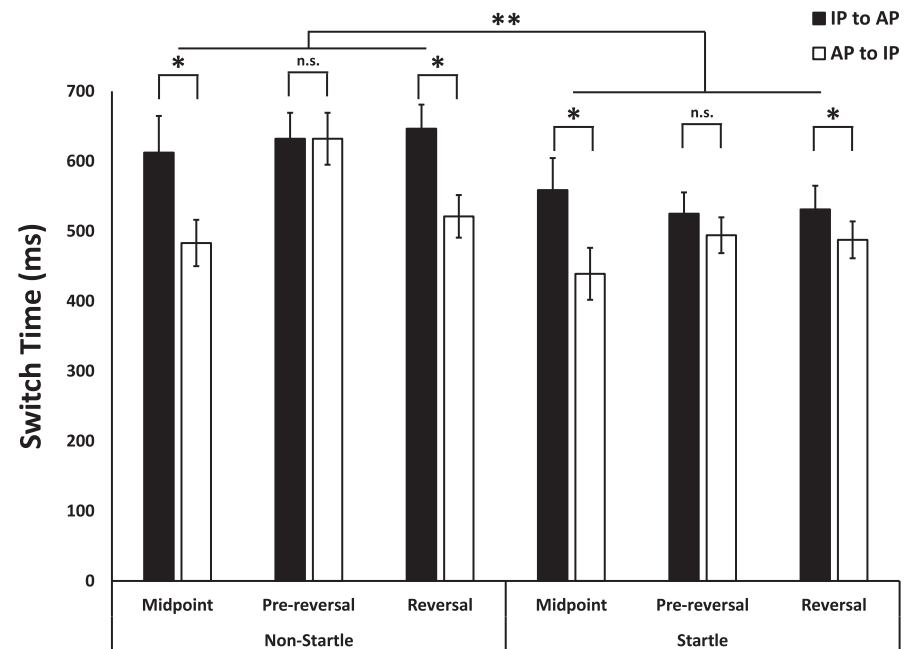


Fig. 4. Switching time data showing mean values with standard error bars, separated by stimulus type (non-startle, startle), and stimulus location (midpoint, pre-reversal, and reversal). Switching time from IP to AP is shown in black bars, whereas AP to IP is shown in white bars. *Significant difference between switch direction, $P < 0.05$. **Significant main effect of stimulus type, $P < 0.01$.

Effects of startle indicator presence/absence. The comparison of switch RT and switching time depending on whether SCM activation was present or absent is shown in Fig. 5. Analysis of switch RT confirmed a main effect of SCM presence, $F(1, 7) = 43.93$, $P < 0.001$, $\eta_p^2 = 0.86$, whereby SCM+ trials were initiated at significantly shorter latency ($M = 253$ ms, $SD = 37$ ms), as compared with SCM- trials ($M = 350$ ms, $SD = 55$ ms). No effects were found for direction, $F(1, 7) = 1.73$, $P = 0.230$, $\eta_p^2 = 0.20$, and no significant interaction effect was found, indicating that the presence of SCM activation had a similar effect for pattern switches in both directions (Fig. 5A). Similarly, a main effect of SCM presence was found for switching time, $F(1, 7) = 8.88$, $P = 0.046$, $\eta_p^2 = 0.46$, whereby SCM+ trials were completed with a significantly shorter switch time ($M = 493$ ms, $SD = 74$ ms), as compared with SCM- trials ($M = 577$ ms, $SD = 153$ ms). No effects were found for direction, $F(1, 7) = 3.12$, $P = 0.121$, $\eta_p^2 = 0.31$, and no significant interaction effect was found, indicating that the presence of SCM activation was not affected by direction of pattern switch (Fig. 5B).

Relative limb contribution. Data from the IC analysis is presented in Fig. 6. The one sample t -tests (Fig. 6A) confirmed that only the IP to AP nonstartle condition was significantly different to 0.5, $t(9) = 2.57$, $P = 0.030$, $d = 0.81$. No significant effects were found for conditions involving AP to IP nonstartle, $t(9) = 0.95$, $P = 0.365$, $d = 0.30$, IP to AP startle, $t(9) = 0.80$, $P = 0.444$, $d = 0.25$, or AP to IP nonstartle, $t(9) = -1.30$, $P = 0.226$, $d = 0.41$. Results of the ANOVA (Fig. 6B) indicated a main effect for stimulus, $F(1, 9) = 13.58$, $P = 0.005$, $\eta_p^2 = 0.60$, due to significantly larger IC values on nonstartle trials ($M = 0.59$, $SD = 0.20$), as compared with startle trials ($M = 0.49$, $SD = 0.21$). There was also a significant Direction \times Location interaction, $F(2, 18) = 9.21$, $P = 0.002$, $\eta_p^2 = 0.50$, which was due to a significantly larger IC value for AP to IP trials when the stimulus location occurred at the reversal compared with the midpoint.

