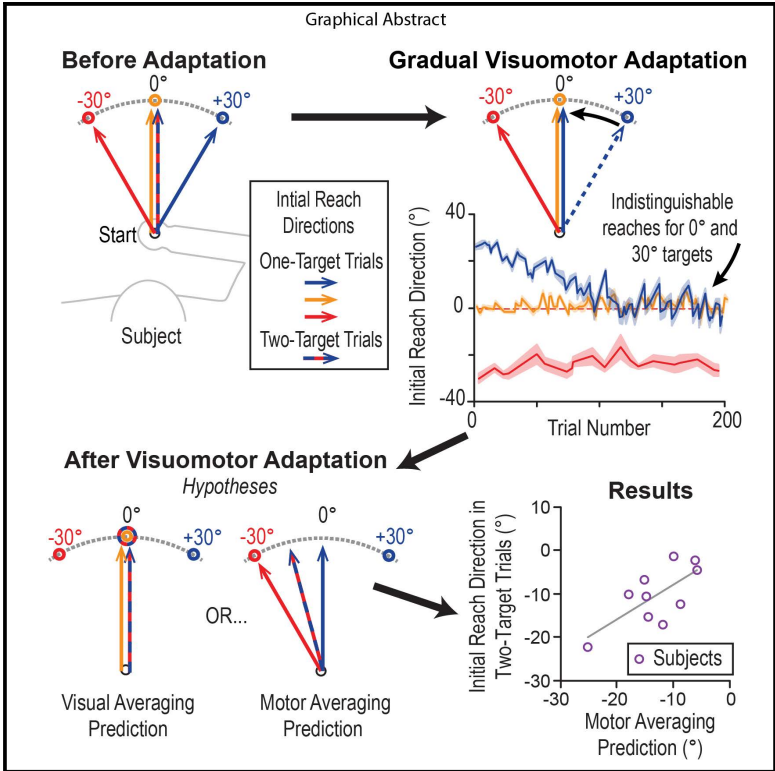# Cell Reports

Rapid Automatic Motor Encoding of Competing Reach Options

Graphical Abstract

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In Brief

Gallivan et al. show, by dissociating the visual direction of potential targets from the movement directions required to reach them, that reaches under target uncertainty reflect an average of corresponding movement, and not visual, directions. This suggests that competing action options are directly mapped onto corresponding motor representations in cortex.

Highlights

- Previous work suggests that competing movements are prepared for potential targets

- We dissociated, unbeknownst to subjects, the motor versus visual directions of targets

- Movement direction toward potential targets reflects a rapid coding of reach paths

- This suggests an automatic conversion of action options into associated movements

CellPress

Report

Rapid Automatic Motor Encoding of Competing Reach Options

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SUMMARY

Mounting neural evidence suggests that, in situations in which there are multiple potential targets for action, the brain prepares, in parallel, competing movements associated with these targets, prior to implementing one of them. Central to this interpretation is the idea that competing viewed targets, prior to selection, are rapidly and automatically transformed into corresponding motor representations. Here, by applying target-specific, gradual visuomotor rotations and dissociating, unbeknownst to participants, the visual direction of potential targets from the direction of the movements required to reach the same targets, we provide direct evidence for this provocative idea. Our results offer strong empirical support for theories suggesting that competing action options are automatically represented in terms of the movements required to attain them. The rapid motor encoding of potential targets may support the fast optimization of motor costs under conditions of target uncertainty and allow the motor system to inform decisions about target selection.

INTRODUCTION

During the course of any given day, we make myriad decisions about which action, from among those immediately available to us, to perform next. It has been shown, in the context of goal-directed reaching (Cisek and Kalaska, 2005; Cui and Andersen, 2011; Klaes et al., 2011), that competing potential targets elicit separate neural representations in sensorimotor brain areas prior to one of the targets being selected. One influential but controversial idea, which resonates with Gibson's notion of action affordances (Gibson, 1979), is that this activity represents competing motor representations associated with the targets (Cisek, 2007; Cisek and Kalaska, 2010). However, given that these brain areas exhibit both sensory- and motor-

related response properties, it is also possible, and difficult to rule out, that this neural activity instead represents purely visual or spatial information about the targets (Ochiai et al., 2002; Pesaran et al., 2006; Pearce and Moran, 2012).

