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

Neuroscience (accepted)

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

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Abstract

A loud auditory stimulus (LAS), delivered during movement preparation, can help the initiation and execution of planned actions. LAS is often used as a tool to investigate motor preparation in simple reaction time (RT) tasks, where all movement parameters are known in advance. In this report, we used LAS to examine direction specification in simple and choice RT tasks. This approach allowed us to investigate how the specification of movement direction unfolds during preparation. In two experiments, participants responded to the appearance of an imperative stimulus (IS) with a ballistic wrist force directed towards one of two targets. In probe trials, LAS (120 dBa) was delivered around the time of IS presentation. In Experiment 1, reaction times in the simple RT task were faster when the LAS was presented, but the effect on the movement kinematics was negligible. In the Choice RT task, however, movement direction variability increased when the LAS was presented. In Experiment 2, when we primed movements towards one direction, our analyses revealed that the longer participants took to start a movement, the more accurate their responses became. Our results show not only that movement direction reprogramming occurs quickly and continuously, but also that LAS can be a valuable tool to obtain meaningful readouts of the state of the motor system for action.

Keywords: acoustic stimulus, motor control, movement direction, preparation

Introduction

Execution of voluntary acts is preceded by preparatory processes in the central nervous system (CNS). The task specifies the act required – a speech act, a manipulative act, a locomotor act – and preparatory processes specify when and how the act will be executed so that the task requirements are met in the prevailing conditions (Jeannerod, 1994; Requin et al., 1991). Preparatory processes must therefore incorporate information about task requirements and environmental conditions in order to specify task-appropriate movement parameters that are passed to the neural machinery that generates motor commands to the muscles. The process of preparation is therefore often referred to as *motor planning* or *motor programming* (Kawato, 1999; Keele et al., 1990; Schmidt and Lee, 2011).

The process of incorporating task and environmental information into a motor plan has been studied using reaction time (RT) and other speeded tasks in which the response is a target-directed movement of some kind (Ghez et al., 1990; Haith et al., 2015; Leonard, 1958; Marinovic et al., 2010; Rosenbaum and Kornblum, 1982; Schouten and Bekker, 1967). The person executing the task is provided with some initial information, which may be either sufficient or insufficient to determine the necessary response. At a later time, but prior to executing the response, additional information is provided that either changes the task requirements initially specified (in the case that the initial information was sufficient; Haith et al., 2015) or supplements initially insufficient information so the required response is fully specified (Ghez et al., 1990; Rosenbaum and Kornblum, 1982; Schutte and Spencer, 2007). Using these methods it has been found that motor plans are initially established using information available from task instructions, prior experience with the task, and perception of the task layout (Ghez et al., 1997; Ghez et al., 1990; Haith et al., 2015; Hudson et al., 2007; Schutte and Spencer, 2007). Where the target is not initially specified, the initial planning state represents the information available concerning all potential targets (Cisek and Kalaska, 2002; Favilla et al., 1990; Findlay, 1982; Gallivan et al., 2015; Ghez et al., 1997; Haith et al., 2015; He and Kowler, 1989; Hudson et al., 2007; Stewart et al., 2014), and many forms for this representation have been proposed (Cisek and Kalaska, 2005; Erlhagen and Schoner, 2002; Gallivan et al., 2015; Haith et al., 2015; Kopecz and Schoner, 1995; Stewart et al., 2014). Incorporation of new information into the motor plan can occur at any time prior to initiation of descending motor commands (Favilla et al., 1990; Ghez et al., 1997), and indeed there may be little or no distinction between the processes that underlie this plan updating and those responsible for feedback corrections of ongoing movements (Flanagan et al., 1993;

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 rapid, but not instantaneous: following presentation of new information during the reaction time, 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 simultaneous 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 might interfere with the ability to attend to and incorporate new target information. Data from double step RT experiments, in which no temporal demands are imposed upon the participants, provide similar estimates of the time cost of plan updating (van Sonderen et al., 1988; van Sonderen et al., 1989). However, double step-paradigms, where the target can suddenly jump from one initial location to another, require that participants divide their attention across multiple potential reaching targets, making the behavioral task more challenging. A case in point regarding the influence of task instructions and demands on estimates of motor planning was made by Haith et al. (2016). 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. Here we investigate movement direction plan updating when the use of strategies to deal with short preparation intervals in speeded tasks are minimized and participants have only a binary choice (right or left) for which to prepare during a trial. More precisely, this study aimed to reveal the time course of direction specification when the state of preparation for action required fast adjustments. 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.

An LAS presented unexpectedly during movement preparation can speed the initiation of the prepared action, a phenomenon termed the StartReact effect (Valls-Solé et al., 1999). Although most research on the StartReact involved 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 an 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. In contrast, however, some authors failed to detect any facilitation of movement initiation in tasks where participants had multiple movement choices (Carlsen et al., 2004). Thus, it seems that under certain circumstances, 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. Because no studies have investigated the impact of LAS on the directional accuracy of movement trajectories and the results might be task dependent, the aim of Experiment 1 was to investigate whether LAS could speed the initiation of motor responses in our task and also examine how it affects initial movement direction in simple and choice RT conditions. The results of experiment 1 suggest that LAS speeds the initiation of movements but has no effect on response accuracy in simple RT tasks, where all movement parameters can be specified well in advance of the movement imperative. By contrast, LAS affects both movement initiation and accuracy under choice RT conditions, also indicating that movement accuracy progressively increases as initiation time is delayed and more time is available to prepare the specified movement. The aim of Experiment 2 was to further examine how direction reprogramming develops over time, by manipulating target probability to induce larger directional biases during planning, and the inter-stimulus-interval (ISI) between the imperative stimulus (IS, or visual target) and the LAS. Our results showed that as reaction time increased, movement accuracy also increased. Although this process is continuous, it evolves rapidly.

