

Title: Unexpected acoustic stimulation during action preparation reveals gradual re-specification of movement direction.

Running Head: Sounds reveal gradual re-specification of actions.

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Abstract

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3 A loud acoustic stimulus (LAS) is often used as a tool to investigate motor preparation in simple
4 reaction time (RT) tasks, where all movement parameters are known in advance. In this report, we
5 used a LAS to examine direction specification in simple and choice RT tasks. This allowed us
6 to investigate how the specification of movement direction unfolds during the preparation period. In
7 two experiments, participants responded to the appearance of an imperative stimulus (IS) with a
8 ballistic wrist force directed towards one of two targets. In probe trials, a LAS (120 dBa) was
9 delivered around the time of IS presentation. In Experiment 1, reaction times in the simple RT task
10 were faster when the LAS was presented, but the effect on the movement kinematics was negligible.
11 In the Choice RT task, however, movement direction variability increased when the LAS was
12 presented. In Experiment 2, when we primed movements towards one direction, our analyses
13 revealed that the longer participants took to start a movement, the more accurate their responses
14 became. Our results show not only that movement direction reprogramming occurs quickly and
15 continuously, but also that LAS can be a valuable tool to obtain meaningful readouts of the motor
16 system's preparatory state.
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31 **Keywords:** acoustic stimulus, motor control, movement direction, preparation
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Introduction

1 Execution of voluntary acts is preceded by preparatory processes in the central nervous
2 system (CNS). The task specifies the act required – a speech act, a manipulative act, a
3 locomotor act – and preparatory processes specify when and how the act will be executed so
4 that the task requirements are met in the prevailing conditions (Jeannerod, 1994; Requin et
5 al., 1991). Thus, preparatory processes must incorporate information about task requirements
6 and environmental conditions in order to specify task-appropriate movement parameters,
7 which are passed to the neural machinery that generates motor commands to the muscles. The
8 process of preparation is therefore often referred to as *motor planning* or *motor programming*
9 (Kawato, 1999; Keele et al., 1990; Schmidt and Lee, 2011).
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11 The process of incorporating task and environmental information into a motor plan
12 has been studied using reaction time (RT) and other speeded tasks in which the response is a
13 target-directed movement of some kind (Ghez et al., 1990; Haith et al., 2015; Leonard, 1958;
14 Marinovic et al., 2010; Rosenbaum and Kornblum, 1982; Schouten and Bekker, 1967). The
15 person executing the task is provided with some initial information, which may be either
16 sufficient or insufficient to determine the necessary response. At a later time, but prior to
17 executing the response, additional information is provided that either changes the task
18 requirements initially specified (in the case that the initial information was sufficient; (Haith
19 et al., 2015) or supplements initially insufficient information so the required response is fully
20 specified (Ghez et al., 1990; Rosenbaum and Kornblum, 1982; Schutte and Spencer, 2007).
21 Using these methods it has been found that motor plans are initially established using
22 information available from task instructions, prior experience with the task, and perception of
23 the task layout (Ghez et al., 1997; Ghez et al., 1990; Haith et al., 2015; Hudson et al., 2007;
24 Schutte and Spencer, 2007). Where the target is not initially specified, the initial planning
25 state represents the information available concerning all potential targets (Cisek and Kalaska,
26 2002; Favilla et al., 1990; Findlay, 1982; Gallivan et al., 2015; Ghez et al., 1997; Haith et al.,
27 2015; He and Kowler, 1989; Hudson et al., 2007; Stewart et al., 2014), and many forms for
28 this representation have been proposed (Cisek and Kalaska, 2005; Erlhagen and Schoner,
29 2002; Gallivan et al., 2015; Haith et al., 2015; Kopecz and Schoner, 1995; Stewart et al.,
30 2014). Incorporation of new information into the motor plan can occur at any time prior to
31 initiation of descending motor commands (Favilla et al., 1990; Ghez et al., 1997), and indeed
32 there may be little or no distinction between the processes that underlie this plan updating and
33 those responsible for feedback corrections of ongoing movements (Flanagan et al., 1993;
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Flash and Henis, 1991; Hudson et al., 2007; Nashed et al., 2014; Prablanc and Martin, 1992; van Sonderen et al., 1989).

Incorporating new information into an existing motor plan appears to be rapid, but not instantaneous. If new information is provided during the reaction time interval, new task parameters are not reflected in the resulting movement for hundreds of milliseconds (e.g., Ghez et al., 1997; Marinovic et al., 2010; van Sonderen et al., 1988; van Sonderen et al., 1989). However, it is uncertain to what degree estimates of the time-costs of motor plan updating are inflated by processing demands related to task instructions (e.g. pay attention to a sequence of tones to start moving, (Ghez et al., 1997; Ghez et al., 1990; Haith et al., 2015), which could interfere with the ability to attend to and incorporate new information. For example, using traditional and forced RT tasks, Haith and colleagues (2016) showed that up to one-third of the reaction time is expended on processes unrelated to movement programming but were rather concerned with adhering to task instructions and meeting task demands. Here we investigate movement direction plan updating when the use of strategies to deal with short preparation intervals are minimized and participants only need to prepare for a binary choice (right or left) during a trial. More precisely, this study aimed to reveal the time course of direction specification when the state of preparation for action required rapid adjustments to update the plan. To achieve this, we used reaction time (RT) tasks in combination with the delivery of loud acoustic stimuli (LAS) to induce the early release of prepared actions at different levels of preparation.

A LAS presented unexpectedly during movement preparation can trigger the initiation of the prepared action, a phenomenon termed the StartReact effect (Valls-Solé et al., 1999). Although most research on the StartReact has employed simple RT tasks (for recent reviews, see Marinovic and Tresilian, 2016; Nonnekes et al., 2015), some studies have investigated the early release of motor actions by LAS using choice RT tasks. Kumru et al. (2006) showed that a LAS could trigger whatever motor response was prepared at the time of stimulation (e.g. a correct or an incorrect hand movement). Similarly, Forgaard et al. (2011) found participants released motor acts whose amplitude fell between targets when their movements were triggered by LAS. However, some authors failed to detect any facilitation of movement initiation in tasks where participants had multiple movement choices (Carlsen et al., 2004). Thus, this relatively simple technique may be able to provide a readout of the state of motor preparation slightly prior to the voluntary decision to move in some circumstances and/or tasks, but not in others. We sought to obtain a read-out of the state of preparatory direction specification, but no studies have yet investigated the impact

1 of a LAS on the directional accuracy of movement trajectories. Thus, it is necessary to
2 determine whether a LAS can speed the initiation of motor responses in our task and to
3 examine how it affects initial movement direction in simple and choice RT conditions. The
4 results of experiment 1 showed that a LAS speeds movement initiation, but has no effects
5 on response accuracy in simple RT tasks (where all movement parameters can be specified
6 well in advance of the movement imperative). In contrast, the results showed that a LAS
7 affects both movement initiation and accuracy under choice RT conditions, which indicates
8 that movement accuracy progressively improves as initiation time is delayed and more time
9 is available to prepare the specified movement. The aim of Experiment 2 was to further
10 examine how direction reprogramming develops over time, by manipulating (i) target
11 probability to induce larger directional biases during planning, and (ii) the inter-stimulus-
12 interval (ISI) between the imperative stimulus (IS, or visual target) and the LAS, to probe
13 different preparatory states. Our results showed that as reaction time increased, movement
14 accuracy improved: the process appears to be continuous, but evolves rapidly.

27 **Experimental Procedures**

29 **Participants**

31 Nineteen volunteers (3 women) participated in Experiment 1 (mean age = 20.5, range = 18 to
32 39). Twenty-six volunteers (3 women) participated in Experiment 2 (mean age = 20.4, range
33 = 18 to 39). Participants gave written informed consent prior to commencement of the study,
34 which was in accordance with the Declaration of Helsinki and approved by the local Ethics
35 Committee of the University of Queensland. All participants reported normal or corrected to
36 normal vision, stated that they were right handed, and had no known neurological conditions
37 that could have affected their performance in the tasks. Participants received course credit for
38 their participation in the studies.

48 **Procedures and Design**

50 Participants sat in a chair in front of a 22-in Samsung LCD monitor (120 Hz refresh rate,
51 1680 x 1050 resolution) located 0.9 m away from them. The experiments involved isometric
52 wrist contractions using a custom-built device (see de Rugy et al., 2012) that held the hand
53 and forearm in a neutral position throughout the experiment (see Figure 1A). Participants had
54 their hands snugly fit into the device to reduce any time lag between muscle contractions and
55 recording of forces generate by their wrists. Participants moved a circular cursor from the
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1 centre of the monitor to targets presented radially, by applying forces with the wrist in two-
2 dimensions (abduction/flexion-extension). Forces were measured by a six-degree of freedom
3 force/torque sensor (JR3 45E15A-I63-A 400N60S, Woodland, CA), and converted to cursor
4 location such that 20 N was required to move the cursor to the targets. In control trials, the
5 cursor was visible throughout the trial and provided participants with information about the
6 distance and the directional error to reach the target, as shown in Figure 1C. In probe trials,
7 the circular cursor was replaced by an expanding ring that provided information about the
8 distance to the target but no information regarding the directional error (see Figure 1D). The
9 reason visual feedback was constrained in probe trials was to minimize the chances that
10 participants associated probe trials with errors in a particular direction and, consequently,
11 developed compensatory feedforward strategies when the LAS was presented in those trials.
12 Two target locations were used: 45 and 135° from horizontal in relation to the origin (see
13 Figure 1B). As shown in Figure 1C & D, the target presentation occurred 1.3 seconds (\pm 400
14 ms) after the appearance of the cursor on the screen. Participants were asked to move the
15 cursor towards the target as quickly as possible upon its presentation. In probe trials, the LAS
16 was presented in synchrony with the presentation of the target (Experiment 1) or at one of
17 three times (-25, 0, 25 ms) relative to the presentation of the targets (Experiment 2). Feedback
18 on reaction time was provided on the monitor screen after all control trials to encourage fast
19 responses, no feedback was provided after probe trials.

20 Before the beginning of the experiments, participants performed 30 practice trials to
21 familiarise themselves with the task. Acoustic stimulation was presented twice during
22 familiarization. Visual stimuli were generated with Cogent 2000 Graphics running in
23 MATLAB 7.5.

