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Inhibition of motor-related activation during a simple reaction time task requiring visuomotor mental rotation

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Abstract

The present study investigated whether differences in reaction time (RT) between movements initiated to a visual cue (directly cued) versus movements initiated to a location other than the visual cue (indirectly cued) arise due to varying levels of inhibition within the motor system during response preparation. Unlike typical visuomotor mental rotation (VMR) experiments, this study employed a simple RT paradigm to allow response preparation to occur in advance of the imperative stimulus (IS). Participants responded to the IS by either moving directly to the location of a visual cue or to a location that required a mental transformation between the visual cue and the intended movement goal (i.e., a location 60°, 90°, or 120° rotated with respect to the visual cue). To probe motor-related activation during response preparation, a startling acoustic stimulus (SAS, 124 dB) was randomly presented 500 ms, 1000 ms, or 1500 ms following visual cue onset, but before the IS. Results showed similar RTs during non-startle control trials regardless of rotation angle and whether trials were completed in a random or blocked design. Interestingly, SAS trials showed a low incidence of early response triggering across all time points regardless of whether the movement was directly or indirectly cued. In contrast, directly cued movements performed outside of the VMR context showed a high incidence of SAS response triggering. These results suggest that when a stimulus to target-goal transformation might be required, inhibitory suppression of motor-related activation arises regardless of whether the final movement is directly or indirectly cued.

Keywords: Visuomotor mental rotation; Startle; Response preparation; Inhibition; Motor activation

Introduction

In a typical visuomotor mental rotation (VMR) task, participants point from a central home position to a location that deviates from a visual cue by a predetermined / instructed angle of rotation (Drummond, Carlsen, & Cressman, 2013; Georgopoulos & Massey, 1987; Neely & Heath, 2010). Broadly speaking, there are two types of movements in this task: directly cued and indirectly cued. Directly cued movements are those in which the stimulus and movement goal overlap (i.e., 0° angle of rotation), whereas indirectly cued movements require a movement to be made towards a location other than the stimulus (i.e., rotation angle other than 0°). Typically, these indirectly cued movements incur a longer reaction time (RT) compared to directly cued movements (see Georgopoulos & Pellizzer, 1995 for a review; Neely & Heath, 2010), whereby RT increases as a function of increasing angle of rotation (Georgopoulos & Massey, 1987), although a non-linear increase in RT has been demonstrated with the addition of perceptually familiar angles (Neely & Heath, 2010).

Two major hypotheses have been forwarded to account for the increase in RT seen in indirectly vs. directly cued movements: a mental rotation model, and a response substitution hypothesis. Georgopoulos & Massey (1987) proposed a mental rotation model (MRM) that posits that during indirectly cued movements, participants mentally rotate a movement vector from its starting position (i.e., a movement directed to the visual cue) through increasing angular degrees until the movement goal is obtained (see Georgopoulos & Pellizzer, 1995 for a review). Although not explicitly stated, the process of rotating the movement vector from its initial stimulus position to the new movement goal location would presumably require inhibition of intermediate angles as the movement vector rotates. In contrast to the MRM, Cisek and Scott (1999) proposed the response substitution hypothesis (RSH), suggesting that during indirectly cued movements, the initial motor activity related to the visual location of the stimulus (i.e., a directly cued response) must be inhibited, and replaced with motor activity related to the rotated movement goal in order for the movement to be initiated as required. Thus, RT differences between direct and indirectly cued movements result from the initial inhibition and the additional cognitive transformation that must occur

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prior to initiation of the indirectly cued motor response. Although these models differ with respect to their specific explanations of the processes underlying a VMR, they both suggest additional inhibitory processes may be required during indirectly cued movements compared to directly cued movements. Specifically, prior to initiation of an indirectly cued movement, inhibition of unwanted movements occurs to prevent an incorrect response being initiated to either the visual cue or to a location between the visual cue and the new rotated movement goal.

While inhibitory activation is associated with the processes involved in indirectly cued movements, it is unknown how this inhibition affects motor preparatory neural activity during the RT interval of a VMR task. Thus, the purpose of the present study was to investigate the time course of motor preparatory activation during a VMR task. Specifically, we asked whether direct and indirectly cued movements involve differential levels of preparatory activation prior to response initiation. Previous research has shown that response preparation can be probed by presenting a loud (>120 dB) startling acoustic stimulus (SAS) during the motor preparatory phase of a RT task (see Carlsen, Maslovat, & Franks, 2012 for a review). Presenting a SAS not only results in a typical reflexive startle response (Brown et al., 1991; Landis, Hunt, & Strauss, 1939), but also results in the early and involuntarily initiation of the planned voluntary movement (termed a StartReact response). It has been argued that because of the extremely short onset latencies observed in SAS trials (<80 ms from SAS onset), it is unlikely that StartReact responses are mediated by typical cortical initiation pathways (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004; Valls-Solé, Rothwell, Goulart, Cossu, & Muñoz, 1999; Valls-Solé et al., 1995). However, a response must be sufficiently "prepared" for it to be susceptible to SAS triggering (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004). Thus the "susceptibility" of a response to SAS triggering may not only reflect preparatory activation related to excitation of the motor system, but a lowered incidence of response triggering could also be indicative of the presence of inhibition on the motor system.

In typical VMR RT tasks, the onset of the target location coincides with the go-signal, and thus processes related to preparation and initiation of the action must occur during the RT interval. In contrast, in the present study, participants performed a VMR task within the context of a simple RT paradigm in which the visual cue was presented prior to the go-signal (imperative stimulus [IS]). Thus, motor preparatory processes for direct and indirectly cued movements could be performed *in advance of* the IS. A SAS was then used to examine differences in preparatory activation between direct and indirectly cued movements at various time points prior to movement initiation, by examining the susceptibility of direct and indirectly cued movements to early movement triggering. It was hypothesized that a reduction in the observed proportion of StartReact responses would be observed for indirectly cued movements compared to directly cued movements at various time points prior to the go-signal if RT increases typically observed in VMR tasks is in part due to increased inhibition of the motor system. Secondarily, it was hypothesized that this inhibition might be mitigated if the trials were presented in a blocked vs. random trial order, as completing all trials of a particular angular rotation consecutively may allow for an increased amount of preparation and reduced inhibition due to reduced uncertainty between trials. In contrast, completing a different angular rotation every trial may cause a decrease in preparation activation and increased inhibition due to increased uncertainty between trials.