Experimental Procedures

Participants

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

Procedures and Design

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

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

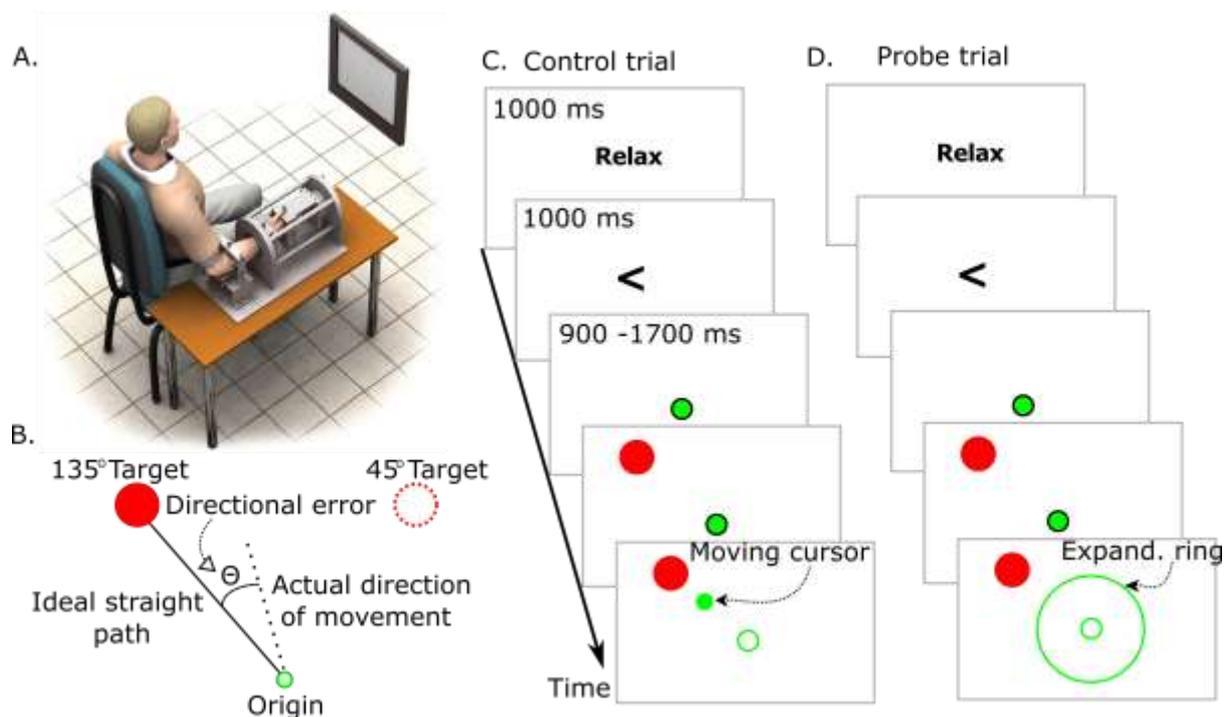


Figure 1: **A**- Experimental setup showing the wrist device. **B** - Example of directional error calculation when the target was presented at 135°. Note that the dotted red circle represents the location of the target at 45°. **C** & **D** - Time course of sequence of visual events presented on the 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.

Auditory stimuli

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

EMG

The electromyogram (EMG) signals were recorded from the extensor carpi radialis brevis (ECRB), flexor carpi radialis (FCR), and sternocleidomastoid (SCM) 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 taken as 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-

way ANOVAs and follow-up post-hoc tests were computed using the functions *med1way* and *mcppb20* (2000 iterations each), respectively, from the WSR2 package. Simple t-tests (*yuend* function) and correlations (*pbcor* function) were also performed using the robust methods suggested by Wilcox (Wilcox, 2012) and implemented with the WSR2 package. For Experiment 2, we also computed cumulative distribution functions (CDF) for each individual's directional error, according to their reaction time data. These CDFs were analysed with robust procedures using the function *rmanova* (WRS2 package). Follow-up polynomial contrasts to detect trends in the data were performed using standard parametric procedures. If corrections were occurring gradually over time, we expected that directional bias would decrease linearly as the deciles increased. Error count across the probe conditions in Experiment 2 were analysed using a Friedman's test. Note that for Experiment 2, we focused our analysis on trials directed to targets positioned at 45° of the origin as our experimental manipulation (see Methods below) was designed to induce larger directional errors on those trials, allowing the analysis of directional adjustments over time. Alpha was set to 0.05 for all comparisons. We report Cohens' *d* effect sizes for the difference of means of pairwise comparisons.

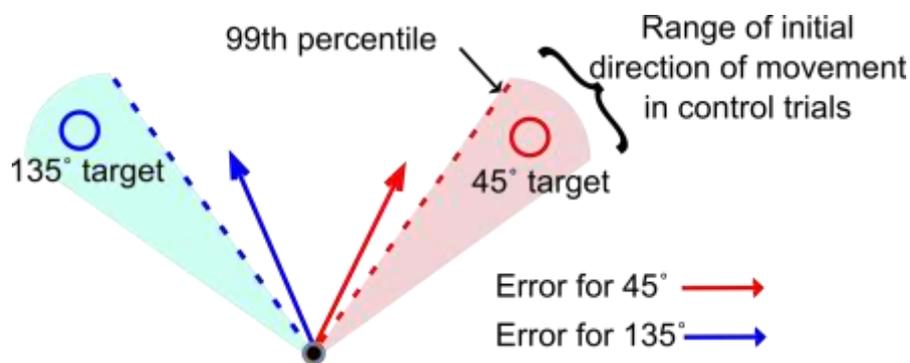


Figure 2: Directional error determination. The shaded areas represent the range of initial direction of movement in control trials for targets at 45° (pink shaded area) and 135° (light blue shaded area). The dashed lines represent the 99th percentile for initial movement direction in control trials for 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.