DISCUSSION

The purpose of the current study was to examine whether the motor commands involved in intentionally switching between relatively stable interlimb coordination patterns are prepared in advance. Unlike previous studies that have used a dynamical systems framework to generate predictions regarding switching behavior, the current study used a SAS, which has been employed within an information-processing framework to probe the processes associated with response preparation and execution. Although the same pattern of results was observed for startle and nonstartle trials, the data clearly showed that presentation of a SAS substantially reduced the time to initiate the switching behavior (Fig. 3). Because only those movements prepared in advance exhibit the short latency response, triggered effects when presented with a SAS (Carlsen et al. 2012), this result can be taken as evidence that participants were engaging in motor-specific preparatory processes in anticipation of the switch stimulus. This result not only confirms that the switch response is preprogrammed, but also provides new and complementary evidence that a secondary task can be prepared while performing a continuous bimanual movement (Maslovat et al. 2015b).

We were also interested in whether any RT differences in response to the SAS would be observed, on the basis of whether participants were preparing to switch from AP to IP or IP to AP and where in the movement cycle the switch stimulus occurred. The RT results showed no effects of switch direction or stimulus location (Fig. 3), which suggests a similar preparatory state regardless of the starting pattern or where in the cycle the SAS occurred. While many intentional switching studies have been most concerned with switching time and thus have not reported RT values (e.g., Byblow et al. 1999; Carson et al. 1996), Leunissen et al. (2013) reported faster switch RTs when transitioning to the symmetric vs. asymmetric pattern. Although this result contrasts the current null finding of switch direction, this earlier study used a more complex two-dimensional bimanual circling task, and their RT values were con-

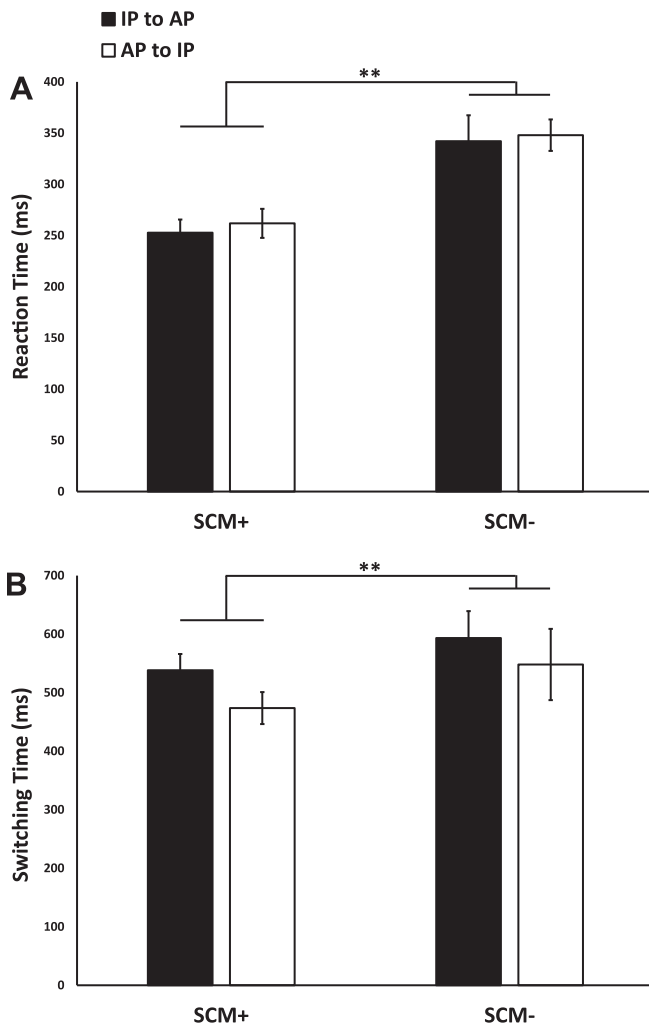


Fig. 5. Reaction time (A) and switching time (B) data for switching startle trials showing mean values with standard error bars, separated by SCM activation presence (SCM+) or absence (SCM-). Performance for trials switching from IP to AP is shown by the solid bars, whereas switching from AP to IP is shown by the open bars. **Significant main effect of SCM activation, $P < 0.01$.

siderably longer (500–700 ms) than we observed on nonstartle trials (350–450 ms), which may explain the discrepancy in findings.