24 [Insert Figure 1 here]

25 Auditory stimuli

26 The auditory stimuli were bursts of 50 ms broadband white noise with a rise/fall time shorter
27 than 1 ms. Stimuli were generated with a custom made noise generating box triggered via the
28 parallel port of the computer controlling the visual stimulus and presented binaurally via
29 high-fidelity stereophonic headphones (Sennheiser model HD25-1 II; Germany). The input
30 signal to the headphones had a bandwidth of approximately 10 Hz–30 kHz. Auditory stimuli
31 had a peak loudness of 120 dB. Sound intensity was measured with a Bruel and Kjaer sound
32 level meter (type 2205, A weighted; Brüel & Kjaer Sound & Vibration Measurement,
33 Naerum, Denmark) placed 2 cm from the headphone speaker.

EMG

The electromyogram (EMG) signals were recorded from the extensor carpi radialis brevis (ECRB) and flexor carpi radialis (FCR) muscles using disposable Ag-AgCl electrodes. The EMG signal was amplified, band-pass filtered between 30 and 1 kHz (Grass P511 isolated amplifier), sampled at 2000 Hz, and stored on computer. Torque data and EMG signals were time locked and sampled at the same frequency.

Data analysis

The variables of interest were: premotor reaction time, variable directional error (VDE), constant directional error (CDE), and error count. Premotor reaction time was defined as the difference between the earliest EMG onset time in either ECRB or FCR and the time of target appearance. EMG onset time was determined as the time when the rectified EMG signal from the muscle exceeded two standard deviations from baseline activity. VDE was determined by calculating the standard deviation of the directional error across trials at 100 ms after movement onset time. This timing was chosen because it reflects the intended direction of movement before visual feedback mechanisms can affect the trajectory of the cursor (Elliott et al., 2001) and is identical to those used by recent studies analysing the initial direction of movement in similar contexts (Haith et al., 2016; Verstynen and Sabes, 2011). CDE was determined by calculating the median signed directional error across trials at 100 ms after movement onset time (negative errors mean an initial trajectory direction between targets irrespective of whether the target was at 45 or 135° in relation to the origin). For example, if the initial directional of the movement was 60° for a target positioned at 45°, the directional error was -15°. Movement onset time was calculated using the tangential speed time series derived from the torque data employing the algorithm recommended by Teasdale et al. (1993). Error count was defined as the number of trials in which the directional error exceeded the 99th percentile value of the distribution of movement angles made by each subject in the control trials that involved no LAS, in the direction towards the incorrect target (see Figure 2). The effects of experimental conditions on premotor reaction times, VDE and CDE were analysed using the robust methods proposed by Wilcox (2012). In Experiment 1, we used the *bwtrim* function from the R package WRS2 to run two-way within subjects' ANOVAs on the trimmed means (trim level was set to the default value of 20%). Significant interactions were followed-up with the *nparcomp* function from the R package nparcomp, which allows the computation of simultaneous non-parametric confidence intervals and p-values using the Tukey contrast (Konietschke et al., 2008). In Experiment 2, the robust one-

1 way ANOVAs and follow-up post-hoc tests were computed using the functions *medlway* and
2 *mcppb20* (2000 iterations each), respectively, from the WSR2 package. Simple t-tests (*yuend*
3 function) and correlations (*pbcor* function) were also performed using the robust methods
4 suggested by Wilcox (2012) and implement with the WSR2 package. For Experiment 2, we
5 also computed cumulative distribution functions (CDF) for each individual's directional error,
6 according to their reaction time data. These CDFs were analysed with robust procedures
7 using the function *rmanova* (WRS2 package). Follow-up polynomial contrasts to detect
8 trends in the data were performed using standard parametric procedures. If corrections were
9 occurring gradually over time, we expected that directional bias would decrease linearly as
10 the deciles increased. Error count across the probe conditions in Experiment 2 were analysed
11 using a Friedman's test. Note that for Experiment 2, we focused our analysis on trials
12 directed to targets positioned at 45° of the origin as our experimental manipulation (see
13 Methods below) was designed to induce larger directional errors on those trials, allowing the
14 analysis of directional adjustments over time. Alpha was set to 0.05 for all comparisons. We
15 report Cohens' *d* effect sizes for the difference of means of pairwise comparisons.
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27 [Insert Figure 2 here]

28 **Experimental procedures**

29 Experiment 1 tested the effect of LAS on movement direction variability in simple and choice
30 RT tasks. Participants performed 244 trials divided in two blocks. In one block, the location
31 of the target was cued by arrows as shown in Figure 1 (simple RT task) and participants had
32 to react as quickly as possible to the target's appearance. In the other block, the cue was not
33 presented (choice RT task). The order of the blocks was counterbalanced across participants
34 and, with the exception of the visual cue, the order of temporal events during a trial was
35 identical between blocks. In each block, 20 trials (10 for each of the two directions, ≈16% of
36 the total number of trials within a block) were probe trials in which the appearance of the
37 target was synchronised with that of the LAS. Participants were asked to ignore the LAS and
38 perform the task normally. The order of presentation of the probe trials was pseudo-
39 randomised so that trials with LAS were not presented sequentially.
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51 Experiment 2 examined the effect of LAS on a choice RT task when the probability of
52 targets at 135° was greater than targets at 45°. Participants performed a total of 290 trials: 60
53 trials to the target positioned at 45° (36 probe and 24 control) and 230 trials to the target
54 positioned at 135° (12 probe and 218 control). This unbalanced number of trials served to
55 prime the participants to prepare their movements to the most likely target at 135° and induce
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larger directional errors when the probe was presented for targets at 45°. Probes were delivered at three times in relation to the appearance of the IS: -25, 0, and 25 (12 trials per condition). Instructions, feedback, and the temporal order of events within trials were identical to those used in the choice RT task of experiment 1.

Results

Experiment 1

[Insert Figure 3 here]

Figure 3A shows the premotor reaction time for control and probe trials (LAS) during choice and simple RT tasks. The results indicate that participants responded more quickly to the target's appearance in probe trials relative to the control trials and also in the simple RT task relative to the choice reaction time task. The RM analysis of variance indicated a statistically reliable effect of type of trial (control vs. LAS) on premotor reaction time, $F = 155.5$, $p < 0.0001$, $d = 1.77$. As expected, the effect of type of task (choice vs. simple) was also statistically reliable, $F = 30.18$, $p < 0.0001$, $d = 1.31$. The interaction between task and trial type was not statistically significant, $F = 1.21$, $p = 0.27$, suggesting that LAS did not affect RT differentially in the two tasks.

Figure 3B shows the mean variable directional error as a function of task and trial type. The results suggest that directional variability was not affected by LAS when participants had *a priori* information about the target location in probe trials. The analysis of variance showed a statistically significant effect of trial type, $F = 12.38$, $p = 0.0017$, $d = 0.31$. The main effect of task $F = 8.90$, $p = 0.005$, $d = 0.40$, and the interaction between task and trial type were also statistically significant, $F = 12.65$, $p = 0.0015$. The robust post-hoc tests showed that the combination of the choice RT task and the LAS presentation (probe trial) resulted in the largest variability in movement direction in relation to all other conditions. No other differences were observed between experimental conditions (see Figure 3B).

As shown in Figure 3C the constant directional error did not change systematically as a function of type of trial and task. The ANOVA found no reliable main effects of type of trial, $F = 0.32$, $p = 0.57$, $d = 0.13$, nor task, $F = 1.08$, $p = 0.30$, $d = 0.18$. Although there appears to be a tendency for negative errors (indicating bias towards the incorrect target) for LAS trials in the choice reaction time task, the ANOVA interaction between task and trial type failed to reach statistical significance, $F = 3.16$, $p = 0.083$.

[Insert Figure 4 here]

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2 As shown in Figure 4, the scatterplot of premotor reaction time by absolute
3 directional error suggests a negative association between the two variables, with
4 participants who responded more quickly directing initial forces closer to the incorrect
5 target. The robust Spearman test confirmed a reliable correlation between variables, $r = -$
6 0.81 , $p = 0.0001$. This result indicates that as the premotor reaction time increased,
7 participants made smaller directional errors. The correlation between premotor reaction
8 time and error count shown in Figure 4B was also negative but the robust correlation failed
9 to reach statistical significance, $r = -0.42$, $p = 0.10$.

[Insert Figure 5 here]

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11 The gradual decrease in the magnitude of angular errors as preparation time increases
12 can also be seen in Figure 5, where we plot the aiming direction of incorrect trials according
13 to premotor RT. In Figure 5A, most responses are directed towards the incorrect target for the
14 shortest premotor RTs (< 100 ms). Between 100 to 150 ms, aiming directions span the whole
15 range between targets. At the premotor RT interval between 150-200 ms, there are few
16 responses toward the incorrect target and most responses were directed to intermediate points
17 between targets. At the longest premotor RT interval (Figure 5D), most responses were
18 intermediate between targets or close to the correct target position.

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20 Given that participants could be affected by their recent history of action (Verstynen
21 and Sabes, 2011), we also analysed whether the median absolute directional errors (error
22 trials only, see Figure 2) across participants were influenced by the position of the target on
23 the previous trial (i.e. trial N-1). We found that the mean absolute error across participants
24 was 18.8° ($SD = 17.6$) when the previous movement was directed toward the same target,
25 whereas it was 13.4° ($SD = 7.8$) when the movement was made toward the opposite target in
26 trial N-1. Because we were interested in determining whether repeated presentation of a
27 target tended to increase or decrease the size of errors with respect to the previous movement,
28 rather than testing the null hypothesis that repetition has no effect, we took advantage of
29 Bayesian statistics to contrast these alternatives. For this analysis, we used the Bayesian
30 alternative to t-tests introduced by Morey and colleagues (Morey and Rouder, 2011; Rouder
31 et al., 2009), implemented using the BayesFactor package for R (*ttestBF*). Because the
32 *ttestBF* function of the R package provides 2 Bayes factors, both against the same
33 denominator model, it was possible to estimate a Bayes factor comparing whether the effect
34 was to increase or decrease directional errors after movements toward specific targets by
35 dividing the probability of an increased error over that of a decreased directional error. This
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Bayesian approach yielded a Bayes factor of 6.41 in favour of an increased error after a movement made to the same target (3-10 = moderate evidence ; (Jeffreys, 1961). Although this effect is small ($d = 0.27$), it suggests participants were more likely to be biased away from the target to which they had moved to in trial N-1 (for similar results see (Tanaka and Shimojo, 1996, 2000)).

