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A motor planning stage represents the shape of upcoming movement trajectories

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Wong AL, Goldsmith J, Krakauer JW. A motor planning stage represents the shape of upcoming movement trajectories. *J Neurophysiol* 116: 296–305, 2016. First published April 20, 2016; doi:10.1152/jn.01064.2015.—Interactions with our environment require curved movements that depend not only on the final position of the hand but also on the path used to achieve it. Current studies in motor control, however, largely focus on point-to-point movements and do not consider how movements with specific desired trajectories might arise. In this study, we examined intentionally curved reaching movements that navigate paths around obstacles. We found that the preparation of these movements incurred a large reaction-time cost. This cost could not be attributed to nonmotor task requirements (e.g., stimulus perception) and was independent of the execution difficulty (i.e., extent of curvature) of the movement. Additionally, this trajectory representation cost was not observed for point-to-point reaches but could be optionally included if the task encouraged consideration of straight trajectories. Therefore, when the path of a movement is task relevant, the shape of the desired trajectory is overtly represented as a stage of motor planning. This trajectory representation ability may help explain the vast repertoire of human motor behaviors.

complex action; desired trajectory; motor planning; optimal feedback control; reaction time

NEW & NOTEWORTHY

This work demonstrates that to produce an intentionally curved movement, it is necessary to invoke a unique process that plans the shape of the desired movement path of the endpoint effector. The existence of such an abstract representation of kinematics may explain the large human repertoire of complex movements and may help explain the dissociation seen between simple endpoint-directed movements and complex tool-use and imitative actions in ideomotor apraxia.

THROUGHOUT DAILY LIFE, we frequently plan and execute intentionally curved movements to interact with our environment. For movements such as reaching around obstacles, writing, or expressing oneself through hand gestures, the shape of the movement path is part of the overall motor goal. Hence, we propose a motor planning stage that generates a representation of movement trajectory shape (Wong et al. 2014). For example, when a numeral 8 is to be drawn, this stage would determine whether to draw the shape with either one continuous sinuous line or two discrete ovals, one on top of the other. In other words, this stage would define the intended path to the final goal location that then guides the preparation of motor commands for execution.

Several lines of evidence support the existence of this trajectory representation stage. First, written letters exhibit characteristic trajectory features that are invariant across different movement effectors (Rijntjes et al. 1999; Wright 1990) or size scales (van Galen and Teulings 1983; Wing 2000). Consistent with these behavioral data, brain activity appears to represent scale-invariant letter shape in parietal cortex (Kadmon Harpaz et al. 2014), and effector-independent letter shape in parietal and premotor cortices (Rijntjes et al. 1999). Thus the evidence for motor equivalence supports the existence of an abstract representation of an intended movement trajectory at an early stage of motor planning.

Second, making simultaneous incongruent movements with the two arms incurs a reaction time (RT) and execution quality cost (Albert and Ivry 2009). However, direct cueing of the incongruent movement goals, which presumably eliminates the need for two simultaneous but distinct trajectory representations, reduces this bimanual interference effect (Albert and Ivry 2009; Diedrichsen et al. 2001). Similarly, no interference is noted when the shapes are congruent such that a single trajectory representation could guide the production of both movements. Thus generating a trajectory representation is resource intensive and consumes RT.

Third, reaching around an obstacle primes the next reach to be similarly curved rather than straight, even after the obstacle is removed (Jax and Rosenbaum 2007; van der Wel et al. 2007). Surprisingly, merely observing another individual reach around an obstacle is sufficient to prime behavior (Griffiths and Tipper 2009, 2012). This suggests that the trajectory shape representation may be visually based (e.g., a mental image of the shape of the movement path) and does not require coupling with subsequent execution of the movement.

