

Motor, not visual, encoding of potential reach targets

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We often encounter situations in which there are multiple potential targets for action, as when, for example, we hear the request “could you pass the ...” at the dinner table. It has recently been shown that, in such situations, activity in sensorimotor brain areas represents competing reach targets in parallel prior to deciding between, and then reaching towards, one of these targets [1]. One intriguing possibility, consistent with the influential notion of action ‘affordances’ [2], is that this activity reflects movement plans towards each potential target [3]. However, an equally plausible explanation is that this activity reflects an encoding of the visual properties of the potential targets (for example, their locations or directions), prior to any target being selected and the associated movement plan being formed. Notably, previous work showing spatial averaging behaviour during reaching, in which initial movements are biased towards the midpoint of the spatial distribution of potential targets [4–6], remains equally equivocal concerning the motor *versus* visual encoding of reach targets. Here, using a rapid reaching task that disentangles these two competing accounts, we show that reach averaging behaviour reflects the parallel encoding of multiple competing motor plans. This provides direct evidence for theories proposing that the brain prepares multiple available movements before selecting between them [3].

Behavioural studies have shown that individuals, when simultaneously presented with multiple competing reach targets and required to rapidly act before knowing the final target location, initially launch their movements towards the ‘spatially averaged’

midpoint of the targets before correcting their movements to the selected target location [4–6]. The mechanisms underlying this ubiquitous behaviour are unclear; it may reflect the simultaneous implementation of multiple competing motor plans (i.e. a motor average of competing movement paths) or the preparation of a single movement towards an averaged visual-spatial target location (i.e. a visual average of target directions). Here, we show that reaching movements toward multiple potential targets reflect the simultaneous implementation of competing action plans. Previous work has shown that multiple competing eye movement plans can be maintained in parallel in oculomotor brain structures (for example [7,8]). Our new results suggest that the same is true for the preparation of complex reaching movements.

Participants ($n = 10$) moved the handle of a robotic manipulandum to control the position of a cursor on a horizontal screen. In each trial, either one target (at -30° , 0° or $+30^\circ$; see Figure 1A) or two potential targets (at -30° and $+30^\circ$) were presented and, following a brief delay period (750 ms), an auditory beep cued participants to initiate a movement, within 425 ms, towards the target(s). The actual target (randomly selected in 2-target trials) was only cued (filled-in) at movement onset and the movement was to be completed within 500 ms. On some of the trials, an obstacle (simulated with the robot) was displayed to the right of midline and carefully positioned such that participants would select straight ahead initial movements for both the 0° and $+30^\circ$ targets. Accordingly, when presented with two potential targets (-30° and $+30^\circ$), participants

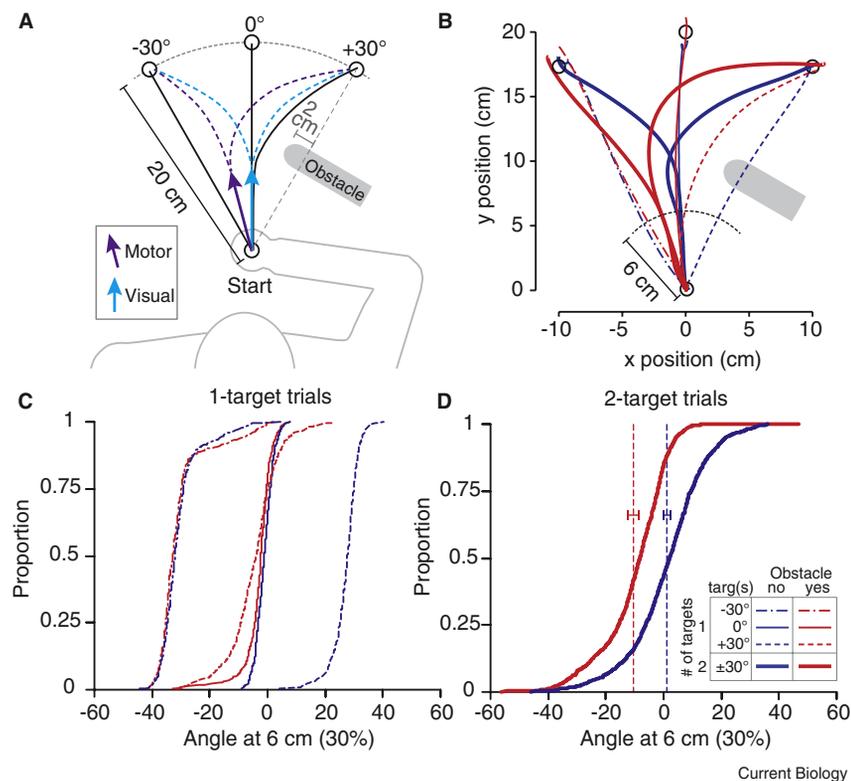


Figure 1. Experimental paradigm and results.

