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Research report

Short-term motor plasticity revealed in a visuomotor decision-making task

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ABSTRACT

Selecting and executing an action toward only one object in our complex environments presents the visuomotor system with a significant challenge. To overcome this problem, the motor system is thought to simultaneously encode multiple motor plans, which then compete for selection. The decision between motor plans is influenced both by incoming sensory information and previous experience—which itself is comprised of long-term (e.g. weeks, months) and recent (seconds, minutes, hours) information. In this study, we were interested in how the recent trial-to-trial visuomotor experience would be factored into upcoming movement decisions made between competing potential targets. To this aim, we used a unique rapid reaching task to investigate how reach trajectories would be spatially influenced by previous decisions. Our task required subjects to initiate speeded reaches toward multiple potential targets before one was cued in-flight. A novel statistical analysis of the reach trajectories revealed that in cases of target uncertainty, subjects initiated a spatially averaged trajectory toward the midpoint of potential target locations before correcting to the selected target location. Interestingly, when the same target location was consecutively cued, reaches were biased toward that location on the next trial and this effect accumulated across trials. Beyond providing supporting evidence that potential reach locations are encoded and compete in parallel, our results strongly suggest that this motor competition is biased by recent trial history.

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1. Introduction

Among the most challenging problems faced by our visuomotor system is the selection of targets in a cluttered world filled with many objects that could be acted upon. One possible solution to this problem is revealed by neurophysiological studies that suggest the brain plans multiple motor programs in parallel [1–5], allowing for several targets to compete for action selection at any one time. This strategy facilitates and simplifies target selection. Because all the potential actions are simultaneously coded, selection of the final action becomes the more straightforward process of one action plan 'winning out' over the others. This motor competition requires that each potential plan be associated with levels of activation reflecting its likelihood of being selected [e.g. [1]], but it is rather poorly understood what specific target and task properties modulate this competitive process.

In a recent experiment, we found that when subjects performed rapid reaches toward two equally likely targets before one target was cued in-flight, subjects initiated a 'spatially' averaged trajectory toward the midpoint of the potential target locations [6]. This is consistent with other eye-movement and reach paradigms demonstrating that movements made in the presence of competing stimuli tend to deviate between the stimulus locations [7–10]. In a second experiment, we also showed that reach trajectories were biased both by the spatial location of the potential targets and by the number of targets on each side of space, suggesting that location and probability are factors that influence motor plan competition [6]. This pattern of results, however, is consistent with the idea that all the potential targets (and actions) have identical weights. Yet it is necessary to have a visuomotor system that can independently adjust the weightings of each potential target and action. Indeed, motor decisions are based not only on the information currently available to the sensory system, but also on previous visuomotor experience [e.g. [11]]. Visuomotor experience and the changes associated with that experience can accrue over timescales of weeks or months [12,13] but can also be seen to operate over much shorter intervals [e.g. [9,14,15,16]]. Specifically, it has been shown that the parameters of a current movement are influenced by the characteristics and intentions of the previous movement. It

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is precisely this trial-to-trial motor plasticity that we investigated in the current experiment: how the selection of a given target on one trial alters its weighting in the competition between targets on the subsequent trial.

Trial history effects reveal how visuomotor decision-making processes evolve across multiple movements [e.g. [14,15,17,18]] and have been investigated in a wide range of paradigms. For example, subjects are faster to detect targets when the location is repeated [19], and grasping kinematics are affected by the recent availability of visual feedback [20,21]. Target-directed eye movements provide a particularly good illustration of the effects of trial history: the colour, shape and location of the target on a previous trial influences both the neural activity in eye-movement-related structures during motor planning and the subsequent behavioural response [e.g. [7,22,23]]. In addition, behavioural studies have shown that reach targets embedded among distractors that vary in colour from trial-to-trial produce more variable reach trajectories than targets that maintain a colour across trials [24]. Of particular relevance is recent work investigating the effects of previously performed arm movements on subsequently performed actions. For example, avoiding a virtual obstacle on one trial will result in a more curved trajectory on the next trial even when no obstacle is present [25,26]. These results suggest that successive movements in a sequence are not programmed de novo but instead are created by slightly modifying the blueprints of the preceding movement(s) [27]. In the current study, we wanted to capitalize on this proposed holdover of motor parameters from trial-to-trial as a way of creating a disparity in the weightings assigned to two potential targets. As such, we tested if the spatial averaging between potential targets that we have previously reported [6] would be biased toward the location of a previously cued target, and if so, whether this bias would accumulate across multiple trials.

