

Current Biology
Supplemental Information

Motor, not visual, encoding of potential reach targets

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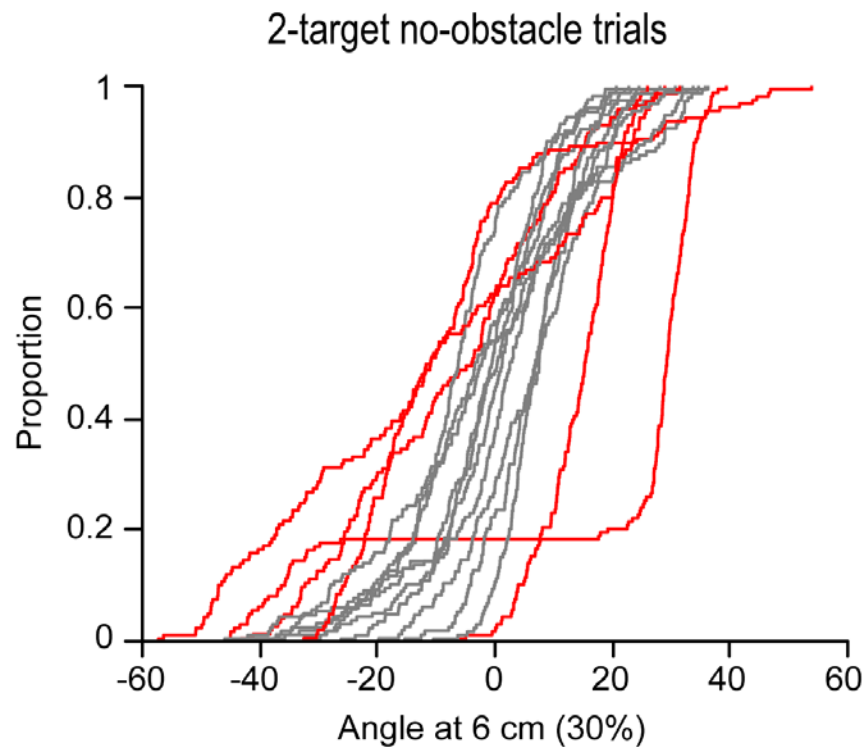


Figure S1: Cumulative frequency distributions of initial movement direction for 2-target no-obstacle trials for each participant. The reach angle at 30% of movement distance is displayed on the abscissa with frequency, expressed as a proportion of trials, displayed on the ordinate. Separate distributions are shown for each participant. The red lines show participants who did not show consistent spatial averaging effects, either because they tended to pick one of the two potential targets and move directly towards it or were highly variable. These 5 participants were excluded from further analysis.

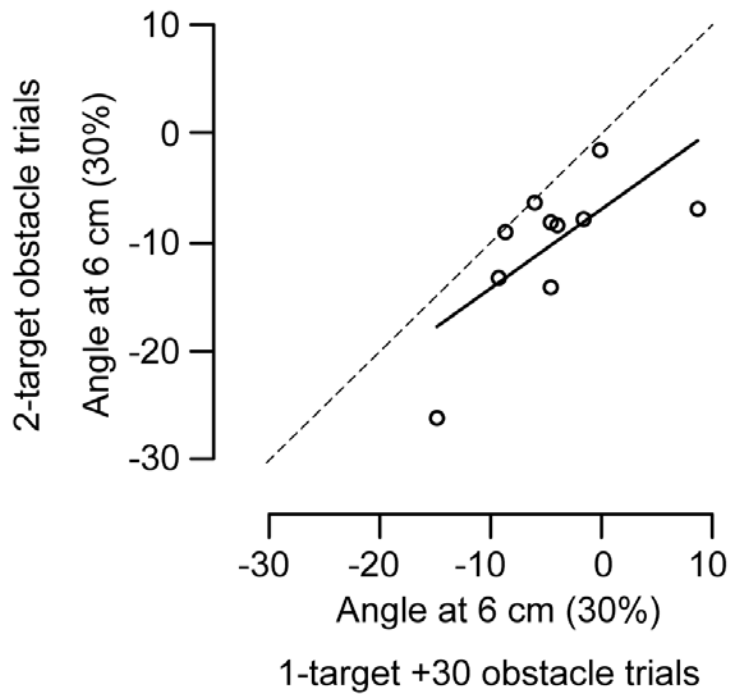


Figure S2: Relation between initial movement direction in 2-target obstacle trials and 1-target +30 obstacle trials. Average reach angle at 30% of movement distance (6 cm) in 2-target obstacle trials (ordinate) versus the corresponding angle in 1-target obstacle trials with the +30 target (abscissa). The dashed line is a unity line. Each data point represents one participant.

