Evidence for a common mechanism supporting invigoration of action selection and action execution

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Abstract
The speed, or *vigor*, of our movements can vary depending on circumstances. For instance, it is well established that the promise of a reward leads us to make faster movements. Potential rewards also lead to lower reaction times, suggesting that the process of action selection can be similarly invigorated by reward. It has been proposed that invigoration of action selection and of action execution might occur through a common mechanism, and thus these aspects of behavior might be coupled. To test this hypothesis, we instructed participants to make reaching movements to "shoot" through a target at varying speeds and we assessed whether moving more quickly was also associated with more rapid action selection. We found that action selection was significantly slower when participants moved more slowly. This finding was recapitulated in a further dataset in which participants determined their own movement speed and moved slowly in order to stop their movement inside the target. Our results support the hypothesis that action selection and action execution are invigorated by a common underlying mechanism.

Introduction

A key aspect of volitional movement is the speed at which we move – often referred to as the "vigor" of our movements. We can easily voluntarily choose to move at a particular speed. The speed of our movements can also be affected more implicitly by the circumstances surrounding our movements. In particular, it is well established that the promise of earning a reward leads us to move faster. Nonhuman primates and humans make faster saccadic eye movements toward targets that are paired with rewards (Manohar et al., 2017, 2015; Takikawa et al., 2002) while in humans, velocity of reaching movements is increased by expectation of reward (Summerside et al., 2018).

As well as influencing how quickly we move, reward can also influence how quickly we decide what movement to make. Reward can simultaneously reduce reaction times and error rates

(Hübner and Schlsser, 2010; Krebs et al., 2011; Manohar et al., 2015; Salinas et al., 2014), improving the speed–accuracy trade-off for selecting an action. This improvement can be viewed as an "invigoration" of action selection.

The invigorating effects of reward on action execution and action selection have both been explained by normative computational theories in which the benefits of moving more quickly are balanced against the cost of the effort required to either physically move more quickly (Haith et al., 2012; Rigoux and Guigon, 2012; Schweighofer et al., 2015; Shadmehr et al., 2019; Summerside et al., 2018) or to select actions more quickly (Manohar et al., 2015). According to these theories, reward invigorates both action selection and action execution for analogous reasons, but potentially through distinct mechanisms (Fig. 1A, left).

Recent proposals, however, have suggested that there may be a closer, mechanistic link between the vigor of action selection and action execution (Thura, 2020). Recent work by Thura and Cisek showed that, in a deliberative decision-making task, the urgency of an ongoing decision strongly influenced the speed and duration of the ensuing movement (Thura et al., 2014). These results prompted the suggestion that the process of choosing which action to execute may be modulated in tandem with invigorating the action (Fig. 1A, right), possibly via a signal computed in the basal ganglia (Bogacz et al., 2010; Forstmann et al., 2010; Thura and Cisek, 2017). Evidence in favor of coupling between movement vigor and action selection vigor is inconclusive, however (Reynaud et al., 2020).

Although the prospect of reward can reliably elicit changes in movement vigor, it is not the only way that movement vigor can be altered. People can also explicitly decide to vary the speed of their movements. It is unclear, though, how volitional changes in movement speed might affect the speed of their action selection. If action selection and movement vigor do indeed share a common mechanism of invigoration, then instructing people to vary their movement speed ought to also affect the vigor with which they select their actions (the coupled-vigor hypothesis). Alternatively, if there is no shared mechanism underlying movement vigor and action selection, instructed changes in movement vigor ought not to affect the vigor of action selection (the independent-vigor hypothesis)(Fig. 1A, right). We therefore performed an experiment to establish how instructed changes in movement vigor would affect the speed of participants' action selection. Specifically, we asked whether moving more quickly or more slowly affected the speed–accuracy trade-off for action selection.