Finally, there is neuropsychological evidence for a movement trajectory representation. Patients with ideomotor apraxia, arising predominantly from left frontoparietal cortex lesions, have normal point-to-point reaches (Botvinick et al. 2009; Buxbaum et al. 2005; Hermsdorfer et al. 1996; Ietswaart et al. 2006) but impaired gesture imitation (Buxbaum et al. 2014; Goldenberg and Hagmann 1997; Hermsdorfer et al. 1996) and tool-use pantomime (Buxbaum et al. 2014; Goldenberg and Hagmann 1998), movements that require a consideration of trajectory shape. Similarly, studies of nonhuman primates implicate neurons in parietal and premotor cortices of representing movement shape, not just endpoint goal (Hocher-

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man and Wise 1990, 1991; Pearce and Moran 2012; Torres et al. 2013). These data argue that movement trajectories are explicitly represented by neurons as part of motor planning.

In the present study we sought direct evidence for a motor planning stage that overtly represents trajectory shape. Using a task that requires subjects to plan curved movements around barriers, we assessed whether there is a difference in RT for the same executed movement when it does or does not require the construction of a de novo trajectory representation.

MATERIALS AND METHODS

Sixty-two right-handed, adult (age 18–40 yr, 28 male), neurologically healthy subjects were recruited for this study, and each participated in one of the three experiments. All subjects were naive to the purposes of this study and provided written informed consent before participation. All procedures were approved by the Johns Hopkins School of Medicine Institutional Review Board. Subjects made planar reaching movements on a glass-surfaced table with their right forearm restrained by a wrist splint and supported by pressurized air jets to allow frictionless movements of the elbow and shoulder. Vision of the arm was obstructed by a mirror through which subjects viewed an LCD monitor (60 Hz) displaying target cues and a cursor representing the position of the index finger in a veridical horizontal plane.

Movement of the index finger was tracked at 130 Hz using a Flock-of-Birds magnetic tracker (Ascension Technology, Milton, VT). All subjects completed 256 movements per condition, divided evenly into two 128-movement blocks.

Experimental Paradigms

Subjects were instructed to produce a reaching movement toward a target while avoiding barriers located around both the starting position and the target (Fig. 1*A*). Targets appeared at one of eight possible locations uniformly spaced 45° apart along a circle of radius 12 cm. Barriers could be presented at any of eight possible orientations (rotated in 45° increments); each target was surrounded by a barrier, constraining both the initial and final movement directions of the reach. This task was a modified version of a barrier-constrained reaching paradigm previously introduced by Pearce and Moran (2012), with the addition of a second barrier positioned around the goal target to ensure that subjects were planning entire movement trajectories and were not simply concerned with the direction to initiate the movement.

On a typical trial (Fig. 1), subjects began the trial by moving their hand into the start target. After a brief delay of random duration (600-1,600 ms), the display (consisting of the reach target and the 2 barriers) appeared. Subjects were instructed to respond to the display by initiating a reaching movement to the goal target as soon as possible and to complete the movement within 1,200 ms. As soon as the subject moved his or her hand out of the start target, all visual information except the start target and the hand cursor were removed, encouraging the subject to plan the entire movement trajectory before movement onset. If a subject initiated his or her movement before the target and barriers appeared, the hand was required to return to the start target and wait for another interval before the trial would begin. At the conclusion of the movement, subjects were asked to hold their hand still on the location where they thought the reach target was located until the end of the trial, whereupon subjects were shown feedback about their movement by seeing an image of the entire reach trajectory drawn on top of the target and barriers.

Subjects in each experiment were divided into groups. Certain groups were presented, in addition to the barriers, with a path cue in the form of a line drawn on the screen between the start target and the reach target that navigated around the barriers. This cue instructed subjects to generate a reach with a particular trajectory, although

