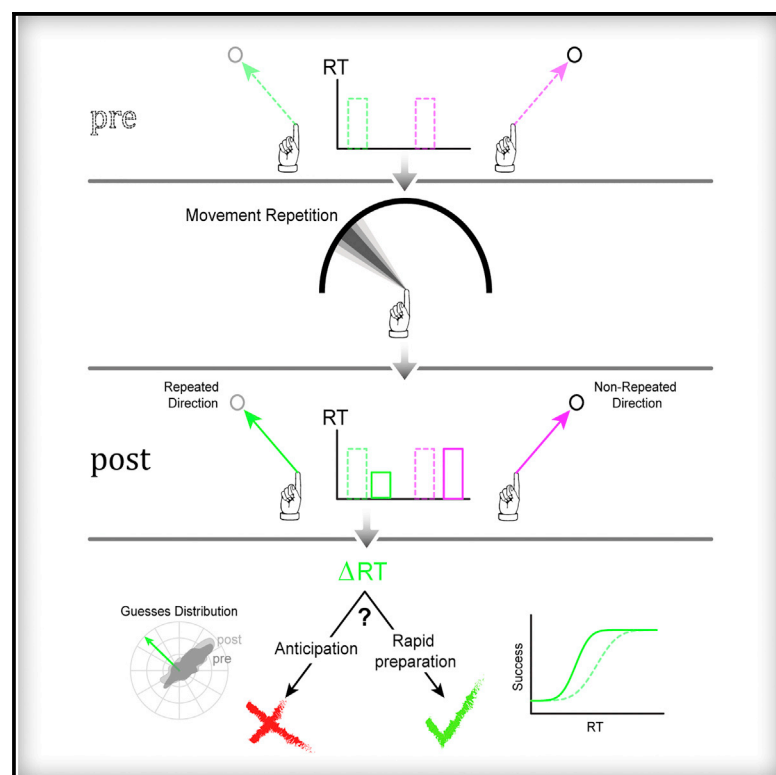


## Movement Repetition Facilitates Response Preparation

### Graphical Abstract



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### In Brief

Mawase et al. show that repeating a specific movement reduces reaction times for generating the same movement in the future. This effect is not attributable to anticipation of the required movement but instead is due to the ability to more rapidly select and prepare a previously repeated movement.

### Highlights

- Reaction times are reduced for movements that have been repeated in the recent past
- This effect is not attributable to anticipatory preparation of the repeated movement
- Instead, repetition enables the repeated movement to be prepared more rapidly
- We speculate that this effect relates to physiological changes caused by repetition



# Movement Repetition Facilitates Response Preparation

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## SUMMARY

Our sensorimotor system appears to be influenced by the recent history of our movements. Repeating movements toward a particular direction is known to have a dramatic effect on involuntary movements elicited by cortical stimulation—a phenomenon that has been termed use-dependent plasticity. However, analogous effects of repetition on behavior have proven elusive. Here, we show that movement repetition enhances the generation of similar movements in the future by reducing the time required to select and prepare the repeated movement. We further show that this reaction time advantage for repeated movements is attributable to more rapid, but still flexible, preparation of the repeated movement rather than anticipation and covert advance preparation of the previously repeated movement. Our findings demonstrate a powerful and beneficial effect of movement repetition on response preparation, which may represent a behavioral counterpart to use-dependent plasticity effects in primary motor cortex.

## INTRODUCTION

It is well established that our motor behavior is shaped not only by current sensory and environmental context but also by our recent history of experiences and actions (Wolpert and Kawato, 1998; Crammond and Kalaska, 2000; Körding and Wolpert, 2004; Pruszynski et al., 2011). Previous neurophysiological studies have shown that involuntary motor responses elicited by transcranial magnetic stimulation (TMS) over M1 tend to be biased toward movements that were previously repeated (Classen et al., 1998; Bütefisch et al., 2000). Similarly, intracortical microstimulation of primary motor cortex leads to use-dependent effects in macaques (Nudo et al., 1990).

At the behavioral level, there are well-documented effects of movement repetition on the kinematics of movement. For instance, repeating a particular movement biases future movements toward that direction (Diedrichsen et al., 2010;

Mawase et al., 2017) and speed (Hammerbeck et al., 2014). However, it is by no means clear whether these effects bear any relation to neurophysiological changes assessed with TMS (Bestmann and Krakauer, 2015). Indeed, it has been suggested that the effect of repetition on movement kinematics may largely reflect the influence of high-level expectations about where the target may appear (Verstynen and Sabes, 2011; Wong et al., 2017).