Experiment 2

A robust paired t-test contrasting the premotor reaction time in control trials to targets at 45 ($x = 233.5$ ms, $SD = 31.8$) and 135° ($x = 206.6$ ms, $SD = 32.6$) found reactions were faster toward the more likely target (135°), $t_{15} = 5.84$, $p < 0.0001$, $d = 1.03$. A comparison between the mean variable directional errors in both control trials (45: $x = 14.8$, $SD = 9.4$; 135°: $x = 12.7$ standard deviation, $SD = 9.6$) also revealed that participants were less variable when aiming toward the more likely target, $t_{15} = 3.59$, $p < 0.0026$, $d = 0.90$. These results indicate that our experimental manipulation succeeded in priming the participants to weight movement preparation more heavily toward the target at 135°.

[Insert Figure 6 here]

Figure 6A shows the premotor reaction time for control and probe trials at different intervals between IS and LAS. The RM analysis of variance indicated a statistically reliable effect of trial type (control, LAS at -25, 0, and 25 ms in relation to IS) on premotor reaction time, $F = 7.91$, $p < 0.001$. The robust post-hoc test showed reliable differences between control trials and probes presented before or synchronised with the IS as shown in Figure 6A. Responses were also faster when probes were delivered before the target's appearance in relation to probes synchronised with or after the IS onset. This post-hoc test also showed that responses were faster for synchronised probes in relation to probes presented after the IS. An additional analysis of polynomial contrasts, excluding control trials, revealed a reliable linear trend on the data, $F_{1, 25} = 26.36$, $p < 0.0001$, but not a quadratic trend, $F_{1, 25} = 2.18$, $p = 0.15$. These results indicate LAS induced earlier responses in all probe conditions and that the size of the effect was affected by LAS timing.

Figure 6B shows the variable directional error for control and probe trials. The analysis of variance found a reliable effect of trial type on directional variability, $F = 2.60$, $p = 0.0005$. The post-hoc test indicated that variable error was significantly greater for trials in which the probe was delivered before the IS in relation to all other conditions, as shown in

Figure 6B. The polynomial trend analysis detected no reliable trends in this variable (Linear trend: $F_{1,25} = 3.51$, $p = 0.073$; Quadratic: $F_{1,25} = 0.14$, $p = 0.70$).

Figure 6C shows the constant directional error for control and probe targets at 45°. The robust ANOVA failed to find a reliable main effect of type of trial, $F = 0.25$, $p = 0.82$. The polynomial contrast analysis, with the exclusion of the control trials, found a statistically reliable linear trend in this variable, $F_{1,25} = 5.31$, $p = 0.030$, but not a quadratic trend, $F_{1,25} = 0.12$, $p = 0.73$.

As shown in Figure 7, error count decreased as time for preparation increased. An analysis of variance on error count across the 3 probe times indicated significant differences among means, Friedman test - *Chi-square* = 8.12, $p = 0.017$. A Wilcoxon signed rank test found a statistically reliable difference between means before and after IS onset as shown in Figure 7.

[Insert Figure 7 here]

[Insert Figure 8 here]

Figure 8 shows the scatterplots of mean premotor reaction times by the mean directional errors for the three probe timings. The robust correlation test revealed statistically reliable negative correlations between premotor RT and directional error when the LAS were presented before, $r = -0.56$, $p = 0.007$, and in synchrony with the IS, $r = -0.82$, $p < 0.0001$. For probe trials presented after the IS, any relationship also tended negative, but the test failed to reach statistical significance, $r = -0.31$, $p = 0.23$.

[Insert Figure 9 here]

As shown in Figure 9A, for short premotor RTs (< 100 ms), most responses were directed towards the incorrect target. For the next interval (100-150 ms), responses were still more likely to be near the incorrect target but clearly more responses were either directed to an intermediate position between targets or close to the correct target. At the premotor RT interval between 150-200 ms, we observe fewer responses toward the incorrect target and most responses seem to be beyond an intermediate point between targets. At the longest premotor RT interval (Figure 9D), the majority of responses were near the correct target despite a few mistakes towards intermediate positions.

We also conducted a robust correlational analysis using individual trials pooled across all participants in Experiment 2. As depicted in a polar plot in Figure 10A, this analysis showed there is a negative correlation between variables, $r = -0.53$, $p < 0.0001$. This negative correlation between premotor reaction time and directional error was also significantly

reliable for the three participants in Experiment 2 who consistently made systematic directional errors (more than 12 out of 30) as shown in Figure 10B (S1: $r = -0.59$, $p = 0.0017$; S2: $r = -0.40$, $p = 0.023$; S3: $r = -0.58$, $p = 0.002$). Thus, the intra-individual analysis supports the inter-individual correlational analysis.

[Insert Figure 10 here]

[Insert Figure 11 here]

To gain further insight on the speed of error correction implementation, we also calculated the average directional error at each decile based on the cumulative distribution function (CDF) of RTs for 8 participants that made at least 8 directional errors during LAS trials. Figure 11A shows the change in directional error as a function of the CDF of reaction time across 10 deciles (5th to 95th %). The RM analysis of variance indicated a statistically reliable effect of reaction time decile on directional error ($F = 4.85$, $P = 0.007$). A follow-up polynomial contrast analyses indicated a statistically significant linear trend on the data ($F_{1,7} = 11.11$, $P = 0.013$). As shown in Figure 11A, a simple linear regression fit on the directional error across the RT deciles provided a reasonable approximation of the data ($R^2 = 0.86$). Note that at the shortest reaction time decile, responses were mainly directed at the primed target. In contrast, the two longest reaction time deciles indicate directional errors were directed at an intermediate position between targets. This additional analysis reinforces that directional errors decrease gradually as reaction times increase. Figure 11B illustrates the cumulative distribution function of reaction times. As expected, the analysis of variance indicated a significant effect of deciles on reaction time ($F = 16.21$, $P = 0.005$; Linear trend: $F_{1,7} = 36.03$, $P = 0.001$).

Discussion

In the experiments reported here, we took advantage of the capacity of LAS to induce the early initiation of movement to probe how direction reprogramming unfolds in a choice RT task with few task constraints, such as preparation time deadlines or instructions regarding online movement corrections.

Consistent with some findings in the StartReact literature (Forgaard et al., 2011; Kumru et al., 2006), the results of Experiment 1 showed that movement initiation in our task occurred earlier in both simple and choice RT versions. As expected, the LAS had a large effect on movement direction variability in the choice RT task, but the same effect was not detected in the simple RT task (effect size: Cohen's $d = 0.33$; difference between control and

1 LAS means in the simple RT task 95%CI [-1.7, 3.7]). The observation that directional
2 variability was relatively unaffected by LAS in our simple RT task suggests that the effect of
3 the LAS is not to add significant noise to the circuits responsible for response programming:
4 if the LAS merely added noise, then directional variability would be expected to increase.
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6 Rather, a LAS appears to increase the gain of these circuits, affecting reaction time, duration,
7 and forcefulness of prepared responses (Castellote and Valls-Solé, 2015; Fernandez-Del-
8 Olmo et al., 2014; Kumru et al., 2006; Marinovic et al., 2014a; Marinovic et al., 2013;
9 Marinovic et al., 2014b), without negatively affecting movement parameters such as
10 direction.
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16 The analysis of directional errors in the choice RT task in Experiment 1 showed that
17 when the LAS was presented, the participants with longer reaction times had smaller errors
18 than participants who had shorter reaction times (see Buetti and Kerzel, 2009) for a similar
19 finding using the Simon task). This same pattern of results was clear across all the LAS-IS
20 intervals (-25, 0, and +25 ms) used in Experiment 2, where we primed participants to weight
21 movement preparation more heavily toward one target. Moreover, because we delivered the
22 LAS at three times in relation to the IS in Experiment 2, we could confirm a progressive
23 improvement in movement direction specification using polynomial contrasts to check for
24 trends in constant error and movement variability. Thus, as more time was available to
25 process visual information, participants gradually improved directional accuracy. These
26 findings indicate that despite the separation between targets being above the threshold from
27 which participants move stochastically towards one specific target irrespective of the
28 preparation time (Ghez et al., 1997), our participants adjusted their movements continuously,
29 with a linear decrease in directional errors as reaction times increased. These results are
30 consistent with those reported by Schutte and Spencer (2007) (see also Erlhagen and Schoner,
31 2002), who found that movement parameters were adjusted gradually for large target
32 separations (80°) when task instructions allowed online corrective movements. Different from
33 Schutte and Spencer (2007), however, we did not constrain time of movement onset to force
34 participants to choose the best initial parameters of the movement, which could interfere with
35 the time available to implement corrective adjustments to their movements. Instead, in
36 Experiment 2, we induced them to prepare for the incorrect target and examined how initial
37 movement accuracy evolved as more time was provided before the movement was triggered
38 by the LAS, allowing the study of motor behaviour in less contrived conditions.
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58 Unlike reports showing that participants aim toward intermediate positions between
59 targets at short response latencies (Ghez et al., 1997; Haith et al., 2015), the results of
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1 Experiment 1 indicate that participants sometimes use a strategy of aiming close to the
2 targets. Note that a simple averaging strategy would cause directional errors in probe trials to
3 be about 45° (half of the distance between targets, see Figure 4) or less. Our analysis,
4 therefore, suggests that even though there was a 50/50 chance of targets appearing at 45 and
5 135°, some participants guessed the location of the upcoming targets as a strategy to shorten
6 reaction time (n.b. participants who displayed the shortest RTs also had errors above 60°).
7 This "guessing strategy" is likely to be affected by the recent movement history (trial N-1)
8 (de Lussanet et al., 2002; see also Dorris et al., 1999) as errors were relatively larger toward
9 repeated targets, as supported by our Bayesian analysis of directional errors.
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11 Cisek and Kalaska (Cisek and Kalaska, 2002, 2005) demonstrated that when the final
12 target for action is uncertain, the specification of multiple movement directions can occur
13 simultaneously in the dorsal premotor cortex. After a decision is made, however, there is a
14 rise in activation of neurons tuned to the correct target direction, and a suppression of neurons
15 tuned to the incorrect direction. These results are consistent with the proposal that when the
16 level of neural activation reaches a certain threshold, a motor response with a particular
17 direction is executed (Cisek and Kalaska, 2010). We propose that LAS adds activation to the
18 circuits involved in response execution, to induce a generalised increase in neural activation
19 throughout the CNS that summates with voluntary motor preparation, and thereby shortens
20 the time required for neural activation to reach threshold (see Marinovic et al., 2014b). In the
21 choice RT task, this could sometimes lead to the release of responses for which activation
22 related to the correct target was not fully developed, and the suppression of the activation
23 related to the incorrect target was not completed. This would explain the observation of
24 response bias towards the mostly likely target when participants were probed with LAS.
25 Because the reprogramming of movement direction takes time to complete, responses became
26 increasingly more accurate as preparation time increased (see Figure 9, 10 and 11).
27 Consistent with recent reports, our data indicate movement reprogramming is not as sluggish
28 as one would expect if the process of aiming to the alternative target requires a complete
29 reprogramming of a motor action (over 200 ms in control trials of Experiment 1), as there is
30 no need to return to a state of preparation similar to that found before a commitment to
31 prepare had started (Ames et al., 2014; Haith et al., 2016). Our analysis of directional errors
32 based on the cumulative distribution function of RTs suggests a correction of 45° in our task
33 may take approximately 110 ms to be implemented (see Figure 11). Therefore, even tens of
34 milliseconds can be beneficial to reduce directional errors associated with a late target switch.
35 Given our criterion to determine movement errors and our experimental design, our estimate
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1 of 110 ms to adjust movement direction would still not be enough to bring movements much
2 closer than half-way between targets in Experiment 2. This indicates that more time would be
3 required to fully reprogram movement direction when participants strongly favoured
4 preparation towards a specific target (e.g. more frequent target). Our estimate of the time to
5 adjust movement direction is not far from that the 130 ms estimate provided by Haith et al.
6 (2016). Different from our study, however, Haith et al (2016) did not vary the probability of
7 the targets, an experimental manipulation that could make the neural competition between
8 representations of potential actions (see Cisek, 2007; Oostwoud Wijdenes et al., 2016) faster
9 to conclude than in our study when the less frequent target was presented.
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18 **Conclusion**