Methods

Participants

Fourteen right-handed participants (5 males, 9 females; age 21.8 ± 2.2 years) completed a VMR task with a random presentation order of mental rotation (MR) angles (Experiment 1 - RND). Eleven right-handed participants (6 males, 5 females; age 23.6 ± 2.6 years) completed the same VMR task where MR angles were presented in a blocked fashion (Experiment 2 - BLK). All participants had normal or corrected to normal vision, and no history of neurological, sensory, or motor disorders. Testing of each participant took place in a single testing session, and took approximately 1.5 hours to complete. All participants provided informed consent, and the study was conducted in accordance with ethical guidelines approved by the University of Ottawa's Research Ethics Board. Data from three participants in Experiment 1 and one participant in Experiment 2 were not included in the analyses described below due to the absence of a reliable startle response (see Data reduction section for details). Therefore, the final analyses for Experiment 1 were based on data from eleven participants (5 males, 6 females; age 22.0 ± 2.3 years) and Experiment 2 were based on data from 10 participants (5 males, 5 females; age 23.8 ± 2.7 years).

Experimental Set-up

Participants sat facing a computer monitor with a circular aperture placed over the monitor in order to eliminate orientation cues related to the cardinal axes (Coppola, White, Fitzpatrick, & Purves, 1998). The participant's right forearm was semi-prone and placed in a custom made brace, such that their wrist and hand hung over the edge of the brace (see Figure 1A). The forearm was secured using Velcro straps placed around the proximal and distal ends of the radius and ulna, allowing for forearm pronation and supination. The shoulder was abducted approximately 15˚ and the elbow was flexed in a comfortable position at approximately 70˚ to allow for an

optimal balance between agonist and antagonist maximal voluntary electrical activity (O'Sullivan & Gallwey, 2002). Vision of the distal arm and hand was obstructed. Participants grasped a handle (120 mm long x 25 mm in diameter) with their right hand which could be rotated in the coronal plane via pronation/supination of the forearm (see Figure 1A).

The task for participants was to rotate the handle using a supination movement to point to "movement goal" targets. The axis of rotation of the handle corresponded to the center of a circle displayed on the monitor and participants used the upper end of the handle to point to the goal location (Figure 1B) (for details pertaining to the visual display and trials see the Visual Stimuli & Trials sections respectively). For example, when the handle was parallel to the floor with the forearm pronated, it pointed at the 9 o'clock position, and when the forearm was supinated such that the handle was perpendicular to the floor, it pointed at the 12 o'clock position.

Visual Stimuli

The visual stimuli displayed to participants are shown in Figure 1B and were generated using a custom written LabVIEW (National Instruments Inc.) program. On the computer monitor a black circle was displayed (diameter = 185 mm, surrounded by a 20 mm wide circular border). In the center of the circle was a circular IS (go-signal; diameter = 90 mm), which turned from black to green (shown as grey in Figure 1) after a variable foreperiod ranging from 1650 – 2350 ms following visual cue onset.

At the start of each trial, the hand (and handle) was oriented parallel to the floor such that the forearm was pronated with the palm down (i.e., 9 o'clock position). This was indicated by a small green dot (diameter = 8 mm) appearing in the border of the circle on the far left (shown in Figure 1B, Time 1 as a grey dot). Once this home position was maintained for 2000 ms, the dot disappeared and an instructed "mental rotation angle" appeared above the IS (Figure 1B, Time 2). The visual cue (white circle with diameter = 10 mm) appeared inside the circular border of the display 2000 ms after the MR angle was presented (Figure 1B, Time 3). Participants were instructed to make a movement that corresponded to a location that deviated by the mental rotation (MR) angle in the clockwise direction from the visual cue (i.e., the "movement goal"), once the IS turned green (shown as grey in Figure 1B, Time 4). Participants were instructed to initiate the required supination movement as quickly and as accurately as possible. The IS (i.e., go-signal) was randomly presented between 1650 ms and 2350 ms following visual cue onset, so that it would not be anticipated.

Trials

A schematic representation of each of the four MR angles, including the locations of the visual cues and corresponding movement goals is shown in Figure 1C. In (i), the MR angle is 0°, thus these trials were directly cued trials in which the location of the visual cues (solid white circles) and movement goal targets (dotted white circles) overlapped. Additional MR angles included (ii) 60°, (iii) 90°, and (iv) 120°. As illustrated in Figure 1C, the movement goals remained consistent at 50° (position a), 40° (position b), and 30° (position c) of arm supination in the clockwise direction from the start position for all MR angles. These movement goals were chosen such that movement end-point occurred between the starting position (0°) and approximate maximal supination ($\simeq$ 110°).

Participants completed a brief practice session involving 3 randomized trials for each MR angle (total of 12 trials). Feedback, including RT and movement accuracy with respect to the required target, was displayed on the computer monitor after each practice trial. However, only RT feedback was provided in the testing trials. No feedback regarding movement accuracy was provided during testing trials in order to mitigate the possibility of participants simply memorizing the movement goal locations.

Experiment 1 (RND)

Following the practice trials, participants performed 300 testing trials (5 blocks of 60 testing trials). Within each testing block, 48 control trials were completed such that all 12 combinations of MR angle and movement goal were presented four times each in a randomized fashion (see Figure 1C). As well, in each block 12 additional test trials were performed in which the SAS was presented. The SAS (1000 Hz, 40 ms) was generated by a custom LabVIEW (National Instruments Inc.) program, and was amplified and presented via a loudspeaker (M54-H, MG Electronics, Inc.) placed 50 cm behind the head of the participant. SAS intensity was calibrated to 124 dB using a precision sound level meter (Casella-254, A-weighted scale, impulse setting), located at a distance corresponding to the location of participants' ears. The SAS was presented pseudo-randomly such that the SAS never occurred on 2 consecutive trials. Participants were instructed that the SAS tone was irrelevant to the task and could be ignored. The SAS was only presented on trials in which the movement goal was 40° in order to limit the number of SAS exposures experienced by participants, and to control for movement distance when comparing across MR angles. Moreover, the SAS was delivered once in each block at 500 ms, 1000 ms or 1500 ms following visual cue onset (i.e., -1150 ms, -650 ms or -150 ms with respect to the earliest possible go-signal; times based on previous studies; Carlsen &

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MacKinnon, 2010), for each MR angle. In order to limit fatigue, rest periods were given between blocks.