Behavioral studies have investigated the encoding of competing reach targets using variants of the "go-before-you-know" task, in which individuals are required to launch a movement toward two or more potential targets before knowing the final target. In such tasks, participants often exhibit spatial averaging behavior whereby reaches are initially aimed toward the midpoint of the distribution of potential targets (Ghez et al., 1997; Chapman et al., 2010a; Gallivan et al., 2011), which is effective in terms of reducing the cost of the in-flight corrective actions required once the target is selected following movement onset (Hudson et al., 2007; Stewart et al., 2013; Haith et al., 2015a). A fundamental question, with important ramifications for understanding the mechanisms underlying both movement planning and decision making, is how spatial averaging behavior emerges. One possibility is that, when presented with competing potential targets, the brain prepares and then executes a movement in the average visual direction of these targets. From a computational perspective, this "visual encoding" strategy could be viewed as advantageous, as it would not require that the brain devote further resources to forming motor representations of each potential reach target. However, it is also possible that the brain does, in fact, form motor representations of each potential target and then prepares a movement based on these representations. According to this alternative "motor encoding" account, spatial averaging could arise either from averaging the movement parameters (i.e., the initial movement directions or the final hand positions) of reach plans formed for each potential target or from computing an optimal movement based on motor representations of these targets. In instances in which the target is selected prior to movement onset, such motor encoding may facilitate the rapid launching of the associated movement (Cisek, 2007; Gallivan et al., 2015, 2016a). Moreover, the motor encoding of potential targets could also provide a mechanism through which movement-related parameters (e.g., costs) are factored into decisions among competing options (Cos et al., 2012).
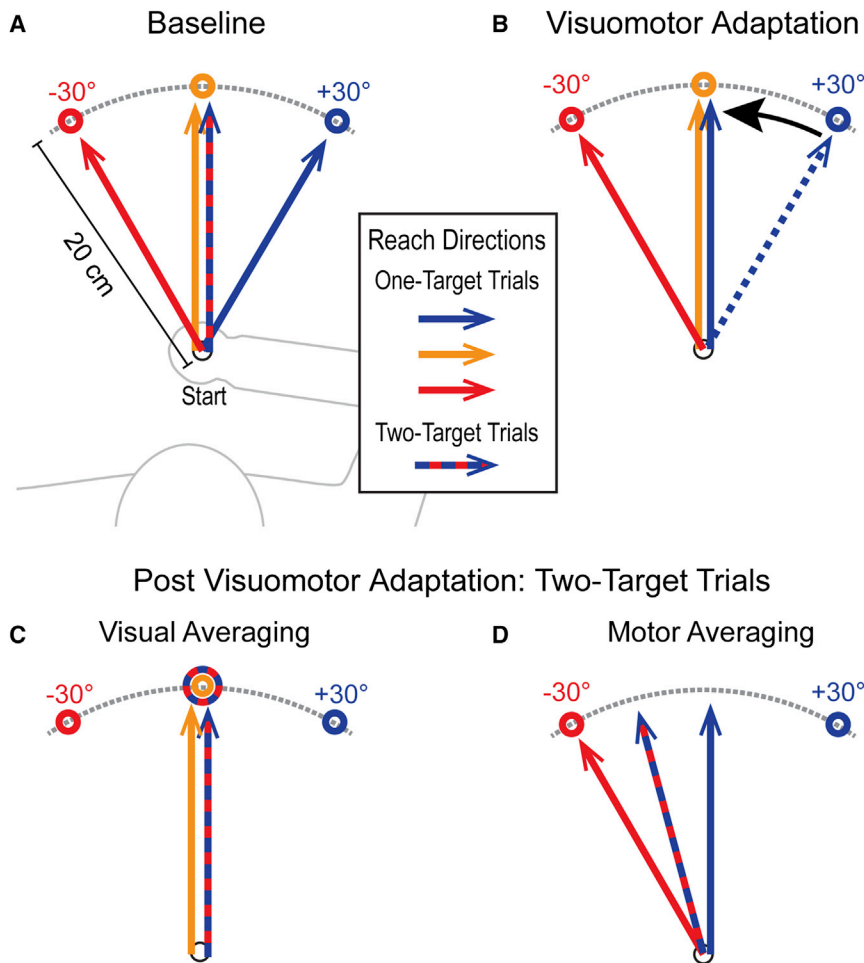
Figure 1. Experimental Paradigm and Hypotheses

(A) Predicted initial reach directions for one- and two-target trials involving the −30°, 0°, and +30° targets prior to adaptation to visuomotor rotations (day 1 of testing). A straight-ahead initial movement in −30°/+30° two-target trials (striped arrow) is expected regardless of whether participants aim for the average target position (visual averaging) or execute an average of movement paths for the two potential targets (motor averaging).

(B) Predicted initial reach directions following adaptation to visuomotor rotations gradually applied to the 0° and +30° targets and designed such that participants moved their hands straight ahead (∼0°) for both the 0° and +30° targets and directly to the −30° target in one-target trials (day 2 of testing).

(C) Under visual averaging, the initial movement direction in post-adaptation −30°/+30° two-target trials should be straight ahead if participants aim for the average visual target position (striped arrow).

(D) Under motor averaging, due to this compression of motor space, the initial movement direction in post-adaptation −30°/+30° two-target trials (striped arrow) should be rotated leftward if participants execute an average of the potential motor paths.

To determine which of these above accounts is correct (i.e., visual versus motor encoding of potential targets), we designed an experimental task in which participants moved the handle of a robotic manipulandum in a horizontal plane to move a virtual cursor from a start position toward one or two potential targets (see Experimental Procedures for details). In the key trials in our experiment, participants performed reaching movements toward single targets located at −30°, 0°, and +30°, as well as go-before-you-know reaches toward two potential targets located at −30° and +30°. In the baseline condition, we found that participants reached directly toward single targets (Figure 1A, solid lines) and launched reaches in the spatially averaged direction in two-target trials (Figure 1A, striped arrow). Such behavior, as noted above, is consistent with both the visual and motor encoding of potential targets. So, to directly test between these alternate accounts, we then gradually adapted participants to visuomotor rotations such that they unwittingly produced identical straight ahead (∼0°) one-target movements for both the 0° and +30° targets (Figure 1B; see also Hirashima and Nozaki, 2012). Here, following adaptation, the visual and motor encoding hypotheses now make different predictions with respect to the initial movement direction in two-target trials. The visual encoding hypothesis predicts that the initial direction will be toward the

spatial midpoint of the targets (Figure 1C, striped arrow), because the visually averaged direction is ∼0° and reaches to the 0° target are unaffected by the applied visuomotor rotations. In contrast, the motor encoding hypothesis predicts that the initial direction (Figure 1D, striped arrow) should be midway between the adapted one-target movement toward the +30° target (Figure 1D, blue arrow) and the (non-adapted) one-target movement toward the −30° target (Figure 1D, red arrow). Critically, we applied the visuomotor rotations gradually so that participants were unaware of the dissociation between their visual and motor space. In addition, participants were required to initiate reaches as soon as the targets were presented. These two features of the task, importantly, guard against the use of deliberate cognitive strategies (Stewart et al., 2014; c.f. Gallivan et al., 2015) and allow us to assess whether putative motor encoding is automatic (i.e., non-conscious) in nature. We also removed performance feedback in these two-target trials so as to prevent any error feedback learning (c.f. Stewart et al., 2014).