19 Our results provide further evidence that the preparatory processes required in both simple
20 and choice RT tasks can be facilitated by loud acoustic stimulation. They also show that
21 relatively large adjustments in movement direction are implemented progressively over tens
22 of milliseconds. Thus, the larger the discrepancy between an initially prepared motor act and
23 a suddenly specified alternate action, the longer it takes to generate a revised motor plan that
24 will attain task success. Our data demonstrate the utility of the loud acoustic stimulation in
25 providing meaningful readouts of the neural state of the motor system during the final stages
26 of preparation for action.
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36 **Acknowledgements**

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Figure captions

Figure 1: **A**- Experimental setup showing the wrist device. **B** - Example of directional error calculation when the target was presented at 135°. Note that the dotted red circle represents the location of the target at 45°. **C & D** - Time course of sequence of visual events presented on the monitor screen. **C** - Control trial. The green cursor could be moved by the participants providing online feedback about their directional error. **D** - Probe trial. The green expanding ring only provided information about the distance travelled from the origin but contained no information about the directional errors made by the participants to move toward the target.

Figure 2: Directional error determination. The shaded areas represent the range of initial direction of movement in control trials for targets at 45° (pink shaded area) and 135° (light blue shaded area). The dashed lines represent the 99th percentile for initial movement direction in control trials for target at 45 (red) and 135° (blue). The blue and red arrows represent movements on hypothetical example trials on which LAS is applied. Directions which lie outside the 99th percentile of the control distribution (as illustrated) are specified as “error trials” and analysed separately.

Figure 3: **A** - Premotor reaction time for choice (left) and simple (right) RT tasks during control (light blue) and probe trials (dark blue). **B** - Variable directional error measured 100 ms after movement onset. **C** - Constant directional error measured 100 ms after movement onset. Error bars represent the 95% confidence intervals. Confidence intervals were calculated following Morie’s (2008) suggestion for repeated measures designs. * $p < 0.05$.

Figure 4: **A** - Scatter plot of the mean premotor reaction time versus mean absolute directional error in LAS “error trials” during the choice RT task. **B** - Scatter plot of the mean premotor reaction time versus error count. Note that 3 participants did not move outside the 99th percentile of the movement direction distribution observed in control trials (see Figure 2), so their data do not contribute to the correlational scatterplot.

Figure 5: Polar histograms for aiming direction for “error trials” pooled across all participants who made directional errors in Experiment 1. Red line represents the direction of the incorrect target. Green represents the direction of the correct target. **A** – Histogram of responses in which premotor RT was less than 100 ms. **B** - Histogram of responses in which

1 premotor RT ranged from 100 to 150 ms. **C** - Histogram of responses in which premotor RT
 2 ranged from 151 to 200 ms. **D** - Histogram of responses in which premotor RT was over
 3 200 ms. Note that for simplicity we adjusted the aiming directions for targets at 135° so the
 4 green line represents the position of the correct target and the red line represents the
 5 incorrect target irrespective of the real position of the target during the experiment.
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10 **Figure 6:** **A** - Premotor reaction time for probe and control targets at 45°. **B** - Variable
 11 directional error measured 100 ms after movement onset. **C** - Constant directional error
 12 measured 100 ms after movement onset. Error bars represent the 95% confidence intervals.
 13 Confidence intervals were calculated following Morie's (2008) suggestion for repeated
 14 measures designs. * $p < 0.05$.
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21 **Figure 7:** Average number of directional errors participants made in the three probe
 22 conditions. Each condition comprised 12 probe trials. Error bars represent the 95%
 23 confidence intervals. Note that participants who made no errors also contribute to this
 24 analysis. * $p = 0.004$.
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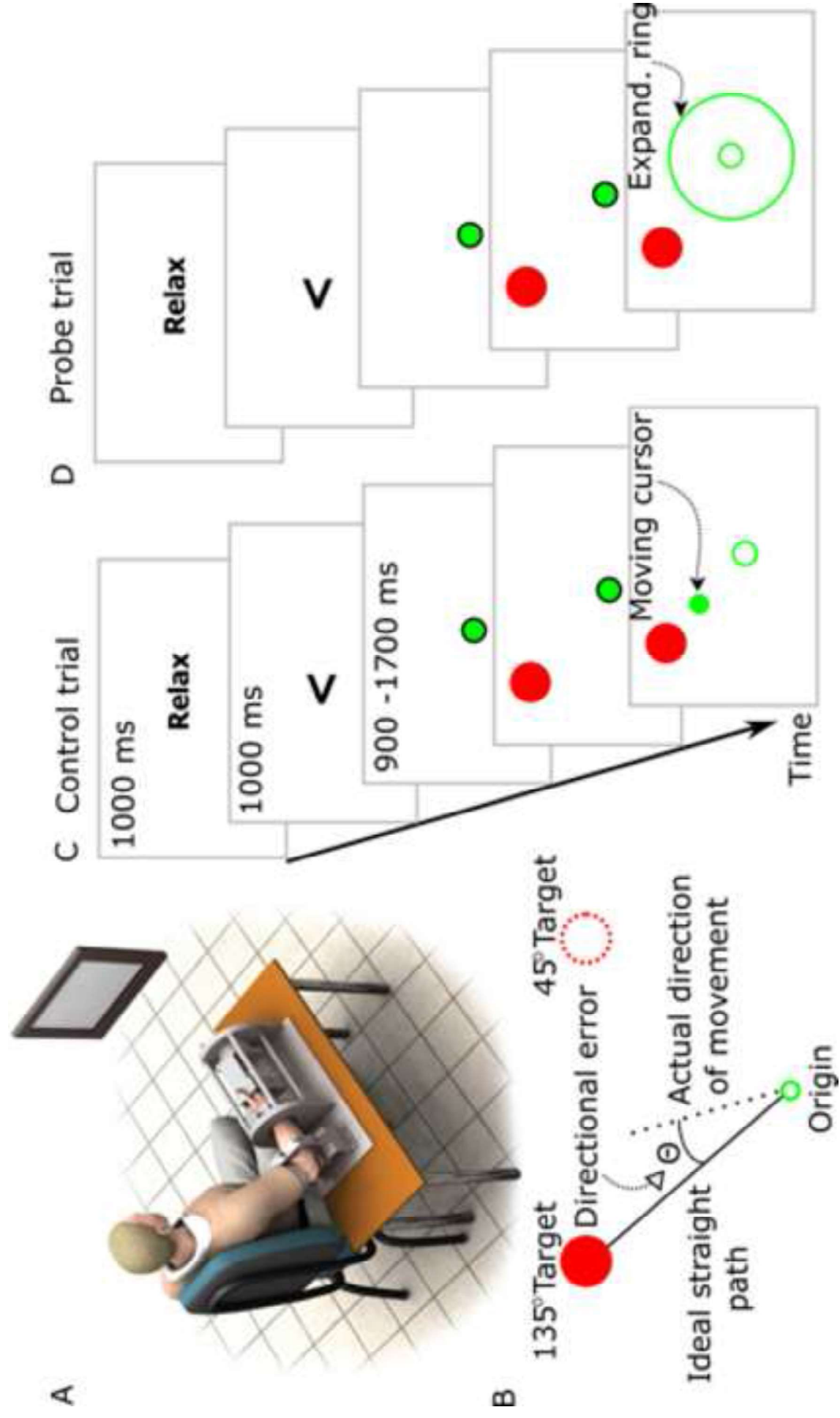
31 **Figure 8:** **A** - Correlation between mean premotor RT and mean directional errors ("error
 32 trials" only) across participants when the LAS were delivered 25 ms prior to the IS ($N = 21$).
 33 **B** - Correlation between mean premotor RT and mean directional errors across participants
 34 when the LAS occurred in synchrony with the IS ($N = 18$). **C** - Correlation between mean
 35 premotor RT and directional errors across participants when the LAS were delivered 25 ms
 36 after the IS ($N = 17$). Note that not all participants displayed directional errors according to
 37 our criterion so their data did not contribute to the correlation analyses.
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45 **Figure 9:** Polar histograms for aiming direction for "error trials" pooled across all
 46 participants and probe times, and binned into 4 intervals according to premotor reaction time.
 47 Note that participants were primed to aim for the target positioned at 135° (represented by the
 48 red line) but the correct target was placed at 45° (represented by the green line) in relation to
 49 the cursor origin. **A** - Histogram of responses in which premotor RT was less than 100 ms. **B**
 50 - Histogram of responses in which premotor RT ranged from 100 to 150 ms. **C** - Histogram
 51 of responses in which premotor RT ranged from 151 to 200 ms. **D** - Histogram of responses
 52 in which premotor RT was over 200 ms.
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1 **Figure 10: A** – Polar plot of the correlation between premotor RT and directional errors
2 using trials collapsed across all participants who made directional errors in at least one of the
3 probe timings. ($N = 21$). **B** – Polar plot of the correlations between premotor RT and
4 directional errors for three participants that made over 12 errors across all probe trials in
5 Experiment 2. S1-S3 = Participant number.
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10 **Figure 11:** Bootstrapped medians of the means across participants for each decile of the
11 cumulative distribution function (CDF) of reaction times ($N = 2000$). **A** - Directional errors
12 across participants as a function of RT decile time in Experiment 2. **B** - CDF of reaction time
13 in Experiment 2. Error bars represent the SE of the bootstrapped medians. Both variables
14 were calculated based on the data of 8 participants who made at least 8 directional errors
15 (mean number of errors = 15.9, $SD = 8$). The fits represent simple linear regressions on the
16 data. Directional error $R^2 = 0.86$; Reaction time $R^2 = 0.97$.
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Figure 1