Results

We performed an experiment to determine whether instructed changes in movement vigor would influence the vigor of action selection. Participants made planar reaching movements

from a central start position toward one of four potential targets (Fig. 1BC). The participants were asked to initiate their movement at a specific time cued by a metronome and "shoot" through the target (Fig. 1CE). Participants were also instructed to move at a particular speed (based on post-movement feedback, see Materials and Methods), which varied by block to be either fast, medium or slow (Fig. 1D). Participants easily varied their speed within each block according to these requirements (Fig. 2A), with peak velocities significantly different across the three speed conditions (one-way ANOVA, $P < 10^{-19}$, $F(2,33) = 251.75$).

To determine whether instructed changes in movement speed also affected the vigor of action selection, we used a forced–response approach to assess how quickly participants were able to select the correct action. We systematically varied, on a trial-to-trial basis, the amount of time available to participants to prepare their movements by requiring participants to initiate their movement at a fixed time in each trial (cued by a metronome) while varying the time at which the target was displayed (Fig. 1E, Forced-response approach (Ghez et al., 1997; Haith et al., 2016; Schouten and Bekker, 1967); see Methods), allowing us to determine the minimum time required for accurate action selection.

In line with previous experiments that varied allowed preparation time, participant's performance followed a speed–accuracy trade-off (Chittka et al., 2009) whereby reaches made with very short preparation times (initiated 0 ms – 100 ms after the target appeared) were directed randomly relative to the true target direction while reaches made at longer preparation times (> 300ms) were more likely to be accurate (i.e., directed within ±22.5° of the target)(Haith et al., 2016). The center of this speed–accuracy trade–off corresponded to the average time at which participants could correctly select and prepare an appropriate movement. We therefore used this point on the speed–accuracy trade–off curve to quantify the vigor of participant's action selection (Fig. 2B), and we estimated this by fitting a cumulative Gaussian distribution to participants' data (Haith et al., 2016).

