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RESEARCH ARTICLE

Response preparation changes during practice of an asynchronous bimanual movement

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Abstract For synchronous bimanual movements, we have shown that a different amplitude can be prepared for each limb in advance and this preparation improves with practice (Maslovat et al. 2008). In the present study, we tested whether an asynchronous bimanual movement can also be prepared in advance and be improved with practice. Participants practiced (160 trials) a discrete bimanual movement in which the right arm led the left by 100 ms in response to an auditory "go" signal (either 80 dB control stimulus or 124 dB startle stimulus). The startle stimulus was used to gauge whether inter-limb timing could be pre-programed. During startle trials, the asynchronous bimanual movement was triggered at early latency suggesting the entire movement could be prepared in advance. However, the triggered movement had a shorter between-arm delay and a temporally compressed within-arm EMG pattern, results that we attribute to increased neural activation caused by the startling stimulus. However, as both startle and control trials improved over time, it does appear response preparation of interval timing can improve with practice.

Keywords Response preparation · Programing · Practice · Timing · Startle

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Introduction

The learning of novel motor skills is an essential part of human existence. Researchers have long examined numerous aspects of skill acquisition, typically examining how a behavioral measure (e.g., time to complete a movement, error score, reaction time) changes with the amount and/or quality of practice undertaken by the learner. While we know that practice is a predominant factor in skill acquisition, determining the actual process by which learning occurs has provided a considerable challenge. One way to simplify the investigation of the learning process is to consider the production of a task from an information-processing perspective. For example, if a simple movement is to be produced in response to the appearance of a "go" stimulus, a number of stages are thought to occur, including stimulus identification and recognition, response selection, and response programing (Donders 1969). The purpose of the current study was to examine response programing changes that occur during acquisition of a movement. More specifically, this experiment was designed to study what aspects of a movement could be prepared in advance (i.e., pre-programed), and how this preparation changed with practice.

A number of different methodologies have been employed to examine motor preparation. One avenue has used a simple reaction time (RT) paradigm whereby the response to the "go" stimulus is known in advance. In this situation, it has been suggested that response preparation may occur prior to the "go" signal, depending on the nature of the required movement (see Klapp 1996 for a review). To examine when advance preparation can occur, reaction time is used as a measure of time needed to process information following the "go" signal. It is assumed that an increase in reaction time is due to preparation being performed after the "go" signal. In a series of studies, Klapp

(1995, 2003) showed that a sequenced movement could not initially be pre-programed. However, with sufficient practice a multiple component movement could be recoded into a single element (i.e., "chunked"), and thus fully prepared in advance (see also Fischman and Lim 1991; cf. Sherwood and Canabal 1988).

A more recent methodology used to examine response preparation involves the use of a startling acoustic stimulus (SAS). During a simple reaction time task, replacing the auditory "go" signal with a loud (>124 dB) SAS has been shown to elicit the required action at a much shorter latency, with kinematics and EMG configurations largely unchanged (Valls-Solé et al. 1995, 1999; Siegmund et al. 2001; Carlsen et al. 2003, 2004a, b, 2007; Cressman et al. 2006; MacKinnon et al. 2007). Due to dramatic shortening of premotor reaction times (i.e. premotor RT < 60 ms), it has been hypothesized that the startle can bypass the usual voluntary command and act as a trigger for a pre-programed response (Valls-Solé et al. 1999; Carlsen et al. 2004b). Support for this hypothesis has come from a number of studies that have shown that startle effects are distinct from and larger than stimulus intensity effects (Carlsen et al. 2007), and only occur when the participant has prepared the response in advance (Valls-Solé et al. 1999; Carlsen et al. 2004a; Rothwell 2006). Alternately, when uncertainty exists regarding what movement is required such as a discrimination (Carlsen et al. 2008) or choice reaction time task (Carlsen et al. 2004a) advance preparation may not occur, and thus the startle does not trigger the movement.

The use of an SAS can act as a probe for what is pre-programed, as fully prepared movements would be expected to be triggered at a shorter latency than control trials, with similar movement characteristics. In addition, the startle paradigm can also be used as a tool to examine how pre-programing changes during the learning process. By examining the response to startle trials provided at various points in the acquisition process (i.e., early, middle, late), it is possible to determine what is being prepared as learning progresses. We have previously used a startling stimulus to examine preparation changes for a synchronous bimanual movement of asymmetrical amplitudes (Maslovat et al. 2008). In response to an auditory "go" signal, participants were required to perform simultaneous elbow extension movements with the right arm to a 20° target and the left arm to a 10° target. Prior to and following practice, startle trials were interspersed with control trials to examine the effects of an SAS on the bimanual movement. The comparison of startle to control trials indicated that a different amplitude movement could indeed be prepared in advance for each limb, and that this preparation improved with practice. In addition, while startle trial reaction times were much faster than control trials, the configuration of the EMG patterns was unchanged. This was taken as evidence for the prepared movement being triggered at an early latency by the startling stimulus.