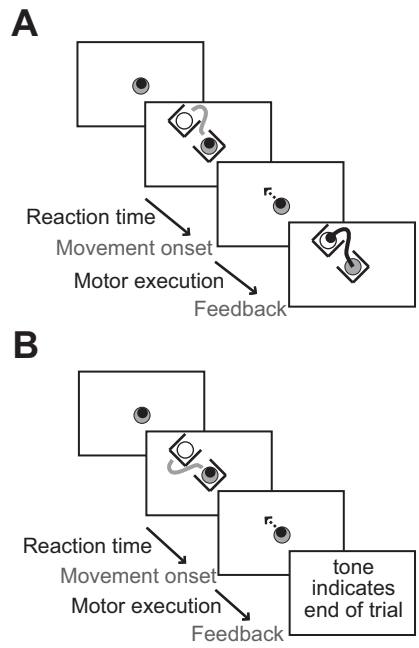

Fig. 1. Experimental methods. *A*: subjects initiated a trial by moving onto the start target. After a random delay, the reach target and barriers appeared. Under No-Planning (T^{NoPlan}) conditions, a path cue (gray curved line) also appeared to prompt subjects about the path they should take. At movement onset, the target and barriers disappeared. After completion of the movement, subjects were given visual feedback about their movement trajectory (black line). *B*: in *experiment 3*, the presented path cue was occasionally incorrect; on these trials, the path cue (gray curved line) correctly led out of the start target but directed subjects into the closed end of the goal barrier. Subjects were given no feedback at the end of the reach on these incorrect-cue trials.

subjects were informed that they did not have to constrain their movement path to exactly overlay the path cue. Instead, they were simply instructed to navigate around the barriers in the same manner as the path cue. The path cue disappeared along with the barriers at movement onset; hence, the nominal working-memory requirements of each group were comparable (i.e., to recall the target location and the path necessary to get there), and both groups were tasked with the same execution requirements.

Experiment 1 assessed the RT cost of trajectory representation. Twenty subjects were recruited for this study. They were exposed to 128 unique barrier and target configurations (8 target locations, 8 goal-barrier orientations, and 2 start-barrier orientations). This large number of possible movements was chosen so that we could acquire a reasonable sample of reaches for analysis without allowing subjects to become overly familiar with any particular barrier configuration, encouraging de novo trajectory planning on every trial.

Subjects were randomly assigned to one of two groups (10 subjects per group). The trajectory with planning (T^{Plan}) group was shown only the target and the barriers; the trajectory without planning (T^{NoPlan}) group was additionally shown a suggested path to avoid the barriers and was asked to move in the same general direction that the line instructed.

Experiment 2 addressed whether point-to-point movements require trajectory representation. Twenty-four subjects were recruited for *experiment 2* (divided into 4 groups of 6). We compared the RTs of point-to-point movements (to 8 possible targets) for two groups of six subjects who were shown the target, barriers, and either a path cue (point-to-point without planning; P^{NoPlan}) or not (point-to-point with planning; P^{Plan}). *Experiment 2* also explored whether the small but significant RT difference between making 1 of 8 possible point-to-point movements in the P groups and making 1 of 128 possible curved reaches in the T^{NoPlan} group could be attributed to Hick's law (i.e.,

that RT depends on the number of possible movement alternatives). Two additional groups of six subjects were exposed to a subset of 64 possible barrier configurations in the presence (T^{NoPlan}_{64}) or absence (T^{Plan}_{64}) of a path cue. Subjects in these 64-configuration groups had the added benefit of always knowing the orientation of the barrier around the goal target, which was fixed throughout the session; this allowed us to also perform an additional control analysis to examine how perception contributed to the RT cost. We also exposed the P^{Plan} group to a smaller subset of 16 possible uncued barrier configurations. A Hick's law curve was fit separately to all of the planning (16, 64, or 128 barrier configurations) or no-planning (64 or 128 barrier configurations) conditions.

Experiment 3 addressed whether the T^{NoPlan} group may have inferred the barrier orientations directly from the path cue rather than spending time perceptually discriminating the barrier orientations. We asked 10 new subjects to complete a T^{NoPlan}_{64} condition (in which only 64 possible barrier configurations were used) where, on a minority of trials, the displayed path cue was incorrect: it guided subjects to the back of the goal barrier 180° opposite the barrier opening (Fig. 1*B*). As before, once the movement was initiated, the barriers and path cue disappeared; any movements that properly avoided the barriers thus required perception of the barrier orientations before movement onset. We examined whether subjects could properly avoid the barriers on these incorrect trials without exhibiting an RT cost, compared with the T^{NoPlan}_{64} group from *experiment 2*, who were matched for the total number of possible movements (i.e., barrier configurations) to avoid a Hick's law effect on measured RTs.