(A) Schematic of experimental setup and predicted hand paths for 1-target (black traces) and 2-target (purple and cyan traces) obstacle trials. The purple and cyan arrows indicate the predicted initial hand directions for motor plan and visual target averaging, respectively. (B–D) The key in (D) applies to (B), (C) and (D). (B) Single trial data from a representative participant. For analysis, reach angle at 30% of movement distance (i.e., arc at 6 cm) was extracted. (C) Cumulative frequency distributions, for all trials and participants, of initial movement direction in 1-target trials for the no-obstacle and obstacle conditions. (D) Corresponding distributions for 2-target trials, computed the same as in (C). Vertical dashed lines and horizontal error bars denote group-level means and associated standard errors.

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were fully able to adopt the visual strategy of aiming toward their spatially averaged position (i.e. 0° position; cyan arrow vector in Figure 1A), before correcting their trajectory in-flight to the cued target position. However, because the obstacle's position necessarily affected the prepared movement path associated with one of the potential targets (+30° target), a weighted average of motor plans to the two potential targets would instead result in a counterclockwise rotation of the initial reach vector (purple arrow vector in Figure 1A). Thus, the critical test of whether the potential reach targets were being encoded in visual versus motor coordinates was the direction of the initial reach vector in 2-target obstacle trials, in comparison to 2-target no-obstacle trials.

Figure 1B shows trajectories from a representative participant for both one and two target trials in both the no-obstacle and obstacle conditions. To quantify the direction of the initial movement, we determined the angle of the reach vector from the start position to the position of the handle when it reached 6 cm from the start position (30% of the distance to any target), a point before corrective movements to the cued target were made (see Supplemental Information). Figures 1C and 1D show cumulative distributions, combining all trials and participants, of the initial movement direction for one and two target trials, respectively, with separate distributions shown for the no-obstacle and obstacle conditions. Importantly, the initial movement direction for the 0° target in 1-target trials did not differ ($P = 0.15$) in the no-obstacle ($-1.1 \pm 0.5^\circ$, mean \pm SE) and obstacle ($-3.0 \pm 1.0^\circ$) conditions, indicating that the obstacle did not interfere with participants' ability to aim toward the averaged visual position of the -30° and $+30^\circ$ targets (i.e. 0°).

Clearly, however, the obstacle position markedly affected the 1-target movements towards the $+30^\circ$ target, such that the initial movement direction in these trials ($-4.6 \pm 2.0^\circ$) was similar to the direction in 1-target trials, with and without the obstacle, to the 0° target ($P > 0.16$ in both cases). Consistent with previous work

[4,9], on 2-target no-obstacle trials, participants initially aimed toward the visual midpoint of the two potential targets, before correcting to the cued target (after the handle had travelled 6 cm; see solid blue trace Figure 1D). Critically, with respect to the hypotheses being tested, the initial reach direction in 2-target obstacle trials ($-10.1 \pm 2.1^\circ$; red solid trace in Figure 1D) was significantly ($P < 0.001$) rotated counterclockwise, relative to 2-target no-obstacle trials ($1.3 \pm 1.5^\circ$; solid blue trace). This finding is consistent with the idea that the initial movement, in the obstacle condition, arises from a weighted average of the movement paths to the -30° and $+30^\circ$ targets (purple arrow in Figure 1A) and not with the notion that the initial movement is launched towards the visually averaged target position (cyan arrow in Figure 1A).

The current findings suggest that spatial averaging effects during reaching (for example [4,9]) — as well as activity in sensorimotor areas associated with potential reach targets [1] — arise from the simultaneous encoding of multiple competing motor plans, and not a simple visual-spatial averaging of potential target locations and/or a high-level cognitive strategy of launching an initial movement in a spatially-averaged direction prior to accumulating sensory evidence in favour of one target versus another. The parallel specification of multiple fully elaborated reaching movements, each of which can be implemented in a moment's notice, may reflect a more ancient, evolutionarily conserved mechanism for producing rapid, effective behaviour in the presence of environmental dynamics and uncertainty [3,10].

Supplemental Information

Supplemental Information includes two Figures, Experimental Procedures, Results, and Discussion and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.08.046>

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