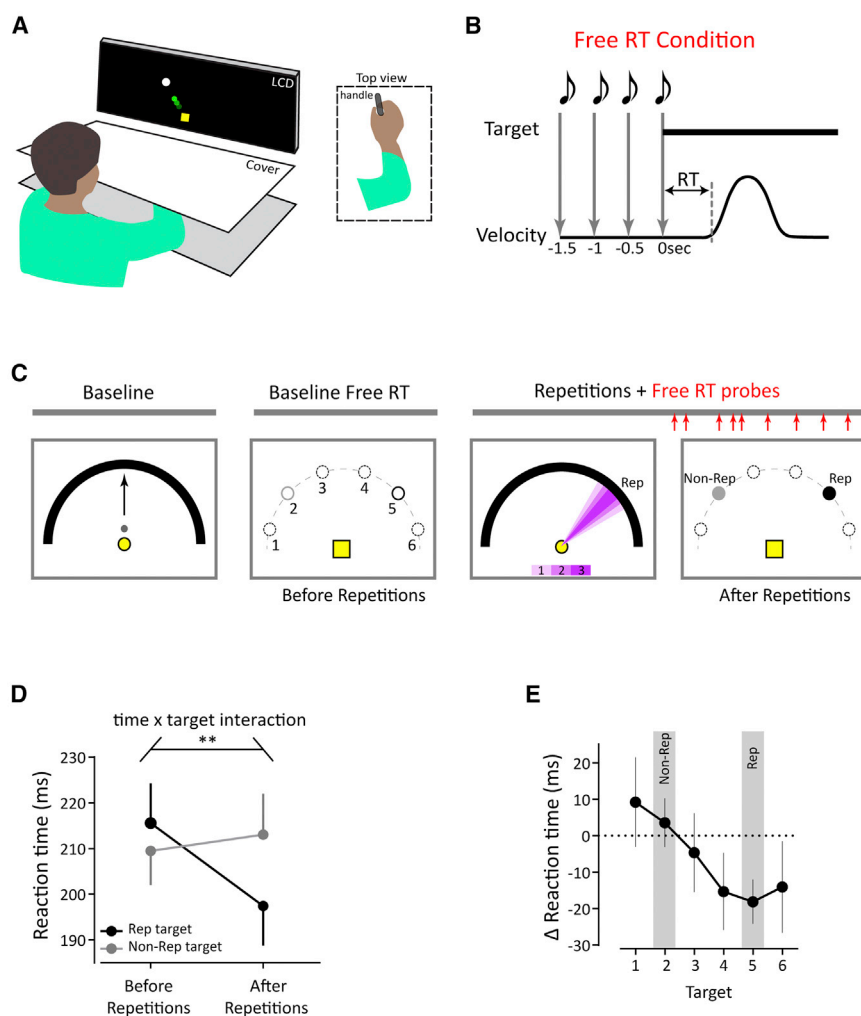
Repetition has also been found to lead to lower reaction times (RTs) (Hyman, 1953). It is unclear exactly how repetition causes this improvement. The most likely possibility seems to be that this effect is due to anticipation, in the same way that pre-cuing the required movement before a “GO” cue reduces RT. Participants might, following repetition, begin to prepare the repeated movement by default, in accordance with their expectations about which movement would most likely be required. Such a “default” state of planning would naturally lead to reduced RTs for targets presented in the repeated movement, because the action would already be prepared. Anticipatory preparation could also account for movement directions being biased toward a recently repeated movement direction (Verstynen and Sabes, 2011; Bonaiuto et al., 2016; Marinovic et al., 2017), because limiting RTs tends to bias movement toward a default preparatory state (Ghez et al., 1997; Haith et al., 2015). It is also possible, however, that repetition might allow lower RT in a choice RT task through improving the latency at which an action can be generated (Hyman, 1953; Pachella, 1973; Welford, 1980).

## RESULTS

### Movement Repetition Selectively Reduces Reaction Time

In experiment 1, we sought to test whether repeating a specific movement would selectively affect RTs for that movement in the future. Among an array of six potential targets, we selected one target direction to be the repeated direction and another one symmetrically opposite the midline to be the non-repeated direction (see [Experimental Procedures](#) for details). We measured baseline choice RTs for these two target directions in an initial block, in which participants were instructed to move as soon and as accurately as possible after the target appeared (Figures 1A–1C). Before the repetition block, the average





**Figure 1. Repetition Reduces RT**

(A) Experimental setup. Participants sat in front of a computer monitor and made reaching movements while holding a handle, whose position was recorded on a digitizing tablet.

(B) Free RT condition in experiment 1. RT was measured as the time between stimulus presentation and movement onset.

(C) Trial schedule of experiment 1.

(D) Mean RT in free RT trials across participants before and after repetition for the repeated (black) and non-repeated (gray) targets.  $**p < 0.01$ .

(E) Generalization of improvement in RT from the repeated direction (at  $45^\circ$ ) to neighboring target directions. Note that the smaller SEM for the repeated and the non-repeated targets is because these targets were probed more often than the other targets. Error bars indicate  $\pm$  SEM.

Post hoc analysis revealed that, after repetition, the average mean RT across all participants in the repeated direction was significantly lower than before the repetition ( $t_{15} = 3.569$ ;  $p = 0.006$ ) and was significantly lower ( $t_{15} = 2.890$ ;  $p = 0.022$ ) than the average RT in the non-repeated direction. The average RT in the non-repeated direction did not change ( $t_{15} = 0.70$ ;  $p = 0.74$ ). Importantly, the improvement in RT occurred despite the fact that no visual targets were ever present during repetition trials and thus was attributable to repetition of the movement rather than to repetition of the stimulus that cued the movement.

The improvement in RT from the repeated direction generalized narrowly

in neighboring target directions. Figure 1E plots the average change in RT across participants for each target direction. We found that the RT effect generalized to immediately neighboring targets ( $30^\circ$  away) but less so to more distant targets ( $>30^\circ$  away).