Methods

Experiment 1 tested the effect of LAS on movement direction variability in simple and choice RT tasks. Participants performed 244 trials divided in two blocks. In one block, the location of the target was cued by arrows as shown in Figure 1 (simple RT task) and participants had to react as quickly as possible to the target's appearance. In the other block, the cue was not presented (choice RT task). The order of the blocks was counterbalanced across participants and, with the exception of the visual cue, the order of temporal events during a trial was identical between blocks. In each block, 20 trials (10 for each of the two directions, $\approx 16\%$ of the total number of trials within a block) were probe trials in which the appearance of the target was synchronised with that of the LAS. Participants were asked to ignore the LAS and perform the task normally. The order of presentation of the probe trials was pseudo-randomised so that trials with LAS were not presented sequentially.

Experiment 2 examined the effect of LAS on a choice RT task when the probability of targets at 135° was greater than targets at 45° . Participants performed a total of 290 trials: 60 trials to the target positioned at 45° (36 probe and 24 control) and 230 trials to the target positioned at 135° (12 probe and 218 control). This unbalanced number of trials served to prime the participants to prepare their movements to the most likely target at 135° and induce larger directional errors when the probe was presented. 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

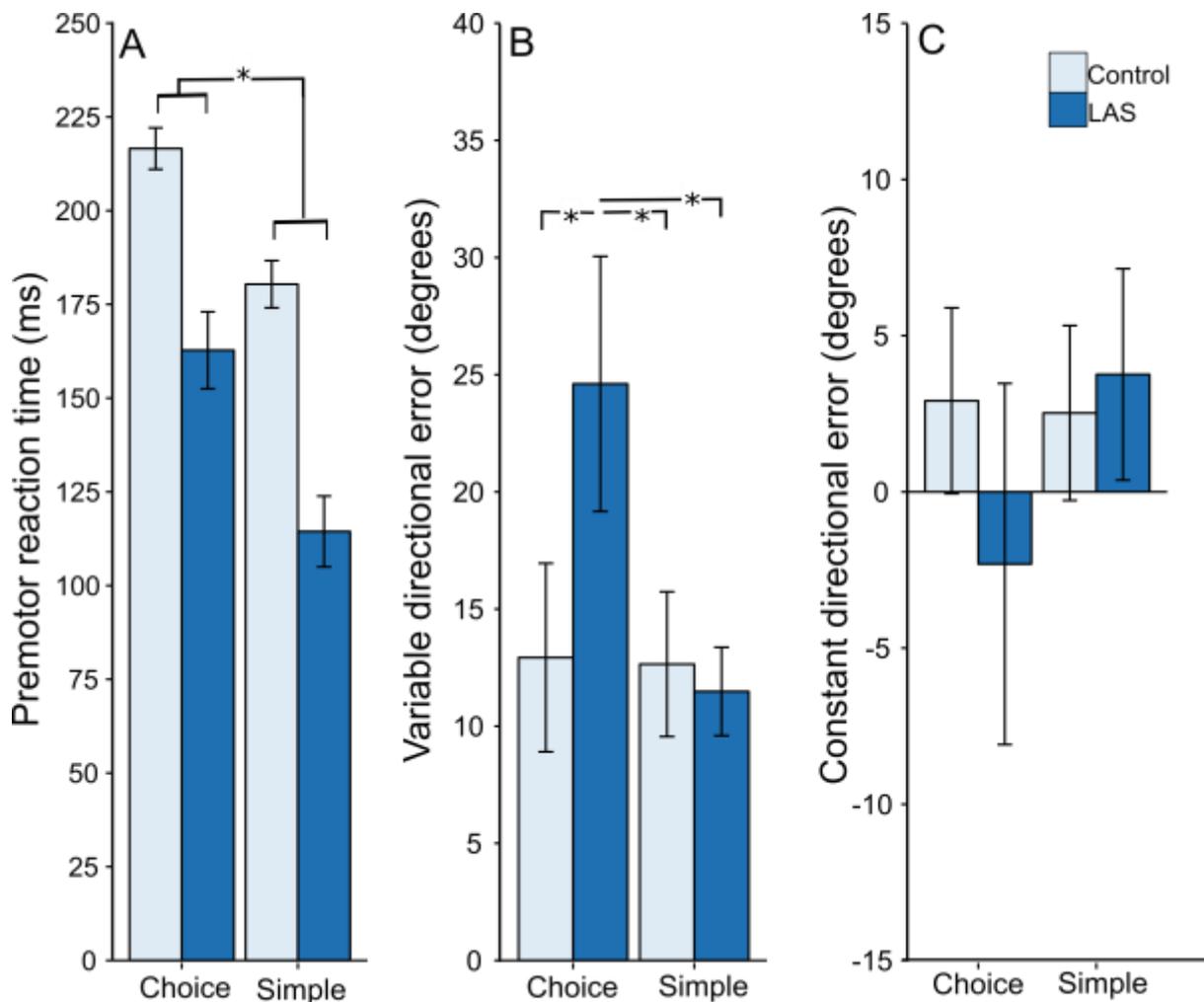


Figure 3: **A** - Premotor reaction time for choice (left) and simple (right) RT tasks during control (light blue) and probe trials (dark blue). **B** - Variable directional error measured 100 ms after movement onset. **C** - Constant directional error measured 100 ms after movement onset. Error bars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

Figure 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, $F = 3.16$, $p = 0.083$.