Our previous work (Maslovat et al. 2008) confirmed that a synchronous bimanual movement of different amplitudes could be prepared in advance. The focus of the current experiment was to extend these findings by examining whether an asynchronous bimanual movement of equal amplitudes could be prepared in advance, and whether this preparation would change as a result of practice. The task we chose was a bimanual elbow extension movement whereby both limbs moved to a 20° target; however, initiation of the left limb was required to be delayed by 100 ms relative to initiation of the right limb. A 100-ms delay was chosen to be sufficiently short to promote advance preparation of both arm movements (rather than on-line preparation of the second movement), yet long enough that participants could distinguish the difference in arm initiation, and thus improve with practice. We were unsure whether this movement could be pre-programed early in the acquisition period. On the one hand, based on the theoretical model proposed by Klapp (1995, 2003), an asynchronous movement should not be prepared in advance due to a sequencing requirement of the limb movements. This model has been supported by studies involving two-step *unimanual* movements that have shown that only the first movement is prepared in advance, with the second movement programed on-line (Adam et al. 2000; Vindras and Viviani 2005; Khan et al. 2006). However, to our knowledge, this model has not been specifically tested for sequenced *bimanual* movements. An asynchronous bimanual movement may be prepared in a different manner to a two-step unimanual movement, as the two movement elements are independent (i.e., do not require the same limb) and may overlap temporally (i.e., the second movement element may start before the first element is complete). These differences may allow both components of the bimanual movement to be prepared in advance.

The results of this study should further our knowledge of the preparation process for asynchronous bimanual movements. Additionally, the use of a learning paradigm will allow for examination of how the preparation process changes with practice. If advance preparation is not possible early in acquisition, we would not expect the asynchronous bimanual movement to be triggered by the startling stimulus. However, with practice we would predict that movement "chunking" would occur, thus allowing for advance preparation and triggering by the startling stimulus. Alternatively, if the movement is able to be prepared early in acquisition, we would predict that as performance changes with practice, the movement triggered by the startling stimulus would reflect these changes.

Method

Participants

Thirteen right-handed volunteers with no obvious upper body abnormalities or sensory or motor dysfunctions participated in the study after giving informed consent. However, only data from ten right-handed volunteers (3 males, 7 females; age 25 ± 5 years) were employed in the final analysis. Three participants did not show activation in the sternocleidmastoid muscle during any startle trials (which is thought to be the most reliable indicator of a startle response), and thus were excluded from the analysis (see Carlsen et al. 2003, 2004a, 2007 for more detail regarding the exclusion criteria for participants). All participants were naïve to the hypothesis under investigation, and this study was conducted in accordance with ethical guidelines established by the University of British Columbia.

Task and experimental design

Participants sat in a height-adjustable chair in front of a 15-inch color monitor (ADI Microscan A505, 1,024 × 768 pixels, 75 Hz refresh) resting on a table. Attached to the table on each side of the monitor were lightweight manipulanda that participants used to perform horizontal flexion–extension movements about the elbow joint. Participants' arms and hands were secured with Velcro straps to the manipulanda with the elbow joint aligned with the axis of rotation and the hands pronated. The home position for each arm was located such that a 20° extension movement resulted in the arms being straight ahead (i.e., perpendicular to the monitor on the table), and was defined as 0°. Targets were located on the table top at 20° of extension from each home position. In response to an auditory "go" signal, the participants were asked to rapidly extend the right and left limb to the targets such that the left arm moved from the home position 100 ms after the right arm. Participants were instructed to look straight ahead at the monitor and respond by making a movement "as fast and as accurately as possible" from the starting position and to stop at the final targets.

All trials began with a warning tone consisting of a short beep (80 ± 2 dB, 100 ms, 100 Hz), followed by a random variable foreperiod of 1,500–2,500 ms, then by the imperative "go" signal. The "go" signal could either consists of a control stimulus (80 ± 2 dB, 100 ms, 1,000 Hz) or startling stimulus (124 ± 2 dB, 40 ms, 1,000 Hz, <1 ms rise time). All auditory signals were generated by a customized computer program and were amplified and presented via a loudspeaker placed directly behind the head of the participant. The acoustic stimulus intensities were measured using a sound level meter (Cirrus Research model CR:252B) at a distance of 30 cm from the loudspeaker (approximately the distance to the ears of the participant).

Participants performed a total of 160 trials in a single testing session (approximately 45 min), alternating between "testing" and "practice" trials. Participants began with a block of ten testing trials whereby three trials included a startling "go" stimulus in a pseudo-random order (the first trial was never a startle, and startle trials were never presented consecutively). This was followed by two blocks of 20 practice trials where no startle trials were presented. This pattern was repeated two additional times (testing, practice, testing, practice) and then ended with a final testing block. Thus, a total of four testing blocks (ten trials each—seven control, three startle) and six practice blocks (20 trials each) were performed by each participant. No augmented feedback was provided during each trial; however, terminal feedback was provided on the monitor for 3 s following the trial that included reaction time (RT, in ms) and arm delay (practice trials only, in ms). At the end of each trial, participants were allowed to examine the final position of their arms, relative to the targets. To encourage fast and accurate responses, a monetary bonus was offered for fast RT and accurate delay times.