Experiment 4 examined the possibility that subjects were using the path cue to assist in determining how to initiate the movement without regard for the shape of the movement trajectory, and that once the movement was underway, the remainder of the trajectory was then determined online. Twelve new subjects were asked to participate and completed two tasks during the experiment. Subjects were randomly assigned to one of two groups. In the first task, subjects completed a task nearly identical to that in *experiment 1* in that they were reaching to targets while avoiding barriers, with the exception that the start barrier appeared early and remained on the screen for a brief delay (600-1,600 ms) before the onset of the goal target and barrier. Six subjects completed this early-start barrier onset task with no path cue (T^{Plan}_{ES}), whereas the remaining six subjects were provided with a path cue that appeared at the same time as the goal target following the delay (T^{NoPlan}_{ES}). Subjects were instructed to begin moving when the goal target appeared. This first task allowed for an assessment of whether knowledge of the initial movement direction eliminated the RT advantage provided by the path cue.

In the second task, subjects were presented with a target array showing all eight potential target locations. Subjects were shown only a start barrier and were required to produce a point-to-point reach to the target indicated by the opening of the start barrier. The start barrier appeared either at the time of the go cue (completed by T^{Plan}_{ES} subjects) or at the beginning of the trial before the go cue (completed by the T^{NoPlan}_{ES} subjects); the go cue was a tone indicating that the subjects should begin moving, which occurred 600-1,600 ms after the beginning of the trial. This second task allowed for an estimate of how long it actually took to discriminate the orientation of the start barrier.

Data Analysis

All data were analyzed offline using programs written in MATLAB (The MathWorks, Natick, MA). Movements were selected using a semi-automated program that identified reaches according to a velocity criterion (tangential velocity >0.05 m/s); all movements were verified by visual inspection. Measures of RT were computed as the time between onset of the target and initiation of the movement. Inherent delays in the experimental setup were measured to be, on average, 105 ms; all reported RTs have been corrected to compensate for these delays.

Trials were excluded if subjects did not complete the movement within 1,200 ms. Also, since most barrier configurations had more than one possible solution path, we preselected one possible path as the "canonical" one and presented that solution to the no-planning groups; any "noncanonical" reaches (e.g., distinct in how the barriers were circumnavigated) generated by the planning group (as well as any non-canonical mistakes made by the no-planning group) were excluded to allow for a fair comparison of RTs for movements with comparable kinematics. Paths that hit a barrier were not specifically excluded from analysis unless they were also noncanonical movements. On average, 14.3% of all trials in the T^{Plan} condition and 6.3% of all trials in the T^{NoPlan} condition were excluded.

RTs were compared via mixed-effects models using the lme4 package (Bates et al. 2014) in R, treating group and barrier configuration as fixed effects and subject as a random effect. Significant effects were determined using a likelihood ratio test to compare pairs of models (with and without the particular factor of interest). Where appropriate, step-down Bonferroni-Holm-corrected two-tailed *t*-tests were applied to examine groupwise RT differences. Error bars in all depicted data report SE across subjects.

Reach kinematics. Trajectories were first grouped according to the relative position and orientation of the target barrier to the start barrier; this yielded 64 unique rotationally invariant target-barrier configurations. Reach-trajectory kinematics were then analyzed using tools for functional data analysis. Specifically, a trajectory was considered to be the outcome variable in a function-on-scalar regression model that treated group status $X_i(t)$ as the predictor:

$$Y_i(t) = B_0(t) + B_1(t)\ X_i(t) + e(t),$$

where $Y_i(t)$ is the observed trajectory for subject i, $B_0(t)$ is the average trajectory in the T^{NoPlan} condition, and $B_1(t)$ is the average difference between T^{Plan} and T^{NoPlan} groups. We fit this model using a Bayesian method that allows for correlation in the errors $e(t)$ (Goldsmith and Kitago 2015). A 95% simultaneous posterior credible interval was used to identify significant differences between groups while accounting for the multiple comparisons implicitly made when comparing functions. This analysis was performed on trajectories that were time-normalized and resampled to have 40 segments (41 points) per trajectory. This analysis was repeated for all possible combinations of target location and barrier orientation; reported P values were not further corrected for multiple comparisons across configurations.