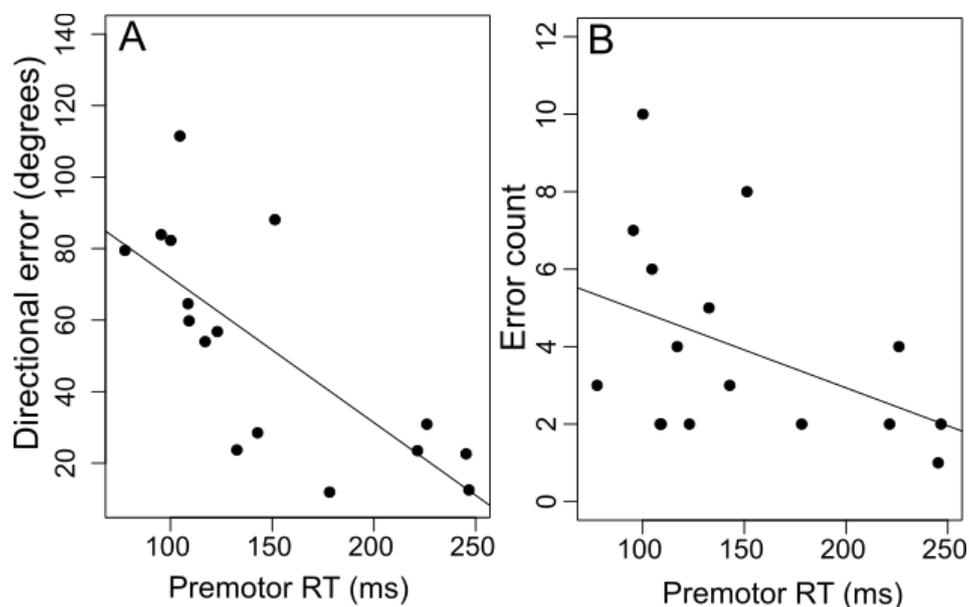


Figure 4: **A** - Scatter plot of the mean premotor reaction time versus mean absolute directional error in LAS “error trials” during the choice RT task. **B** - Scatter plot of the mean premotor reaction time versus error count. Note that 3 participants did not move outside the 99th percentile of the movement direction distribution observed in control trials

(see Figure 2), so their data do not contribute to the correlational scatterplot.

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

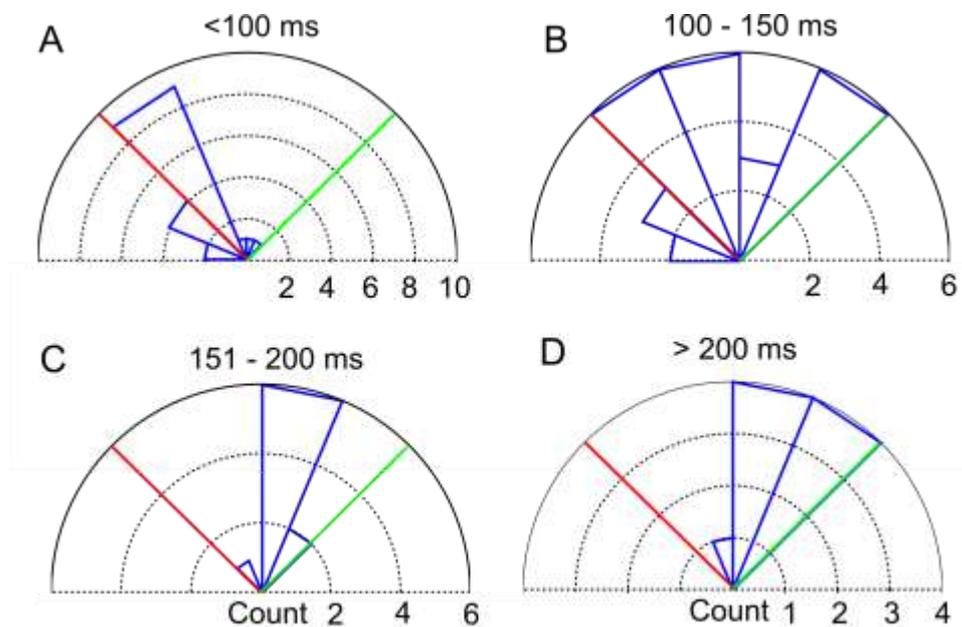


Figure 5: Polar histograms for aiming direction for “error trials” pooled across all participants who made directional errors in Experiment 1. Red line represents the direction of the incorrect target. Green represents the direction of the correct target. **A** – Histogram of responses in which premotor RT was less than 100 ms. **B** - Histogram of responses in which premotor RT ranged from 100 to 150 ms. **C** - Histogram of responses in which premotor RT ranged from 151 to 200 ms. **D** - Histogram of responses in which premotor RT was over 200 ms. Note that for simplicity we adjusted the aiming directions for targets at 135° so the green line represents the position of the correct target and the red line represents the incorrect target irrespective of the real position of the target during the experiment.

The gradual decrease in the magnitude of angular errors as preparation time increases can also be seen in Figure 5, where we plot the aiming direction of incorrect trials according

to premotor RT. In Figure 5A, most responses are directed towards the incorrect target for the shortest premotor RTs (< 100 ms). Between 100 to 150 ms, aiming directions span the whole range between targets. At the premotor RT interval between 150-200 ms, there are few responses toward the incorrect target and most responses were directed to intermediate points between targets. At the longest premotor RT interval (Figure 5D), most responses were intermediate between targets or close to the correct target position.