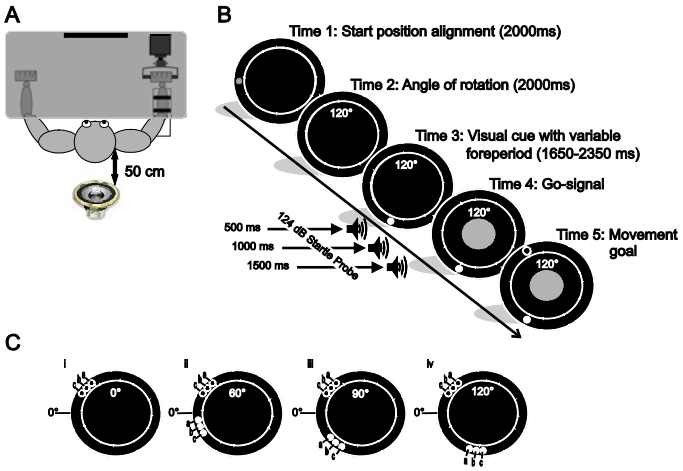

Figure 1. Overview of experimental set-up. A. Schematic illustration of participant position. Participants sat facing the monitor with no vision of their right arm. The speaker that delivered the SAS was located 50 cm behind the participants' ears. Participants started each trial with their right hand pronated (0°). Movement goals were located at 30°, 40°, and 50° of forearm supination. The movement was completed by the right hand while gripping a handle (120 mm long x 25 mm diameter). B. Temporal schematic of the visual stimuli displayed within a trial. In this trial the visual cue was to be mentally rotated 120°, such that the participant was to move to a movement goal corresponding to 50° of forearm supination (as shown by the dashed circle at Time 5).* note that due to the grey scale format green elements are shown as grey in B (see Materials and Methods section for clarification). C. Schematic illustration representing the four instructed angles of rotation and their corresponding visual cues and movement goal locations (i: 0°, ii: 60°, iii: 90°, iv: 120°). Solid white circles represent the three possible visual cue locations. Dotted white circles represent the three corresponding movement goals at 30° (position c), 40° (position b) and 50° (position a) of forearm supination from the starting position of the hand. Visual cue (a) corresponds with movement goal (a), visual cue (b) corresponds with movement goal (b), and visual cue (c) corresponds with movement goal (c). Note that the startling acoustic stimulus (SAS trials) was only delivered on trials in which the movement goal was 40° (i.e., movement goal [b]).

Experiment 2 (BLK)

Participants in the BLK experiment completed 4 blocks of 75 testing trials where in each block, only one of the four instructed MR angles described above was presented. Blocks were randomly ordered and the movement goal location was randomized within each block such that there were 20 control trials to each movement goal (a, b, c; see Figure 1C). In addition 15 SAS trials were presented in each block with 5 SAS trials at each of the three SAS presentation times outlined above. The SAS was presented pseudo-randomly such that the SAS never occurred on 2 consecutive trials and only occurred on trials in which the movement goal was 40°. In order to limit fatigue, rest periods were given between blocks.

Recording Equipment

Surface electromyographic (EMG) data were collected from the muscle bellies of the right biceps brachii (BB, agonist), right pronator teres (PT, antagonist), and left sternocleidomastoid (SCM, startle indicator), using bipolar pre-amplified (gain=10) surface electrodes (Delsys Bagnoli DE-2.1) connected via shielded cabling to an external amplifier system (Delsys Bagnoli-8). The EMG recording sites were prepared and cleansed in order to decrease electrical impedance. The electrodes were placed such that they were oriented parallel to the muscle fibers and then attached to the skin using double sided adhesive strips. A reference electrode was placed on the participant's left lateral epicondyle.

For all experiments forearm angular position data were collected using a potentiometer connected to the central axis of the handle. On each trial, data collection was initiated by the computer 3000 ms prior to the IS on all trials. Unfiltered EMG and position data were digitally sampled at 1 kHz (National Instruments PCI-6030E) for 4000 ms using a customized program written in LabVIEW (National Instruments Inc.) and stored for offline analysis.

Data Reduction

Movement onset was defined as the first point in time at which angular displacement was greater than 0.2° from the home position location following the IS or SAS. Actual "final position" corresponded to the angular position of the handle with respect to the home position at the first time point at which angular velocity fell below 8°/s and then remained below 8°/s for at least 150 ms. Any secondary corrections after the first endpoint were ignored. Movement time was defined as the time from movement onset to the time that final position was achieved. Peak displacement and peak velocity were defined as the greatest angular displacement and velocity achieved during the movement respectively.

EMG data from all muscles measured were analyzed for timing of burst onsets and offsets as well as EMG amplitude. Signals were rectified and filtered using a 25Hz low pass elliptic filter, and displayed on a computer monitor using a custom written LabVIEW (National Instruments Inc.) program. EMG burst onsets were defined as the point in time at which the rectified and filtered EMG activity first reached a value 2 standard deviations above baseline levels (i.e., mean EMG activity in a 100 ms interval starting 500 ms prior to the IS). Similarly, EMG burst offset was defined as the point in time where EMG activity first fell below 20% of peak burst amplitude, with the activity between EMG onset and EMG offset defined as a distinct burst. EMG markers were manually adjusted if

necessary to compensate for any errors due to the strictness of the LabVIEW algorithm. EMG activity in the SCM, as well as movement related EMG activity from two distinct bursts in the biceps (agonist 1 and agonist 2) and one burst in the pronator teres (antagonist) were marked for each trial (e.g, triphasic EMG pattern, see Wadman, Denier Van der Gon, Geuze, & Mol, 1979). Peak EMG amplitudes were defined as the largest EMG amplitude recorded within an interval of 100 ms following EMG burst onset. Premotor RT during control trials was calculated as the time between the IS and agonist 1 onset.

A StartReact response was deemed to have occurred if a) the participant showed startle related SCM activation following the SAS, and b) the intended movement was initiated (i.e., premotor RT) within 250 ms of the SAS (Carlsen & MacKinnon, 2010). For 4 participants SCM activation was not observed in 60% or more of the trials in which the SAS was presented at the longest latency following visual cued onset, thus data from these "low responders" were excluded from the analyses (see Brown et al., 1991).

Statistical Analysis

Dependent variables were analyzed using Repeated Measures Analysis of Variance (RM ANOVA) to determine whether differences existed between control and SAS trials, between different presentation times of the SAS (i.e., 500, 1000 or 1500 ms following visual cue onset), and between different MR angles (i.e., 0°, 60°, 90° or 120°). For comparisons between control and SAS trials, only control trials with a movement goal of 40° were used since the SAS was only presented on trials in which the movement goal was 40° (see Trials section above). Performance on control trials were analyzed between MR angles and all movement goal locations (i.e., 30°, 40° or 50°). Prior to statistical analysis, proportion values were subjected to an arcsine square root transformation (Osborne, 2010). In cases where sphericity was violated, Greenhouse-Geisser corrected *p*-values are reported. Differences with a probability of less than 0.05 were considered significant and Tukey's Honestly Significant Difference (HSD) post-hoc tests were administered to determine the locus of any significant differences.