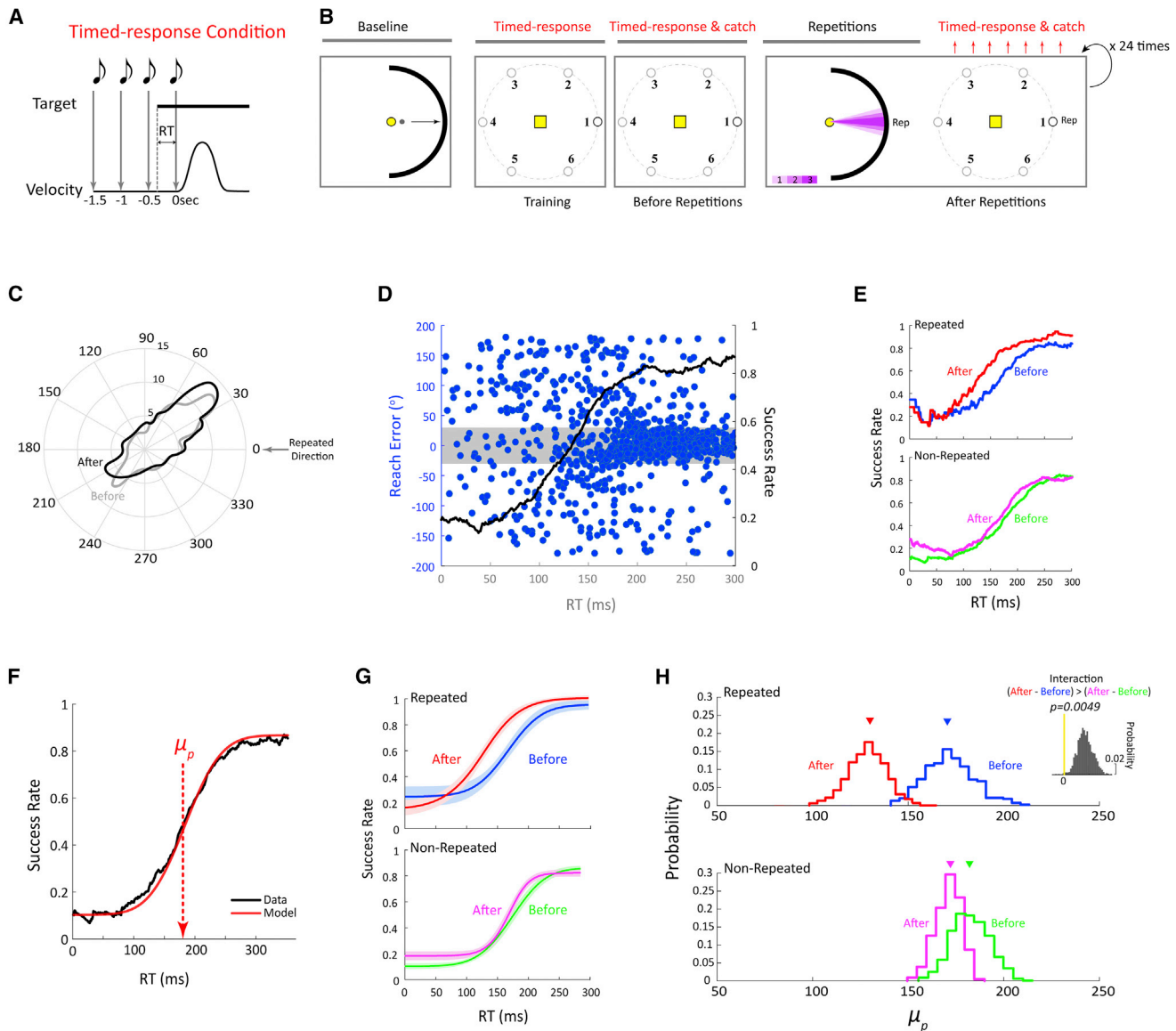
### Repetition Improves RT by Reducing the Time Required to Select and Prepare a Response

Experiment 1 showed that movement repetition reduced RTs for subsequent movements. As described in the Introduction, this reduction in RT might have occurred either through anticipatory preparation of the repeated movement or through being able to prepare the repeated movement more rapidly. To disambiguate these possibilities, we performed a second experiment (experiment 2), controlling available response preparation time using a timed-response paradigm (Figure 2A), which allowed us to effectively impose a particular RT on each trial. We characterized the dynamics of response preparation for each target by assessing the accuracy of participants' movements as a function of the imposed RT. Furthermore, we included a number of "catch" trials, in which no target ever appeared but participants were still

RT across all participants in the repeated and non-repeated directions was not statistically different ( $t_{15} = 1.378$ ;  $p = 0.341$ ; Figure 1D; Table S1).

Participants then performed 408 movements toward the repeated direction. Importantly, they were not cued where to move by a target but instead viewed a broad, semi-circular target but were prompted to repeat a specific movement direction through a combination of verbal instruction and trial-by-trial score-based feedback (allowing us to assess the effects of movement repetition per se, rather than stimulus repetition). Participants successfully followed this instruction and performed consistent repetition during the repetition block with an average movement direction of  $47.5^\circ \pm 2.2^\circ$  (mean  $\pm$  SD) for the  $45^\circ$  group and  $134.7^\circ \pm 0.9^\circ$  for the  $135^\circ$  group. The SD of the repeated directions was  $3.6^\circ \pm 1.6^\circ$  for the  $45^\circ$  group and  $3.3^\circ \pm 0.5^\circ$  for the  $135^\circ$  group.