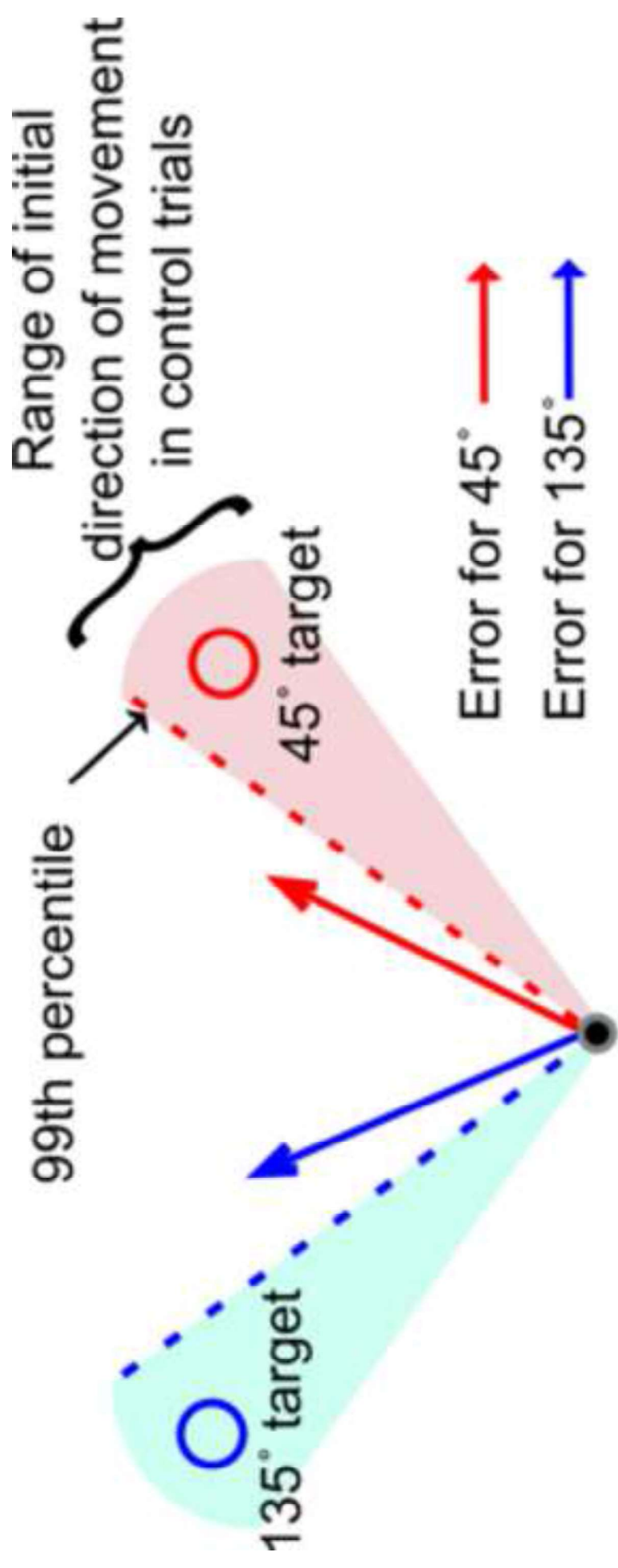


Figure 2

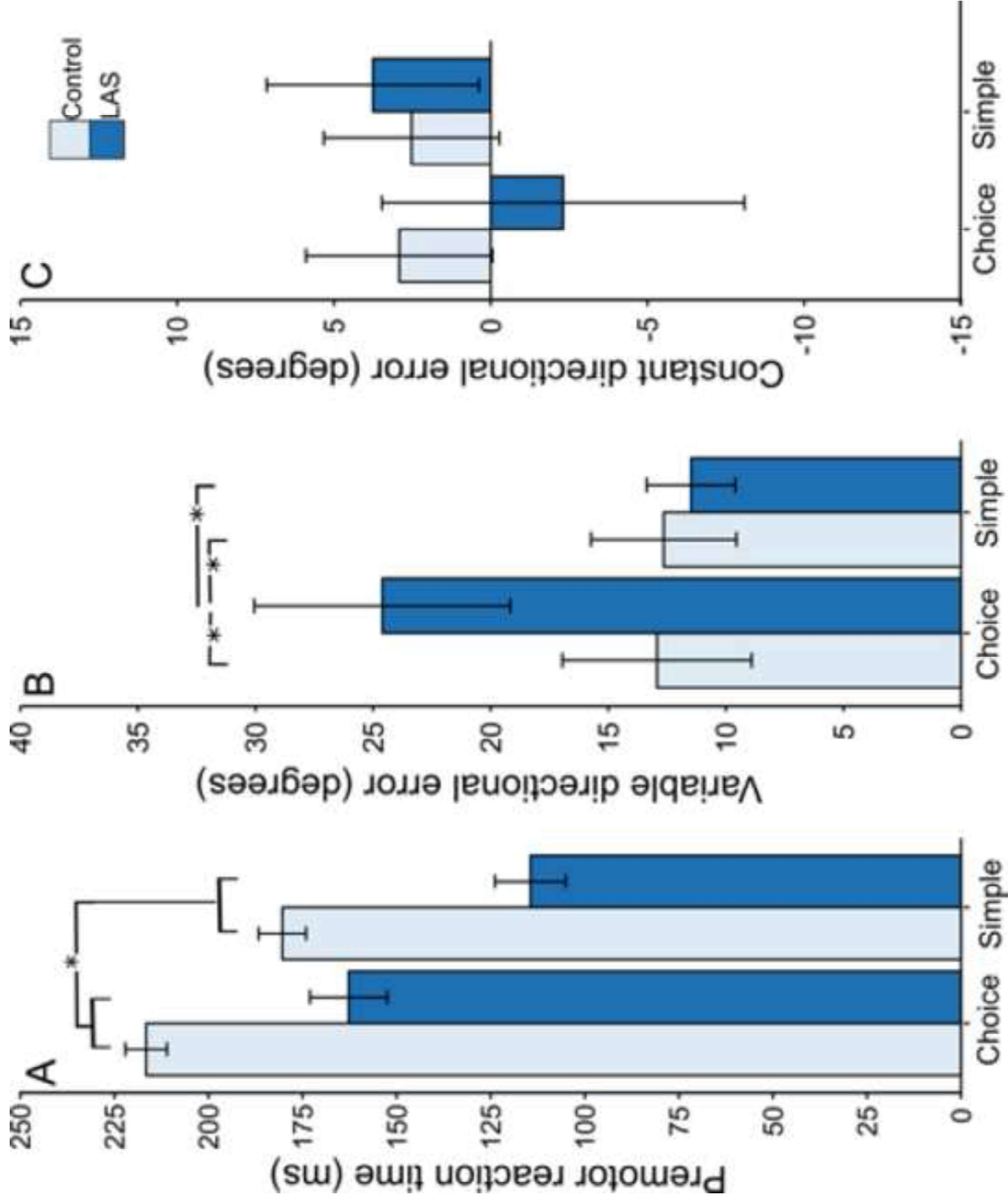


Figure 3

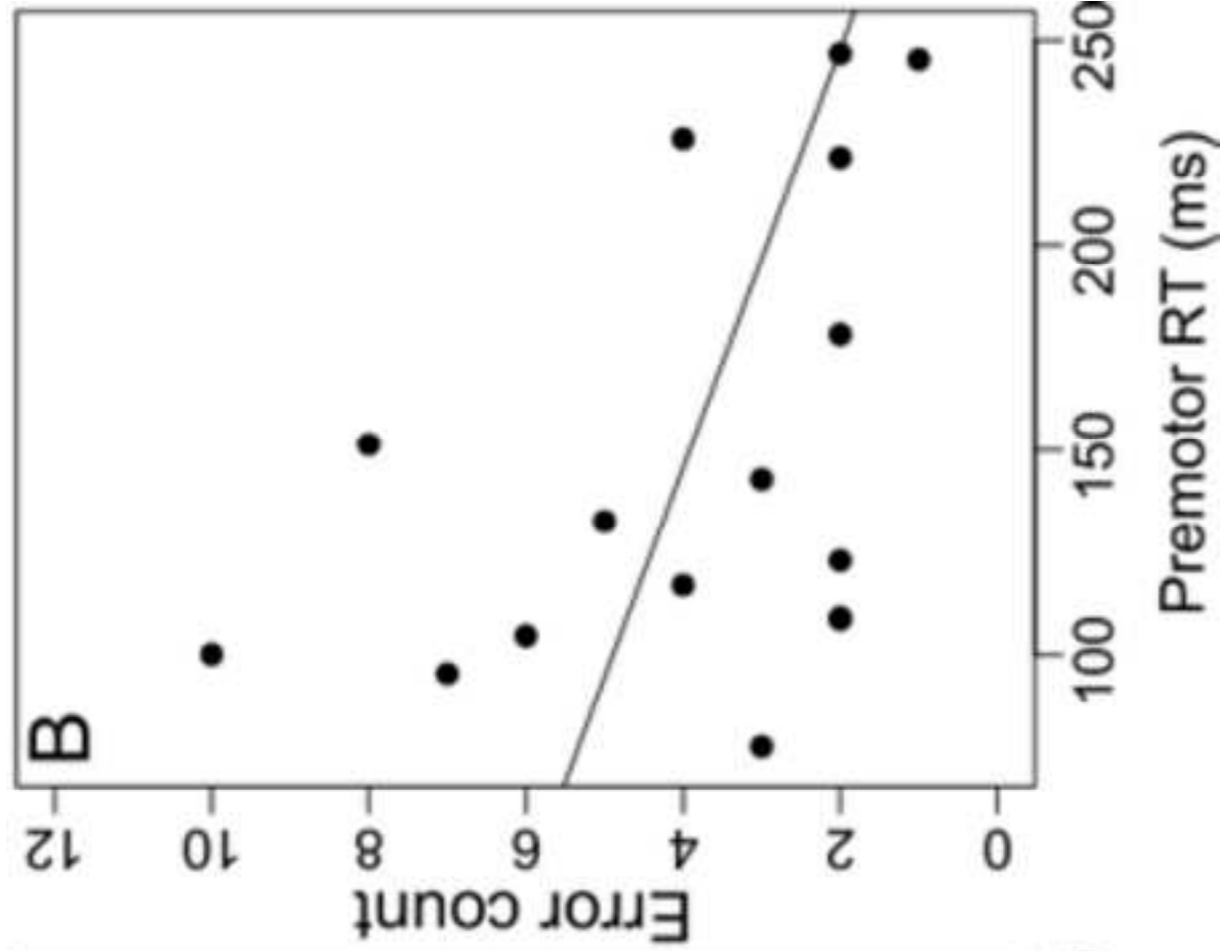
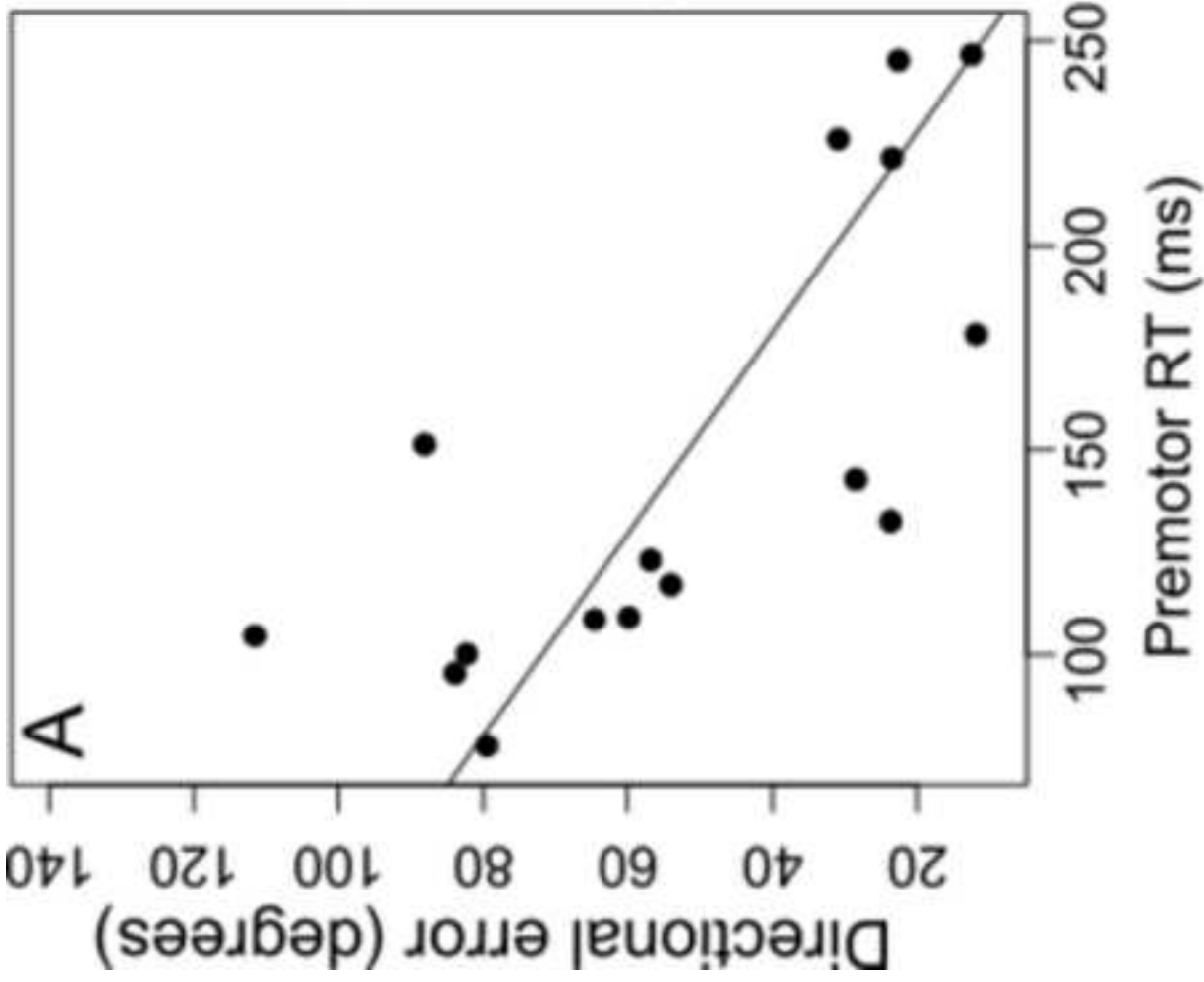