Trajectory complexity. Complexity was quantified by ranking the average movement trajectories for each of the 64 unique barrier and target combinations from the kinematic analysis according to a stratified criterion. Trajectories were first sorted according to the number of inflection points present in the curve (intuitively, an "S" shape is more complex than a "C" shape even though both might have similar mean curvatures, because an inflection point would require that the arm exhibit more changes in acceleration compared with a C-shaped movement). Curves having the same number of inflection points were then ordered by curvature. To measure curvature, the average trajectory for each barrier configuration was computed and smoothed using a B-spline fit. Trajectories were arc-length normalized, and the radius of curvature was evaluated at each point along the length of the trajectory by fitting a circle that included the four neighboring points. Curvature was then computed as the average absolute value of the inverse radius of curvature.

Hick's law curves. RTs for each individual subject were computed across all barrier configurations. Hick's law curves were then fit to the relationship between average RT and number of possible movements for all subjects having the same planning requirement (e.g., Planning or No-Planning) using a weighted least-squares regression to fit a logarithmic (base 2) equation with two free parameters to the data; errors were weighted by the squared inverse logarithm of the independent variable (number of movement choices) to account for the inherent biased weighting of errors that occurs when a logarithm of

the data is taken before the data are fit to a linear least-squares regression.

Path decision-making cost. To test whether some of the RT cost could be attributed to decision-making, barrier conditions were identified in which subjects in the T^{Plan} group frequently, as a group, opted to take different paths to get to the target (i.e., when chosen movement paths differed from the canonical one presented to the T^{NoPlan} group on at least 25% of all trials pooled across the group). The mean RTs for those configurations were compared with those of barrier conditions in which subjects in the T^{Plan} group were highly consistent in their choice of movement path. A *t*-test was used to compare mean RTs for these two sets of configurations.

Change-of-mind trajectory classification. In *experiment 3*, we wanted to evaluate when subjects changed their movement to adjust for an incorrect path cue. To examine this, we used baseline movements from two different types of correctly cued trials (cases) to train a classifier. *Case 1* movements included the same path cue as the incorrect trial, but barriers were configured to make the displayed path cue appropriate; *case 2* movements included the same barrier configuration as the incorrect-cue trial but showed the path cue that was actually appropriate for that configuration. A *k*-nearest neighbors algorithm was used to classify whether the trajectory, at each time point, belonged to *case 1* or *case 2*. This classification was performed along each two-dimensional point (horizontal and vertical) of the smoothed velocity profile using the 10 nearest neighbors; neighbors were inversely weighted according to the Mahalanobis distance from the point. Rather than treat *case 1* as a prior, the first five points along the incorrect trajectory were assigned to have a *case 1* classification, and the classification analysis always included the five most recently classified points from the incorrect trajectory as potential neighbors. The first time when the trajectory was classified to be more like *case 2* than *case 1* was identified as the point at which subjects changed their mind; a change-of-mind point was successfully computed for all but three trials. The change-of-mind time for each barrier configuration was taken to be the median time obtained from the classification analysis across all incorrect trials.