Given that participants could be affected by their recent history of action (Verstynen and Sabes, 2011), we also analysed whether the median absolute directional errors (error trials only, see Figure 2) across participants were influenced by the position of the target on the previous trial (i.e. trial N-1). We found that the mean absolute error across participants was 18.8° ($SD = 17.6$) when the previous movement was directed toward the same target, whereas it was 13.4° ($SD = 7.8$) when the movement was made toward the opposite target in trial N-1. Because we were interested in determining whether repeated presentation of a target tended to increase or decrease the size of errors with respect to the previous movement, rather than testing the null hypothesis that repetition has no effect, we took advantage of Bayesian statistics to contrast these alternatives. For this analysis, we used the Bayesian alternative to t-tests introduced by Morey and colleagues (Morey and Rouder, 2011; Rouder et al., 2009), implemented using the BayesFactor package for R (*ttestBF*). Because the *ttestBF* function of the R package provides 2 Bayes factors, both against the same denominator model, it was possible to estimate a Bayes factor comparing whether the effect was to increase or decrease directional errors after movements toward specific targets by dividing the probability of an increased error over that of a decreased directional error. This 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°.

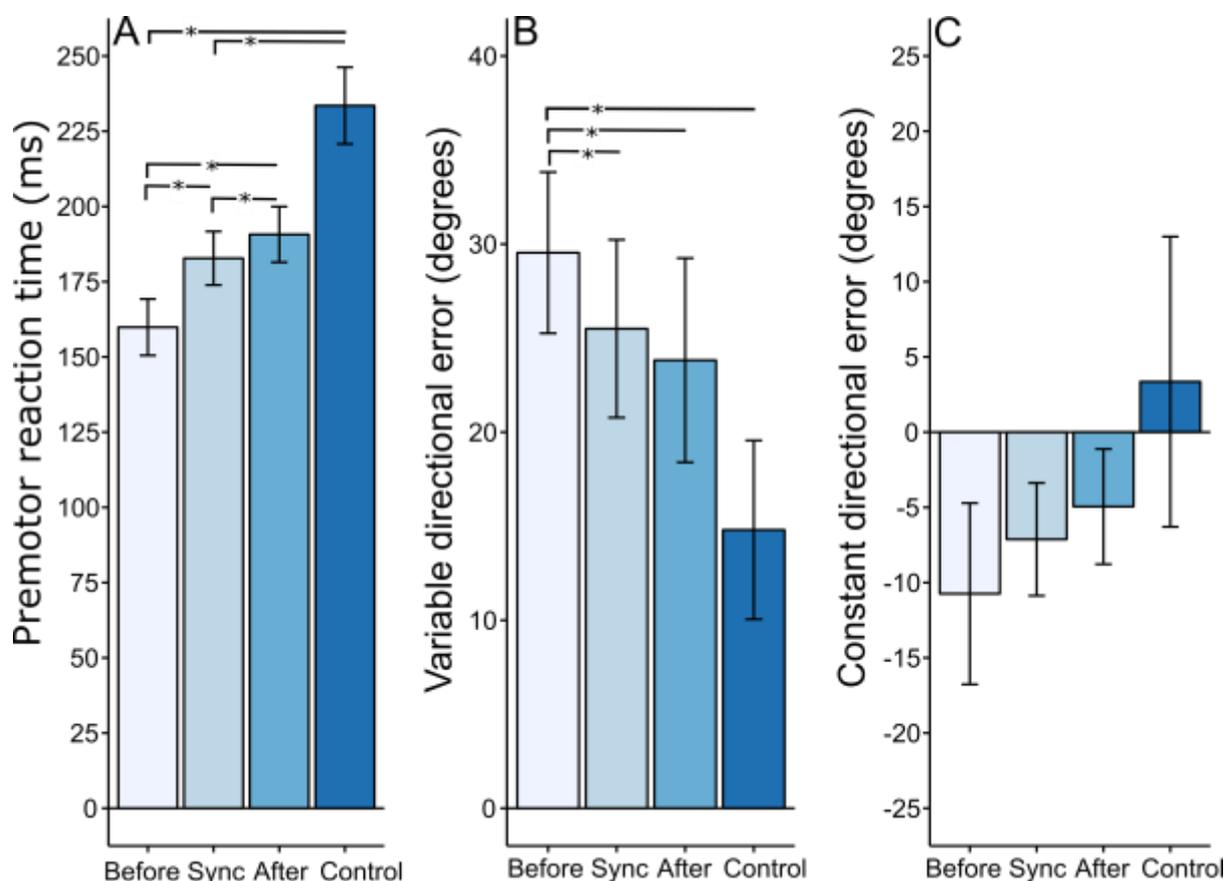


Figure 6: **A** - Premotor reaction time for probe and control targets at 45°. **B** - Variable directional error measured 100 ms after movement onset. **C** - Constant directional error measured 100 ms after movement onset. Error bars represent the 95% confidence intervals. Confidence intervals were calculated following Morie's (2008) suggestion for repeated measures designs. * $p < 0.05$.

Figure 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.