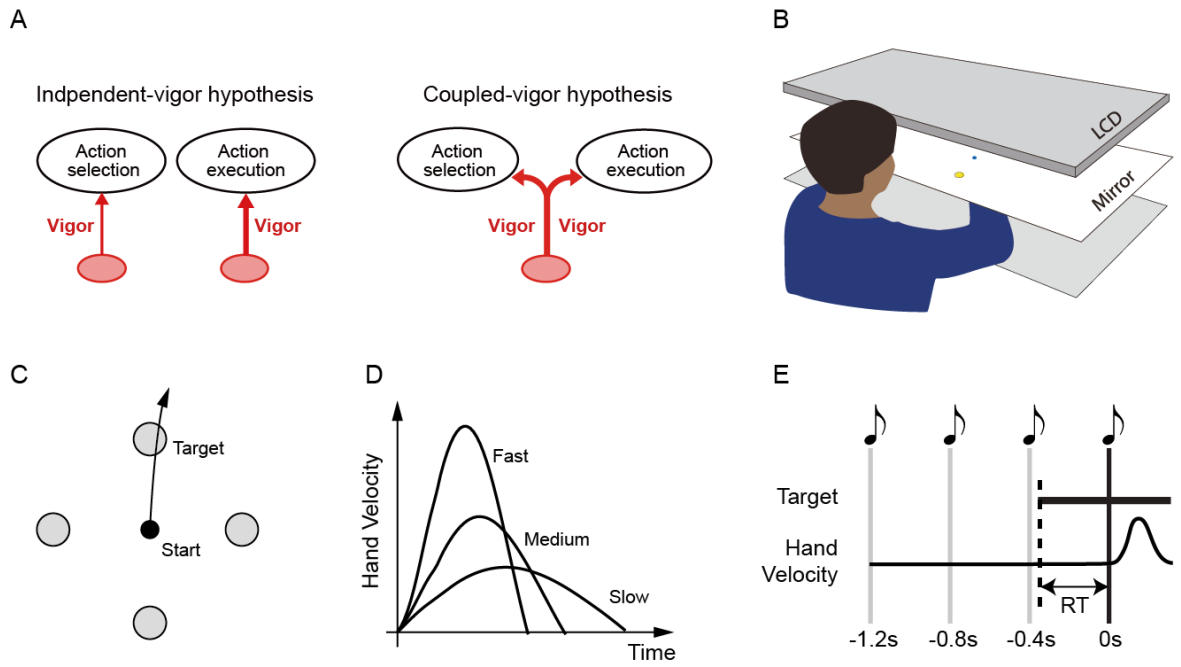

Figure 1. **Experimental setup.**

A, Possible mechanistic link between invigoration of action selection and action execution. left: independent-vigor hypothesis and right: coupled-vigor hypothesis. *B*, Participants performed center-out reaching movements towards targets presented via mirrored display. *C*, One of four equally-space targets were shown and participants asked to go through a target (shooting task). *D*, Participants were instructed to ensure that peak tangential velocity within certain ranges (fast, 0.8 ± 0.08 m/s, medium, 0.45 ± 0.045 m/s and slow 0.25 ± 0.025 m/s) on each trial. *E*, Participants completed forced-response tasks. Participants heard a sequence of four metronome tones, and were instructed to respond synchronously with the fourth tone. Varying the onset of the stimulus relative to this deadline allowed us to effectively control participant's reaction times.