RESULTS

On day 1 of testing, the purpose of which was to obtain baseline performance measures, participants completed the pre-adaptation phase. Here, in each trial, either one target (−30°, −15°, 0°, and +30°) or two potential targets (with the left target at −30° and the right target at −20°, −10°, 0°, +10°, +20°, or +30°) were presented, and immediately following target presentation, an auditory beep cued participants to initiate a movement toward the
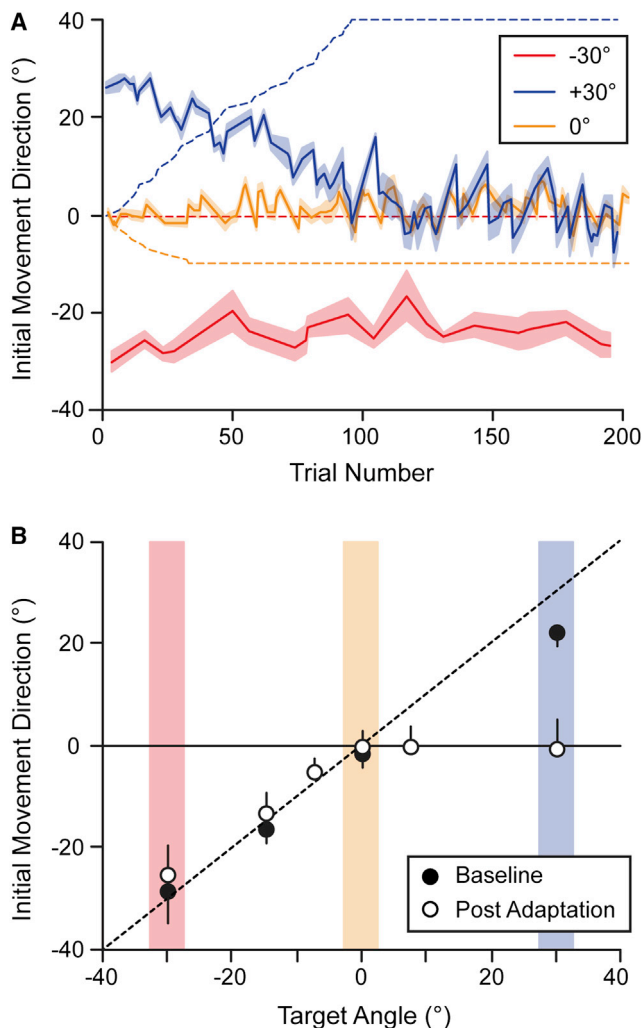
Figure 2. Initial Movement Directions during and after Visuomotor Adaptation

(A) Direction of the robot handle, relative to the start position, at 30% of the distance to the targets as a function of trial number during the adaptation phase. The red, orange, and blue lines represent one-target trials involving the −30°, 0°, and +30° targets, respectively. Each line represents the mean across participants, and the shaded region represents ±1 SE. The color-matched dashed lines show the visuomotor rotations applied to each target. Note that the +40° and −10° rotations were increased linearly over each trial of the +30° and 0°, respectively, and the rotations applied appear jagged in the plot due to the spacing of these trials among the other trials.

(B) Average initial movement direction for one-target trials (based on participant medians) as a function of target angle during baseline testing on day 1 (black circles) and after adaptation on day 2 (white circles). The dashed line is the unity line, and the vertical black lines represent ±1 SD.

target(s). Importantly, the actual target (randomly selected in two-target trials) was only cued (filled in) at movement onset. For each target display, visual feedback was removed on half of the trials.

On day 2 of testing, participants completed the adaptation and post-adaptation phases. During the adaptation phase, we gradually applied opposing visuomotor rotations (up to +40° and

−10°, respectively) to the +30° and 0° targets (Figure 2A, dashed lines). This caused the participants to adapt the initial direction of their movements for the 30° target while maintaining the initial reach direction for the −30° and 0° targets (Figure 2A, solid lines). Critically, we found that, during the latter half of the adaptation trials, during which the visuomotor rotations were held constant, participants' initial movement directions were approximately straight ahead (0°) for both the 0° and +30° targets and approximately in the direction of the target for the −30° target. Notably, during post-experiment debriefing, participants reported being unaware of the visuomotor rotations being applied.

During the post-adaptation phase, participants then completed two-target trials, all without visual feedback of the cursor, and one-target trials (at −30°, −15°, −7.5°, 0°, +7.5°, and +30° targets) both with and without this visual feedback (see Supplemental Experimental Procedures and Figure S1). Figure 2B shows the average initial movement direction for one-target trials as a function of target angle during baseline testing on day 1 (black circles) and after adaptation on day 2 (white circles). On day 1, we found that movements were aimed approximately in the direction of the targets. On day 2, following adaptation to the visuomotor rotations applied to the +30 and 0° targets, we instead found that movements to the 0°, +7.5°, and +30° targets tended to be directed straight ahead (0°) whereas movements to the −30°, −15°, and −7.5° targets were approximately in the direction of the target (Figure 2B).

The fact that participants learned to produce similar straight-ahead movements for separate visual target locations (i.e., the 0° and +30° targets) allowed us to critically test whether, when simultaneously presented with competing +30° and −30° targets, initial movement directions correspond to the average visual direction of the potential targets (visual averaging) or rather the average direction of the movement paths toward the potential targets (motor averaging). That is, if a participant aimed to the average target position, we would expect the initial movement direction to be roughly straight ahead because movements toward the 0° target location were not rotated away from that position (Figure 1C, striped arrow). Conversely, if the initial movement corresponds to an average of the constituent single-target movement directions, we would expect the initial direction to be biased to the left (i.e., rotated counterclockwise) because of the visuomotor rotation applied to the +30° target (Figure 1D, striped arrow).