In order to assess whether repetition affected RTs for a particular direction, we interleaved a subset of trials, in which we measured RT for movements to targets presented in various directions. Our data revealed an interaction between the effects of movement direction and time ( $F_{1,15} = 9.111$ ;  $p = 0.009$ ; Figure 1D).



**Figure 2. Movement Repetition Facilitates Response Preparation**

(A) Timed-response condition.  
 (B) Trial schedule of experiment 2.  
 (C) Circular histogram showing the distribution of guessed directions in catch trials (trials in which no target appeared) in the timed-response condition before (gray) and after (black) repetition.  
 (D) Data during the timed-response condition pooled across participants and targets. Blue points indicate RT and initial reach direction error ( $^{\circ}$ ) for individual trials; black line shows the moving average of the probability that a movement is successful for a given RT, which corresponds to the speed-accuracy trade-off.  
 (E) Top: speed-accuracy trade-off for the repeated target before (blue line) and after repetition (red line). Bottom: speed-accuracy trade-off for the non-repeated targets before (green line) and after repetition (magenta line) is shown. Success rates were estimated based on the pooled data of all participants.  
 (F) Illustration of maximum likelihood model fit (red line) to empirical speed-accuracy trade-off data (black line). Dashed line indicates the estimated mean of latency of preparation ( $\mu_p$ ).  
 (G) Same as (E) but showing the model fits to data pooled across participants. Shaded regions indicate the 95% CI determined by bootstrap analysis.  
 (H) Top: bootstrap distribution of  $\mu_p$  for the repeated target before (blue) and after (red) repetition. Bottom: bootstrap distribution of  $\mu_p$  for the non-repeated targets before (green) and after (magenta) repetition is shown. Inset shows the bootstrap distribution of the difference in the change (after-before) in  $\mu_p$  between the repeated target and non-repeated targets and corresponding p value for this time  $\times$  direction interaction.

required to move. These catch trials allowed us to directly observe the presence of any anticipatory preparation before presentation of any target.

During the repetition trials (the repeated target was located at  $0^{\circ}$ ), participants performed consistent movements with an average movement direction of  $1.9^{\circ} \pm 2.8^{\circ}$  (mean  $\pm$  SD) and

SD of the repeated directions of  $4.2^\circ \pm 1.9^\circ$ . In addition, the average RT in these trials was  $476.7 \pm 100.3$  ms.

In the timed-response condition, we found that the distribution of the guessed directions in catch trials was not uniform but was biased toward particular directions, dominated by the far right ( $30^\circ$ – $60^\circ$ ) and near left directions ( $210^\circ$ – $240^\circ$ ; [Figures 2C and S1](#)). These movement directions were likely preferred because they are the least effortful ([Shadmehr et al., 2016](#)). Critically, there was no significant change of the guessed direction toward the repeated direction after movement repetition (paired t test;  $t_9 = 0.01$ ;  $p = 0.91$ ). This result provides strong evidence against the possibility that movement repetition confers a significant execution advantage through anticipatory preparation.

We next examined whether movement repetition affected the latency of preparation toward the repeated target. [Figure 2D](#) shows the reach errors (blue points) as a function of the effective RT for the pooled data across participants during the timed-response condition. We estimated the speed-accuracy trade-off function for each target based on the proportion of accurately initiated movements within a sliding window around each given RT ([Figure 2E](#)). To enable a quantitative comparison between speed-accuracy trade-off curves, we fit a parametric model to the speed-accuracy trade-off for each target using a maximum likelihood approach ([Figure 2F](#)). We were primarily interested in the latency parameter of the speed-accuracy curve ( $\mu_p$ ), given that experiment 1 showed a reduction in RT following movement repetition. [Figure 2G](#) shows the estimated latency of preparation (parameter  $\mu_p$ ) and the 95% confidence interval (CI) for the repeated and non-repeated directions before and after repetition. The estimated latency of preparation for the repeated direction was 168.4 ms (95% CI; [144.9–197.7]) before repetition and 134.0 ms [114.6–155.8] after repetition. In the non-repeated directions, the estimated latency was 181.3 ms [163.2–200.1] before repetition and 168.7 ms [153.5–185.2] after repetition ([Figure 2H](#)). A paired comparison of the fitted parameters for the pooled data (using bootstrap method) showed a significant time  $\times$  direction interaction ( $p = 0.0049$ ) in the estimated latency of preparation ( $\mu_p$ ; [Figure 2H](#), inset), demonstrating that movement repetition improved the preparation time for the repeated direction to a larger extent than preparation of movements toward the non-repeated directions. Post hoc test revealed repetition led to significantly lower latency of preparation in the repeated direction ( $p = 0.002$ ), but not in the non-repeated directions ( $p = 0.158$ ). This finding is consistent with the result of experiment 1, indicating that movement repetition affects the latency of the speed-accuracy curve. A similar analysis of the steepness of the speed-accuracy trade-off through the parameter  $\sigma_p$  showed no significant time  $\times$  direction interaction ( $p = 0.208$ ) and no changes in the repeated and non-repeated directions ( $p = 0.771$  and  $p = 0.331$ , respectively).