While it would be expected that a louder stimulus would result in shorter response latency due to the well-known stimulus intensity effects (Woodworth 1938), the magnitude of RT decrease observed on startle trials (~140 ms) was much greater than what is typically reported due to simply a more intense stimulus. In addition, the comparison of reaction time on startle trials with and without SCM activation confirmed there was a significant and substantial decrease in RT for SCM+ vs. SCM- trials (~100 ms; see Fig. 5A), even though both trial types involved the more intense SAS. This result provides additional evidence that the reduced latency resulting from the SAS was not solely caused by stimulus intensity effects but rather was more likely due to the involuntary triggering of a prepared response associated with engagement in the startle reflex circuitry. The difference between SCM+ and SCM- trials is consistent with several previous startle studies involving the use of a SAS (Carlsen et al. 2007; Honeycutt et al. 2015; Maslovat et al. 2015b, 2015d), confirming that substan-

tial reductions of RT coupled with the presence of a startle reflex (as indicated by SCM) indicate early response triggering that is different than simple stimulus intensity effects, even when RTs are in the 250-ms range (Fig. 5). Although switching startle trials were still initiated at latencies well above those reported during the simple RT task, the results are similar to previous studies that have used a SAS to show advance preparation in paradigms involving more complex coordinated tasks (e.g., Maslovat et al. 2015b).

In addition to a decrease in time to switch onset, the SAS also resulted in a significant decrease in the switching time required to transition between patterns (Fig. 4). Interestingly, the effects of the SAS did not interact with any other factors, indicating the switching time decrease was of similar magnitude in both directions and at all locations. This suggests that this effect may be due to a general increase in neural activation caused by the SAS, which may either facilitate disruption of

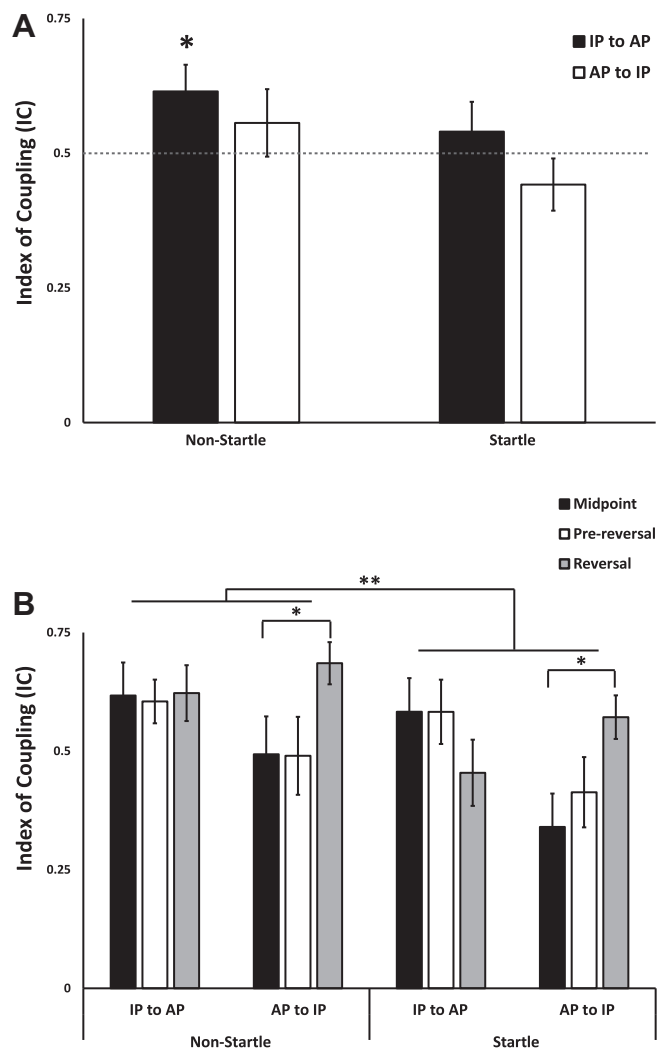


Fig. 6. Index of coupling (IC) data separated by switch direction and stimulus type (A) and by stimulus location (B), showing mean values with standard error bars. An IC > 0.5 indicates the phase transition was mediated to a greater degree by the left limb, whereas an IC < 0.5 indicates the phase transition was mediated to a greater degree by the right limb. A: IP to AP switch for nonstartle trials resulted in an IC that was significantly ($*P < 0.05$) larger than 0.5. B: when the switch stimulus was located at the reversal point, AP to IP transitions showed significantly ($*P < 0.05$) greater IC values, and startle trials resulted in significantly ($**P < 0.01$) lower IC values.