Figure 4

Figure 5

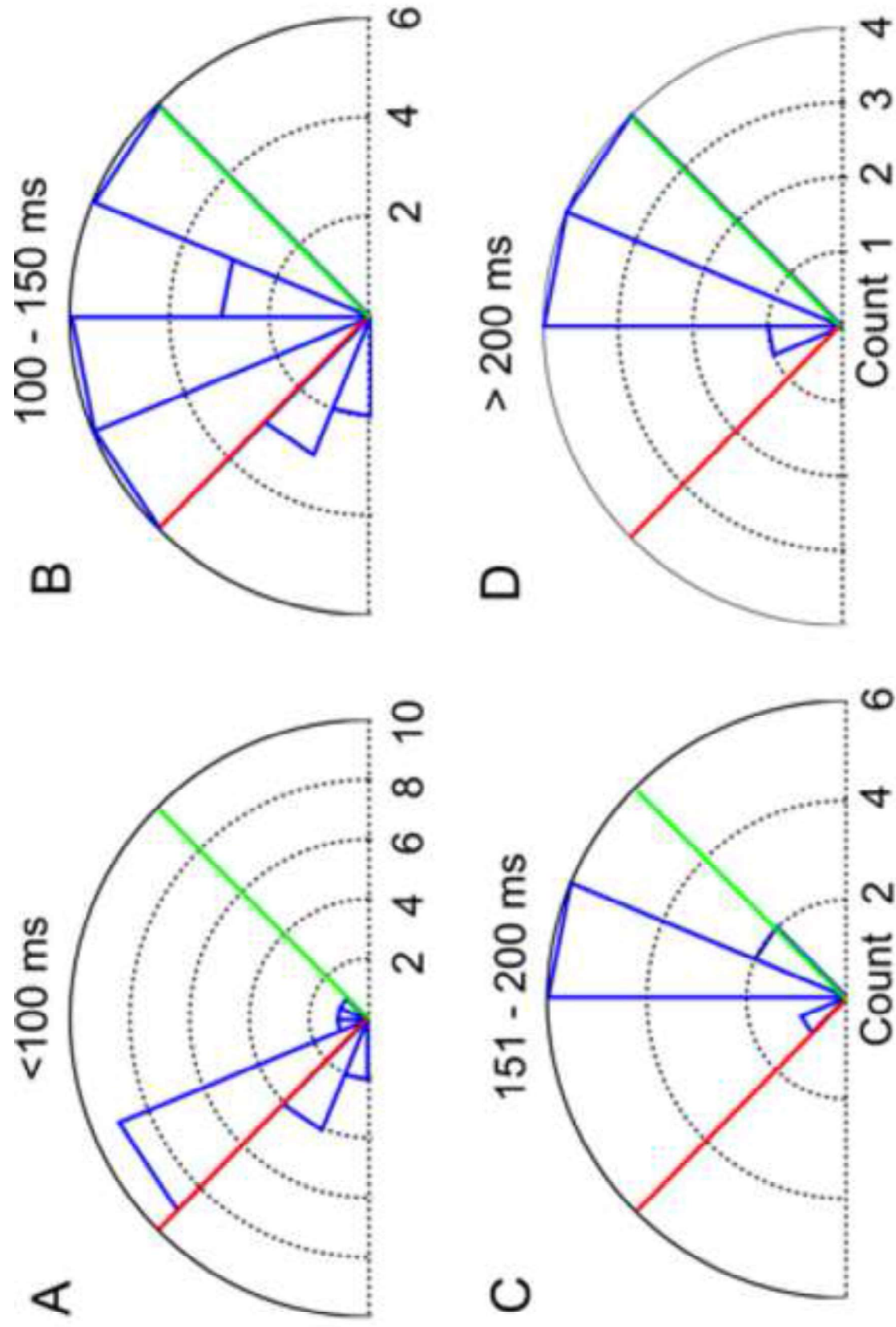


Figure 6

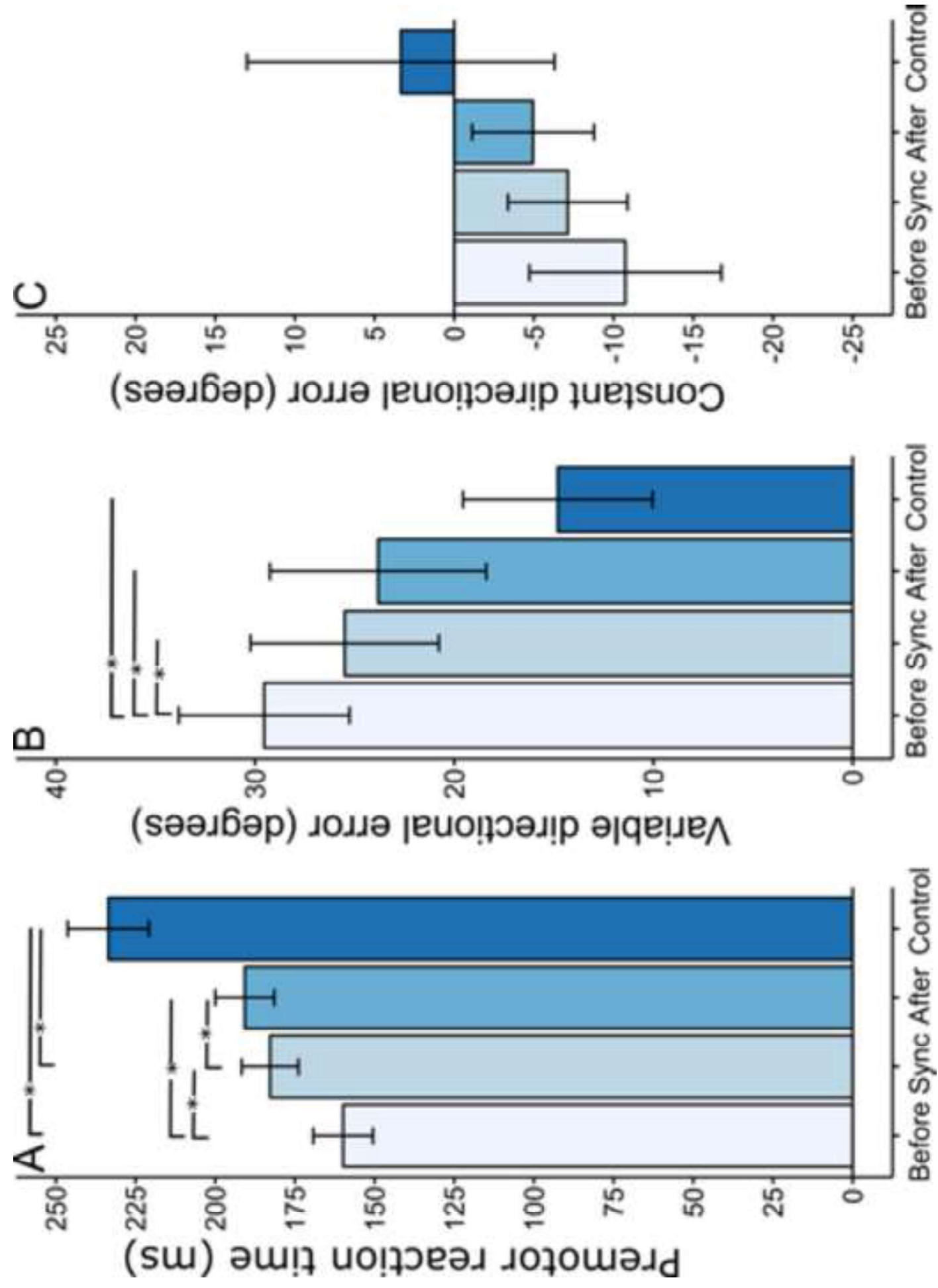


Figure 7

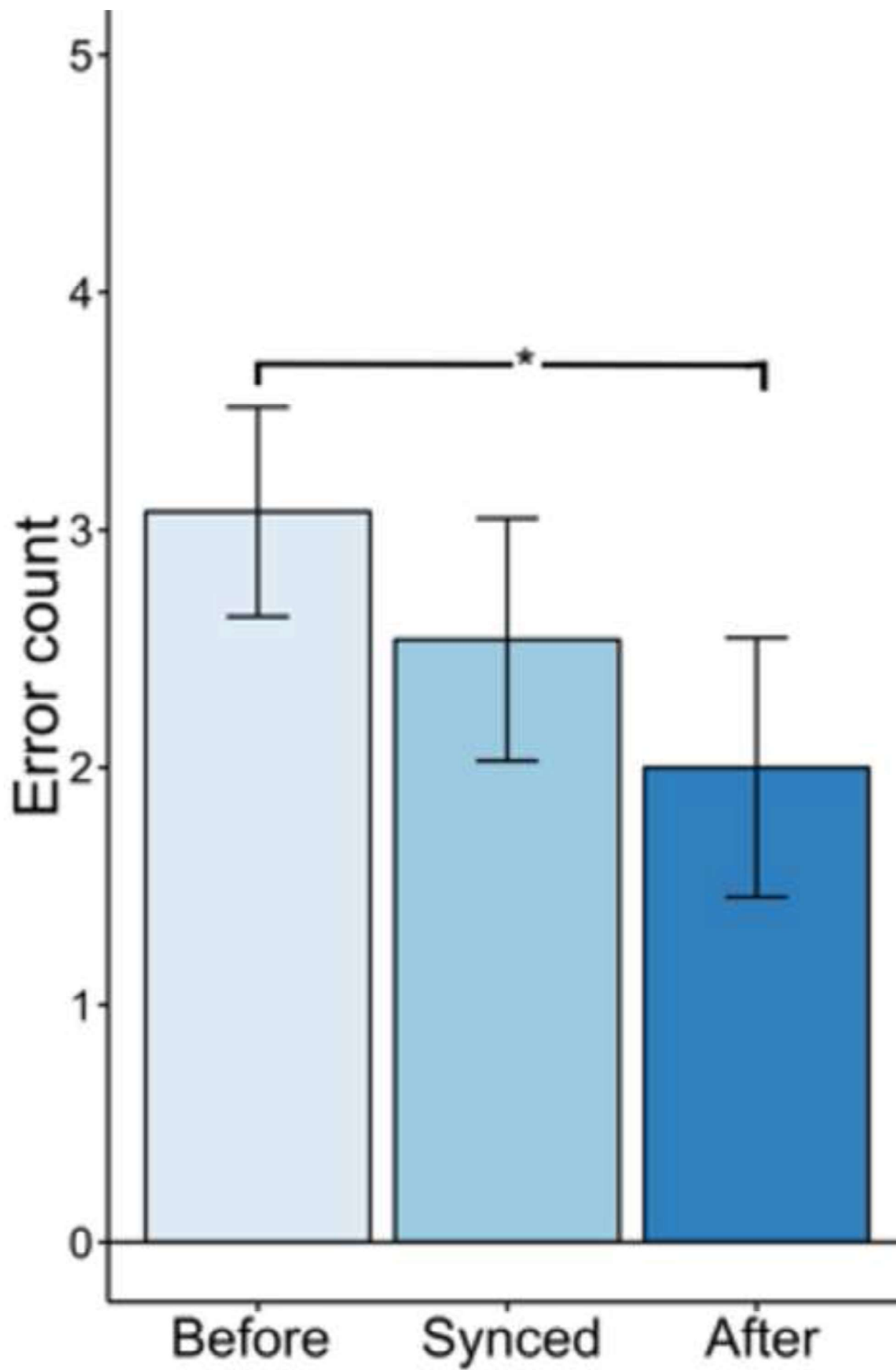