Recording equipment

Surface EMG data were collected from the muscle bellies of the following superficial muscles: right and left lateral head of the triceps brachii (TRI—agonist), right and left long head of the biceps brachii (BIC—antagonist), and left sternocleidomastoid (SCM—startle indicator) using preamplified surface electrodes connected via shielded cabling to an external amplifier system (Delsys Model DS-80). Recording sites were prepared and cleansed in order to decrease electrical impedance. The electrodes were oriented parallel to the muscle fibers, and then attached using double sided adhesive strips. A grounding electrode was placed on the participant's left lateral malleolus. Arm angular displacement was measured using potentiometers (Precision, MD157) attached to the central axis of the manipulanda. A customized LabView® computer program controlled stimulus and feedback presentation, and initiated data collection at a rate of 1 kHz (National Instruments, PC-MIO-16E-1) 500 ms before the presentation of the "go" signal and terminated data collection 2,000 ms following the "go" signal.

Data reduction

Movement onset was defined as the first point when velocity reached and remained above 0°/s following the "go" stimulus. Final position was defined as the first point at which angular velocity fell below 8°/s and remained below

this value for 50 ms. Surface EMG burst onsets were defined as the point at which the EMG first began a sustained rise above baseline levels. The location of this point was determined by first displaying the EMG pattern with a superimposed line indicating the point at which activity increased to more than two standard deviations above baseline (mean of 100 ms of EMG activity preceding the go signal). Onset was then verified by visually locating and manually adjusting the onset mark to the point at which the activity first increased. This method allowed for correction of errors due to the strictness of the algorithm. EMG offsets were marked in a similar fashion, with the activity between EMG onset and EMG offset being defined as the duration of a muscle burst. Startle trials in which no detectable startle response (SCM activity) was observed were discarded (total of five out of 120 trials—4%), as were trials when reaction time was longer than 400 ms (total of 14 out of 1,600 trials—<1%) or when movement occurred prior to the "go" signal (total of 12 out of 1,600 trials—<1%).

Dependent measures and statistical analyses

Premotor reaction time (PMT) was analyzed to examine whether the startling stimulus initiated the movement at latency values that would suggest the movement was prepared in advance and triggered by the startle (Valls-Solé et al. 1999; Carlsen et al. 2004b). PMT was defined as the time difference between the "go" stimulus and the onset of the first agonist burst in the right arm. Kinematic-dependent measures included arm delay, movement time (MT), and endpoint point constant error (CE). Arm delay was defined as the time interval between movement onset of the right and left arm, and was the primary measure used to determine improvements in performance. Endpoint error and MT were used as secondary measures to determine if any changes in speed and accuracy occurred with practice, and for a comparison between startle and control trials to determine if similar movements were produced. MT was defined as the difference in time between movement onset and final position. Endpoint CE was determined by calculating the mean error of the final endpoint for each limb.

To compare EMG patterns, burst onsets and durations were calculated for each arm. The onset of the first agonist burst (AG1, TRI) was measured from the time of the "go" stimulus, while onset of the antagonist (ANT, BIC) and second agonist burst (AG2, TRI) were calculated as the time from the onset of the AG1. This allowed for determination of the relative timing of the triphasic EMG pattern. To quantify activation amplitude of the first agonist burst, we integrated the rectified raw EMG trace for the first 30-ms of the AG1 burst (Q30, Corcos et al. 1989; Gottlieb et al. 1989; Khan et al. 1999; Maslovat et al. 2008). The Q30 measure represents the initial slope of the agonist burst and is minimally affected by feedback, thus providing a useful measure of neural activation.

We limited our statistical analysis to the four testing blocks to allow us to directly compare startle and control trials throughout the practice period. PMT and arm delay were independently analyzed via a 4 Block × 2 Stimulus Type (control, startle) repeated measures analysis of variance (ANOVA). All other dependent measures were independently analyzed via a 4 Block × 2 Stimulus Type (control, startle) × 2 Arm (left, right) repeated measures ANOVA. The alpha level for the entire experiment was set at 0.05. Partial eta squared (η_p^2) values are reported as a measure of effect size. Significant results for the repeated measures ANOVAs were examined via Tukey's honestly significant difference (HSD) test and simple effects tests to determine the locus of the differences.

Results

A summary of the results for all dependent measures, including mean and standard deviations are provided in Table 1. Figure 1 shows limb displacement and EMG data (rectified and smoothed by 20-point averaging) for a representative control trial (top) and startle trial (bottom). Overall PMT values during startle trials suggest that the movement was prepared in advance and triggered by the startle throughout the acquisition period. With practice, participants showed improvement at the between-limb timing delay in both control and startle trials; however, during startle trials the delay was consistently shorter. Furthermore, startle trials produced faster movements, larger endpoint error, and a within-limb muscle activation pattern that was temporally compressed.