Supplemental Experimental Procedures

Participants

Fifteen right-handed individuals (8 males, 7 females; age range: 18 to 27 yr.) participated in the experiment after providing informed written consent. These participants were undergraduate or graduate students from Queen's University and received financial compensation (15 CAD) for their time. The Queen's University General Ethics Board approved all experimental procedures. Participants were naïve with respect to the purposes of the experiment.

Apparatus

Seated participants grasped a vertical cylindrical handle, attached to a planar robotic manipulandum (WristBOT [S1]) that moved freely in a horizontal plane and measured the position of the handle (resolution 0.01 mm). Participants moved the handle to control the position of a circular cursor (diameter 5 mm). The cursor as well as the start position and one or two targets (circles of diameter 20 mm) were displayed on a horizontal 30-inch computer screen, suspended above a horizontal mirror located halfway between computer screen and the middle of the handle. Thus, the visual stimuli appeared in the same plane as the handle. The mirror also prevented participants from seeing their hand or the manipulandum.

Stimuli

In a given trial, either one target (1-target trials) or two potential targets (2-target trials) were presented at a distance of 20 cm from the start position. In 1-target trials, the target could appear at one of three possible locations: -30° from the midline, at the midline (0°), or $+30^\circ$ from the midline (see Fig. 1A). In 2-target trials, the targets were always located at -30° and $+30^\circ$. In the obstacle condition, an obstacle, simulated by the robotic manipulandum, was displayed. The obstacle was composed of a rectangle (width 2 cm and length 30 cm) capped at one end by a semicircle (radius = 1 cm). It was oriented such that its long axis was perpendicular to the straight line between the start position and the $+30^\circ$ target and positioned such that it bisected this straight line with the tip extending 2 cm past the line (see Fig. 1A). This position, which was determined during pilot testing, ensured that the obstacle interfered with direct movements to the $+30^\circ$ but did not interfere with straight ahead movements to the 0° (or -30°) target. The obstacle was simulated as a rigid object using the robotic manipulandum, which prevented the handle from entering the obstacle. Specifically, the outside wall of the obstacle was simulated as a very stiff spring (3 N/mm) with damping (0.01 N/mm/s).

Note that we also included a condition in which the obstacle was positioned on the left (i.e., reflected across the midline). However, this condition did not turn out to be suitable for the purposes of hypothesis testing. Specifically, with the obstacle positioned on the left, participants tended to generate curved hand paths that deflected away from the obstacle when reaching for the 0° target, considerably biasing the initial direction of movement to the right of midline (i.e., clockwise). As a consequence, the condition with the obstacle positioned on the left was not ideal for disentangling whether targets were encoded in motor versus visual coordinates. Therefore, we only considered the condition with the obstacle on the right (referred to as the obstacle condition) in our analysis.

Procedure

To begin each trial, the participant moved the cursor into the start position and held it there for one second. Thereafter, either one or two targets were presented, along with the obstacle in the obstacle condition, and the participant was required to keep the cursor at the start position for an additional 750 ms. After this brief preview period an auditory 'beep' (800 Hz, 50 ms) cued

the participant to reach toward the target(s). The allowable reaction time, between the beep and movement onset, was 425 ms. Movement onset was deemed to have occurred when the center of the cursor moved 20 mm from the start position. At movement onset, one of the two potential targets in 2-target trials was cued (filled in solid) as the target. Each potential target had an equal (0.5) probability of being cued such that, at the time of movement onset, the participant did not have knowledge of which potential target would become the target. In 1-target trials, the single target was also filled in at movement onset. Following movement onset, the participant was required to move the cursor to the cued target and click on it, using a button located on top of the manipulandum handle, within 500 ms. In 2-target trials, these strict timing criteria, coupled with the target uncertainty prior to movement, encouraged participants to equally consider all the available target options prior to movement.

If the participant initiated the movement before the auditory go cue, the feedback message “too early” was displayed on the screen, and the trial was aborted. If the participant stayed in the start position for more than 425 ms following the go cue, the feedback message “too late” was displayed and the trial was aborted. If the participant’s movement took longer than 500 ms, the feedback message “too slow” was displayed. If these timing criteria were met, a trial was considered a “hit” if any part of the cursor contacted any part of the target at the time the button was pressed. Alternately, the trial was considered a “miss” if the cursor position was not in contact with the target when the button was clicked.

Each participant completed three blocks of trials. In the left and right obstacle blocks, the obstacle was presented on the left or right side of the screen and in the no-obstacle block it was absent. Each block contained 120 1-target trials (40 trials for each of the three target positions) and 160 2-target trials (280 total trials in each block). The 1- and 2-target trials were randomly distributed within each block and the order in which the blocks were completed was counter-balanced across participants. Mandatory breaks were given between each block; however, participants were permitted to take additional breaks whenever they wished.