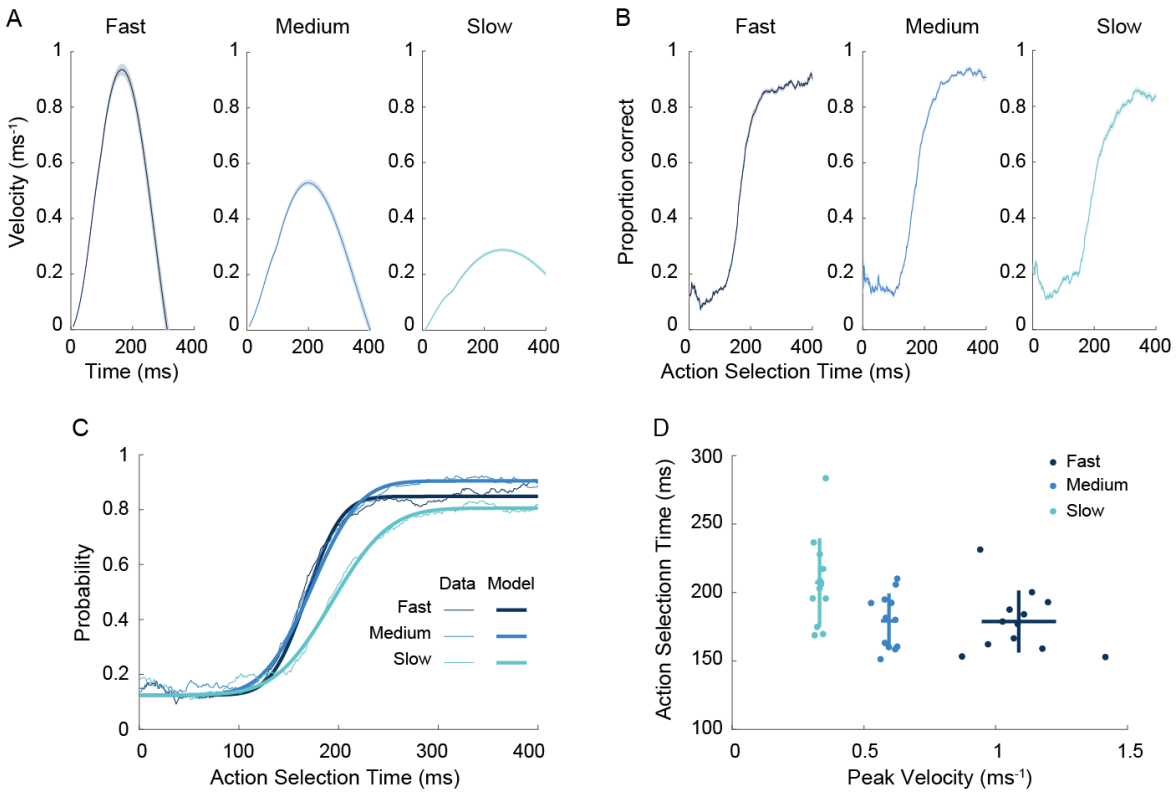

Figure 2. **Performance of three different movement speed conditions in the Shooting Tasks.** *AB*, Average velocity profiles (*A*) and speed-accuracy trade-off (*B*) across participants (N = 12) in the Shooting Task (Fast-, Medium- and Slow-speed conditions). Shaded regions indicate ± 1 s.e.m. *C*, Average speed-accuracy trade-off (N = 12, thin lines) and average model fit (bold lines) for each movement speed conditions. *D*, Estimated action selection time (y - axis) against peak velocity (x - axis). In all panels, dark blue is the Fast-, blue is the Medium- and light blue is the Slow-speed condition.

Fig. 2C plots the fits of the speed–accuracy trade-off function when fitted to group-level data, showing a good correspondence with the data. We also fit this model to individual participant data to estimate the speed of action selection for each individual participant in each condition (see Supplementary Figure 1). We found that the time needed for accurate action selection was different across movement-speed conditions (using a mixed-effects ANOVA model with movement conditions a fixed factor and with random intercept and slope, $P < .0001$, $F(2,33) = 17.915$). The estimated action-selection time in the Slow-speed condition (207.24 ± 32.26 ms) was significantly longer than in the Medium- (179.18 ± 20.10 ms) and Fast-speed (178.78 ± 22.71 ms) conditions (Fig. 2D, Tukey post-hoc test: $P < .0001$ in both cases), in accordance with the prediction of the coupled-vigor hypothesis.