Figure 3A shows cumulative distributions, combining data from all participants and trials, of initial movement directions in one- and two-target non-visual feedback trials involving the −30° and +30° targets, with separate distributions shown for the day 1 baseline (dashed lines) and day 2 post-adaptation phases (solid lines). Consistent with previous work, we found that the distribution of initial directions in −30°/+30° two-target trials on day 1 (dashed purple line) was centered close to 0° (Chapman et al., 2010a; Gallivan et al., 2011; Stewart et al., 2014). Critically, however, the distribution for these trials on day 2 (solid purple line) was shifted significantly leftward (i.e., counterclockwise). Figure 3B shows representative day 2 hand paths, from a single participant, for −30° and +30° one-target trials and for −30°/+30° two target trials in which either the −30° or +30° target was selected. The open circles show, for
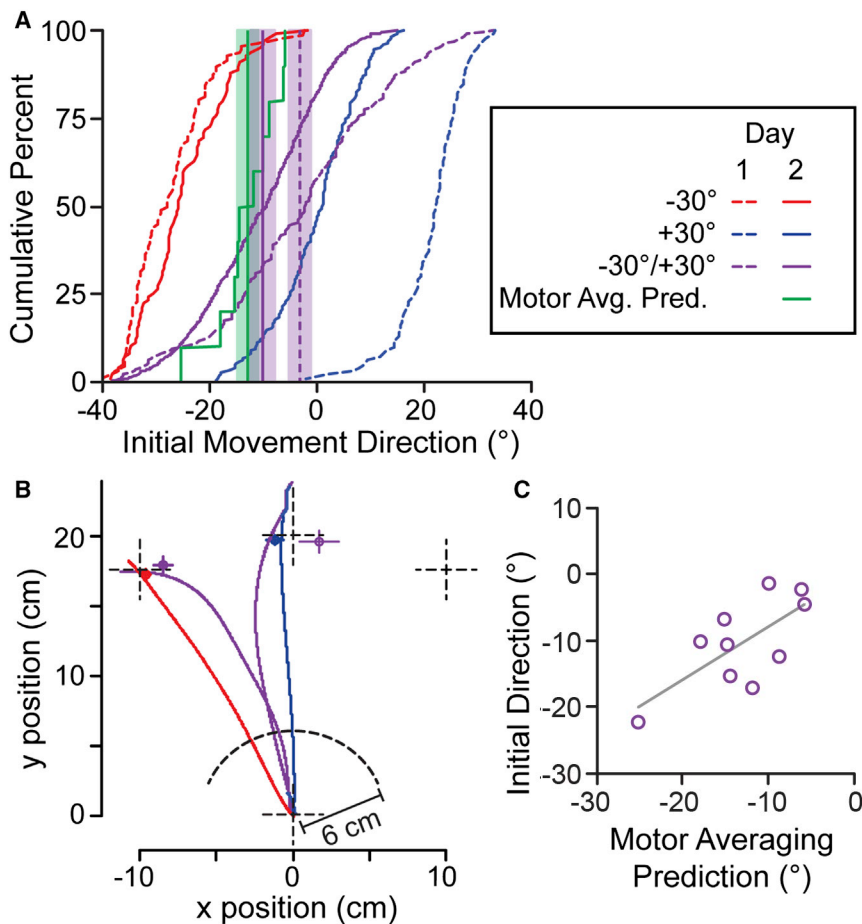
Figure 3. Test of the Motor Averaging Hypothesis

(A) Cumulative distributions of initial movement directions (i.e., handle direction at 30% of the target distance) and the predicted initial movement direction on day 2 assuming motor averaging. Note that the distribution for the motor averaging prediction is based on a single value per participant (n = 10). The vertical lines show mean initial directions for the −30°/+30° trials on days 1 and 2 and the predicted motor average on day 2. The widths of the shaded regions represent ±1 SE. The legend applies to all panels.

(B) Representative hand paths from a single participant in trials without visual feedback following adaptation on day 2. Note that movement corrections in two-target trials (purple traces) occurred after the hand traveled 6 cm or 30% of the distance to the targets. The circles represent the mean reach endpoint locations (i.e., handle "click" positions), based on participant medians, for the four trial types; the x and y error bars represent ±1 SE. The dashed crosshairs indicate the locations of the −30°, 0°, and +30° targets and the start position.

(C) Relation between median initial movement direction in −30°/+30° trials on day 2 and the day 2 motor averaging prediction. Each point represents a participant, and the gray line is the linear regression line (r = 0.70; p = 0.024).

each of these trial types, the mean endpoint positions, averaged across participant medians, at which participants "clicked" the handle, believing they had reached the target. To quantify the shift in the initial direction of −30°/+30° two-target trials, we computed, for each participant, the median direction in these trials on days 1 and 2 (see dashed- and solid-lined vertical purple lines in Figure 3A, respectively). A paired t test using these median values revealed that the direction on day 2 (M = −10.25°; SE = 2.12°) was significantly less (t_9 = −2.79; p = 0.021) than on day 1 (M = −3.26°; SE = 1.92°). This shift in initial direction is consistent with the motor averaging hypothesis. Furthermore, this shift is inconsistent with the visual averaging hypothesis, if we assume (under the visual averaging hypothesis) that movements directed toward the visual averaged target are largely unaffected by the visuomotor rotations. (See the Supplemental Experimental Procedures and Figure S2, where we directly test the visual averaging hypothesis and show that this hypothesis is not consistent with our results.)

To directly test the idea that the reaches executed toward multiple potential targets are predicted by a weighted average of the movement paths to each single target individually (i.e., a motor average), we computed, from the one-target trials, the initial reach direction that we would expect to observe in −30°/+30° two-target post-adaptation trials if this was indeed the case.

To derive this predicted direction, we first developed a weighting, for each participant, based on their initial directions in −30° and +30° one-target pre-adaptation trials without cursor feedback (from day 1). The weighting (w), which captures participants' inherent trajectory biases in the −30°/+30° two-target trials, was computed as follows: $w = (\Theta_{-30°/+30°} - \Theta_{-30°})/(\Theta_{30°} - \Theta_{-30°})$, where Θ is the initial direction and a value above 0.5 indicates a rightward (or clockwise) bias. We then applied this subject-specific weighting to the initial directions in post-adaptation −30° and +30° one-target trials without cursor feedback (from day 2) to obtain the predicted motor average direction for each participant. (Note that, in carrying out this procedure for each participant, we used median values for each trial type.) The weights across participants ranged from 0.34 to 0.62, with an average of exactly 0.50.