the preswitch pattern or stabilization of the postswitch pattern. Further evidence for this conclusion is provided by the comparison of switching times for startle trials with and without SCM activation. As with switching RT, switching time was significantly shorter on SCM+ trials (Fig. 5B), confirming the switching time reduction was not simply an effect of the more intense switching stimulus. This result is consistent with previous research showing that a SAS can result in a decrease in movement time due to the engagement of the startle reflex circuitry (Maslovat et al. 2011b, 2015c). An alternative mechanism for this effect could be attributed to the SAS temporarily increasing the movement frequency, which has been shown to reduce the transition duration (Carson et al. 1996). Although dynamical pattern theory predicts only a small decrease in transition time as movement frequency increases, reductions in the magnitude of 100 ms have been reported (Scholz and Kelso 1990), similar to what was observed for startle trials in the current experiment. It is also worth noting that although the SAS significantly reduced the transition time between patterns, the mean switch time of both nonstartle (~550–650 ms) and startle trials (~450–550 ms) was consistent with past studies that have emphasized fast transitions (e.g., Byblow et al. 2000; de Poel et al. 2006).

Switching time was also affected by the switch direction and where in the movement cycle the switch stimulus occurred (Fig. 4). As expected, and consistent with previous research (Carson et al. 1994; Kelso et al. 1988; Scholz and Kelso 1990), participants were faster to switch toward the more stable pattern (i.e., from AP to IP). However, a novel finding of the current study is that this directional effect was only present when the switch stimulus occurred at either the midpoint or reversal location, as no differences were found at the pre-reversal point. Thus, the benefits of switching to a more stable pattern may only occur if the switch stimulus occurs at certain locations that may be more salient to the performer. When producing continuous cyclical movements, it has been shown that both spatial and temporal variability are lowest at reversal points, which may represent “anchor” points to stabilize the movement (e.g., Beek et al. 1992; Byblow et al. 1994). Additionally, when a pacing metronome is synchronized with reversal points, pattern stability increases and less spontaneous transitions are observed (Byblow et al. 1994; Fink et al. 2000). It appears from our data that when the switch stimulus appeared at a less salient location (i.e., pre-reversal), that the time required to switch from IP to AP was unaffected, and this our null effect was due to an increase in the time to switch from AP to IP. Although this explanation does not account for the directional advantage when the switching stimulus was presented at the midpoint, it does indicate that the benefits of switching to the more stable IP pattern may only be realized when the switch stimulus occurs at specific points in the movement cycle. This effect may have been masked in previous intentional switching studies due to either presentation of the switching stimulus only at the reversal point (De Luca et al. 2010; Tallet et al. 2010) or a lack of emphasis on reaction time to the switch stimulus (e.g., Byblow et al. 1999, 2000; de Poel et al. 2006), which would not require participants to begin the switching process at a less stable location in the movement cycle.

Further investigation of the switching behavior was achieved by examination of the relative phasing adaptation of each limb

during the transition period. Similar to the results reported by de Poel et al. (2006), nonstartle trials were mediated by a greater contribution of the nondominant (left) limb, although only the IP to AP direction reached statistical significance (Fig. 6A). In addition, and similar to the results of the switching time, the index of coupling was affected by the switch direction and stimulus location (Fig. 6B). Significantly greater left limb contribution during the transition was observed when the switch stimulus was presented at the reversal vs. the midpoint, but only when participants were required to switch from AP to IP. This result provides additional confirmation that the location in the movement cycle where the switch stimulus occurs is an important consideration in the understanding of transitions between coordination patterns. An unexpected result of the switching analysis was that the startling stimulus caused a significant decrease in left limb contribution during the transition between patterns. While it is unclear why this effect would occur, the increased activation caused the SAS resulted in a reduction in switch time and appears to have also altered how the transition occurred, with a response that was more equally mediated by both limbs.

The use of a SAS within an intentional switching paradigm allowed for novel insight into a task that is traditionally examined within a dynamical systems model. Within this perspective, the switching behavior is thought to occur reactively as a result of a modification in the performer’s intention, leading to the destabilization of the ongoing neural pattern and an alteration in the dynamics of the system and ultimately, a change in coordination pattern (Kelso 2012). This approach does not typically consider if any motor commands are prepared in advance of the change of intention and is more concerned with the execution of the switch response itself. The current data provide convincing evidence that the advance knowledge of the required pattern switch encourages preprogramming and storage of the switching behavior, and thus results in a response that is able to be triggered at reduced latency by the SAS. It would be expected that increased preparation time would be required for the switch to the more difficult AP pattern, as this involves nonhomologous muscle contractions. However, this preprogramming would occur in advance of the switch stimulus, leading to the expectation of no RT effect of switch direction for both nonstartle and startle trials. These results suggest a modification of the description of intentional switching behavior, such that preparatory processes occur before the change of intention in expectation of the required pattern change. Once the switch stimulus has been perceived, the change in intention of the performer leads to the execution of the preprogrammed motor commands associated with the switch response, with more time required to switch to the more complex AP pattern. This conclusion highlights the benefit of a theoretical approach that combines various models, which can provide a complementary perspective.