Preliminary Control Experiments

VMR RT Experiment

The RND and BLK VMR Experiments required the use of a handle to point to "virtual" targets corresponding to a location seen on a computer screen - as opposed to traditional VMR tasks where participants commonly point directly to the movement goal (e.g., Georgopoulos & Massey, 1987; Neely & Heath, 2010). Thus a control experiment was conducted in order to determine whether the apparatus and task used in Experiments 1 and 2 could be used to replicate the previous VMR RT results whereby larger MR angles lead to increases in RT when a preparation interval is not provided.

For the VMR RT Experiment, eight naïve participants (6 M, 2 F; age 21.9 ± 2.6 years) were recruited and provided informed consent. Using the same experimental set-up and stimulus display as described above, participants performed a more traditional VMR RT experiment (see Neely and Heath (2010)). Specifically, the testing session began with participants being instructed that they were to move to a location that deviated in a clockwise direction from the visual cue provided by the instructed MR angle. Furthermore, participants were instructed to make a quick and accurate movement to this movement goal location as soon as possible following appearance of the visual cue (i.e., visual cue onset served as the IS). In addition, a pictorial representation (i.e., line drawing) of the MR angle was provided on the stimulus display prior to cue onset (zero was defined as the same position as the home position, with angles drawn clockwise from zero). Participants were also provided with vision of their hand prior to each block of trials, allowing them to re-orient themselves with the home position as well as 90° of supination.

Participants performed 60 RT trials for each MR angle (0°, 60°, 90°, and 120°) in a blocked fashion (i.e., only one MR angle of rotation was presented in each block of trials), with ten trials completed to each of 6 different movement goals (30°, 40°, 50°, 60°, 70°, and 80° clockwise from the home position). Block order was counterbalanced across participants and the presentation of the visual cue location and hence movement goal was randomized within each block of trials. Prior to the testing session all participants completed a brief practice session involving six randomized trials for each angle of rotation (total of 24 trials). Participants began with their hand at the home position (9 o'clock). Once the position was achieved and held for 2000 ms the MR angle appeared in the center of the circular display. After a variable foreperiod (1000 – 2000 ms) the visual cue appeared which served as the IS for movement initiation. Feedback regarding accuracy, RT, and limb position was not provided during the testing session.

Similar to Neely & Heath (2010), movement onset (i.e., displacement RT) was analyzed between MR angles (0°, 60°, 90°, and 120°) using a one-way RM ANOVA. The analysis of RT revealed a significant main effect for angle of rotation, $F(3,21) = 9.795$, $p = 0.004$, $\eta^2p = 0.583$. Similar to previous VMR tasks, post-hoc analysis indicated that RT for directly cued movements (0° [M = 355.6 ms, SD = 57.5]) was significantly ($p < 0.05$) faster than all indirectly cued movements (60° [M = 449.1 ms, SD = 126.5]; 90° [M = 476.5 ms, SD = 144.4]; 120° [M = 475.4 ms, SD = 121.9]). Furthermore, there was a significant linear trend

towards increased RT with increasing MR angle (p = 0.005). Even though there were no differences in RTs for the indirect targets, these results indicate that our experimental set-up is suitable for investigating differences between direct and indirectly cued movements.

Non-VMR Startle Experiment

In order to determine whether presenting a SAS would lead to the early release of the prepared movement using the apparatus and task used in Experiments 1 and 2, a non-VMR startle experiment was conducted. We hypothesized that the stimulus-driven, directly cued movement (0° angle of rotation) used in the current experiment, is no different than the stimulus-driven, directly cued movements used in previous startle studies, and thus the presentation of a SAS would result in a similarly high proportion of StartReact responses as previously observed (e.g., Carlsen & MacKinnon, 2010).

Eight naïve participants (4 M, 4 F; age 26.0 ± 6.9 years) took part in the non-VMR Startle Experiment after providing informed consent. The experiment used the same experimental set-up, stimulus display, trial sequence, and SAS procedure as described for Experiment 2 (BLK), except that all participants performed only a single block of directly cued movements. Specifically, following 12 directly cued practice trials, 75 directly cued testing trials were performed, in which 20 control trials were directed at each movement goal (a, b, c; see Figure 1C) and 15 SAS trials were pseudo-randomly presented in each block with 5 SAS trials at each of the three SAS presentation times with a 40° movement goal.

In order to confirm that presenting the SAS led to the early release of the prepared movement, a paired sample t-test was conducted to compare premotor RT during control trials and trials when a SAS was delivered 1500 ms following visual cue onset. A significant difference in premotor RT was observed, $t(7)=19.146$, $p<0.001$, such that StartReact trials had significantly shorter RTs (M = 88.3 ms, SD = 15.4) than control trials (M = 161.1 ms, SD = 17.2).

Similar to Carlsen and MacKinnon (2010) a high proportion of startle responses were detected across all SAS time points (500 [M =0.84]; 1000 [M =0.93]; 1500 [M =0.97]) and an increasing incidence of StartReact responses was observed as the SAS was presented at a longer latency following the cue onset (500 [M =0.4]; 1000 [M =0.62] ; 1500 [M =0.91]). Given the similar high proportion of startle and StartReact responses observed in the current study as previous studies when performing directly cued movements, we were confident that the experimental set-up and paradigm used here was suitable for investigating preparatory activation differences between direct and indirectly cued movements in a VMR task using startle.

Results: Experiments 1 and 2

Task Performance: Control Trials

Experiment 1 (RND)

Final positions achieved during control trials were analyzed using a 3 movement goal (30°, 40°, vs. 50°) x 4 MR angle (0°, 60°, 90°, vs. 120°) RM ANOVA. Analysis revealed a significant main effect for movement goal, $F(2,20) = 66.81$, $p < 0.001$, $\eta^2p = 0.870$, as well as MR angle, $F(3,30) = 9.704$, $p < 0.001$, $\eta^2p = 0.492$. Post-hoc analysis confirmed the expected finding that mean final position achieved was significantly different between movement goals: 30° (M = 27.1°, SD = 6.5), 40° (M = 29.1°, SD = 6.7), 50° (M = 31.1°, SD = 7.1). Furthermore, the final position attained (collapsed across targets) was significantly larger for the 120° MR angle (M = 32.7°, SD = 8.8) compared to 0° (M = 27.2°, SD = 6.1), 60° (M = 27.5°, SD = 6.8) and 90° (M = 29.0°, SD = 6.5). These main effects were superseded by a significant interaction between the factors, $F(6,60) = 6.780$, $p < 0.001$, η^2p = 0.404, whereby final position attained was only significantly different between the 30° and 50° movement goals for the 0° MR angle. However, a significant linear trend ($p< 0.001$) indicates that there was a relative increase in final position achieved at greater movement goal targets angles for each MR angle.