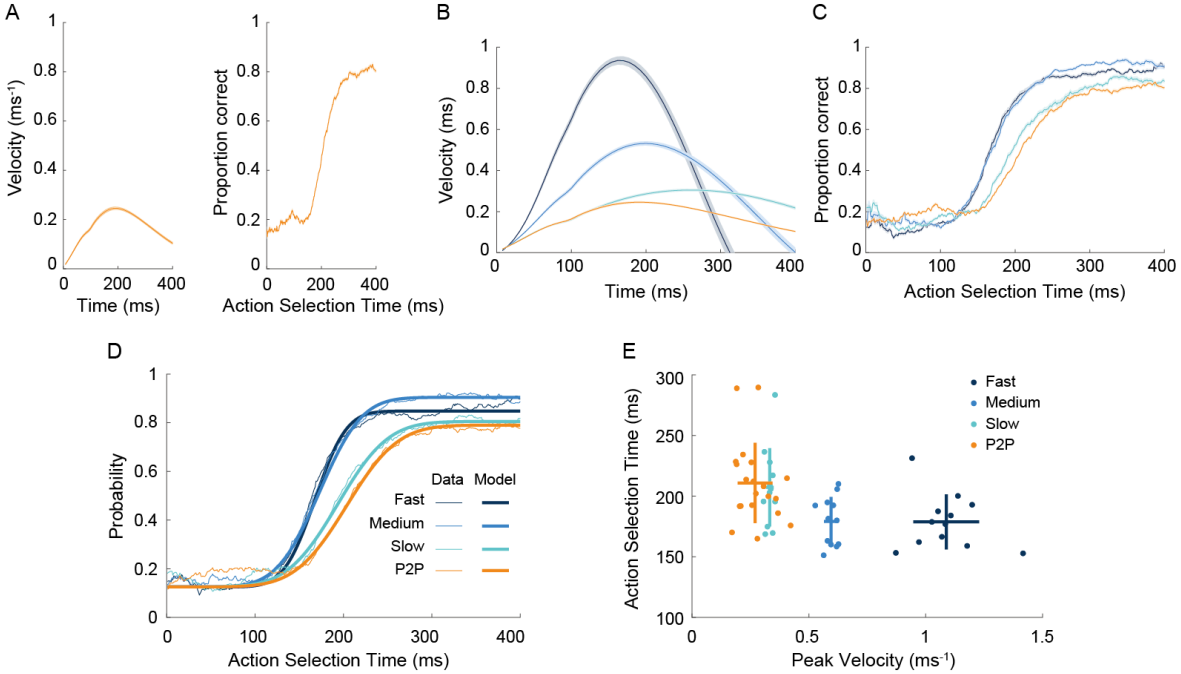

Figure 3. **Performance of Point-to-Point Task and Shooting Tasks.**
A, Velocity profile (left) and speed-accuracy trade-off (right) across participants (N = 20) in the point-to-point task. Shaded regions indicate ± 1 s.e.m. *BC*, Average velocity profiles (*B*) and speed-accuracy trade-off (*C*) of the Shooting Task and the Point-to-Point Task plotted together. *D*, Average speed-accuracy trade-off (thin lines) and average model fit (bold lines) for the Shooting Task and the Point-to-Point Task. *E*, Estimated action selection time (y - axis) against peak velocity (x - axis). In all panels, dark blue is the Fast-, blue is the Medium-, light blue is the Slow-speed condition in the Shooting Task, and orange is the Point-to-Point Task.

To confirm that the result of the Shooting Task was not due to specific choices we made in our data analysis, we repeated our analyses with different choices for exactly how we determined the initial movement direction, and how we designated each trial as being accurate or inaccurate. Our initial results were robustly reproduced under these alternative approaches to analyzing the data (see Supplementary).

One potential concern with the results of the Shooting Task is that movement in the Slow-speed condition is unnaturally slow; when participants make shooting movements through a target at a self-selected speed, they are much more likely to select speeds consistent with the Fast- or Medium-speed conditions, rather than the Slow-speed condition (Haith et al., 2016). It is possible that the need to comply with instructions to move at an unnaturally slow speed may have been responsible for participants' slowed action selection. To address this concern, we compared the results from the Shooting Task to data from a similar experiment in which

participants made point-to-point movements, i.e. in which they had to stop at the target, rather than shoot through the target. Participants received no instructions about their movement speed in this Point-to-Point Task and were free to select a natural movement speed. In all other respects, this Point-to-Point Task was identical to the Shooting Task.

Participants' mean peak velocity in the Point-to-Point Task (0.27 ± 0.07 m/s, Fig. 3A, left) was very similar to that of participants in the Slow-speed condition of the Shooting Task (0.33 ± 0.02 m/s, Fig.3B). As with the Shooting Task, we estimated the action-selection time needed by participants by fitting a cumulative Gaussian distribution to participants' performance to estimate a speed–accuracy trade-off (Fig. 3A, right, Fig. 3CD, Supplementary Figure 2, along with the Shooting Task). We found that action-selection time (the center of the trade-off function) was different across the Fast- and Medium-speed Shooting Tasks and Point-to-Point Task (using mixed effects ANOVA with movement conditions a fixed factor and with random intercept and slope, $F(2,41) = 17.915$). The estimated action-selection time in the Point-to-Point task (210.87 ± 33.07 ms) was slower than the Medium- (Tukey post-hoc test: $P < 0.0001$) and Fast-speed conditions (Tukey post-hoc test: $P < 0.0001$). The estimated action-selection times in the Point-to-Point task (210.87 ± 33.07 ms) was, however, comparable to that in the Slow-speed condition in the Shooting Task (two sample t-test: $P = 0.764$) (Fig. 3E). This analysis depended on reusing data from the Shooting Task, and therefore, might not have been independent of the analysis for that task. In particular, a false positive result due to unusually fast preparation in the Medium and Fast conditions might have been recapitulated in our second analysis. However, the action-selection times estimated in these conditions were consistent with prior datasets that used a similar task (Haith et al., 2016).