Typically, in simple RT tasks involving the use of a SAS, a specific response is initiated from a resting state, allowing for the movement output to be compared between startle and nonstartle trials to ensure a similar response was triggered by the SAS. One potential concern associated with the current experiment is that any change in speed of either limb might be considered the start of transition between patterns. This raises the possibility that the reduction in RT on startle trials could be due to a generic response to the SAS rather than the accelerated

release of a planned switch response. Although we cannot definitely rule this out, if the early response seen following the SAS was not the planned switch response, it would be expected that the switching time would be increased on startle trials as the participant would require additional time to recover from the generic startle response (Maslovat et al. 2015a, 2017) before transitioning to the new pattern. Contrary to this prediction, all conditions showed a decrease in switch completion time on startle trials (Fig. 4), which we believe supports our conclusion that the switch response was prepared in advance and, thus, was initiated at a shorter latency by the SAS.

The differences between the current experiment and previous simple RT studies also raise the question as to what exactly is prepared in advance in this special case of an intentional switch during an ongoing coordination movement. In simple RT paradigms, the prepared response can be considered as a group of cortical motor neurons that act as a functional unit to determine the required movement pattern. The neural activation level of this so called “cell assembly” (Wickens et al. 1994) can be raised to a subthreshold level before the go signal, such that only a relatively small input can “ignite” the assembly and, thus, lead to the motor output (Summers and Anson 2009). Although the mechanism by which the SAS accelerates this process is currently the subject of debate, one suggestion is that activation related to the startle reflex acts through ascending reticulo-thalamo-cortical circuits and provides the additional activation to trigger the prepared cell assembly at short latency (Carlsen et al. 2012). However, in the current experiment the specific muscle commands required for the switch response may not be known in advance as the response will change depending on where in the cycle the switch stimulus occurs. Thus, participants may plan a more generic homologous (if switching to IP) or nonhomologous (if switching to AP) muscle contraction. Conversely, the preparation process may be more dynamical in nature, whereby the required switch response is constantly changing within the movement cycle. Although the specific nature of the switch response preparation may require further investigation, the current results clearly show that the SAS speeds up the initiation of the response, similar to the effect observed during simple RT tasks. This result is consistent with previous work that has shown early response triggering by a SAS in situations where not all aspects of the required response are known. In these studies, this result was attributed to either the preparation of a generic response to be modified during execution (Forgaard et al. 2011), or the preparation of multiple response alternatives (Carlsen et al. 2009b), both of which are viable explanations for the current data.

Although we believe the current data provide novel and convincing evidence regarding preparation and execution of intentional switching, the use of a one-dimensional coordination task may oversimplify the dynamics associated with bimanual coordination tasks encountered in everyday life. Indeed, some researchers examining switching behaviors have used a more complex two-dimensional coordination pattern to allow for more possible switch options (e.g., Byblow et al. 1999; Leunissen et al. 2013). However, the use of a SAS limits the number of switching conditions that can be reasonably tested, due to a need to limit exposure to intense sounds (Carlsen et al. 2011). Rather than manipulate the number of switch options, we instead chose to focus on the location in the

movement cycle where the switch stimulus occurred, and thus opted for a simpler, one-dimensional coordination pattern. This approach proved fruitful, as we found that both switching time and relative limb contribution were significantly affected by the location of the switch stimulus.

Lastly, the current study also highlights the potential benefit of considering human behavior from a variety of theoretical frameworks. To understand motor control of the arms, much of the neurophysiological and computational research is based on discrete movements, with conclusions drawn about response planning and execution (e.g., Flash and Sejnowski 2001; Kalaska et al. 1997). However, there is evidence that continuous rhythmic arm movements are not simply a sequence of discrete actions but rather may involve different neural circuitry (Schaal et al. 2004) and the interaction between discrete and rhythmic movements may provide valuable insight regarding control mechanisms (Sternad et al. 2002). The use of an intentional switching task to investigate response preparation and execution allowed for an information-processing perspective to be applied to a continuous movement that has predominantly been examined using a dynamical systems approach. The results revealed novel information pertaining to the processes involved during intentional switching between coordination patterns and provided strong evidence that the switch response is prepared in advance of the switch stimulus, irrespective of switch direction or stimulus location. The data also indicated that while less time was required to complete the switch transition into the more stable IP pattern, this was dependent upon where in the movement cycle the switch stimulus occurred, suggesting that switch location may affect the intrinsic dynamics of the system. Similarly, the relative contributions of each limb to the switching behavior were also dependent upon both switch direction and stimulus location. This new information and alternative description of switching behavior may assist in furthering our understanding of how humans are able to quickly and efficiently transition between different coordination patterns.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