Figure 8

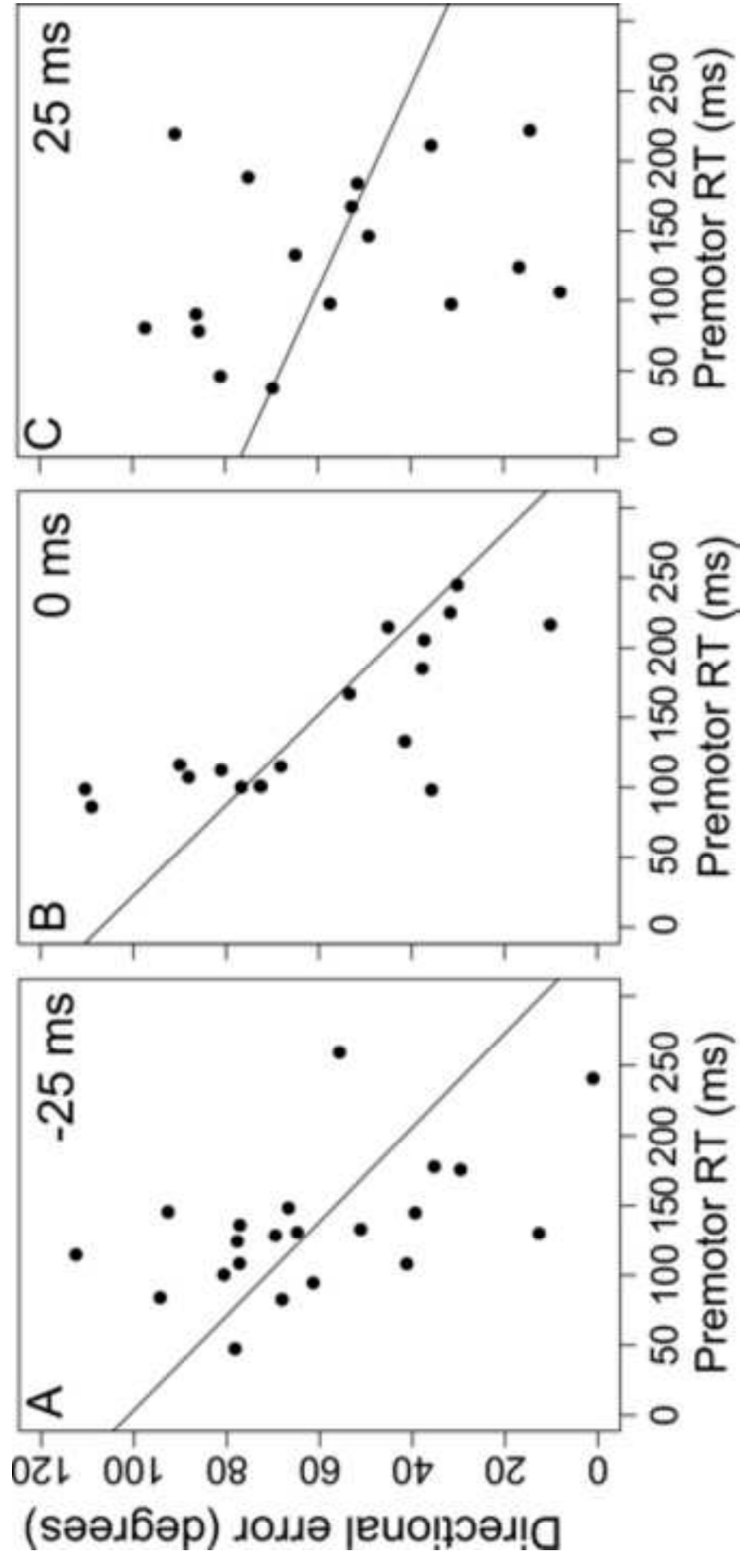


Figure 9

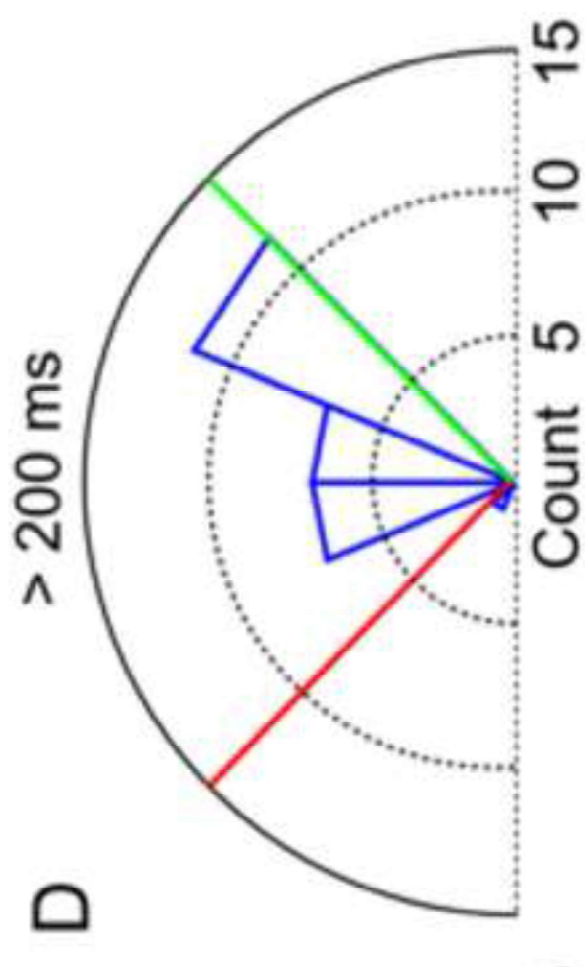
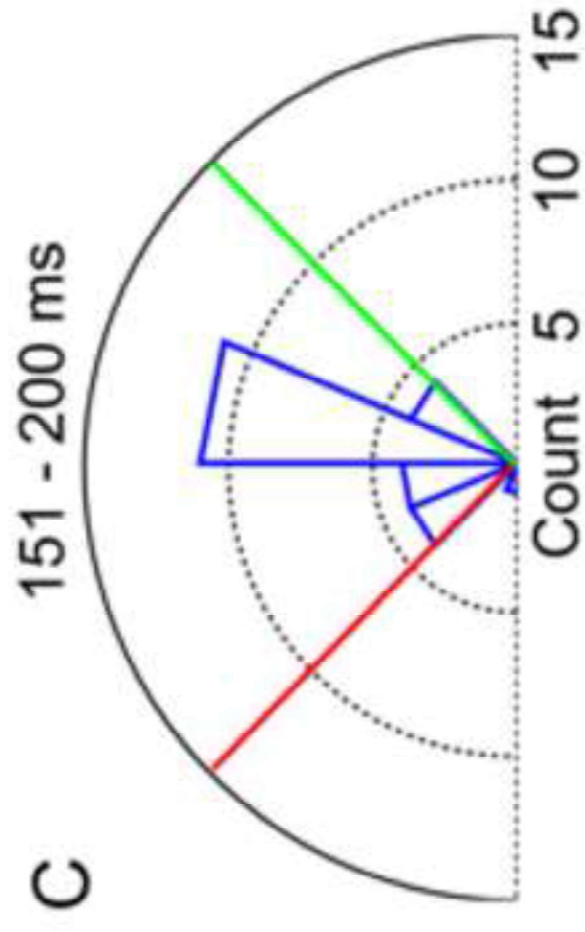