In summary, the relationship between the vigor of action execution and the vigor of action selection was preserved even when participants selected their own movement speed due to varying task constraints.

Discussion

It has been proposed that there is a common neural mechanism governing the invigoration of movement and the invigoration of action selection (Thura, 2020). In the present study, we performed a simple behavioral experiment in human subjects in which participants were instructed to make reaching movements to "shoot" through a target at varying speeds. We found that voluntarily increasing movement speed (i.e., movement vigor) also caused action selection to be faster and more accurate, supporting the hypothesis that there is a common neural mechanism governing the invigoration of movement and the invigoration of action selection.

One possible concern with our experimental results is that participants might have misinterpreted the instructions given to them. Although participants were instructed to move at different speeds and were only provided feedback about movement speed, they might have misinterpreted the instructions as encouraging them to also select actions more quickly. If this were the case, then the changes in action selection that we observed could also have been volitional. We believe this is unlikely, however, since we would have expected any misinterpretation of instructions to be quite idiosyncratic and variable across participants. The difference in the vigor of movement preparation was very consistent across participants, however.

Another potential concern with our results is that our findings could have been an artifact of the way we analyzed the data – in particular, slow movements might have led to a later estimate of the time of movement initiation (Brenner and Smeets, 2019). In this study, movement initiation time was determined as the time at which tangential velocity exceeded 0.026 m/s. This fixed velocity threshold might have systematically inflated our estimates of movement initiation time in the Slow-speed condition (because a slower movement would reach this threshold later), which might account for the rightward-shifted speed–accuracy trade-off. In practice, however, any possible effect of re-estimating reaction time would not be large enough to account for observed shifts in the speed–accuracy trade-off; halving the velocity threshold for determining the time of movement initiation from 0.026 m/s to 0.025 m/s reduced our estimates of the center of the speed-accuracy trade-off by less than 1 ms in each condition and by an amount that did not systematically vary with movement speed (difference in estimate action-selection time with high versus low threshold, Slow: -0.24ms, Medium: -0.77ms, Fast: -0.12ms), demonstrating that our results were not sensitive to this effect. Furthermore, possible artifacts related to estimating the time of movement initiation would only predict a rightward shift in the speed–accuracy trade-off but we also observed a broadening of the speed-accuracy trade-off with slower movements.

Vigor of behavior is often quantified in terms of reaction times (Beierholm et al., 2013; Niv et al., 2007), particularly in settings where detailed kinematics are not measured, such as in free-operant conditioning tasks in rodents, or in button-pressing tasks in humans. In our experiments, we were able to separate vigor into two components: vigor of action selection and vigor of execution of the action itself. Although we could have simply used reaction time to quantify the vigor of action selection, recent work has demonstrated that reaction times alone do not provide a complete characterization of the dynamics of action preparation (Haith et al., 2016; Hardwick et al., 2019; Mawase et al., 2018). Reaction times measure the time at which a movement is initiated, rather than the time at which it is selected and prepared, and

initiation has been found to occur some 80ms later than preparation (a delay that accounts for one third of typical reaction times), and at a time that is independent of movement preparation (Haith et al., 2016). Purely measuring reaction times might, therefore, simply have reflected changes in the relative delay between action preparation and action initiation. To avoid this issue, we used a forced-response paradigm which allowed us to establish a more precise speed-accuracy trade-off for action selection (Mawase et al., 2018; Salinas et al., 2014; Stanford et al., 2010), which we expected to more directly reveal changes in the vigor of action selection.