D.M., M.J.C., and A.N.C. conceived and designed research; D.M., M.J.C., and A.N.C. performed experiments; D.M., M.J.C., and A.N.C. analyzed data; D.M., M.J.C., and A.N.C. interpreted results of experiments; D.M., M.J.C., and A.N.C. prepared figures; D.M. drafted manuscript; D.M., M.J.C., and A.N.C. edited and revised manuscript; D.M., M.J.C., and A.N.C. approved final version of manuscript.

REFERENCES

Beek PJ, Turvey MT, Schmidt RC. Autonomous and nonautonomous dynamics of coordinated rhythmic movements. *Ecol Psychol* 4: 65–95, 1992. doi:10.1207/s15326969eco0402_1.

- Byblow WD, Carson RG, Goodman D.** Expressions of asymmetries and anchoring in bimanual coordination. *Hum Mov Sci* 13: 3–28, 1994. doi:10.1016/0167-9457(94)90027-2.
- Byblow WD, Summers JJ, Semjen A, Wuyts IJ, Carson RG.** Spontaneous and intentional pattern switching in a multisegmental bimanual coordination task. *Mot Contr* 3: 372–393, 1999. doi:10.1123/mcj.3.4.372.
- Byblow WD, Summers JJ, Thomas J.** Spontaneous and intentional dynamics of bimanual coordination in Parkinson's disease. *Hum Mov Sci* 19: 223–249, 2000. doi:10.1016/S0167-9457(00)00011-7.
- Carlsen A, Chua R, Inglis JT, Sanderson DJ, Franks IM.** Prepared movements are elicited early by startle. *J Mot Behav* 36: 253–264, 2004b. doi:10.3200/JMBR.36.3.253-264.
- Carlsen AN, Chua R, Inglis JT, Sanderson DJ, Franks IM.** Can prepared responses be stored subcortically? *Exp Brain Res* 159: 301–309, 2004a. doi:10.1007/s00221-004-1924-z.
- Carlsen AN, Chua R, Inglis JT, Sanderson DJ, Franks IM.** Differential effects of startle on reaction time for finger and arm movements. *J Neurophysiol* 101: 306–314, 2009a. doi:10.1152/jn.00878.2007.
- Carlsen AN, Chua R, Summers JJ, Inglis JT, Sanderson DJ, Franks IM.** Precues enable multiple response preprogramming: evidence from startle. *Psychophysiology* 46: 241–251, 2009b. doi:10.1111/j.1469-8986.2008.00764.x.
- Carlsen AN, Dakin CJ, Chua R, Franks IM.** Startle produces early response latencies that are distinct from stimulus intensity effects. *Exp Brain Res* 176: 199–205, 2007. doi:10.1007/s00221-006-0610-8.
- Carlsen AN, Maslovat D, Franks IM.** Preparation for voluntary movement in healthy and clinical populations: evidence from startle. *Clin Neurophysiol* 123: 21–33, 2012. doi:10.1016/j.clinph.2011.04.028.
- Carlsen AN, Maslovat D, Lam MY, Chua R, Franks IM.** Considerations for the use of a startling acoustic stimulus in studies of motor preparation in humans. *Neurosci Biobehav Rev* 35: 366–376, 2011. doi:10.1016/j.neubiorev.2010.04.009.
- Carson RG.** The dynamics of isometric bimanual coordination. *Exp Brain Res* 105: 465–476, 1995.
- Carson RG, Byblow WD, Abernethy B, Summers JJ.** The contribution of inherent and incidental constraints to intentional switching between patterns of bimanual coordination. *Hum Mov Sci* 15: 565–589, 1996. doi:10.1016/0167-9457(96)00028-0.
- Carson RG, Goodman D, Kelso JAS, Elliott D.** Intentional switching between patterns of interlimb coordination. *J Hum Mov Stud* 27: 201–218, 1994.
- Carter MJ, Maslovat D, Carlsen AN.** Anodal transcranial direct current stimulation applied over the supplementary motor area delays spontaneous antiphase-to-in-phase transitions. *J Neurophysiol* 113: 780–785, 2015. doi:10.1152/jn.00662.2014.
- Carter MJ, Maslovat D, Carlsen AN.** Intentional switches between coordination patterns are faster following anodal-tDCS applied over the supplementary motor area. *Brain Stimulat* 10: 162–164, 2017. doi:10.1016/j.brs.2016.11.002.
- De Luca C, Jantzen KJ, Comani S, Bertollo M, Kelso JA.** Striatal activity during intentional switching depends on pattern stability. *J Neurosci* 30: 3167–3174, 2010. doi:10.1523/JNEUROSCI.2673-09.2010.
- de Poel HJ, Peper CL, Beek PJ.** Intentional switches between bimanual coordination patterns are primarily effectuated by the nondominant hand. *Mot Contr* 10: 7–23, 2006. doi:10.1123/mcj.10.1.7.
- Donders FC.** On the speed of mental processes. In: *Attention and Performance II. Acta Psychologica*, edited by Koster WG. Amsterdam: North Holland, 1969, p. 412–431.
- Fernandez-Del-Olmo M, Río-Rodríguez D, Iglesias-Soler E, Acero RM.** Startle auditory stimuli enhance the performance of fast dynamic contractions. *PLoS One* 9: e87805, 2014. doi:10.1371/journal.pone.0087805.
- Fink PW, Foo P, Jirsa VK, Kelso JA.** Local and global stabilization of coordination by sensory information. *Exp Brain Res* 134: 9–20, 2000. doi:10.1007/s002210000439.
- Flash T, Sejnowski TJ.** Computational approaches to motor control. *Curr Opin Neurobiol* 11: 655–662, 2001. doi:10.1016/S0959-4388(01)00265-3.
- Forgaard CJ, Maslovat D, Carlsen AN, Franks IM.** Default motor preparation under conditions of response uncertainty. *Exp Brain Res* 215: 235–245, 2011. doi:10.1007/s00221-011-2893-7.
- Haken H, Kelso JAS, Bunz H.** A theoretical model of phase transitions in human hand movements. *Biol Cybern* 51: 347–356, 1985. doi:10.1007/BF00336922.