2. Methods

We recorded rapid reach movements (OPTOTRAK, 150 Hz) from 17 right-handed (mean age 25.5 years, 10 female) subjects as they reached from a start button to a touch screen (40 cm away). Trials began with participants holding down the start button and fixating a cross centered on screen for a variable time ranging from 1000 to 2000 ms. A beep signalled when fixation was replaced by a target display, consisting of one or two outline targets (1-cm radius circle, black, on a white background), and also provided the cue for subjects to initiate a reach (within 325 ms). Upon button-release, one of the target(s) in the display was cued (filled-in black) and subjects had to correct their trajectory in-flight to that location (within 425 ms) [see Fig. 1A]. To ensure rapid and accurate movements, subjects received visual feedback about their performance at the center of the screen following each trial (to see a video of the task see Supplemental Material online). There were four possible types of errors each of which would cause a different line of text to be centrally displayed: Too Early (if the start button was released before 100 ms had elapsed), Time Out (if the start button was not released within 325 ms), Too Slow (if the screen was not touched within 425 ms of button-release), or Miss (if subjects did not touch within a 6 cm × 6 cm box centered on the target). Good was displayed on trials without errors. On Too Early and Time Out trials, the final target was never cued and the trial was removed and immediately repeated (9% of trials), preserving the sequencing (see below). For analysis, we removed only those trials with the slowest movement times (slowest 5% across all participants) as well as trials where participants missed the target (6%-for analysis of Miss errors, see Supplemental Material). After trial removal, two participants were excluded from analysis, failing to meet our criterion of at least four successful repetitions of each type of trial across the experiment (leaving 15 participants for statistical analyses).

The centers of the two potential targets were 9 cm to the left and right of fixation. Single-target trials served as a baseline since subjects knew in advance what the final location of the cued target would be. In two-target trials, prior to movement onset, subjects needed to prepare for either target to be cued. We embedded specific sequences of target-cueing across trials to test the effect of a previous trial on the next trial's movement, while ensuring that the left and right targets were cued equally often across the entire experiment. Each block of trials consisted of four repetitions of the sequence shown in Fig. 1B, which itself was composed of one repeat-left and one repeat-right micro-sequence. The direction (left or right) of the first micro-sequence in each block was determined randomly and alternated thereafter. The trials of interest within a micro-sequence consisted of the set of two-target 'Repetition' trials where the final target was consecutively cued on the same side of space. A 'Repetition' sequence contained two to five repeated trials (repetition

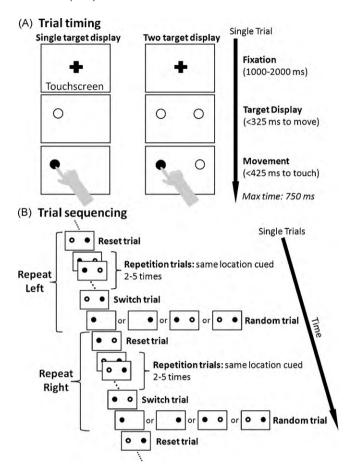


Fig. 1. (A) *Trial timing*: Trials began with the subject fixating a cross for a variable time interval (1000–2000 ms). This was followed by a target display containing one or two possible targets (shown schematically, size not to scale), which also provided the cue for subjects to initiate a reach to touch a target that would be filled in at movement onset. Upon presentation of the target display, subjects had 325 ms to lift their finger off the start button, and then an additional 425 ms to reach and touch the cued target. (B) *Trial sequencing*: Each repetition sequence consisted of one repeat-left and one repeat-right micro-sequence. Each micro-sequence began with a Reset trial (target cued opposite to the upcoming Repetition trials) followed by 2–5 Repetition trials (target cued consecutively to one side), then a Switch trial (target cued opposite preceding Repetition), and finally a Random trial (target cued on either side in a single- or two-target display).

length selected randomly but presented only once per block, per side). To ensure that the participants were unaware of the repetition manipulation, and to mitigate the effects of trial repetition on a subsequent repeat sequence, we inserted trials before and after each set of 'Repetition' trials. Thus, each micro-sequence began with a 'Reset' trial in which the cued target was presented on the side opposite the upcoming Repetition sequence. Following the Repetition sequence, there was a 'Switch' trial where the target was cued on the side opposite the repeated sequence. Finally, following the 'Switch' trial, there was a 'Random' trial where the target could be cued on either side of space and could be either a two-target or single-target trial. Following the conclusion of one micro-sequence (e.g. repeat-left), a micro-sequence in the opposite direction was presented (e.g. repeat-right). Participants completed 10 blocks for a total of 540 trials. Each block began and ended with one additional randomly selected two-target trial to again ensure that participants were unaware of the sequence manipulation. Importantly, participants in post-experiment interviews never reported detecting any contrived patterns in trial sequencing.

3. Results

We employed functional data analysis techniques [28] to fit mathematical functions (using b-splines, see Supplemental Material and our previous work [6] for description of this technique) and to spatially normalize the reach trajectories. This enabled us to use functional analyses of variance (FANOVAs) to compare reaching behaviour across the conditions of interest. A

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