PMT

As predicted, analysis of PMT confirmed a main effect for stimulus type [$F(1, 9) = 54.19$, $P < 0.001$, $\eta_p^2 = 0.86$] whereby startle trials exhibited a significantly shorter PMT ($M = 90$ ms) compared to control trials ($M = 156$ ms). PMT values during startle trials were consistent with previous experiments involving arm movements that have suggested that such short reaction times are due to triggering of the pre-programed response (i.e., Carlsen et al. 2004a, 2007, 2009). There was also a main effect for block [$F(3, 27) = 3.60$, $P = 0.026$, $\eta_p^2 = 0.29$], which was due to a significant decrease in PMT from block 1 ($M = 132$ ms) to block 3 ($M = 116$ ms). This relatively small decrease in PMT with practice also suggests that participants fully prepared the required response in advance throughout the acquisition period (see Maslovat et al. 2008 for similar results), as a change in advance preparation is usually accompanied by a larger decrease in RT (e.g., Klapp 1995).

Table 1 Experimental results for each stimulus type, arm and testing condition, showing means and standard deviations (bracketed)

Variable	Right arm				Left arm			
	Test block 1	Test block 2	Test block 3	Test block 4	Test block 1	Test block 2	Test block 3	Test block 4
Control condition								
Movement time (ms)	284.6 (36.3)	303.9 (44.1)	287.9 (41.8)	270.1 (29.9)	338.7 (45.9)	354.4 (32.3)	321.4 (40.0)	309.4 (55.5)
Arm delay (ms)	–	–	–	–	80.5 (18.9)	97.2 (21.5)	95.0 (25.0)	92.0 (21.4)
Endpoint CE (degrees)	4.4 (3.6)	2.3 (1.8)	3.0 (2.9)	3.0 (2.9)	5.2 (6.8)	1.6 (2.8)	1.3 (2.8)	1.2 (2.6)
AG1 onset (ms)	163.2 (33.8)	154.9 (40.5)	148.0 (18.3)	157.8 (28.1)	237.1 (52.5)	240.8 (49.0)	232.4 (35.8)	234.9 (39.5)
AG1 to ANT onset (ms)	97.1 (22.0)	103.6 (22.0)	100.6 (33.5)	90.7 (23.6)	112.3 (40.2)	108.9 (27.7)	99.5 (35.3)	93.9 (26.6)
AG1 to AG2 onset (ms)	224.7 (35.8)	228.5 (38.0)	220.1 (42.6)	204.5 (34.7)	244.7 (44.6)	237.3 (32.0)	230.3 (35.0)	227.5 (38.7)
AG1 duration (ms)	101.3 (14.3)	105.0 (19.4)	107.1 (21.8)	105.8 (21.1)	106.5 (20.5)	111.7 (18.9)	113.0 (28.8)	108.2 (18.7)
ANT duration (ms)	97.3 (13.7)	104.0 (18.4)	107.6 (22.1)	102.1 (21.5)	96.8 (17.6)	106.3 (20.0)	108.1 (23.8)	108.0 (23.8)
AG2 duration (ms)	88.6 (10.4)	95.4 (11.4)	91.3 (8.5)	86.8 (12.6)	93.9 (12.8)	96.1 (10.2)	91.6 (12.1)	86.7 (11.0)
Q30 (mV ms)	1.27 (1.15)	0.90 (0.52)	1.00 (0.54)	1.09 (0.60)	1.02 (0.42)	0.74 (0.24)	0.80 (0.30)	0.81 (0.46)
Startle condition								
Movement time (ms)	217.8 (56.5)	220.6 (45.8)	212.7 (49.2)	218.9 (31.5)	329.1 (77.2)	306.0 (80.9)	291.3 (65.3)	309.8 (81.7)
Arm delay (ms)	–	–	–	–	35.4 (20.9)	47.5 (27.9)	53.0 (30.1)	58.9 (26.4)
Endpoint CE (degrees)	9.7 (4.8)	6.6 (6.0)	7.1 (4.2)	5.9 (6.1)	7.2 (9.6)	5.1 (5.7)	4.4 (5.7)	3.7 (6.6)
AG1 onset (ms)	100.2 (14.3)	88.7 (9.0)	84.5 (13.0)	88.1 (12.6)	126.3 (31.0)	118.5 (28.1)	124.4 (38.0)	130.8 (34.6)
AG1 to ANT onset (ms)	82.0 (27.1)	73.8 (23.7)	77.4 (26.8)	74.0 (21.5)	86.5 (34.3)	84.9 (30.9)	80.4 (31.1)	85.6 (29.8)
AG1 to AG2 onset (ms)	184.0 (24.1)	181.9 (34.6)	182.7 (38.4)	177.7 (34.6)	206.9 (47.7)	191.3 (50.8)	196.0 (50.8)	200.8 (49.2)
AG1 duration (ms)	105.8 (21.1)	104.1 (26.9)	106.4 (22.3)	99.3 (22.6)	99.1 (25.8)	102.8 (35.6)	107.8 (27.0)	106.4 (26.6)
ANT duration (ms)	100.5 (22.5)	103.5 (19.2)	101.6 (21.4)	100.1 (12.5)	94.7 (20.2)	95.8 (23.8)	99.8 (18.4)	94.4 (21.1)
AG2 duration (ms)	82.2 (13.9)	90.9 (10.4)	85.4 (11.6)	80.2 (8.5)	85.7 (17.2)	88.1 (17.6)	91.9 (11.2)	83.5 (12.2)
Q30 (mV ms)	2.25 (2.01)	2.25 (2.26)	2.00 (1.63)	2.18 (1.82)	2.44 (1.84)	1.72 (1.35)	1.45 (0.69)	1.58 (0.80)