- Honeycutt CF, Kharouta M, Perreault EJ.** Evidence for reticulospinal contributions to coordinated finger movements in humans. *J Neurophysiol* 110: 1476–1483, 2013. doi:10.1152/jn.00866.2012.
- Honeycutt CF, Tresch UA, Perreault EJ.** Startling acoustic stimuli can evoke fast hand extension movements in stroke survivors. *Clin Neurophysiol* 126: 160–164, 2015. doi:10.1016/j.clinph.2014.05.025.
- Kalaska JF, Scott SH, Cisek P, Sergio LE.** Cortical control of reaching movements. *Curr Opin Neurobiol* 7: 849–859, 1997. doi:10.1016/S0959-4388(97)80146-8.
- Kelso JAS.** Phase transitions and critical behavior in human bimanual coordination. *Am J Physiol Regul Integr Comp Physiol* 246: R1000–R1004, 1984.
- Kelso JAS.** *Dynamic Patterns: The Self-Organization of Brain and Behavior*. Cambridge, MA: MIT Press, 1995.
- Kelso JAS.** Multistability and metastability: understanding dynamic coordination in the brain. *Philos Trans R Soc Lond B Biol Sci* 367: 906–918, 2012. doi:10.1098/rstb.2011.0351.
- Kelso JAS.** The dynamic brain in action: coordinative structures, criticality, and coordination dynamics. In: *Criticality in Neural Systems*, edited by Pleniz D, Niebur E. Weinheim, Germany: Wiley-VCH Verlag, 2014, p. 67–104.
- Kelso JAS, Southard DL, Goodman D.** Dynamics governs switching among patterns of coordination in biological movement. *J Exp Psychol Hum Percept Perform* 5: 229–238, 1979. doi:10.1037/0096-1523.5.2.229.
- Leunissen I, Coxon JP, Geurts M, Caeyenberghs K, Michiels K, Sunaert S, Swinnen SP.** Disturbed cortico-subcortical interactions during motor task switching in traumatic brain injury. *Hum Brain Mapp* 34: 1254–1271, 2013. doi:10.1002/hbm.21508.
- Maslovat D, Chua R, Carlsen AN, May C, Forgaard CJ, Franks IM.** A startling acoustic stimulus interferes with upcoming motor preparation: Evidence for a startle refractory period. *Acta Psychol (Amst)* 158: 36–42, 2015a. doi:10.1016/j.actpsy.2015.04.003.
- Maslovat D, Chua R, Franks IM.** Investigation of timing preparation during response initiation and execution using a startling acoustic stimulus. *Exp Brain Res* 235: 15–27, 2017. doi:10.1007/s00221-016-4774-6.
- Maslovat D, Drummond NM, Carter MJ, Carlsen AN.** Reduced motor preparation during dual-task performance: evidence from startle. *Exp Brain Res* 233: 2673–2683, 2015b. doi:10.1007/s00221-015-4340-7.
- Maslovat D, Drummond NM, Carter MJ, Carlsen AN.** Startle activation is additive with voluntary cortical activation irrespective of stimulus modality. *Neurosci Lett* 606: 151–155, 2015c. doi:10.1016/j.neulet.2015.08.053.
- Maslovat D, Franks IM, Leguerrier A, Carlsen AN.** Responses to startling acoustic stimuli indicate that movement-related activation is constant prior to action: a replication with an alternate interpretation. *Physiol Rep* 3: e12300, 2015d. doi:10.14814/phy2.12300.
- Maslovat D, Hodges NJ, Chua R, Franks IM.** Motor preparation and the effects of practice: evidence from startle. *Behav Neurosci* 125: 226–240, 2011a. doi:10.1037/a0022567.
- Maslovat D, Hodges NJ, Chua R, Franks IM.** Motor preparation of spatially and temporally defined movements: evidence from startle. *J Neurophysiol* 106: 885–894, 2011b. doi:10.1152/jn.00166.2011.
- Schaal S, Sternad D, Osu R, Kawato M.** Rhythmic arm movement is not discrete. *Nat Neurosci* 7: 1136–1143, 2004. doi:10.1038/nm1322.
- Scholz JP, Kelso JA.** Intentional switching between patterns of bimanual coordination depends on the intrinsic dynamics of the patterns. *J Mot Behav* 22: 98–124, 1990. doi:10.1080/00222895.1990.10735504.
- Scholz JP, Kelso JAS.** A quantitative approach to understanding the formation and change of coordinated movement patterns. *J Mot Behav* 21: 122–144, 1989. doi:10.1080/00222895.1989.10735470.
- Schöner G, Kelso JA.** Dynamic pattern generation in behavioral and neural systems. *Science* 239: 1513–1520, 1988. doi:10.1126/science.3281253.
- Serrien DJ, Swinnen SP.** Intentional switching between behavioral patterns of homologous and nonhomologous effector combinations. *J Exp Psychol Hum Percept Perform* 25: 1253–1267, 1999. doi:10.1037/0096-1523.25.5.1253.
- Sternad D, de Rugy A, Pataky T, Dean WJ.** Interaction of discrete and rhythmic movements over a wide range of periods. *Exp Brain Res* 147: 162–174, 2002. doi:10.1007/s00221-002-1219-1.
- Summers JJ, Anson JG.** Current status of the motor program: revisited. *Hum Mov Sci* 28: 566–577, 2009. doi:10.1016/j.humov.2009.01.002.
- Swinnen SP.** Intermanual coordination: from behavioural principles to neural-network interactions. *Nat Rev Neurosci* 3: 348–359, 2002. doi:10.1038/nm807.
- Tallet J, Barral J, James C, Hauert CA.** Stability-dependent behavioural and electro-cortical reorganizations during intentional switching between bimanual tapping modes. *Neurosci Lett* 483: 118–122, 2010. doi:10.1016/j.neulet.2010.07.074.