Altogether, our findings demonstrate that participants in experiment 1 were able to reduce their RTs for the repeated movement direction because movement repetition improved the latency at which participants could select and prepared that movement. We were able to rule out the alternative explanation that participants guessed which movement would be required based on experience and prepared that movement in advance.

### Improvement of Response Preparation Is Not Due to Overt Reward

One potential limitation in the designs of experiments 1 and 2 is that participants were encouraged to repeat a particular movement direction through scalar feedback, informing them how closely their movement direction matched the desired direction. We designed this approach to avoid presenting overt targets and thereby ensure that we assessed the effects of movement repetition rather than target repetition. However, this introduced the possibility that the scalar feedback could have acted like a reward, which is known to have a motivating effect that can improve movement quality and RTs. We did not find any relationship between amount of reward received in experiment 2 and the overall improvement in preparation time ( $r = 0.18$ ;  $p = 0.62$ ; [Figure S2](#)). Nevertheless, to properly control for this potential confound, we performed a third experiment, in which we removed the score-based feedback during the repetition trials and instead asked participants to repeat point-to-point movements toward a particular target (see [Experimental Procedures](#) for details; [Figure 3A](#)). Movements during these repetition trials (the repeated target was located at  $0^\circ$ ) had an average movement direction of  $2.0^\circ \pm 4.8^\circ$  (mean  $\pm$  SD) and SD of  $5.8^\circ \pm 1.5^\circ$ . Additionally, the average RT in these trials was  $463.3 \pm 60.7$  ms.

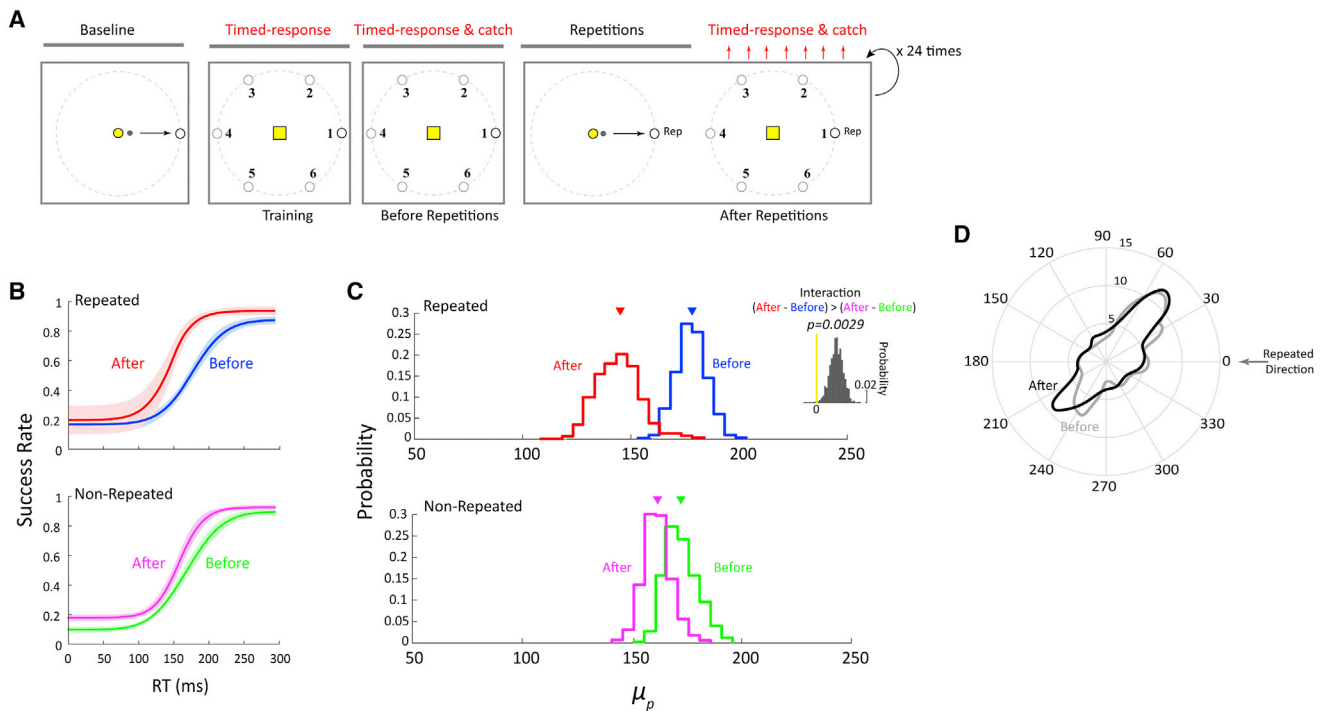
Inducing movement repetition by repeating a target, rather than through score-based feedback, did not qualitatively alter our findings. Participants were able to improve their speed-accuracy trade-off for targets in the repeated direction to a larger extent than the non-repeated directions, evidenced by a significant time  $\times$  direction interaction ( $p = 0.0029$ ) in the estimated latency of preparation ( $\mu_p$ ). The best-fit parameter ( $\mu_p$ ) for the repeated direction was 179.8 ms [165.7–194.1] before and 146.1 ms [128.0–171.4] after repetition ( $p = 0.003$ ), whereas for the non-repeated directions was 171.6 ms [165.9–188.3] before and 160.6 ms [148.8–174.3] after repetition ( $p = 0.01$ ; [Figures 3B and 3C](#)). Similar to experiment 2, we did not find a significant time  $\times$  direction effect ( $p = 0.431$ ) on the parameter  $\sigma_p$ , again indicating that the main effect of movement repetition is on the latency, but not the steepness of the speed-accuracy trade-off.