Note that arm delay has only one value for both limbs. Also note that premotor RT is equivalent to AG1 onset for the right arm

AG1 initial agonist burst (triceps), *ANT* antagonist burst (biceps), *AG2* second agonist burst (triceps)

Kinematics

Arm delay means for the four testing sessions for control and startle trials are shown in Fig. 2. Arm delay showed a significant main effect for block [$F(3, 27) = 3.66$, $P = 0.036$, $\eta_p^2 = 0.29$] and stimulus type [$F(1, 9) = 24.64$, $P = 0.001$, $\eta_p^2 = 0.73$]. No significant interaction effects were found. These results confirmed that while participants improved performance of the arm delay with practice, performance was consistently different in control trials versus startle trials. Post hoc analyses of the block effect confirmed that performance on the first testing block was significantly different to performance on the remaining three blocks. For control trials, participants underestimated the required 100 ms between-arm delay in the first testing block ($M = 81$ ms), but approached the criterion by the second block of testing ($M = 97$ ms). Performance during startle trials also improved with practice; however, the timing of the arm delay was significantly shortened throughout testing (early $M = 35$ ms, late $M = 59$ ms).

Movement time results, separated by block, arm and stimulus type are shown in Fig. 3. The analysis of MT confirmed a main effect for arm [$F(1, 9) = 48.16$, $P < 0.001$, $\eta_p^2 = 0.84$] and stimulus type [$F(1, 9) = 13.10$, $P = 0.006$, $\eta_p^2 = 0.59$]. The main effect of arm was due to a slower MT for the left arm ($M = 320$ ms) compared to the right ($M = 252$ ms) and the main effect of stimulus type was due to a speeded MT during startle trials ($M = 263$ ms) compared to control trials ($M = 308$ ms). These two main effects combined for a significant arm by stimulus type interaction [$F(1, 9) = 5.54$, $P = 0.043$, $\eta_p^2 = 0.38$], as the right arm MT was affected by the stimulus type (startle $M = 217$ ms vs. control $M = 286$ ms) more than the left arm (startle $M = 309$ ms vs. control $M = 331$ ms). There was also a significant stimulus type by block interaction [$F(3, 27) = 5.40$, $P = 0.008$, $\eta_p^2 = 0.38$], whereby the control trials showed a greater effect of practice (block 1 $M = 312$ ms vs. block 4 $M = 290$ ms) compared to startle trials (block 1 $M = 273$ ms vs. block 4 $M = 264$ ms). The only significant effect found for endpoint CE was a main effect for stimulus type [$F(1, 9) = 7.33$, $P = 0.024$, $\eta_p^2 = 0.45$]. This effect was due to a higher positive error value (i.e., overshooting the target) in startle trials ($M = 6.2°$) compared to control trials ($M = 2.7°$).

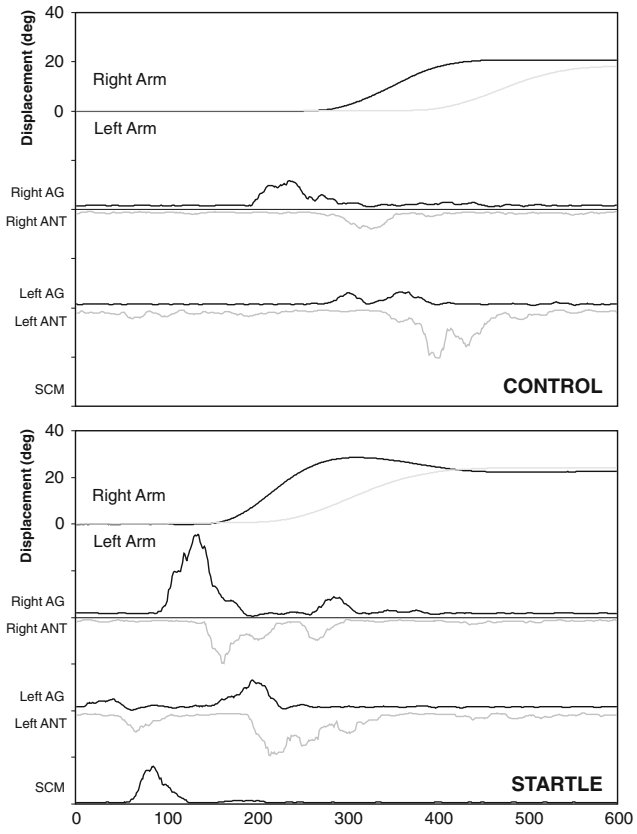

Fig. 1 Limb displacement and EMG data (*AG* agonist, *ANT* antagonist, *SCM* sternocleidomastoid) for a representative control (*top*) and startle (*bottom*) trial. Note that startle trials were performed with a shortened latency, increased EMG activity and increased peak limb displacement. Also note that during startle trials the within-limb EMG pattern was temporally compressed such that antagonist was activated earlier relative to the agonist onset