Experiment 2 (BLK)

Similar to Experiment 1 (RND), participants also completed their movements such that they moved to a greater distance with greater movement goal target angles. Analysis revealed a significant main effect for movement goal, $F(2,18) = 60.395$, $p < 0.001$, $\eta^2p = 0.870$, no main effect for MR angle, $F(3,27) = 2.175$, $p = 0.114$, η^2p = 0.195, and a significant interaction, $F(6,54) = 2.342$, p = 0.044, $\eta^2p = 0.206$. Post-hoc analysis of the interaction indicated that the final position achieved for each MR angle did not differ between the three movement goals. However, similar to Experiment 1 (RND) it appears that participants were moving to different positions for the different movement goals overall. Post-hoc analysis indicated that the final position achieved for each target goal was significantly different (30° [M = 31.2°, SD = 6.1]; 40° [M = 33.9°, SD = 5.3]; 50° [M = 36.7°, SD = 5.2]), with a significant linear trend such that movement endpoint increased with increasing target eccentricity ($p < 0.001$).

Proportions of Startle and StartReact Responses

Experiment 1 (RND)

Analysis of the proportion of startle responses observed revealed no significant main effects of SAS presentation

time, $F(2,30) = 0.725$, $p = 0.497$, $\eta^2p = 0.063$, or MR angle, $F(3,30) = 2.65$, $p = 0.067$, $\eta^2p = 0.209$, indicating that participants were consistently and reliably startled on the majority of trials (81% ±11), irrespective of these factors (Figure 2, black line). Analysis of the proportion of SAS trials in which a StartReact response was deemed to have occurred revealed a significant main effect of SAS presentation time, $F(2,20) = 11.793$, $p<0.001$, $\eta^2p = 0.541$. Post-hoc analysis indicated that the proportion of early StartReact responses was significantly greater ($p < 0.05$) when the SAS was presented at 1500 ms following visual cue onset ($M = 0.39$, SD = 0.34) compared to when the SAS was presented either at 500 ms ($M = 0.21$, SD = 0.29) or 1000 ms ($M = 0.29$, SD = 0.36) following visual cue onset (Figure 3, black line). No main effect of MR angle, $F(3,30) = 1.803$, $p = 0.136$, $\eta^2p = 0.153$, or interaction between the factors was found, $F(6,60) = 0.618$, $p = 0.715$, $\eta^2p = 0.058$.

Experiment 2 (BLK)

Analysis of the proportion of startle responses observed revealed no significant main effect for SAS presentation time (Figure 2, dashed grey line), $F(2,18) = 0.107$, $p = 0.899$, $\eta^2p = 0.0121$and no significant interaction between the factors, $F(6,54) = 0.949$, $p = 0.469$, $\eta^2p = 0.095$. A significant main effect for MR angle, $F(3,27) = 3.146$, $p = 0.041$, $\eta^2p = 0.290$ was found, but post-hoc analysis did not reveal the locus of the differences (p's > 0.05) (0° [$M = 0.74$, SD = 0.29]; 60° [$M = 0.84$, SD = 0.26]; 90° [$M = 0.87$, SD = 0.24]; 120° [$M = 0.73$°, SD = 0.3]).

Similar to Experiment 1 (RND), analysis of the proportion of StartReact responses observed in SAS trials revealed a significant main effect of SAS presentation time, $F(2,18) = 10.001$, $p = 0.001$, $\eta^2p = 0.526$, but no main effect of MR angle, $F(3,27) = 2.885$, $p = 0.054$, $\eta^2p = 0.243$, and no interaction between the factors, $F(6,54) = 0.531$, $p = 0.782$, $\eta^2p = 0.056$. Post-hoc analysis indicated that the proportion of StartReact responses noted was significantly greater when the SAS was presented at 1500 ms following visual cue onset ($M = 0.50$, SD = 0.07) than when the SAS was presented either at 500 ms ($M = 0.22$, SD = 0.04) or 1000 ms ($M = 0.32$, SD = 0.05) following visual cue onset ($p < 0.05$) (Figure 3, dashed grey line).

Experiment 1 vs. Experiment 2

To compare the effect of a random trial order vs. a blocked trial order on the proportion of startle responses and StartReact responses during the VMR task, a 2 (Experiment: RND vs. BLK) x 3 (SAS presentation time: 500 ms, 1000 ms and 1500 ms) mixed model RM ANOVA with repeated measures on the second factor was performed. Given that no effects of MR angle on the proportion of startle or StartReact responses were observed for either experiment, data was collapsed across MR angle for this analysis. Analysis of the proportion of startle responses observed showed no significant main effect for either SAS time, $F(2,38) = 0.431$, $p = 0.653$, $\eta^2p = 0.022$, or Experiment, $F(1,19) = 0.009$, $p = 0.923$, $\eta^2p = 0.935$, and there was no significant interaction between the factors, $F(2,38) = 0.203$, $p = 0.818$, $\eta^2p = 0.011$ (Figure 2).

Analysis of the proportion of StartReact responses observed revealed a significant main effect for SAS presentation time, $F(2,38) = 19.343$, $p < 0.001$, $\eta^2p = 0.504$, but no significant main effect for Experiment, $F(1,19) = 0.146$, $p = 0.707$, $\eta^2p = 0.008$, and there was no significant interaction, $F(2,38) = 1.684$, $p = 0.199$, $\eta^2p = 0.081$ (Figure 3, black vs. dashed grey lines). Post-hoc analysis indicated that the proportion of StartReact responses observed were significantly ($p < 0.05$) different across all three SAS time points (500 ms: 21.6%, 1000 ms: 30.6%, 1500 ms: 44.2%). This was further confirmed by a significant linear trend ($p <0.001$) observed for SAS time whereby the proportion of StartReact responses increased with increasing time following visual cue onset (i.e., as the go-signal approached).