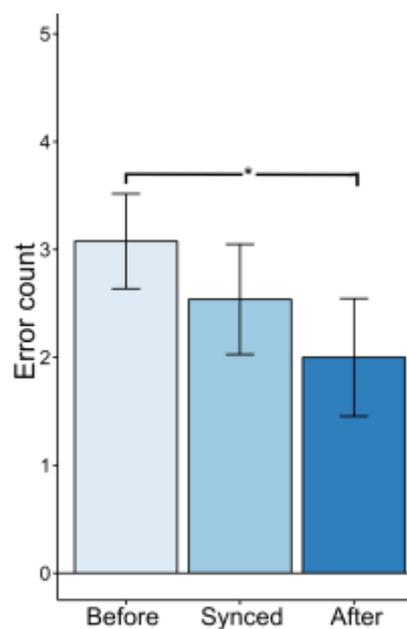


Figure 7: Average number of directional errors participants made in the three probe conditions. Each condition comprised 12 probe trials. Error bars represent the 95%

confidence intervals. Note that participants who made no errors also contribute to this analysis. * $p = 0.004$.

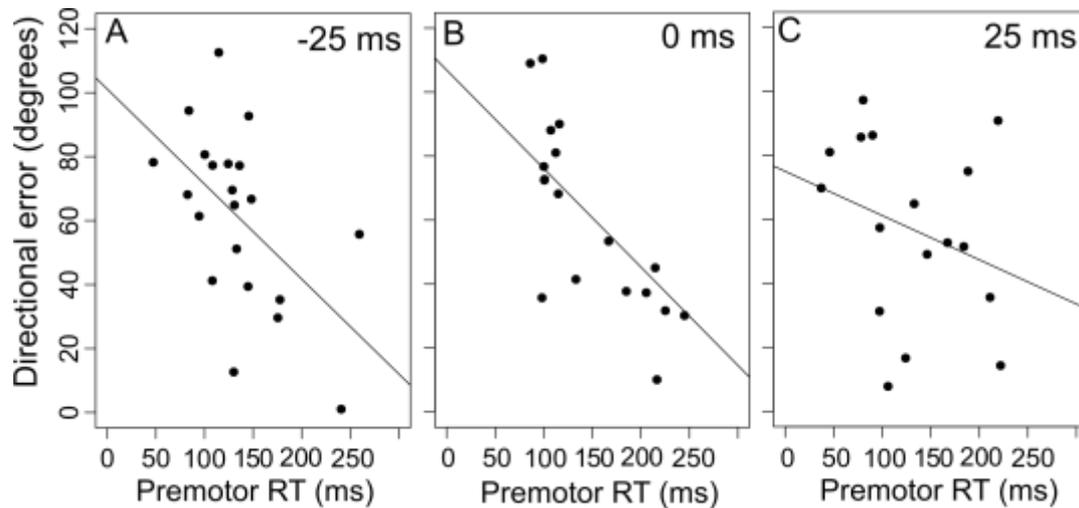


Figure 8: **A** - Correlation between mean premotor RT and mean directional errors (“error trials” only) across participants when the LAS were delivered 25 ms prior to the IS ($N = 21$). **B** - Correlation between mean premotor RT and mean directional errors across participants when the LAS occurred in synchrony with the IS ($N = 18$). **C** - Correlation between mean premotor RT and directional errors across participants when the LAS were delivered 25 ms after the IS ($N = 17$). Note that not all participants displayed directional errors according to our criterion so their data did not contribute to the correlation analyses.

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, $r_s = -0.56$, $p = 0.007$, and in synchrony with the IS, $r_s = -0.82$, $p < 0.0001$. For probe trials presented after the IS, any relationship also tended negative, but the test failed to reach statistical significance, $r_s = -0.31$, $p = 0.23$.

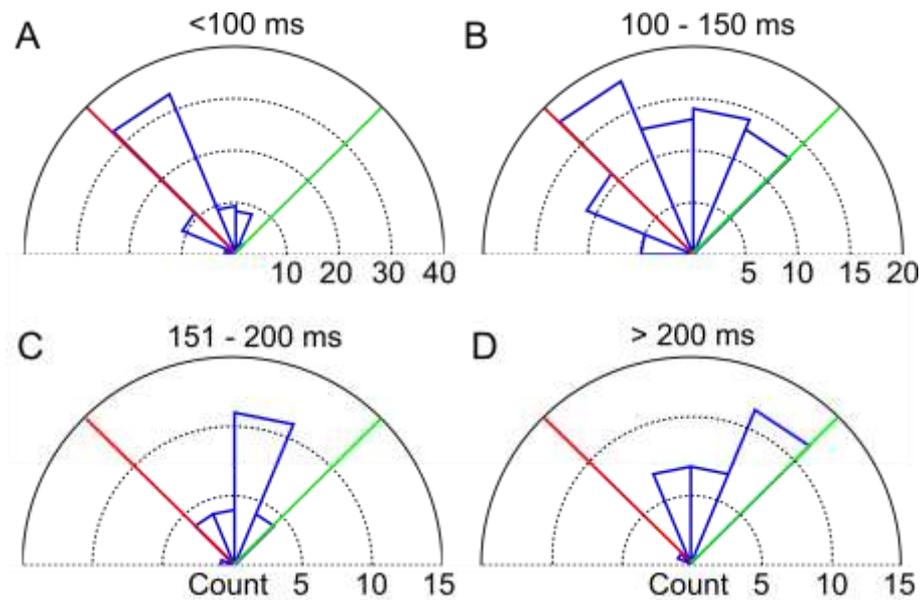


Figure 9: Polar histograms for aiming direction for “error trials” pooled across all participants and probe times, and binned into 4 intervals according to premotor reaction time. Note that participants were primed to aim for the target positioned at 135° (represented by the red line) but the correct target was placed at 45° (represented by the green line) in relation to the cursor origin. **A** – Histogram of responses in which premotor RT was less than 100 ms. **B** - Histogram of responses in which premotor RT ranged from 100 to 150 ms. **C** - Histogram of responses in which premotor RT ranged from 151 to 200 ms. **D** - Histogram of responses in which premotor RT was over 200 ms.