The green curve in Figure 3A shows the cumulative distribution of this predicted motor average on day 2. Note that, because this distribution is based on a single value per participant, this distribution is composed of ten unique values, equaling the total number of participants analyzed. Overall, we found that the predicted motor average (mean = −13.04°; SE = 1.85; see green vertical line in Figure 3A) was highly similar to the initial movement direction (mean = −10.25°) in −30°/+30° two-target day 2 trials, and a paired t test failed to reveal any significant difference (t_9 = 1.79; p = 0.11) between the two. Further analysis showed a significant linear relationship (r = 0.70; p = 0.024) between this predicted motor average and the actual reach movements executed

toward the competing targets (Figure 3C). This finding, combined with all the results presented above, provides compelling evidence for the idea that individuals, when presented with multiple action options, generate initial reach vectors that closely resemble an average vector of the movements toward each target individually.

Because the visuomotor rotations were introduced gradually, such that participants would not be aware of the rotations, adaptation should be driven by implicit processes without a contribution from explicit or cognitive processes (McDougle et al., 2015, 2016). As a consequence, we would not expect to observe an increase in reaction time (i.e., the time from target presentation to reach onset) from the baseline phase on day 1 to the post-adaptation phase on day 2 (Fernandez-Ruiz et al., 2011; Haith et al., 2015b). To assess this prediction, for each participant, we computed, for each phase, the median reaction time in one-target trials ($-30°$, $0°$, and $+30°$ trials) and two-target trials ($-30°/+30°$ trials). A phase by target number repeated-measures ANOVA revealed that, in fact, reaction time was significantly shorter ($F_{1, 9} = 18.3$; $p = 0.002$) in the post-adaptation phase ($M = 271$ ms; $SE = 9$ ms) than in the baseline phase ($M = 307$ ms; $SE = 9$ ms). We found no effect of target number ($F_{1, 9} = 1.54$; $p = 0.246$) and no interaction ($F_{1, 9} = 4.10$; $p = 0.074$). The decrease in reaction time across days, which may reflect general learning of the task, clearly supports the idea that participants adapted to the visuomotor rotations implicitly and without conscious awareness.

DISCUSSION

Here, we found, using a visuomotor adaptation task that dissociated the viewed spatial locations of potential targets from their corresponding reach directions, that the initial direction of reaches rapidly launched toward two potential targets (i.e., under conditions of target uncertainty) constitutes a weighted average of the reach directions associated with the two targets when presented individually (i.e., under conditions of target certainty). This finding indicates that the competing potential targets were rapidly and automatically mapped onto the corresponding motor representations prior to movement selection.

There are several key features of the current task that allow for a robust conclusion that the mapping of viewed potential targets into motor coordinates occurs both rapidly and automatically. First, because the visuomotor rotations were applied gradually, participants were unaware of the dissociation between target and reach directions. Second, participants were required to launch reaches immediately after target presentation. These two features make it highly unlikely that participants would have implemented a deliberate strategy to handle the visuomotor dissociation. Third, because of the large number of different one- and two-target configurations employed, it is improbable that participants could have developed rote responses to the two-target configurations. Finally, participants never received visual feedback of the cursor in two-target trials following adaptation to the visuomotor rotations, and therefore, we can rule out the possibility that they learned to generate motor averaged responses based on error feedback. Note that the current task has several advantages over a previous study we carried out in

which we dissociated target and initial reach directions using an obstacle (Stewart et al., 2014). Whereas the previous results were consistent with motor encoding, other possible interpretations can not be ruled out (see Supplemental Experimental Procedures).

We suggest that, under conditions of target uncertainty, the rapid, automatic motor encoding of targets can support the specification of initial movement directions that tend to optimize motor costs. One possibility, consistent with optimal feedback control models (Todorov and Jordan, 2002), is that the motor system computes an initial movement, based on motor representations of the targets (e.g., the hand positions associated with the targets), that minimizes the ultimate cost of corrected movements to the targets once they are selected (Hudson et al., 2007; Stewart et al., 2013; Haith et al., 2015a). Another possibility is that the motor system averages components of the reach plans specified for the potential targets, such as the initial directions or final hand positions, when generating an initial movement toward these targets. This latter "multiple plans" account could provide an approximate optimization of the motor costs. In addition, in situations in which the target is selected *before* movement onset, forming multiple plans may facilitate the rapid launching of reaches once the target is selected (Gallivan et al., 2015) and may provide key information for deciding which reach option to select in the first place (Cos et al., 2011, 2012; Cisek and Pastor-Bernier, 2014). (Note that, whereas spatial averaging behavior in the context of eye movements may arise from the simultaneous execution of competing movement plans [McPeek et al., 2000, 2003], because of the inherent complexity of arm movement planning and control, we do not believe this is a plausible account of averaging in the case of reaching.)

Our results are consistent with a recently described model in which, under similar conditions of target uncertainty, an optimal feedback control policy is calculated for each potential target and a weighted average of these policies is computed, for each moment in time, based on the relative desirability of the competing targets (Christopoulos and Schrater, 2015). This model not only predicts the averaging of feedback gains for competing targets (as shown in Gallivan et al., 2016b) but also the trajectory averaging frequently observed during both eye and hand movements (e.g., Chou et al., 1999 and Chapman et al., 2010b). In summary, our findings support the hypothesis that, prior to target selection and subsequent movement execution, competing potential reach targets are rapidly and automatically transformed into corresponding motor representations (Cisek, 2007). These behavioral findings provide for a strong interpretation of the results of recent neurophysiological studies showing that multiple spatial goals are represented in sensorimotor regions of the brain (Klaes et al., 2011; Grent-'t-Jong et al., 2015; Dekleva et al., 2016), namely that this activity directly reflects movement-related parameters associated with these goals.

EXPERIMENTAL PROCEDURES

Participants

Sixteen right-handed individuals (five males) between 18 and 26 years of age completed the full experiment after providing informed written consent. The

participants were recruited from the population of undergraduate and graduate students at Queen's University and received financial compensation for their time. The Queen's University General Ethics Board approved all experimental procedures.