Data Analysis

The position of the handle was recorded at 1000 Hz from the robotic manipulandum and digitally low pass filtered at 20 Hz (fourth-order, no-lag, dual-pass Butterworth filter). For analysis, we were primarily interested in the direction of the early portion of the movement that, in 2-target trials, occurred prior to corrections being made to the cued target and thus provides a direct ‘read-out’ of multiple target encoding [S2]. Specifically, we extracted the handle (or cursor) position at 30 % (6 cm) of the displacement from the start position to any one of the targets (20 cm). The initial direction was defined as the direction of the straight line from the start position to this handle position. Previous studies have used 40 % [S3] as well as 60 % [S2, S4, S5] of the distance from the start position as the point prior to correction. However, in the current experiment, we observed occasional corrections at the 40 % mark. Because we were interested in the initial movement that occurred before corrections could be made based on visual feedback, we included both hits and misses, completed within the reaction time requirements, in the final analyses. This results in the exclusion of 6.2 % of all trials.

Previous studies have demonstrated that when participants initiate a reach towards two potential targets, one of which will be cued as the target *after* movement onset, most participants will aim towards the midpoint and then make a correction toward the cued target [S2-5]. This behavioural phenomenon, which also consistently appears in the eye movement literature [S6], has often been labelled ‘spatial averaging’ behaviour. However, for a variety of reasons, some participants fail to exhibit spatial averaging. Thus, some participants appear to adopt a strategy

that involves either picking one target (e.g., the right target) to aim towards on most trials or, alternatively, randomly picking a target, on each trial, to aim towards [S3]. Others participants exhibit a strong rightward or leftward bias and still others simply fail to aim in a consistent direction. Because we were interested in what the presence of the obstacle might reveal about the fundamental mechanisms of spatial averaging behaviour, we excluded participants who did not exhibit consistent spatial averaging. To identify such participants, we examined the cumulative frequency distribution of initial movement directions in the 2-target no-obstacle condition. The red traces in Fig. S1, which shows the distributions for all participants, are from the five participants who failed to exhibit consistent averaging. These participants were removed from further analyses.

Supplemental Results

Error rates

To determine whether the obstacle had any effect on the error rate in 1-target trials, we performed a 3 (single target position) x 2 (presence of obstacle) repeated measures ANOVA. Neither target position ($F_{2, 18} = 2.68$; $p = 0.103$) nor obstacle ($F_{1, 18} = 4.9$, $p = 0.062$) significantly affected error rate, and there was no interaction ($F_{2, 18} = 0.067$; $p = 0.94$). To determine whether the obstacle had any effect on error rate in 2-target trials, we performed a 2 (cued target, $+30^\circ$ versus -30°) by 2 (obstacle, present versus absent) repeated measures ANOVA. Neither cued target ($F_{1, 18} = 0.25$; $p = 0.631$) nor obstacle ($F_{1, 18} = 1.72$, $p = 0.22$) significantly affected error rate, and there was no interaction ($F_{1, 18} = 0.125$; $p = 0.73$). Thus, the obstacle did not influence participants' ability to hit the target in either 1-target or 2-target trials. In addition, any early trajectory differences between the obstacle and no-obstacle conditions in 2-target trials cannot be attributed to different levels of difficulty in obtaining the two targets.

Analysis of initial movement direction in 2-target trials

In our analysis of initial movement direction in 2-target trials in the main manuscript, we collapsed across cued target position. Because the actual target was cued at movement onset, the initial movement direction should not be influenced by whether the $+30^\circ$ or -30° target was cued. To verify that this was the case, we carried out separate paired t-tests for the obstacle and no-obstacle conditions to assess the effect of cued target position on the initial movement direction. In the no-obstacle condition, there was no significant difference ($t_9 = -0.96$; $p = 0.36$) between the initial movement directions when the -30° ($M = 0.9^\circ$, $SE = 1.5^\circ$) and the $+30^\circ$ ($M = 1.8^\circ$, $SE = 1.5^\circ$) targets were cued. Likewise, in the obstacle condition, there was no significant difference ($t_9 = -1.36$; $p = 0.21$) between the -30° ($M = -10.4^\circ$, $SE = 2.2^\circ$) and the $+30^\circ$ ($M = -9.8^\circ$, $SE = 2.0^\circ$) cued targets. The average time, based on participant means, from movement onset—defined as the time at which the handle first moved 0.5 cm from the start position—to when the handle reached 30 % of the distance to the target (i.e., 6 cm from the start position) was 110 ms ($SE = 8$ ms). Thus, on average, we would not expect the initial movement trajectory, from the start position to the 30 % mark, to be influenced by visual feedback [e.g., S7, S8, S9].