Why should we vary the vigor of our behavior at all? In the case of action execution, moving more quickly is known to be perceived to be more effortful and carries greater metabolic cost (Shadmehr et al., 2016) than moving slowly. Moving more vigorously, therefore, is only warranted in the context of large available rewards, where there may an opportunity cost associated with slower movements in that they waste time that could alternatively be spent obtaining further rewards elsewhere (Niv et al., 2007). A prominent theory has suggested that tonic dopamine may regulate movement vigor by signaling these opportunity costs (Niv et al., 2007). Such a theory fits well with the fact that patients with Parkinson's disease, in which dopamine is depleted by the death of dopaminergic neurons, exhibit slow movement (bradykinesia) as a cardinal symptom.

The reasons why the vigor of action selection may be modulated are less clear, since there is no direct analog of the metabolic cost of moving more quickly. Manohar and colleagues (Manohar et al., 2015) proposed that changes in the vigor of action selection could be attributed to improvements in the signal-to-noise ratio of evidence accumulation, which could be presumed to carry a cost that can be traded off against task success. Consequently, the vigor of action selection could be affected by similar circumstances that influence the vigor of action execution. Indeed, in perceptual decision-making tasks, human participants make responses that are faster and less accurate when the average reward rate is higher (Otto and Daw, 2019). Similarly, monkeys exhibit a superior speed–accuracy trade-off when large relative to small rewards are at stake (Salinas et al., 2014).

Reward-related changes in the vigor of both action execution and action selection seem to be absent in patients with Parkinson's Disease (Manohar et al., 2015), suggesting a link between improvements in the vigor of action selection and dopamine. Indeed, administration of L-Dopa – a dopamine precursor which elevates dopamine levels in the brain and is a common medication for Parkinson's Disease – enhances the vigor of action selection in healthy young adults (Beierholm et al., 2013).

More generally, the phenomenon of cognitive effort has been widely studied and it has been clearly established that performing certain cognitive processes carries a sense of effort, that exerting more cognitive effort can accelerate cognitive processing, and exertion of cognitive effort can be modulated by opportunity cost (Otto and Daw, 2019). The exact nature of cognitive effort costs remains unclear (Shenhav et al., 2013) as does its relation to effort costs associated with executing a movement. Our findings, however, reinforce the possibility of a fundamental link between them, as suggested by Thura and colleagues (Thura, 2020; Thura et al., 2014).

Materials and Methods

A total of 32 human participants were recruited for this study (12 in the Shooting task and 20 in the Point-to-Point Task). All participants were right-handed and naive to the purposes of the study, had no known neurological disorder and provided written consent before participation. All procedures were approved by the Johns Hopkins University School of Medicine Institutional Review Board.

Experimental setup

Participants sat on a chair in front of a glass-surfaced table with their right arm resting on a plastic cuff mounted on an air sled which enabled frictionless planar movement of their arm against the glass surface of the table. Tasks, targets and a cursor which reflected participant's hand movement, were displayed in the plane of the hand through a mirror positioned horizontally above their arm (Fig. 1B). The hand position was tracked at 130 Hz using a magnetic tracking device (Flock of Birds; Ascension Technologies). Participants were required to move their hands to guide a blue cursor (2.5 mm diameter) from a fixed central start location (5 mm diameter) to a one of four targets (10 mm diameter). Targets were distributed equally around the start location at a distance of 80 mm. After starting each trial, one of four targets appeared on the screen by a small yellow circle (10 mm diameter).

Experimental tasks

Twelve participants (aged 23.58 ± years; 6 women) were recruited for the Shooting Task (Fig. 1C). On each trial, participants were required to position the cursor inside a start circle and then four tones were provided. The participants were instructed to initiate their shooting movement through the target synchronously with the onset of the fourth tone (forced response paradigm (Ghez et al., 1997; Haith et al., 2016; Schouten and Bekker, 1967), Fig. 1D). Movement initiation time was determined online as the time at which tangential velocity exceeded 0.026 m/s. If participants failed to initiate their movement within 75 ms from the fourth tone, the texts "too early" or "too late" were indicated on the screen. If they were