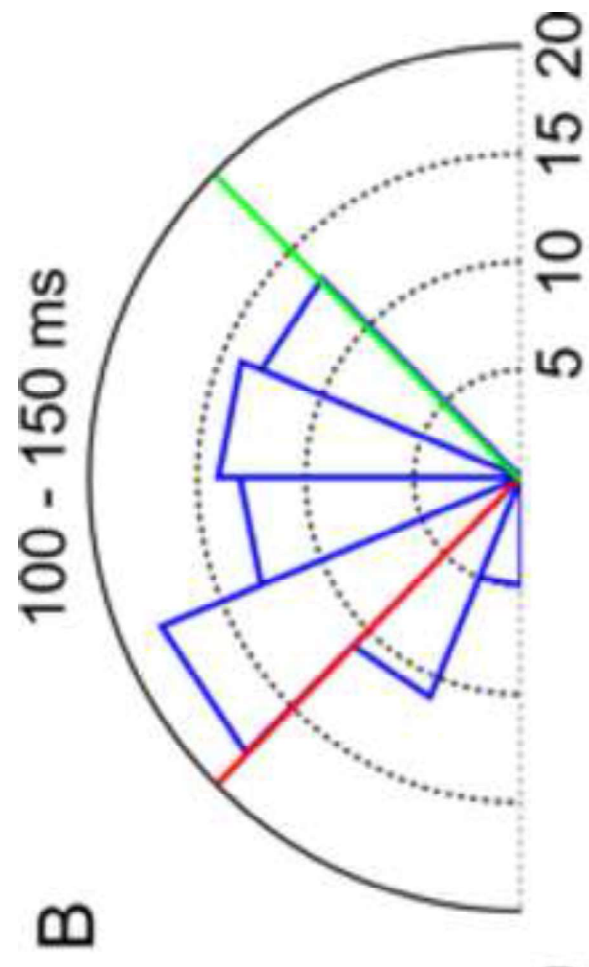
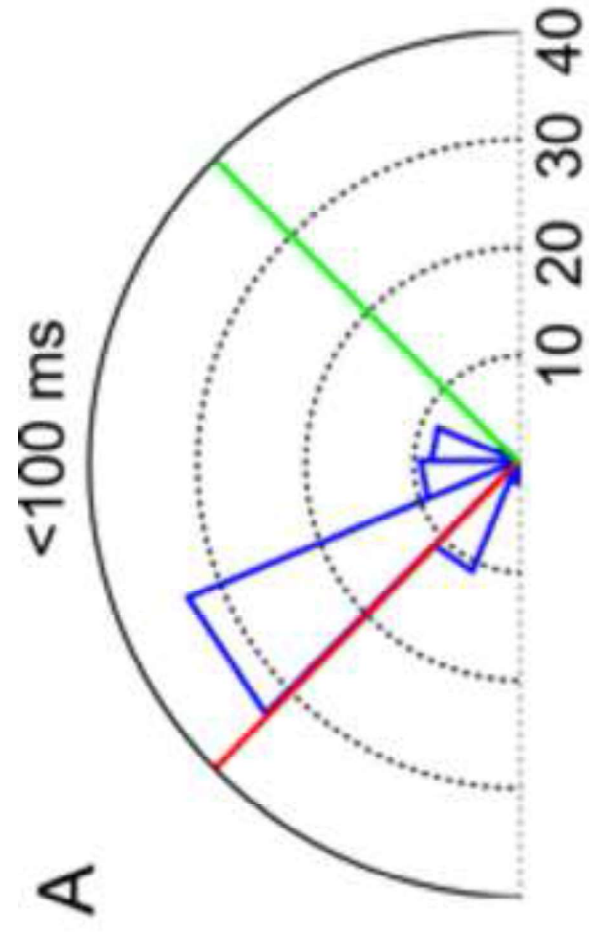


Figure 10

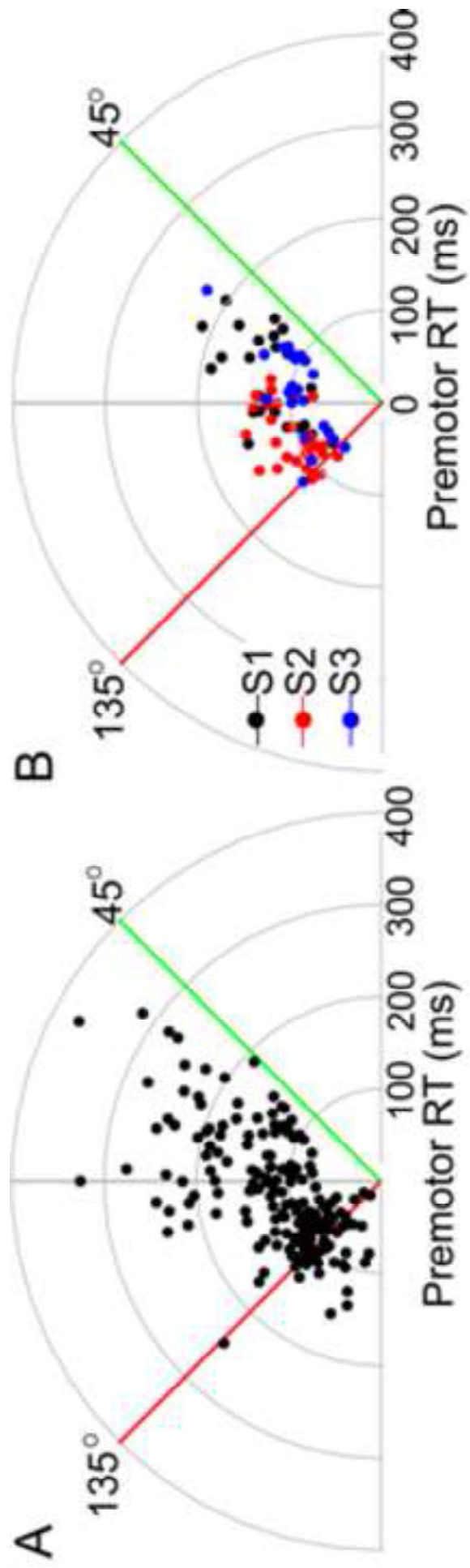


Figure 11