On day 1 of testing, participants completed the pre-adaptation phase of the experiment, in which they performed one-target trials and two-target go-before-you-know trials. Previous studies have shown that, when initiating reaches toward two potential targets, many participants aim toward the midpoint and then make a correction toward the cued target (Chapman et al., 2010a, 2010b; Stewart et al., 2013, 2014; Gallivan and Chapman, 2014). However, one-third to one-half of all participants do not exhibit consistent trial-to-trial averaging behavior and, instead, will at least occasionally adopt a strategy that involves picking one of the two potential targets to aim toward (Stewart et al., 2013, 2014). Because spatial averaging behavior is a prerequisite for testing our hypotheses (noted above), we screened 28 participants on day 1 and continued with those who, based on visual appraisal, exhibited robust trial-to-trial spatial averaging, resulting in 16 participants. Given the importance of participants properly adapting to the applied visuomotor rotations on day 2 for testing our hypotheses (also noted above), only individuals who successfully adapted and maintained this adaptation throughout post-adaptation phase, as assessed by examining cumulative distributions of initial movement directions (see Stewart et al., 2014), were included for analysis (ten participants). Although we selected participants whose performance characteristics allowed for a clear and unambiguous test of our hypotheses, it is important to emphasize that the basic conclusions drawn from the current study are not limited to these participants and the selection criteria by which the participants were selected cannot bias the results.

Apparatus

Seated participants used the right hand to grasp the handle of a robotic manipulandum (WristBOT; Howard et al., 2009) that could be moved in a horizontal plane. The circular start position (diameter 20 mm), circular cursor representing the handle position (diameter 20 mm), and target(s) (diameter 20 mm) were displayed on a 30-in monitor located above the plane of movement. Participants viewed these stimuli in a mirror located halfway between the monitor and movement plane, such that they appeared to be in the plane of movement. Participants could not see their hand or arm.

Procedure

To begin each trial, the participant moved the cursor into the start position (at body midline, 20 cm below the 0° target) and held it there for 200 ms. After this period of time elapsed, either one target or two potential targets were presented (at 20-cm distance), which together with an auditory "beep" delivered at the same time, provided the cue to initiate a reaching movement. If the cursor moved from the start position less than 100 ms after the beep or more than 325 ms after the beep, the message "too early" or "too late" was displayed, respectively, and the trial was aborted. In two-target trials, the participant had to begin moving before knowing which of the two potential targets would be cued as the actual target. In these trials, one of the targets was cued (filled in) once the cursor moved 20 mm from the start position. For consistency, the target was also filled in at this point in one-target trials. In all trials, the participant was required to move the cursor to the cued target and click on it with the button located on the top of the manipulandum within 500 ms of leaving the start position. If the participant took longer than 500 ms to click on the target the message "too slow" was displayed. 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. The trial was considered a "miss" if the cursor was not in contact with the target when the button was clicked.

Day 1: Practice and Baseline Phases

Participants on day 1 first completed 64 practice trials with visual feedback of the cursor. These included four trials for each of four one-target displays (with targets at −30°, −15°, 0°, and +30°) and eight trials for each of six two-target displays (with the left target at −30° and the right target at −20°, −10°, 0°, +10°, +20°, or +30°), presented in random order. Participants then completed an additional set of 160 practice trials with ten trials for each of the same four one-target displays and 20 trials for each of same six two-target

displays, with visual feedback of the cursor randomly removed for half of the trials for each display type and with the order of all trials randomized. After these practice trials, participants completed 320 pre-adaptation phase trials, which included 20 trials for each of the four one-target displays and 40 trials for each of the six two-target displays. For each display, visual feedback was removed on half of the trials and the order of all trials was randomized. Participants were given an optional break after every 50 trials during the pre-adaptation phase as well as the post-adaptation phase described below. Note that the removal of cursor feedback on some day 1 trials was done so as to allow for direct comparison with day 2 trials, in which the removal of cursor feedback on two-target trials was necessary for testing our hypotheses (see below).

Day 2: Adaptation and Post-adaptation Phases

Participants began the day 2 session by completing 96 practice trials to reacquaint them with the task. These included 6 and 12 trials for each of the four one-target displays and each of the six two-target displays, respectively, used on day 1. These practice trials were followed by the adaptation phase, in which we gradually applied opposing visuomotor rotations to the +30° and 0° targets so that, by the end of the phase, participants would generate roughly straight-ahead (0°) hand movements when moving the cursor to either target (Figure 1B). The adaptation phase consisted of 192 one-target trials with visual feedback of the cursor. This consisted of 81 trials with the +30° target, 81 trials with the 0° target, 20 trials with the −30° target, and ten trials with the −15° target (all presented in random order). For the +30° target trials, a visuomotor rotation of +40° was gradually introduced, in one-degree increments, over the first 40 +30° target trials and then held at 40° (see blue dashed line in Figure 2A). For the 0° target trials, a visuomotor rotation of −10° was gradually introduced, in the same one-degree increments, over the first ten 0° target trials and then held at −10° (see orange dashed line in Figure 2A). No rotations were applied to the −30° and −15° targets. We applied 40° and −10° rotations to the +30° and 0° targets, respectively, to compensate for two factors associated with adaptation to visuomotor rotations: incomplete adaptation, seen even when adapting to a single target, and generalization of adaptation across targets; i.e., from the +30° target to the 0° target and vice versa (Krakauer et al., 2000; Hirashima and Nozaki, 2012). As can be clearly seen in Figure 2A, the application of these rotations resulted in our group of participants generating similar, straight-ahead movement directions for both target locations.