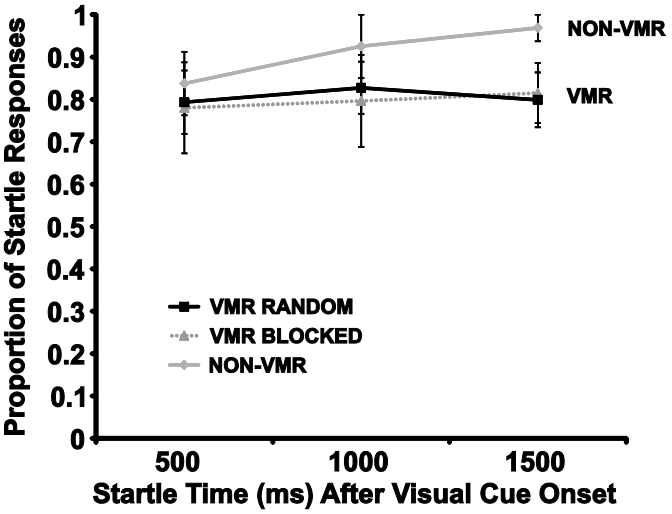

Figure 2. Mean (± 1 SE) proportion of startle responses elicited by the SAS as a function of the time of SAS presentation following visual cue onset (500, 1000 or 1500 ms) for VMR Experiment 1 (Random; solid black/square), Experiment 2 (Blocked; dashed grey/triangle) & Non-VMR Startle Experiment (solid grey/diamond).

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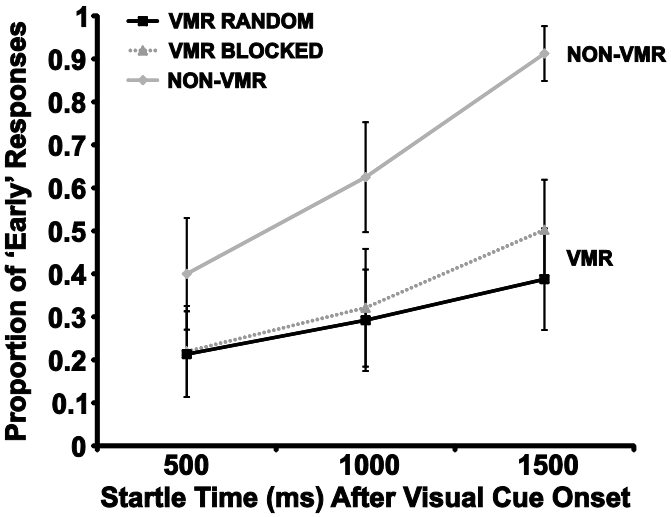

Figure 3. Mean (± 1 SE) proportion of 'early' responses (i.e., StartReact responses) elicited by the SAS as a function of the time of SAS presentation following visual cue onset (500, 1000 or 1500 ms) for VMR Experiment 1 (Random; solid black/square), Experiment 2 (Blocked; dashed grey/triangle) & Non-VMR Startle Experiment (solid grey/diamond).

Effect of SAS on Premotor RT and Final Position

Experiment 1 (RND)

Given the limited number of trials with a StartReact response when the SAS was presented at 500 ms and 1000 ms (Figure 3), premotor RT and final positions were only compared for trials in which the SAS was presented 1500 ms following visual cue onset using a 2 stimulus (Control vs. SAS @ 1500) x 4 MR angle (0°, 60°, 90°, vs. 120°) RM ANOVA. However, a StartReact response was still observed in fewer than 40% of SAS trials even at the 1500 ms SAS presentation time; therefore, in order to perform a factorial analysis, values for missing cells were filled using a linear regression-based multiple imputation procedure in SPSS (IBM Inc.) (imputed values per analysis = 9/36). Data from two participants were not included in these analyses (and values could not be imputed) because no StartReact responses were observed for any of the MR angles at the 1500 ms time point.

Analysis of premotor RT showed a significant main effect for stimulus, $F(1,8) = 117.798$, $p < 0.001$, $\eta^2p = 0.936$, whereby EMG onset occurred earlier during the SAS trials ($M = 88.1$ ms, SD = 21.9) compared to control trials ($M = 173.0$ ms, SD = 24.2) (Figure 4, black). There was also a significant main effect for MR angle, $F(3,24) = 3.020$, $p = 0.049$, $\eta^2p = 0.274$, and a significant interaction, $F(3,24) = 4.180$, $p = 0.016$, $\eta^2p = 0.343$. Post-hoc analysis of the interaction revealed that not only were all startle trials initiated faster than control trials, but startle trial premotor RT was significantly faster for the 0° vs. the 90° and 120° MR angles. Analysis of final position achieved revealed no significant main effect for either stimulus, $F(1,8) = 1.314$, $p = 0.285$, $\eta^2p = 0.141$, or MR angle, $F(3,24) = 2.791$, $p = 0.062$, $\eta^2p = 0.259$, and there was no significant interaction between the factors, $F(3,27) = 1.217$, $p = 0.325$, $\eta^2p = 0.132$.

Experiment 2 (BLK)

Similar to Experiment 1 (RND), premotor RT and final position achieved on StartReact trials were analyzed using a 2 stimulus (Control vs. SAS @ 1500 ms) x 4 MR angle (0°, 60°, 90°, vs. 120°) RM ANOVA, with missing values filled imputed (imputed values per analysis = 6/40) using the same imputation procedure described in Experiment 1 (RND). Analysis of premotor RT revealed a significant main effect of stimulus, $F(1,19) = 66.253$, $p < 0.001$, $\eta^2p = 0.880$, such that EMG onset with respect to either the SAS or go-signal occurred earlier during the SAS trials ($M = 101.2$ ms, SD = 23.4) compared to control trials ($M = 160.5$ ms, SD = 23.1) respectively (Figure 4, light grey). Moreover, there was no significant main effect for MR angle, $F(3,27) = 0.245$, $p = 0.864$, $\eta^2p = 0.027$, and no significant interaction, $F(3,27) = 0.497$, $p = 0.688$, $\eta^2p = 0.052$. Analysis of final position achieved revealed no significant main effects for either stimulus, $F(1,9) = 2.654$, $p = 0.138$, $\eta^2p = 0.228$, or MR angle, $F(3,27) = 0.895$, $p = 0.456$, $\eta^2p = 0.090$, and no significant interaction, $F(3,27) = 0.965$, $p = 0.423$, $\eta^2p = 0.097$.