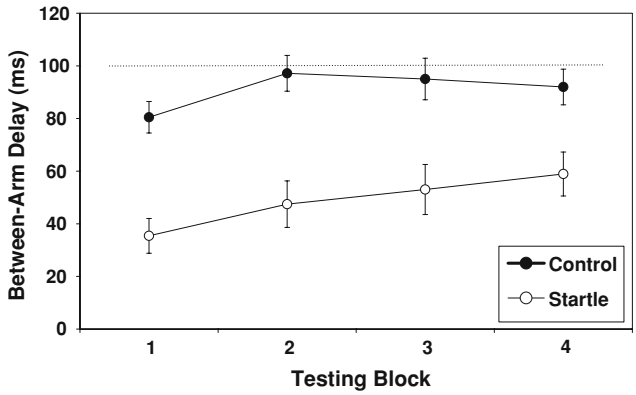

Fig. 2 Mean (SEM) between-arm delay for each of the four testing blocks. The criterion of 100 ms is shown by a *dotted line*. Note the startling stimulus caused a significantly shorter delay

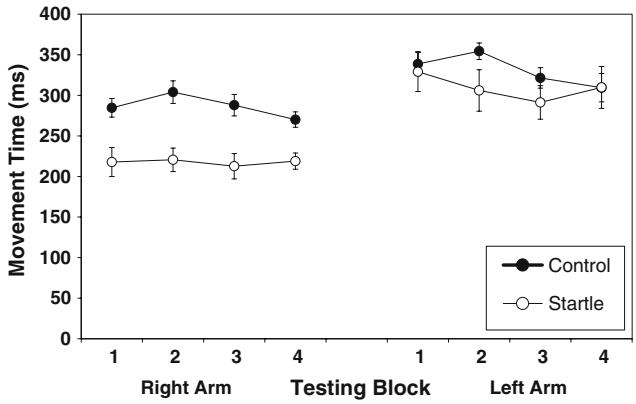

Fig. 3 Mean (SEM) movement time, separated by arm and block. Note the startling stimulus caused a greater decrease in movement time, especially for the right arm

EMG

EMG boxplots, showing the triphasic burst for both limbs during control and startle trials (collapsed by time), are shown in Fig. 4, along with SCM burst for startle trials. Analysis of AG1 onset confirmed a main effect for arm [$F(1, 9) = 133.95$, $P < 0.001$, $\eta_p^2 = 0.94$], stimulus type [$F(1, 9) = 49.26$, $P < 0.001$, $\eta_p^2 = 0.85$], and a significant arm by type interaction [$F(1, 9) = 23.49$, $P = 0.001$, $\eta_p^2 = 0.72$]. The main effect of arm was expected as participants were required to delay initiation of the left arm relative to the right. This resulted in a significantly longer AG1 onset for the left arm ($M = 181$ ms), compared to the right arm ($M = 123$ ms). The main effect of stimulus type was also expected as startle trials should result in a faster arm initiation ($M = 108$ ms), when compared to control trials ($M = 196$ ms). However, we did not expect the arm by type interaction. This result was due to a larger decrease in AG1 onset during startle trials for the left arm (control $M = 236$ ms, startle $M = 125$ ms), compared to the right arm (control $M = 156$ ms, startle $M = 90$ ms). This result is consistent with the reduction in arm delay during startle trials (Fig. 2), but suggests that the between-limb timing was altered when startled. This has not typically been reported in startle research as previous experiments with complex, multi-component movements have shown that the temporal structure of muscle activation patterns remains consistent during startle trials (Valls-Solé et al. 1999; MacKinnon et al. 2007; Maslovat et al. 2008; Queralt et al. 2008).

Although the relative (i.e., between-limb) onset of the initial agonist burst was decreased during startle trials, we were also interested in any changes to the within limb EMG pattern that were observed during startle trials. A main effect for stimulus type was found for the time period between AG1 and ANT [$F(1, 9) = 12.56$, $P = 0.006$, $\eta_p^2 = 0.58$], the time period between AG1 and AG2 [$F(1, 9) = 22.34$, $P = 0.001$, $\eta_p^2 = 0.71$] and the duration of AG2 burst [$F(1, 9) = 17.73$, $P = 0.002$, $\eta_p^2 = 0.66$]. In all cases,