Following this adaptation phase, participants then completed 720 post-adaptation phase trials, which contained two-target trials, all without visual feedback of the cursor, and one-target trials with and without visual feedback of the cursor. In the one-target trials with vision of the cursor, the +40° and −10° visuomotor rotations were applied to the +30° and 0° targets, respectively, with no rotation being applied to other targets. Single targets were presented at one of six possible target locations: −30°; −15°; −7.5°; 0°; +7.5°; and +30°. Through pilot testing, we determined that it was necessary to include a high proportion of one-target trials with visual feedback involving the 0° and +30° targets in order to maintain the visuomotor adaptation achieved during the earlier adaptation phase. Accordingly, there were 200 trials each for the 0° and +30° one-target displays, with 20 of those trials having visual feedback of the cursor removed. Also, there were 100 trials each for the −30° and −15° one-target displays, with again 20 of those trials having cursor feedback removed. Finally, we had 20 trials each for the −7.5° and +7.5°, with half of those having the visual feedback removed.

Three two-target displays, all without visual feedback of the cursor, were presented during the post-adaptation phase: −30°/0°; 0°/+30°; and −30°/+30° trials. Because we were primarily interested in the −30°/+30° two-target trials—trials in which we expected to observe our maximal effects and that would serve as the critical test between the motor and visual averaging hypotheses—we included 60 −30°/+30° trials and only ten each of −30°/0° and 0°/+30° trials. If a participant, when presented with −30°/+30° trials, aimed toward the averaged target position (i.e., visual averaging; Figure 1C), we would expect the initial movement direction to be roughly straight ahead (i.e., ∼0°). Conversely, if a participant instead executed an initial reach movement consistent with the average of the two movements to the potential target (i.e., motor averaging; Figure 1D), then we would expect the initial direction to be biased leftward (i.e., rotated counterclockwise) because of the

influence of the learned visuomotor rotation on the movement direction to the +30° target. Note that we never included visual cursor feedback on any of the two-target trials, as this would have necessarily biased the outcome. Following the completion of day 2 testing and immediately prior to experiment debriefing, participants were asked as to whether they noticed any mismatch between their hand movements and the cursor position during testing. None reported being aware of any incongruence.

Data Analysis

The position of the handle was sampled at 1,000 Hz and digitally smoothed using a fourth-order, zero-phase lag Butterworth filter with a cutoff frequency of 14 Hz. To obtain a measure of the direction of the initial movement vector, prior to when corrections could occur in two-target trials, we determined the direction of the handle, relative to the start position, when the handle reached 30% of the distance (i.e., 6 cm) from the start position to the arc along which the targets were located. We refer to this as the initial movement direction.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and two figures and can be found with this article online at http://dx.doi.org/10.1016/j.celrep.2017.01.049.

AUTHOR CONTRIBUTIONS

All authors contributed to the study design, interpreted the data, and approved the final version of the manuscript for submission. B.M.S. performed the testing and data collection. B.M.S., J.P.G., and J.R.F. performed the data analysis. J.P.G., B.M.S., D.M.W., and J.R.F. drafted the manuscript, and L.A.B. provided critical revisions.

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Supplemental Information

Rapid Automatic Motor Encoding

of Competing Reach Options

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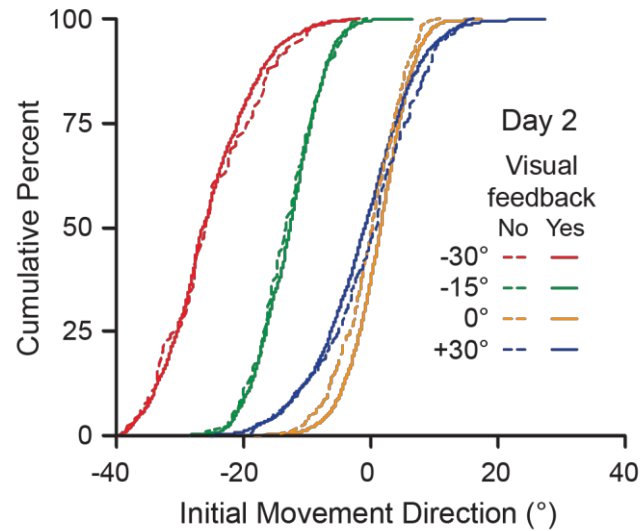
Figure S1: Initial movement directions with and without visual feedback after adaptation (Day 2), Related to Figure 2. Cumulative distributions of initial movement directions (i.e., handle direction at 30% of the target distance) from post-adaptation (Day 2) one-target trials with (solid lines) and without (dashed lines) visual feedback of the cursor controlled by the hand. The distributions include all data from all participants. Note that the initial directions with and without visual feedback are very similar for all four targets shown.
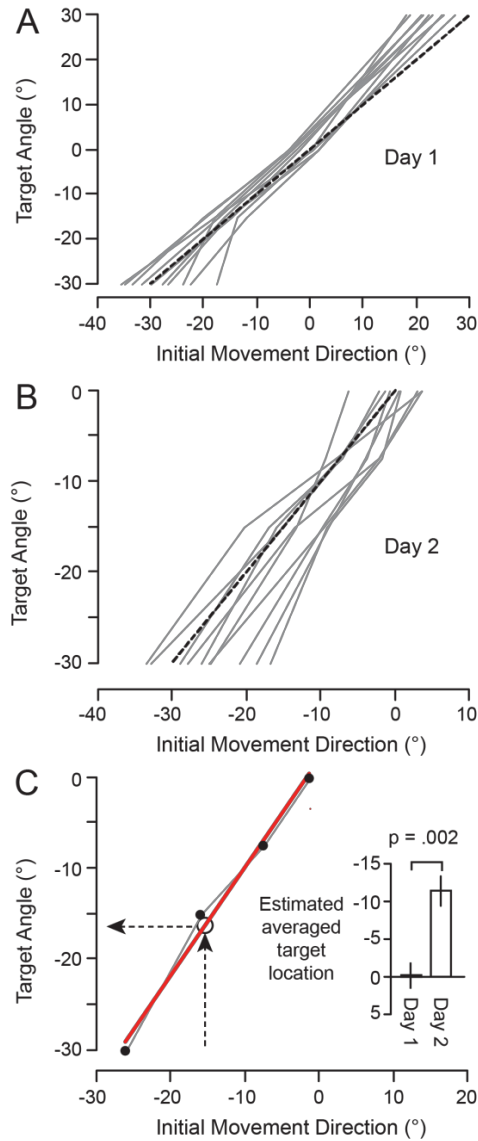
1