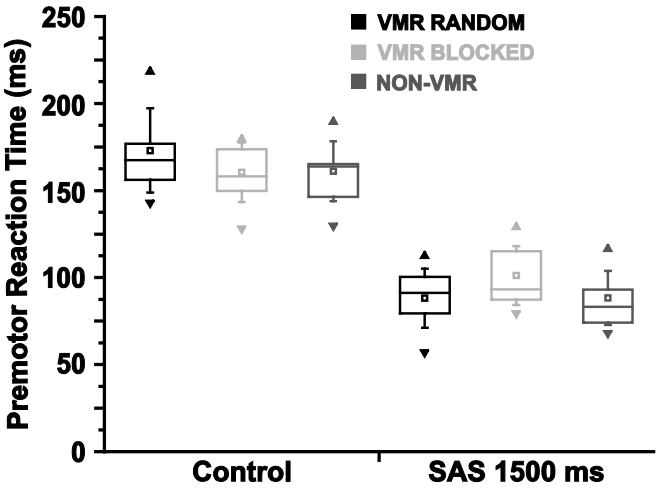

Figure 4. Box and whisker plots of premotor reaction time (ms) for control and StartReact response trials relative to either the control go-signal or the startling acoustic stimulus (SAS) presented at 1500 ms (following visual cue onset) for VMR Experiment 1 (Random; black), Experiment 2 (Blocked; light grey) & Non-VMR Startle Experiment (dark grey). For each data point, the small square indicates the mean, the horizontal line within the rectangular box indicates the median, boundaries of the rectangular box indicate the 25th- and 75th -percentile, the upward and downward pointing triangles indicate maximum and minimum values respectively and the whiskers indicate one standard deviation from the mean.

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Analysis of Experiment 2 (BLK) vs. Non-VMR Startle Experiment

From Figure 3 it appears that the proportion of StartReact responses differed when trials were presented in a VMR task compared to the Non-VMR Startle Experiment. To investigate the effect of task context on the preparation of directly cued movements, the proportion of startle responses and StartReact responses observed following the SAS were compared between the directly cued (i.e., 0°) condition from Experiment 2 (BLK) and the Non-VMR Startle Experiment using a 2 task context (VMR & non-VMR task) x 3 SAS time (500 ms, 1000 ms, 1500 ms) mixed model ANOVA with repeated measures on the second factor. Analysis of the proportion of startle responses revealed no significant main effect of time, $F(2,32) = 3.193$, $p = 0.054$, $\eta^2p = 0.166$, or group, $F(1,16) = 2.184$, $p = 0.159$, $\eta^2p = 0.120$, and there was no significant interaction between the factors, $F(2,32) = 0.027$, $p = 0.599$, $\eta^2p = 0.032$ (Figure 2, dashed-grey vs. grey lines). In contrast, analysis of the proportion of StartReact responses observed revealed a significant main effect of time, $F(2,32) = 17.592$, $p < 0.001$, $\eta^2p = 0.524$. Post-hoc analysis revealed that the incidence of StartReact responses was significantly different ($p < 0.05$) between all SAS time points, increasing with later startle times. Of greater note, there was a significant main effect of task context, $F(1,16) = 5.537$, $p = 0.032$, $\eta^2p = 0.257$, revealing that there was a higher incidence of StartReact responses in the non-VMR trial context (500 [M =0.4]; 1000 [M =0.62]; 1500 [M =0.91]) compared to the VMR context (500 [M =0.18]; 1000 [M =0.3]; 1500 [M =0.48], see Figure 3, dashed-grey vs. grey lines). There was no significant interaction between the factors, $F(2,32) = 0.815$, $p = 0.451$, $\eta^2p = 0.048$. The incidence of StartReact responses observed in the non-VMR context was comparable to that shown in previous studies (e.g., Carlsen & MacKinnon, 2010) suggesting that the low incidence of StartReact responses observed in Experiments 1 and 2 was not caused by the apparatus used, but was rather due to participants completing trials within the context of a VMR task that may or may not have required a mental transformation (i.e., indirectly cued movement).

Discussion

Previous VMR task studies have shown that indirectly cued movements, which require a rotational mental transformation between a target location and a movement goal location, take longer to initiate compared to movements that are completed directly to a visual cue (Georgopoulos & Massey, 1987; Georgopoulos & Pellizzer, 1995; Neely & Heath, 2010). Data from the Control VMR RT Experiment in the present study showed similar results, indicating that the trials that required a mental transformation resulted in longer RTs than directly cued trials. However, unlike typical VMR RT task paradigms, in Experiments 1 (RND) & 2 (BLK) participants were provided with the visual cue and mental rotation (MR) angle prior to the go-signal, allowing them to prepare the required movement in advance within a variable foreperiod RT paradigm. Startle was then used to probe the state of preparation at various time points prior to the go-signal. Performing the VMR task in this type of simple RT paradigm eliminated the differences in RT between MR angles, indicating that subjects had prepared the required response prior to the go-signal. On trials in which the SAS was presented, participants were reliably startled, however, the proportion of SAS trials resulting in the early release of the movement (StartReact responses) was lower than expected based on previous studies, whether the different VMR angles were presented randomly or in a blocked fashion.

Previous experiments have demonstrated that when participants know the required response in advance of a go-signal in a simple RT task, a loud 124 dB SAS can elicit not only a classic startle response (i.e., indicated by SCM activation), but can also trigger a prepared motor response at a latency too short to involve typical cortical initiation processes (see Carlsen, Maslovat, & Franks, 2012 for a review). Moreover, studies examining the time course of motor preparation for directly cued movements have shown that when the temporal predictability of response initiation is relatively low (e.g., in a variable foreperiod RT task), participants tend to prepare the voluntary response well in advance of the earliest possible go-signal (Cressman, Carlsen, Chua, & Franks, 2006); as such, prepared responses can be consistently elicited by a SAS even 1500 ms prior to the go-signal (Carlsen & MacKinnon, 2010). However, in both Experiment 1 (RND) and Experiment 2 (BLK) the proportion of StartReact responses elicited were comparatively low compared to previous studies (e.g., Carlsen & MacKinnon, 2010), irrespective of whether the movements were directly or indirectly cued (Figure 3). In fact, even at the latest SAS time point (1500 ms/ -150ms), when motor preparation would be expected to be highest (Carlsen & MacKinnon, 2010), the observed proportion of StartReact responses was low for both direct (43%) and indirectly (46%) cued movements. Specifically, as the SAS was presented at a longer latency after the visual cue onset (500 ms vs. 1000 ms vs. 1500 ms), or in other words, closer to the earliest possible go-signal (i.e., -1150 ms vs. -650 ms vs. -150 ms), the proportion of StartReact responses increased but remained relatively low across all SAS presentation times (500 ms: 22%, 1000 ms: 31%, 1500 ms: 44% collapsed across angles of rotation and trial order conditions). Interestingly however, similar to our previous findings (Drummond, Carlsen, & Cressman, 2013), there was no effect of MR angle on the incidence of StartReact responses, such that no difference was observed between directly cued movements (MR angle of 0°) or indirectly cued movements (MR angle of 60°, 90°, or 120°). These results suggest that at least some limited motor-related

preparatory activation was occurring soon after the presentation of the visual cue, but irrespective of movement type (direct or indirect) or MR presentation order (random or blocked), the level of advance preparation achieved remained low throughout the foreperiod interval in comparison to previous experiments in which participants only performed a single directly-cued movement (Carlsen & MacKinnon, 2010; Cressman, Carlsen, Chua, & Franks, 2006).