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, $r_s = -0.53$, $p < 0.0001$. 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: $r_s = -0.59$, $p = 0.0017$; S2: $r_s = -0.40$, $p = 0.023$; S3: $r_s = -0.58$, $p = 0.002$). Thus, the intra-individual analysis supports the inter-individual correlational analysis.

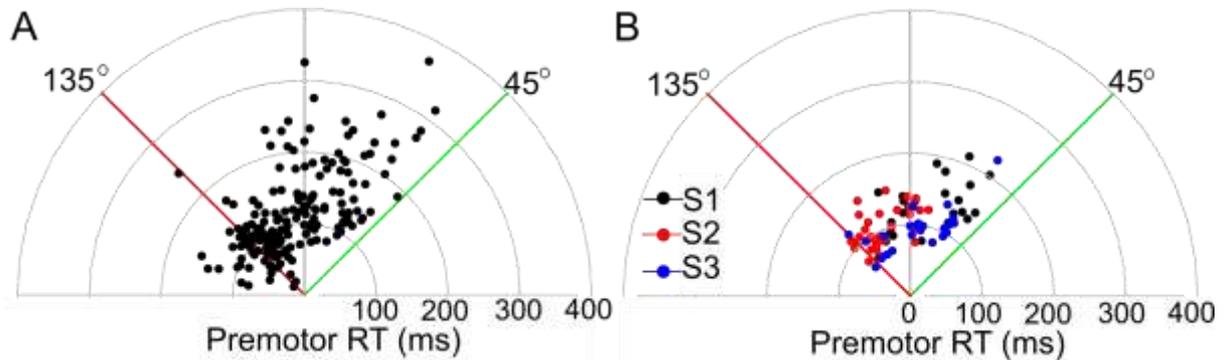


Figure 10: **A** – Polar plot of the correlation between premotor RT and directional errors using trials collapsed across all participants who made directional errors in at least one of the probe timings. ($N = 21$). **B** – Polar plot of the correlations between premotor RT and directional errors for three participants that made over 12 errors across all probe trials in Experiment 2. S1-S3 = Participant number.

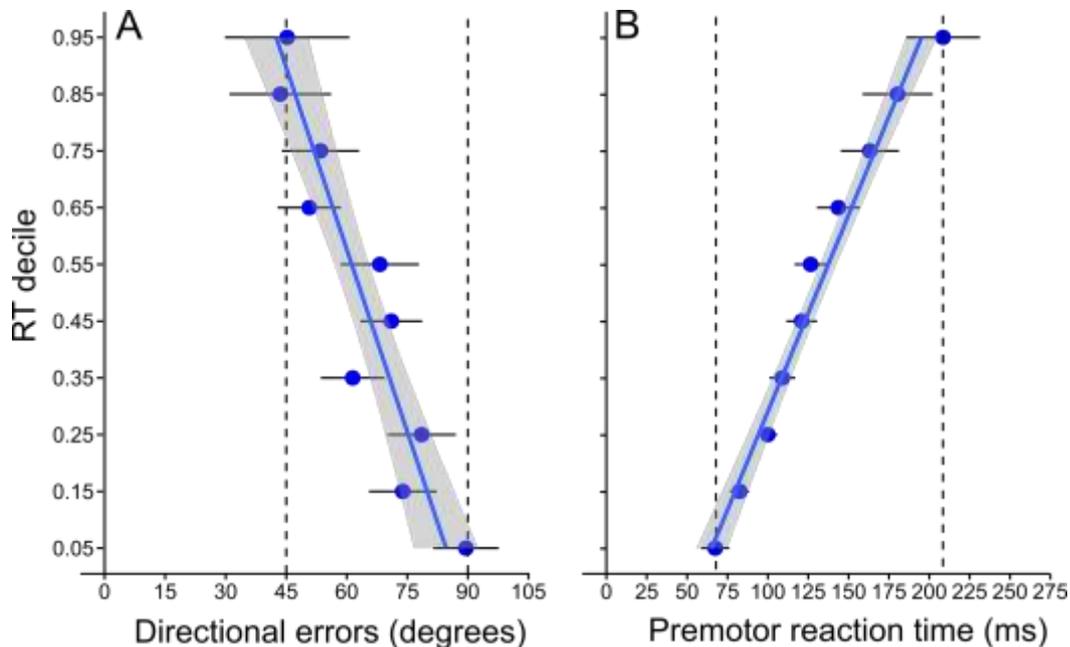


Figure 11: Bootstrapped medians of the means across participants for each decile of the cumulative distribution function (CDF) of reaction times ($N = 2000$). **A** - Directional errors across participants as a function of RT decile time in Experiment 2. **B** - CDF of reaction time in Experiment 2. Error bars represent the SE of the bootstrapped medians. Both variables

were calculated based on the data of 8 participants who made at least 8 directional errors (mean number of errors = 15.9, SD = 8). The fits represent simple linear regressions on the data. Directional error $R^2 = 0.86$; Reaction time $R^2 = 0.97$.

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, the results of Experiment 1 showed that movement initiation in our task occurred earlier in both simple and choice RT tasks (Forgaard et al., 2011; Kumru et al., 2006). 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 LAS means 95% CI [-1.7, 3.7]). The observation that directional variability is unaffected by LAS in our simple RT task is interesting as LAS significantly increases response speed and forcefulness of movements requiring endpoint accuracy (Castellote and Valls-Solé, 2015), suggesting that

LAS does not simply add noise to the circuits responsible for response programming. Rather, it appears to increase the gain of these circuits, affecting reaction time, duration, and forcefulness of prepared responses (Castellote and Valls-Solé, 2015; Fernandez-Del-Olmo et al., 2014; Kumru et al., 2006; Marinovic et al., 2014a; Marinovic et al., 2013; Marinovic et al., 2014b), without negatively affecting movement parameters such as direction.