- Temprado JJ, Zanone PG, Monno A, Laurent M.** Attentional load associated with performing and stabilizing preferred bimanual patterns. *J Exp Psychol Hum Percept Perform* 25: 1579–1594, 1999. doi:[10.1037/0096-1523.25.6.1579](https://doi.org/10.1037/0096-1523.25.6.1579).
- Valls-Solé J, Kumru H, Kofler M.** Interaction between startle and voluntary reactions in humans. *Exp Brain Res* 187: 497–507, 2008. doi:[10.1007/s00221-008-1402-0](https://doi.org/10.1007/s00221-008-1402-0).
- Valls-Solé J, Rothwell JC, Goulart F, Cossu G, Muñoz E.** Patterned ballistic movements triggered by a startle in healthy humans. *J Physiol* 516: 931–938, 1999. doi:[10.1111/j.1469-7793.1999.0931u.x](https://doi.org/10.1111/j.1469-7793.1999.0931u.x).
- Wickens J, Hyland B, Anson G.** Cortical cell assemblies: a possible mechanism for motor programs. *J Mot Behav* 26: 66–82, 1994. doi:[10.1080/00222895.1994.9941663](https://doi.org/10.1080/00222895.1994.9941663).
- Woodworth RS.** *Experimental Psychology*. New York: Holt, 1938.