A low incidence of StartReact responses was observed despite a high proportion of SAS trials that resulted in an observed startle response in SCM (~80%, Figure 2), irrespective of experiment or whether it was a directly or indirectly cued movement. It has been previously shown that when participants are engaged in motor-specific preparatory processing, the startle response in SCM is resistant to habituation (Carlsen, Maslovat, & Franks, 2012). Thus, if there was little motor engagement by participants in the current tasks, the startle response would have been expected to habituate rapidly. As such, we suggest that the low proportion of SAS trials that resulted in StartReact responses was not due to a lack of engagement of motor preparatory processes. Rather, we propose that the StartReact results observed in Experiments 1 and 2 are a result of the motor system modulating the level of mean motor preparatory activation based on the overall task context, rather than simply based on the difficulty of individual movements themselves. This is evidenced by a significantly lower incidence of StartReact responses simply when the task was being performed in a VMR context (Experiments 1 & 2) as compared to a non-VMR context (Figure 3) - even though the same directly cued movement was performed within the same simple RT task. Thus, this seems to suggest that performing the same RT task within the context where a mental transformation will (eventually) be required is sufficient to lead to a dramatic decrease in the level of motor preparatory activation. One might consider this a “cautious” method of governing motor preparation, as processes associated with the modulation of preparation in indirectly cued trials are nevertheless also engaged during directly cued trials, simply due to the direct trials being embedded within the task context of having to perform indirectly cued trials.

Taken together, these findings demonstrate that added task context requirements of a VMR task (i.e., performing a mental rotation: indirectly cued movements) leads to a reduced level of advance preparatory activation in the motor system compared to a simpler task context (e.g., stimulus driven: directly cued movements only). Although the experiments presented in this study do not allow for the precise identification of the mechanism causing this reduction, we suggest that an inhibitory mechanism related to performing a VMR task is responsible for depressing motor-related preparatory activation.

Inhibition and VMR Task Processes

As outlined in the introduction, two major hypotheses (MRM & RSH) have been proposed to account for the observed increase in RT for indirectly vs. directly cued movements. Although they differ in their specific explanations, they both suggest that increased RT seen for indirectly cued movements is due to inhibition that is required to prevent an early incorrect response while additional processing related to the mental transformation occurs. This explanation is also in line with anti-saccade literature, which suggests that the increased latencies associated with indirectly cued eye movements are primarily due to oculomotor inhibition (Olk & Kingstone, 2003). It is important to note that this notion of motor inhibition is specific to indirectly cued movements. However, the differential incidence of StartReact responses observed for directly cued movements between VMR and non-VMR contexts in the current set of experiments suggests that inhibition may not just be specific to indirectly cued movements in a VMR task; rather it appears that an additional inhibitory mechanism was present for both direct *and* indirectly cued movements when trials were performed within a VMR context. Thus, for indirectly cued movements, in addition to cortically mediated vector-specific inhibition of the first stimulus-driven response, there is also inhibition of descending motor output prior to visual cue onset to prevent incorrect responses to the initial stimulus. For *directly cued* movements within a VMR task context, the present data suggests that similar inhibition of descending motor output is also present prior to visual cue onset (even though vector-specific inhibition is not required). This inhibition of the motor system may have acted on one or more structures involved in movement initiation leading to a decreased proportion of StartReact responses. Admittedly, the current data cannot definitively provide evidence regarding the locus and pathways of these inhibitory mechanisms, however, there may have been: 1) suppression at the reticular formation, or 2) suppression at the spinal level. Given the proportion of startle responses observed was similar to that seen in previous studies utilizing a startle response (elicited on 80% of SAS trials), which has a well-documented origin in the reticular formation (Koch, 1999; Yeomans & Frankland, 1996), the spinal level may be a more plausible locus of the inhibition.

The hypothesis that inhibition is occurring at the spinal level is consistent with a “priming and braking” model proposed by Cohen and colleagues (2010), which suggests that there are two parallel but functionally independent and opposing processes operating during movement preparation: 1) Increasing corticospinal excitability to prepare for rapid initiation, and 2) Inhibition of excitability acting at a spinal level in order to prevent premature responses. Effectively, in this scenario the excitatory command is cancelled by the inhibitory command during the preparatory period. Accordingly, the low but increasing amount of motor-related activation observed in VMR

Experiments 1 & 2 across the preparatory foreperiod may be the result of inhibitory activation being slowly released off the excitatory activation in anticipation of the go-signal. Therefore, we suggest that the drive from this inhibitory stream not only prevented premature voluntary release of the planned response, but also limited the ability of SAS to trigger the involuntary release of the planned response (StartReact effect) through a final output gating mechanism. When in the context of the VMR task it may be strategically viable to suppress any activation pertaining to a movement directly to the target location. Neural recordings from monkey M1 clearly demonstrate the automatic stimulus –driven motor activation related to the visual cue location in a VMR task (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989), with similar findings also observed in the anti-saccade literature (see Munoz & Everling, 2004 for a review). Thus, a more complex pattern of initiation and inhibition is likely necessary for performing movements within the context of a VMR task.

Conclusions

The present study investigated the motor-related activation during the preparatory period of a VMR task in a variable foreperiod simple RT paradigm. Performing the task in a simple RT paradigm eliminated response initiation differences between angles of rotation, thus allowing the exploration of potential differences in preparatory activation levels between direct and indirectly cued movements. Independent of mental rotation angle and presentation order (random vs. blocked), results showed a similar incidence of early response triggering by a SAS regardless of whether the movement was directly cued (0˚) or whether a mental rotation was required (indirectly cued: 60°, 90°, 120°). Notably, the absolute level of motor preparation achieved at each time point prior to the go-signal was relatively low in this VMR context compared to a Non-VMR condition (Figure 3). Together, these results suggest that when a stimulus-to-target-goal transformation may be required, a cortically-derived inhibitory signal depresses motor output, perhaps at a spinal level. This inhibitory activity not only prevents unwanted stimulus-driven responses in a VMR task, but also is able to have a profound gating effect on the response triggering effect of a startling acoustic stimulus.

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