succeed, the central initial location turned to yellow from gray color. One of four targets colored by yellow appeared on the screen in between first and fourth tone (Fig. 1E). Participants were allowed various amounts of time to select and prepare their movement by presenting the target at different delays prior to the time of movement initiation. We set three different movement speed: fast (0.8 ± 0.08 m/s), medium (0.45 ± 0.045 m/s) and slow (0.25 ± 0.025 m/s) speed (Fig. 1D). At the end of the movement, if the peak speed for each movement was within the required range, the target changed color from gray to yellow. If the movement was too fast, the target changed color from gray to magenta and, if the movement was too slow, it changed color to blue. The required speed changed from block to block but was fixed within each block of 100 trials. The participants conducted 3 blocks (300 trials total) for each speed condition and the order in which participants experienced these three conditions was counterbalanced across participants. Before each new speed condition began, participants had 20 practice trials in which a target appeared at the onset of first tone, allowing 1200 ms to select and prepare the required action, therefore allowing participants to practice both initiating their movement synchronically with the fourth tone, and to execute their movement at the required speed for that block. In the main blocks for each condition, in 85 out of 100 trials, a target was shown at a random time between 0 and 500ms prior to the fourth tone. In the remaining 15 trials in each block, no target appeared but participants were still required to initiate a movement synchronously with the fourth tone. These catch trials discouraged participants from simply waiting until the target appeared before initiating a movement.

In the Point-to-Point task, participants also made planar reaching movements from a central start position toward one of four potential targets under forced response condition, exactly as in the Shooting task. Participants were asked to move at a natural speed and were required to briefly hold the cursor stationary inside the target at the end of the movement. Participants did not receive any feedback about the speed of their movements, but did receive feedback about the timing of their movement initiation, exactly as in the Shooting task. Twenty participants completed the Point-to-Point task (aged 21.85 ± 5.68 years; 10 women), none of which had participated in the Shooting task. Participants performed 3 blocks of 100 trials.

Data analysis

Raw hand position data were smoothed and differentiated using a Savitzky–Golay filter. Movement onset was detected based on the first time that the tangential velocity of the hand exceeded 0.002 ms^{-1}. Then the mean delays in our system (measured to be 100 ms) were subtracted from this time to obtain an estimate of the true time of movement initiation relative to the target appearing on the screen. The participant's action selection time in each trial was determined as the delay between the time of stimulus presentation and the time of movement initiation. Initial movement direction in each trial was defined based on the

direction of the velocity vector of the hand 50 ms after movement onset. A movement was considered as a correct trial if the initial direction of movement was within ± 22.5° of the target direction, otherwise, the trial was classified as an error. The probability of initiating an accurate movement at a given reaction time was visualized based on the proportion of accurately initiated movements within a 50 ms window around that reaction time, yielding a speed–accuracy tradeoff (Wickelgren, 1977). We quantified the speed of participants action selection time in each condition based on the center of their speed–accuracy trade-off, which we estimated via maximum likelihood by assuming that it had the shape of a cumulative Gaussian distribution (Haith et al., 2016) – equivalent to assuming that the time at which the action was selected followed a Gaussian distribution. In our primary analysis, we calculated initial movement direction at 50 msec from the movement onset and classified a trial as correct trial if its initial movement direction was within 22.5° from the target direction. Our results were reproduced whether we calculated initial movement direction at 100 ms rather than 50 ms, and whether we classified a movement as accurate when it was directed within 45° of the true target direction rather than 22.5° (see Supplementary).

Statistics

We compared the peak velocity between three different speed conditions in the Shooting Task using one-way ANOVA with Tukey post-hoc test. The difference in the estimated action selection time was analyzed with a mixed-effects ANOVA model with movement condition (Fast vs Medium vs Slow-speed conditions in the Shooting task, or Fast vs Medium vs Point-to-Point Task) as a fixed factor and with random intercept and slope. We used Tukey post-hoc tests to compare between movement conditions.

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