Additional support for motor averaging

In 1-target obstacle trials directed towards the $+30^\circ$ target, considerable variability in the initial movement direction was observed across participants. (This is reflected in the larger spread of the cumulative distribution of initial directions in these trials; see Fig. 1C). If the initial movement direction in 2-target trials reflects a weighted average of the movements to each potential target, then, across participants, the initial direction in 2-target obstacle trials should

depend on the initial direction in 1-target obstacle trials. As shown in Fig. S2, a positive linear relation was observed ($r^2 = 0.69$; $p < 0.026$). That is, participants who aimed further to the left when reaching to the single $+30^\circ$ target in the presence of the obstacle, also aimed further to the left in 2-target obstacle trials, consistent with motor averaging.

In addition, the visual averaging hypothesis predicts that the initial movement direction in 1-target obstacle trials directed towards the $+30^\circ$ target should be similar to the initial movement direction in 2-target obstacle trials, whereas the motor averaging hypothesis predicts that the initial direction in 2-target obstacle trials should be rotated leftwards relative to the initial movement direction in 1-target obstacle trials directed towards the $+30^\circ$ target. Consistent with motor averaging, and inconsistent with visual averaging, we find that the initial direction in 2-target obstacle trials ($M = -10.13^\circ$, $SE = 2.08^\circ$) is significantly different ($t_9 = 3.47$; $p = 0.007$) than the initial direction in 1-target obstacle trials with the 30° target ($M = -4.60^\circ$, $SE = 1.98^\circ$). This effect can be appreciated in Fig. S2 where the data points for all participants fall below the unity line.

Supplemental Discussion

Multiple plans for saccadic eye movements versus reaching movements

Work on oculomotor control has demonstrated that multiple saccadic eye movements, associated with different gaze targets, can be prepared prior to an actual eye movement being generated [S10-13]. In particular, activity associated with saccades to multiple potential targets can be observed in the intermediate layers of the superior colliculus, the ‘motor cortex’ of the oculomotor system, only two synapses removed from the motor neurons driving eye movement [S14]. Thus, in the oculomotor system, salient visual targets appear to be directly mapped onto motor responses associated with saccades to these targets, with omnipause neurons in the brainstem preventing this activity from generating the eye movement until the appropriate time [S14]. Notably, however, under the appropriate conditions (e.g., very short saccade latencies), spatial averaging of saccadic eye movement commands associated with multiple competing movement plans can be observed [e.g., S15, S16, S17].

Why then is it not a forgone conclusion that multiple competing reach motor plans be similarly maintained in parallel, as shown in the current paper? First, the circuitry underlying saccadic eye movements is very different from the circuitry underlying reaching movements. The limb motor control system does not have such a direct visual-to-motor mapping as is evident in the oculomotor system. Indeed, although Cisek and Kalaska [S18] reported delay period neural activity associated with multiple potential reach targets in dorsal premotor cortex, such neural response properties were not observed in primary motor cortex, the main source of cortical projections to spinal cord. Furthermore, although there are inhibitory projections from sensorimotor cortical areas to the spinal cord, gating mechanisms equivalent to those achieved by omnipause neurons have not been observed in the limb motor control system. Although there is evidence that there are projections from the superior colliculus to shoulder muscles [S14, S19, S20], which may form part of a general orienting response that facilitates rapid arm movements [S21], we are unaware of any evidence in primates to suggest that this projection is capable of supporting complex, fully specified reaching movements.

Second, the functions performed by saccadic eye movements greatly differ from those of reaching movements. We typically make 2-3 saccades per second to sample our surrounding visual environment and thus, it makes some sense to continuously prepare multiple potential eye movements for the most salient competing visual targets. In contrast, the frequency with which

we typically perform reaching and grasping movements is relatively low. In addition, the complexity of reach movement planning might make it unlikely that circuits involved in limb motor control would specify multiple competing hand movements for potential targets in advance of selecting a target to act on. Reach movement planning is generally thought to involve a number of complex processes including various coordinate transformations (e.g., from gaze centered to hand centered coordinates), the use of internal models to map between motor commands and limb motion, and the implementation of task-specific control policies for intelligent feedback control [S22-27]. The findings presented here suggest that both the oculomotor and limb motor control systems, despite utilizing distinct neural circuitries and having different computational requirements, employ the same basic functional mechanism for dealing with target uncertainty; that is, they both appear capable of specifying multiple movement plans in parallel.

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