We also confirmed that, as in experiment 2, there was no change in the distribution of guesses in catch trials following movement repetition (paired t test;  $t_9 = 0.31$ ;  $p = 0.76$ ; [Figures 3D and S1](#)). The close agreement between our results strongly supports the idea that the improvement in performance in experiments 1 and 2 was due to repetition and not due to inadvertent motivational effects.

## DISCUSSION

In a series of psychophysical experiments, we demonstrated that movement repetition enhances motor performance by facilitating response preparation, enabling reduced RTs. In general, the RT reflects the total amount of time consumed by both sensory and motor processing required to plan an action in response to a sensory cue ([Wong et al., 2015](#); [Salinas et al., 2014](#)). At which level, motor and/or perceptual, does the reduction of RT occur? In our experiments, the benefits of repetition persisted despite a significant change in the stimuli used to cue movement. We





**Figure 3. Enhancement of Response Preparation through Repetition in the Absence of Overt Reward**

(A) Trial schedule of experiment 3.

(B) Top: fitted speed-accuracy trade-off for the repeated target before (blue line) and after repetition (red line). Bottom: fitted speed-accuracy trade-off for the non-repeated targets before (green line) and after (magenta line) repetition is shown. Shaded regions indicate the 95% CI.

(C) Top: bootstrap distribution of  $\mu_p$  of the repeated target before (blue) and after (red) repetition. Bottom: bootstrap distribution of  $\mu_p$  for the non-repeated targets before (green) and after (magenta) repetition is shown. Inset shows the bootstrap distribution of the difference in the change in  $\mu_p$  between the repeated and non-repeated targets and associated p value for this time  $\times$  direction interaction.

(D) Circular histogram showing the distribution of guessed directions in catch trials before (gray) and after (black) repetition.

therefore suggest that the beneficial effect of repetition on RT is due to improvements at the motor rather than perceptual and/or sensory level. We cannot rule out, however, that participants responded faster due to more rapid processing of the visual stimulus when it occurred in a position congruent with the previously repeated movement.

Previous studies have shown that movement complexity can affect the amount of preparation time required for a movement (Henry and Rogers, 1960; Rhodes et al., 2004; Wong et al., 2016) and that this effect is diminished through repetition (Verwey, 1999), potentially attributable to simplifying the process of movement preparation by “chunking” movements together. We believe there is little scope for any analogous simplification of the steps involved in movement preparation in our task, however. We therefore suggest that the same preparatory steps occurred more rapidly as a result of repetition. We cannot, however, definitively rule out that some other qualitative change might have occurred that selectively simplified movement preparation in the repeated direction.

Previous studies have reported that repeated reaching movements to a particular target location reduces the variability of subsequent actions toward that location (Diedrichsen et al., 2010; Verstynen and Sabes, 2011). This phenomenon is well explained by a Bayesian theory, according to which participants

learn the distribution of target locations and integrate this prior expectation of where the target may appear with future observations in order to improve their estimate of future target location. This theory also accounts for the finding that movements aimed toward adjacent targets are biased toward the repeated direction. Thus, the reduction in variability following repetition is compatible with a large literature examining how contextual information influences decisions about where to aim one’s movements (Favilla et al., 1990; Hudson et al., 2008; Haith et al., 2015; Wong and Haith, 2017). Our study suggests the existence of a separate mechanism whereby recent movement history might influence motor performance—in this case through facilitating more rapid response preparation, that is, how quickly we generate a subsequent movement in response to a sensory stimulus (Marinovic et al., 2017). Dissecting the effect of movement history on different components of a behavior (movements versus target dependent) is a clear and important goal for future research.

What happens at the neural level following movement repetition? TMS studies have provided some insight into this question by showing that consistent repetition of thumb movement in a particular direction can change the direction of TMS-evoked (involuntary) movements, a phenomenon that has been termed use-dependent plasticity (Classen et al., 1998; Bütefisch et al.,

2000; Mawase et al., 2017). Similar effects are also observed in involuntary movements elicited by intra-cortical microstimulation (Nudo et al., 1990). The behavioral relevance of changes in involuntary movements elicited by TMS after movement repetition has been questioned (Bestmann and Krakauer, 2015). Our study, however, raises the possibility that this use-dependent plasticity could be related to the ability to prepare particular movements more rapidly. For instance, repetition may allow faster preparation of motor commands in the relevant network through inhibition of activity for less relevant neurons and/or reduction of motor noise.

Recent studies have argued that movement preparation involves setting the state of motor cortex to a particular, movement-specific state (Churchland et al., 2006; Ames et al., 2014) where preparation thought to set the initial state of a dynamical system that generates patterns of activity required for movement. The position of the neural activity trajectory relative to the optimal preparatory subspace correlates with RT (Churchland et al., 2006; Afshar et al., 2011; Michaels et al., 2015). Our results showing that movement repetition significantly reduces RTs might therefore be a consequence of altering the default preparatory state of motor cortex for the repeated direction. This would explain the reduction in RT and would also seem to be a plausible mechanism for the TMS effect. If it were true, however, that repetition affected the default preparatory state of the motor system, we would have expected to see a shift in the distribution of default movements toward the repeated direction. Experiments 2 and 3 show that this is not the case: the distribution of default movements did not change following repetition. We therefore think it unlikely that repetition affects the default preparatory state of the motor system. Furthermore, the fact that repetition did not affect default movement preparation but does usually alter movements evoked by TMS suggests that TMS does not simply provide a readout of the preparatory state of the motor system. Stimulation of the motor cortex may instead reflect a signature of cortical dynamics; movements corresponding to preparatory states that can be attained more rapidly may be more likely to be elicited by TMS. Further work, beyond the scope of the present investigations, will be required to fully understand the relation between TMS-evoked involuntary movement, the neural-state space, the dynamics of movement preparation, and how each of these is affected by repetition.