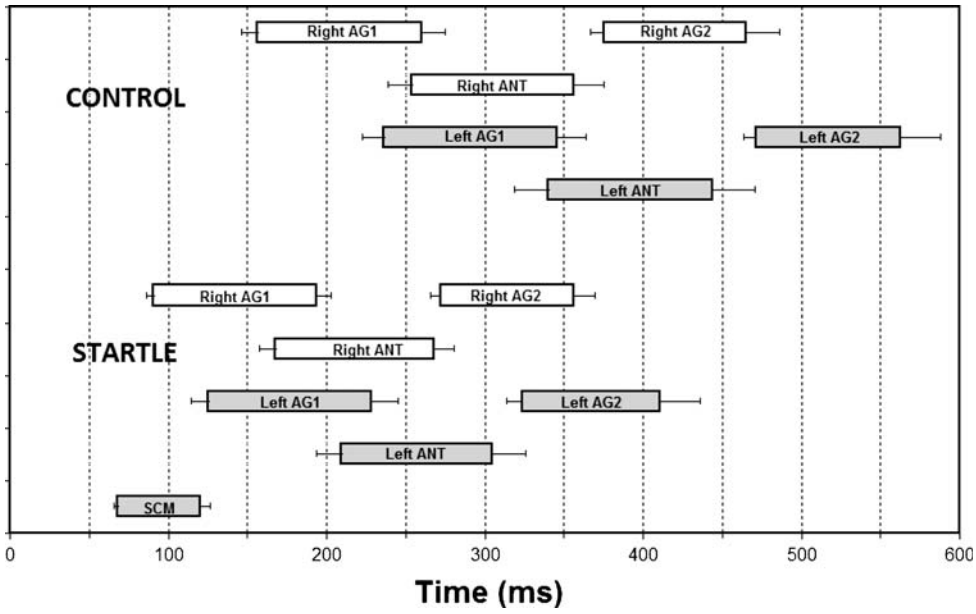

Fig. 4 Plots of triphasic EMG configurations during startle and control trials, collapsed across testing blocks. *Boxes* represent EMG burst durations with mean (SEM) onsets and offsets with respect to stimulus onset. AG1 represents the initial agonist (triceps), ANT represents the antagonist (biceps), AG2 represents the second agonist burst, and SCM represents the startle indicator (sternocleidomastoid). Note the temporal compression of the within-limb EMG during startle trials as well as a reduction in time between left and right AG1

the startling stimulus caused a decrease in time period between muscle activations. Thus, not only did the startling stimulus decrease the delay *between* arms, it also had the effect of temporally compressing the EMG pattern *within* each arm. The only other significant finding was a main effect for arm for the time period between AG1 and AG2 onset [$F(1, 9) = 7.26$, $P = 0.025$, $\eta_p^2 = 0.45$]. The longer time period between agonist bursts for the left arm ($M = 217$ ms) versus the right arm ($M = 201$ ms) is consistent with the finding of increased movement time for the left arm. The analysis of the Q30 scores showed a significant effect for stimulus type [$F(1, 9) = 9.97$, $P = 0.012$, $\eta_p^2 = 0.43$]. This was due to significantly greater EMG activity during startle trials ($M = 1.99$ mV ms), compared to control trials ($M = 0.96$ mV ms).

Discussion

The purpose of the current experiment was to determine if an asynchronous bimanual movement could be prepared in advance, and whether this preparation would change as a result of practice. We were unsure if this movement could be prepared in advance as it was thought that a sequencing component would be required to perform the movement correctly. Our results indicated that this movement could be prepared in advance, as the asynchronous bimanual movement was triggered by the startling stimulus at a latency typically seen in startle experiments involving limb movements (Carlsen et al. 2004a, 2007, 2009; Maslovat et al. 2008), and faster than expected from stimulus intensity effects alone (Carlsen et al. 2007). However, the triggered movement observed during startle trials differed substantially from those in control trials, a result not typically seen in experiments that have used a startling stimulus to trigger a voluntary response. Although a between-arm timing delay was present in early acquisition startle trials, the delay was dramatically shorter than control trials (35 vs. 80 ms). With practice, this delay became significantly closer to the target (100 ms) in both startle and control trials; however, startle trials consistently produced a shortened between-limb delay (Fig. 2). Examination of the muscle activation patterns revealed that the *within-limb* EMG timing was also altered in startle trials, consisting of a reduction in the timing between the initial agonist burst and both the antagonist and second agonist burst, respectively (Fig. 4), and resulting in faster movements to the targets (especially for the right arm, see Fig. 3). Thus, although an asynchronous bimanual movement was triggered by the startling stimulus, the movement appeared to be temporally compressed both in the between-arm delay and within-arm EMG pattern.

To explain this difference in movements during startle and control trials, we hypothesize that the addition of a precise timing requirement to the movement changed how the movement was prepared. Specifically, to accurately delay the left limb by 100 ms, participants would have utilized some form of timing mechanism. While many timing models have been proposed, they often explain time duration estimation via a pulse accumulator (see Macar and Vidal 2004; Taatgen et al. 2007; Block

and Zakay 2008 for recent reviews). For example, Block and Zakay (1996) proposed an attention-gate model whereby a pacemaker produces pulses at a given rate. When attention is focused on timing (rather than an external stimuli), a gate is "opened" to monitor the pulses of the pacemaker. These pulses are accumulated until a threshold is reached which is based on a reference memory store that would be affected by previous performance. Two important points come from the description of this model. First, the pulses of the pacemaker only become meaningful when attention is focused on the timing of an event, such as would be expected for an asynchronous movement with a specified delay. Second, the rate of pacemaker pulses is affected by the participant's arousal level (Triesman 1963; Block and Zakay 1996). In fact, a number of studies have shown that when arousal level is increased, participants are prone to underestimating time intervals which has been attributed to an increase in pacemaker speed (Meck 1996; Penton-Voak et al. 1996; Gruber and Block 2005). We suggest that the use of an intense startling stimulus may have increased participants' arousal level, and thus affected the pacemaker rate. A faster pacemaker would result in a shorter between-arm delay and potentially a condensed within-arm EMG pattern.