The analysis of directional errors in the choice RT task in Experiment 1 showed that when the LAS was presented, the participants with longer reaction times had smaller errors than participants who had shorter reaction times (see Buetti and Kerzel, 2009) for a similar finding using the Simon task). This same pattern of results was clear across all the LAS-IS intervals (-25, 0, and +25 ms) used in Experiment 2, where we primed participants to weight movement preparation more heavily toward one target. Moreover, because we delivered the LAS at three times in relation to the IS in Experiment 2, we could confirm a progressive improvement in movement direction specification using polynomial contrast to check for trends in constant error and movement variability. Thus, as more time was available to process visual information, participants gradually improved directional accuracy. These findings indicate that despite the separation between targets being above the threshold from which participants move stochastically towards one specific target irrespective of the preparation time (Ghez et al., 1997), our participants adjusted their movements continuously, with a linear decrease in directional errors as reaction times increased. These results are consistent with those reported by Schutte and Spencer (2007) (see also Erlhagen and Schoner, 2002)), who found that movement parameters were adjusted gradually for large target separations (80°) when task instructions allowed online corrective movements. Different from Schutte and Spencer (2007), however, we did not constrain time of movement onset to force participants to choose the best initial parameters of the movement, which could interfere with the time available to implement corrective adjustments to their movements. Instead, in Experiment 2, we induced them to prepare for the incorrect target and examined how initial movement accuracy evolved as more time was provided before the movement was triggered by the LAS, allowing the study of motor behaviour in more naturalistic conditions.

Unlike reports showing that participants aim toward intermediate positions between targets at short response latencies (Ghez et al., 1997; Haith et al., 2015), the results of Experiment 1 indicate that participants sometimes use a strategy of aiming beyond intermediate positions between targets. Note that a simple averaging strategy would cause directional errors in probe trials to be about 45° (half of the distance between targets, see Figure 4) or less. Our analysis, therefore, suggests that even though there was a 50/50 chance

of targets appearing at 45 and 135°, some participants guessed the location of the upcoming targets as a strategy to shorten reaction time (n.b. participants who displayed the fastest RTs also had errors above 60°). This "guessing strategy" is likely to be affected by the recent movement history (trial N-1) (de Lussanet et al., 2002; see also Dorris et al., 1999) as errors were relatively larger toward repeated targets, as supported by our Bayesian analysis of directional errors.

Cisek and Kalaska (2002, 2005) demonstrated that when the final target for action is uncertain, the specification of multiple movement directions can occur simultaneously in the dorsal premotor cortex. After a decision is made, however, there is a rise in activation of neurons tuned to the correct target direction, and a suppression of neurons tuned to the incorrect target. These results are consistent with the proposal that when the level of neural activation reaches a certain threshold, a motor response with a particular direction is executed (Cisek and Kalaska, 2010). We propose that LAS adds activation to the circuits involved in response execution, to induce a generalised increase in neural activation throughout the CNS that summates with voluntary motor preparation, and thereby shortens the time required for neural activation to reach threshold (see also Marinovic et al., 2014b)). In the choice RT task, this could sometimes lead to the release of responses for which activation related to the correct target was not fully developed, and the suppression of the activation related to the incorrect target was not completed. This would explain the observation of response bias towards the mostly likely target when participants were probed with LAS. Because the reprogramming of movement direction takes time to complete, responses became increasingly more accurate as preparation time increased (see Figure 9, 10 and 11). Consistent with recent reports, our data indicate movement reprogramming is not as sluggish as one would expect if the process of aiming to the alternative target requires a complete reprogramming of a motor action (over 200 ms in control trials of Experiment 1), as there is no need to return to a state of preparation similar to that found before a commitment to prepare had started (Ames et al., 2014; Haith et al., 2016). However, our analysis of directional errors based on the cumulative distribution function of RTs suggests a correction of 45° in our task may take approximately 110 ms to be implemented (see Figure 11). Therefore, even tens of milliseconds can be beneficial to reduce directional errors associated with a late target switch. Given our criterion to determine movement errors and our experimental design, our estimate of 110 ms to adjust movement direction would still not be enough to bring movements much closer than half-way between targets in Experiment 2. This indicates that more time would be required to fully reprogram movement direction when

participants strongly favoured preparation towards a specific target (e.g. more frequent target). Our estimate to adjust movement direction is not far from that the 130 ms estimate provided by Haith et al. (2016). Different from our study, however, Haith et al (2016) did not vary the probability of the targets, an experimental manipulation that could make the neural competition between representations of potential actions (see Cisek, 2007; Oostwoud Wijdenes et al., 2016) faster to conclude than in our study. Our results also relate to the urgency-gating model proposed by Cisek et al. (2009) to explain the speed of perceptual judgments. More precisely, Cisek and colleagues demonstrated that as the urgency to move increases (e.g. the deadline to commit to a response approaches), so does the gain of evidence accumulation, leading to faster responses when the urgency is high. If the generalised motor arousal induced by the unexpected LAS (see e.g. Jepma et al., 2009; Marinovic et al., 2015) interacts with the endogenous urgency signal (e.g. one's motivation to respond quickly), less accumulation of sensory evidence regarding target location would be required to reach threshold, explaining shorter RTs in the presence of LAS.

Conclusion

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

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