In summary, we have shown that movement repetition improves performance of subsequent movements by enabling response preparation to occur earlier. The results highlight an important benefit of movement repetition that may constitute a previously elusive behavioral counterpart to well-studied physiological effects of movement repetition. These findings might also explain in part why athletes and artists warm up by repeating movements that will be soon executed prior to performance.

## EXPERIMENTAL PROCEDURES

### Participants

A total of 36 right-handed human participants were recruited for the current study (22 female; mean age  $25.02 \pm 4.7$  SD years). Participants provided written consent to participate in the study, which was approved by the Johns Hopkins University School of Medicine Institutional Review Board.

### Experimental Task

Participants were required to move their hands quickly to guide a cursor through a presented target (Figure 1A), which appeared 7 cm from a central start location (5 mm diameter). To ensure consistent movement speed and encourage participants to execute a single, quick movement on each trial, participants were required to maintain their movement duration (the time to reach a displacement of >7 cm from the start location) below 200 ms. They were provided feedback in the form of a low-pitched tone if they failed to meet this criterion on any given trial.

Experiment 1 sought to test whether repetition of a particular movement direction would affect RTs for future movements in that direction. 16 participants (11 female; mean age  $27.25 \pm 5.4$  SD years) were recruited for experiment 1. These participants experienced two types of trials: repetition and free RT trials. In the repetition trials, participants were instructed to repeat the same movement toward a particular direction on a semi-circular target. Participants were required to make accurate and quick movements after the target was presented. In the free RT trials, after entering the central start position in each trial, participants heard a sequence of four tones, spaced 500 ms apart (Figure 1B). One of six potential targets (at  $15^\circ$ ,  $45^\circ$ ,  $75^\circ$ ,  $105^\circ$ ,  $135^\circ$ , and  $165^\circ$ ; each with size of 5 mm diameter) appeared synchronously with the fourth tone, and participants were instructed to move to the target as soon as possible after the target appeared. The predictable sequence of auditory tones served to minimize the ambiguity about the time of target presentation, which is known to increase RTs (Frith and Done, 1986; Haith et al., 2016). The differing contextual cues (presence or absence of a semi-circular target and absence or presence of auditory tones) served as a clear cue to participants as to which type of trial they were performing at the outset of each trial. Furthermore, it allowed us to isolate the effects of movement repetition, rather than target repetition, on RTs.

Participants performed three blocks of reaching movements (Figure 1C), comprised of combinations of these two trial types (repetition trials and free RT trials). The first block (familiarization) consisted of 50 repetition trials of quick reaches toward the center of a large, semi-circular target (7 cm diameter). In the second block (baseline RT block), participants performed 144 free RT trials. Targets were presented in a pseudorandom order, with each target appearing 24 times. In the third block, participants saw the same semi-circular target as in the familiarization block and were instructed to make 476 repetition movements toward a particular location on the arc. This location was varied across participants so that, for half of the participants, movements directed toward  $45^\circ$  were repeated, and for the other half, movements directed toward  $135^\circ$  were repeated. To ensure that participants repeated a consistent movement direction in this block, they were provided score-based feedback based on their distance from the instructed direction. Specifically, they earned +3 points for  $|\text{distance}| < 10^\circ$ , +2 points for  $10^\circ \leq |\text{distance}| < 15^\circ$ , +1 point for  $15^\circ \leq |\text{distance}| < 20^\circ$ , and 0 points otherwise (Figure 1C, third panel). In order to measure the influence of repetition on RT, a subset of trials (1/6) in this block were free RT trials, identical to the free RT trials in the second block (i.e., participants heard a sequence of tones and made a rapid movement toward a single target that was presented with the fourth tone). The only difference from the baseline RT block was in the relative frequency with which each target appeared; the repeated direction and the non-repeated direction (defined as the reflected target across the midline) appeared 24 times each, whereas the other 4 targets appeared 5 times (in total: 68 free RT trials and 408 repetition trials).

Experiment 2 examined whether the effect of repetition on RT was due to anticipating the probability of future targets or, alternatively, because repetition enhanced the latency at which participants could select and prepare the repeated movement after the target was revealed. A new group of 10 participants (4 female; mean age  $24.4 \pm 2.7$  SD years) were recruited for experiment 2. Here, as in experiment 1, we used two separate types of trials for inducing repetition versus measuring its effects. In this experiment, repetition was induced through repetition trials that were similar to those in experiment 1. We assessed the effects of repetition using timed-response trials. In these trials, participants heard a sequence of four tones spaced 500 ms apart and were required to initiate their movement synchronously with the onset of the fourth tone. Movement initiation time was determined online as the time at which the tangential velocity first exceeded 0.05 m/s. If participants failed to initiate their

movement within 75 ms of this time, on-screen text indicated “too early” or “too late” as appropriate.