While arousal was not specifically measured, there is indirect evidence from the current study suggesting that the startling stimulus increased neural activation. During startle trials, participants increased their endpoint error by overshooting the target and showed greater EMG activity (as measured by Q30). Both these results have been found in previous startle experiments and have been attributed to increased activation levels (Carlsen et al. 2004a; Maslovat et al. 2008). If the startling stimulus causes an increase in arousal level and thus the rate of the pacemaker, it may seem surprising that previous startle experiments have not shown a modification in timing of the movement. However, the increase in pacemaker pulse-rate would be evident only for tasks that require participants to specifically focus on timing, a manipulation which has not been explicitly explored in previous startle experiments. There is considerable evidence that how a movement is performed may affect the timing mechanism used. For example, it has been suggested that timing in discrete movements is controlled by an explicit clock-like mechanism, while timing in continuous movements is an emergent property related to movement control (Robertson et al. 1999; Zelaznik et al. 2000, 2002; Summers et al. 2008). Similarly, different neural systems have been implicated in tasks involving explicit timing (i.e., overt estimate of duration) versus implicit timing (i.e., timing is a byproduct of a non-temporal task goal, even if responses adhere to a strict temporal framework) (Coull and Nobre 2008). Thus, we believe the requirement of timing; a specific delay duration between the limbs required participants to implement a different timing mechanism than would be used for a movement not requiring an explicit time estimation.

We have concluded that the current results suggest that the entire asynchronous bimanual movement can be prepared in advance, and that differences between startle and control trials can be explained by an increase in pacemaker pulse-rate due to the startling stimulus. Before we discuss how this finding adds to our knowledge of advance preparation, it is worthwhile investigating whether our results could be explained by a different conclusion. One alternative is that participants prepared only the first movement component in advance, with the second movement programed on-line. However, if this occurred we would predict that the startling stimulus would have only triggered the right arm movement while the left limb movement would have to be prepared after the "go" signal. This should result in longer arm delays during startle trials rather than the shorter arm delays that we observed. Examination of individual startle trials confirmed that only six trials (out of 115) had a between-arm delay that was longer than the required 100 ms, making this alternative explanation unlikely. Another alternative explanation is that participants prepared both limb movements in advance but not the sequencing/delay component. This preparation would have resulted in the startling stimulus triggering both arm movements such that the bimanual movement would be produced in a synchronous manner (i.e., no delay between the arms). Although a short between-arm delay (<10 ms) occurred on some startle trials (9 out of 115 trials, all from three participants); this did not appear to be a consistent result. However, it is possible that the startle triggered both movements, and the reported arm delay simply represents an asymmetry in movement due to a right-hand dominance. Continuous bimanual movements such as circle drawing have shown a delay in the non-dominant hand in the order of 15–40 ms when asked to move synchronously (Stucchi and Viviani 1993; Swinnen et al. 1996). We do not think this explanation is applicable, as we have previously shown that a symmetrical bimanual movement can be performed with a minimal between-arm delay during both startle and control trials (approximately 1–2 ms; Maslovat et al. 2008). Additionally, the delay between arms increased during startle trials as a result of practice, a result which would not be predicted if the delay was solely due to differences in reaction time between the arms.

Although previous research involving unimanual movements has shown that multiple elements cannot be prepared in advance (e.g., Adam et al. 2000; Vindras and Viviani 2005;

Khan et al. 2006), our results suggest that preparation of a sequenced bimanual movement may be qualitatively different.[1] Specifically, the difficulty in preparing a multiple component unimanual movement may relate to uncertainty regarding the exact starting position of the second component due to variability in the first movement. That is, if the performer does not know precisely where and when the second component is to be produced, it may be difficult to prepare the movement characteristics in advance. With practice, advance preparation of a sequenced unimanual movement may be possible (as shown by Klapp 1995), because participants become more consistent with the initial component, thus allowing for the second movement to be prepared in advance and "chunked" with the first movement. These restrictions on preparation would not apply to a bimanual movement, as the effectors used are independent and thus the starting position of both movements is known in advance.

In conclusion, the current results suggest that an asynchronous bimanual movement can be prepared in advance and triggered by a startling stimulus. Furthermore, practice-related changes in preparation were evident in both control and startle trials, confirming that startle methodology is an effective tool to examine the preparation process during skill acquisition. We have also shown that a movement triggered by a startling stimulus can change in temporal structure if the participant is forced into an explicit timing requirement. When required to accurately time an interval, participants may use a timekeeper that is affected by the startling stimulus. Overall these results add to our knowledge of how advance preparation occurs for sequenced bimanual movements, and how practice improves the preparation process.

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[1] A number of methodologies have been used to examine the preparation processes associated with bimanual movements. These have included the examination of spatial assimilation effects for simultaneous and sequential discrete bimanual movements (e.g., Sherwood 1994, 2006), as well as interference effects during dual-task performance conditions (see Pashler 1994 for a review). Similarly, continuous bimanual tasks have also received extensive investigation to explore the control processes involved in limb coordination (see Swinnen and Wenderoth 2004 for a recent review). A common finding in all paradigms is the difficulty in performing bimanual movements when different parameters are required for each limb, such as timing, amplitude, force or direction.

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