Figure S2: Estimation of target direction under the assumptions of visual averaging, Related to Figure 3. (A) Each grey line shows the mapping between target angle and initial reach direction (i.e., handle direction at 30% of the target distance) based on Day 1 one-target trials for each participant. **(B)** Corresponding mappings, for each participant, on Day 2. The dashed lines in A and B are unity lines. **(C)** Target direction estimation procedure. For each participant, a linear regression line was fit through the data points (red line), allowing us to estimate the averaged target position that the participant was putatively aiming for—assuming visual averaging—given their initial movement direction on -30/+30° two-target trials. Example in C is from Day 2. The inset in C (at right) shows the mean estimated angle of the target on Days 1 and 2, based on participant medians. The error bars represent ± 1 SE.

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Supplemental Experimental Procedures

Maintenance of visuomotor adaptation during non-visual feedback trials

In our experiment, it was critical to maintain adaptation during the post-adaptation phase (on Day 2) in one- and two-target trials without visual feedback of the cursor controlled by the hand. With this goal in mind, we provided visual feedback of the cursor in the majority of one-target trials. Figure S1 shows cumulative distributions of initial hand directions—combining data from all trials and participants—from Day 2 one-target trials (to the -30, -15, 0 and +30° targets) with and without visual feedback. The fact that initial hand directions were highly similar with and without visual feedback indicates that we were successful in maintaining adaptation effects during trials without visual feedback.

Assessing the 'visual averaging' hypothesis

As shown in Fig. 3A, we observed a significant counterclockwise rotation of the initial movement direction in -30/+30° two-target trials on Day 2, relative to Day 1. Although this finding provides support for the motor, and not visual, averaging hypothesis, it is nevertheless possible that the learned visuomotor rotations may have had a small overall influence on movement directions on Day 2 that could influence these results. Thus, the test performed in our main paper may not provide a completely fair assessment of the null, visual averaging hypothesis.

A more direct way to evaluate the visual averaging hypothesis is to estimate the averaged target position that participants putatively aimed towards in -30/+30° two-target trials without cursor feedback on Days 1 and 2. Because this averaged visual-perceptual target position should be completely independent of the visuomotor rotations learned by participants (as only the motor, not visual, space was adapted on Day 2), the visual averaging hypothesis predicts that its position should not vary across testing days. To determine the averaged target position that participants putatively aimed towards we computed, for each individual, the median initial direction in Day 1 one-target trials involving the -30, -15, 0, and +30° targets and in Day 2 one-target trials involving the -30, -15, -7.5 and 0° targets (importantly, all trials in which movements were directed approximately to the target).

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The grey lines in Figs. S2A and B show, for each participant, the mapping between their median movement directions and the target angles on Days 1 and 2, respectively. For each participant and day, we fit a linear regression line through the 4 data points (see Fig. S2C, which show the Day 2 data points from a single participant), allowing us to estimate the averaged target location (horizontal arrow) that a participant was ostensibly aiming for—under the assumption of the visual averaging hypothesis—given their initial movement direction (vertical dashed arrow). Note that this approach compensates for any possible effects of the visuomotor rotations applied (to the 0 and +30° one-target trials with visual feedback) on Day 2. The linear regressions provided good fits for all participants on each day (the 20 r^2 values, 10 participants x 2 days, ranged from 0.976 to 0.999).

The inset in Fig. S2C shows the average estimated angle, based on participant medians, of the target in -30/+30° two-target trials on Days 1 and 2, derived from the regression analyses described above. As can be clearly observed, the target angle on Day 2 was rotated counterclockwise relative to Day 1, which was centered approximately at 0°. A paired t-test confirmed that the estimated target angle on Day 2 (M = -11.41°; SE = 1.90°) was significantly less (t_9 = -4.20; p = 0.002) than on Day 1 (M = -0.17°; SE = 1.69°). These findings further argue against the visual averaging hypothesis and suggest that the reaches executed under target uncertainty are related to the learned movement vectors, and not visual directions, associated with each potential target.

Relation of current findings to previous work
In a previous paper (Stewart et al., 2014), we compared the motor versus visual encoding of potential targets by using an obstacle to dissociate target and reach directions (see also Pearce and Moran, 2012). There were three possible target locations: straight ahead (0°), right (+30°), and left (-30°). An obstacle was positioned on the right side of the workspace such that initial direction of reaches to the +30° target were straight ahead while the initial directions of reaches to the other two targets were unaffected. We found that when required to launch a reach movement towards the -30° and +30° potential targets, participants' initial reach directions were deflected to the left of midline. Although this result is consistent with the idea that competing visual targets are directly mapped onto corresponding movements required to attain those

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targets (i.e., a motor encoding of the potential targets), we now recognize a limitation to this study that precludes a definitive conclusion. Specifically, because reaches launched towards two potential targets are far more variable in their initial directions than single-target movements (Chapman et al., 2010; Gallivan and Chapman, 2014; Ghez et al., 1997; Stewart et al., 2013; Stewart et al., 2014), it is plausible that participants, on two-target trials, shifted the distribution of their initial movement directions away from the obstacle's position (i.e., leftward) in order to provide a reasonable margin of safety for avoiding collision (Chapman and Goodale, 2008; Hamilton and Wolpert, 2002; Sabes and Jordan, 1997; Sabes et al., 1998). In this previous study (Stewart et al., 2014), there was also a 750 ms delay between target presentation and the go cue, which may have facilitated the implementation of a cognitive strategy to avoid the obstacle (Fernandez-Ruiz et al., 2011; Haith et al., 2015). For these reasons, we view the current set of results as particularly compelling evidence for the notion that the brain, when presented with multiple competing targets, automatically maps those potential targets onto associated motor representations in cortex.

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