Participants performed five blocks of quick reaching movements (Figure 2B). The first block was similar to the first block in experiment 1, except that it lasted for 30 trials and the semi-circular target was rotated 90° clockwise. The second block (30 trials) consisted of timed-response trials, with one of six potential targets (at 0°, 60°, 120°, 180°, 240°, and 300°; each with size of 5 mm diameter) visible from the onset of the first tone, allowing participants to practice the timing of their initiation. We determined a 60° distance between potential targets in order to minimize possible generalization from the repeated direction to neighboring target directions (see Figure 1E). The third and the fourth blocks were identical and included timed-response trials (108 trials for each block). In each trial of these blocks, the target was presented at times uniformly distributed between 50 and 250 ms prior to the fourth tone (Figure 2A). A subset of twelve trials were catch trials, in which no target ever appeared but participants were still required to move synchronously with the onset of the fourth tone. These catch trials discouraged participants from simply waiting until the target appeared before initiating a movement and also enabled us to assess participants' default preparation in the absence of a specific presented target location and whether this was affected by repetition.

The last block included 24 sub-blocks of 30 repetition trials toward the 0° direction on the semi-circular target, with score-based feedback as in experiment 1 to ensure that participants maintained a consistent movement direction in these trials. Each of these repetition sub-blocks were followed by 7 timed-response ( $n_{\text{ForcedRT}} \geq 5$ ) and catch trials ( $n_{\text{catch}} \leq 2$ ). In order to avoid the target sequence becoming predictable, we randomly shuffled the sequence of targets across all sub-blocks, with the only constraints on the order being that no more than 2 catch trials were allowed per sub-block of 7 trials. In total, there were 720 repetition trials (24 blocks  $\times$  30 trials) and 168 timed-response trials (24 blocks  $\times$  7 trials), including 24 trials for each of the 6 targets and 24 catch trials.

In Experiment 3, we removed the score-based feedback during the repetition trials and instead had participants perform simple point-to-point movements toward a repeated target location. An additional new group of 10 participants (7 female; mean age  $23.4 \pm 3.5$  SD years) were recruited for this experiment. The first block (familiarization) consisted of 10 repetition trials of quick reaches toward a single target at 0°. In the second block, participants practiced the timing of their movement initiation in the timed-response condition (30 trials). Blocks 3 and 4 consisted of timed-response trials (each block included 72 trials; 12 trials for each target). A subset of twelve trials was catch trials, in which no target ever appeared but participants were still required to move. The last block included 24 sub-blocks of 30 repetition trials toward a single target at 0° followed by 7 timed-response and catch trials.

### Data Analysis

Kinematic data were filtered at 10 Hz with a low-pass Butterworth filter and numerically differentiated to calculate velocity. The onset of each movement was determined as the point at which radial velocity crossed 5% of peak velocity (Block and Celnik, 2013). Movement direction in each trial was calculated based on the direction of the position vector of the hand 0.5 cm from start location. In all conditions, we calculated the RT (or effective RT, in the timed-response condition) as the time interval between the time of stimulus presentation (i.e., target) and the time of movement onset.

Trials in which the RT was less than  $-200$  ms (i.e., 200 ms before presentation of the target) or more than 500 ms relative to the target presentation were excluded from further analysis (2% of all trials). A movement was considered to be an error if the initial direction of the movement was not within  $\pm 30^\circ$  of the target direction. Otherwise, the movement was considered to be accurate.

For each target, the probability of initiating an accurate movement (the “success rate”) in the timed-response condition at any given RT was estimated based on the proportion of accurately initiated movements within a 75-ms window around that RT. This yielded an estimate of the speed-accuracy trade-off function (Wickelgren, 1977; Stanford et al., 2010; Haith et al., 2016). In order to quantitatively characterize this trade-off, we followed the model presented in Haith et al. (2016), in which a single preparation event is assumed to occur at a stochastic time  $T_p \sim N(\mu_p, \sigma_p^2)$ , with movements initiated before  $T_p$

directed randomly and movements initiated after  $T_p$  directed accurately toward the target (see Supplemental Experimental Procedures).

### Statistical Analysis

Differences in RT in experiment 1 were assessed with a 2-way repeated-measure ANOVA with factors of time (before versus after) and direction (repeated versus non-repeated). Any differences were explored post hoc using two-sample paired t tests with statistical significance considered at  $p < 0.05$ . Correction for multiple comparisons was conducted using the Holm-Sidak test. To assess between-time (before versus after), between-direction (repeated versus non-repeated) differences and time  $\times$  direction interaction in latency and in steepness of the speed-accuracy trade-off in experiments 2 and 3, we ran a bootstrap analysis on the parameters  $\mu_p$  and  $\sigma_p$  with 1,000 resamples.

### SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, and one table and can be found with this article online at <https://doi.org/10.1016/j.celrep.2018.06.097>.

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### AUTHOR CONTRIBUTIONS

All authors contributed to the study design, interpreted the data, and approved the final version of the manuscript for submission. F.M. and D.L. performed the testing and data collection. F.M. performed the data analysis. F.M., P.A.C., and A.M.H. drafted the manuscript.

### DECLARATION OF INTERESTS

The authors declare no competing interests.

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