RESULTS

Formulation of a Trajectory Representation Incurred a Large RT Cost

In *experiment 1*, we examined the reaches of groups performing cued (T^{NoPlan}) or uncued (T^{Plan}) intentionally curved movements. Both groups executed reaches exhibiting identical movement kinematics. Figure 2*A* shows the mean hand paths for the T^{Plan} and T^{NoPlan} groups across all combinations of target directions and barrier configurations; each panel contains the movements to each of the eight targets for a single goal-barrier orientation (collapsed across the 2 start-barrier orientations). Points that were found to be significantly different between the mean trajectories of the T^{Plan} and T^{NoPlan} groups are highlighted with orange dots. Only a few trajectories exhibited any kinematic differences between the two groups (8 of the 64 rotationally invariant barrier configurations; see MATERIALS AND METHODS), and such trajectory differences persisted only for a small portion of the entire movement: for trajectories that exhibited significant differences between groups, these regions covered only 10.44% of the trajectory on average (range 2.5–20%).

Despite these kinematic similarities, the T^{Plan} group, which was required to plan their movement trajectories, exhibited RTs that were 94.61 ms longer compared with the T^{NoPlan} group, which was given path cues to follow (T^{Plan}, 437.16 ± 22.31 ms; T^{NoPlan}, 342.56 ± 9.28 ms; Fig. 2*B*). This RT

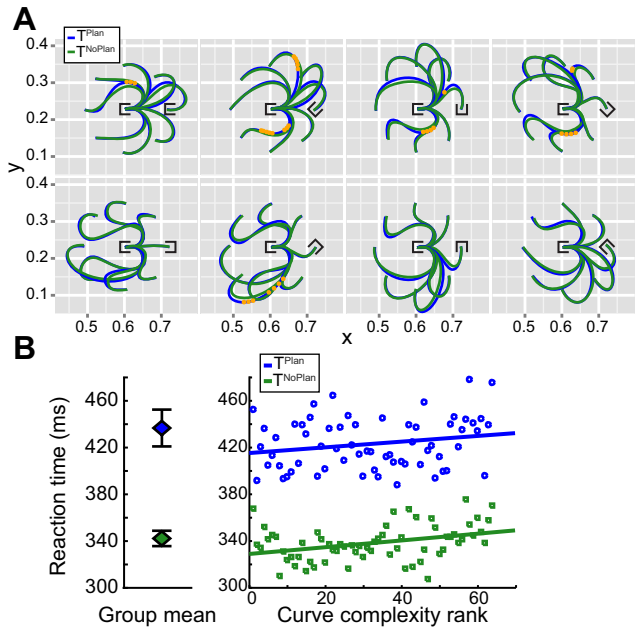

Fig. 2. Results from *experiment 1*. *A*: mean reach trajectories for the T^{Plan} (blue) and T^{NoPlan} (green) groups. Each panel contains trajectories to all 8 targets for a fixed goal-barrier orientation. One representative pair of barriers is shown in black in each panel to indicate the orientation of the goal barrier for all reaches in that panel. Points of significant differences between groups (orange circles) have not been corrected for multiple comparisons across the barrier configurations. *B*: reaction time (RT) was significantly different between the T^{Plan} and T^{NoPlan} groups across all reach trajectories (*left*). RT was found to increase to a small extent with movement complexity (*right*), in a manner independent of the presence of the path cue.

reduction was consistent for every presented movement trajectory [i.e., for each choice of target position and barrier orientation; mixed-effects model, $\chi^2(1) = 11.41$, $P = 0.0007$]. Hence, direct cuing of a movement reduced the RT by about 95 ms without affecting the execution of the movement.

RT Cost was Largely Independent of Movement Complexity

A commonly held belief is that RT is proportional to the difficulty of the movement to be executed (Glencross 1972; Henry and Rogers 1960; Khan et al. 2008; van Mier and Hulstijn 1993); i.e., intuitively a more "complex" movement, in the sense that it is more highly curved, has more changes in acceleration, and therefore requires a more lengthy sequence of muscle activations to execute (Brown and Cooke 1990; Cooke and Brown 1990), should require more time to plan. If this is true, there should be a strong correlation between the observed RT cost and complexity of the corresponding trajectory. Trajectories were assigned a complexity rank, which was quantified by first stratifying trajectories according to the number of inflection points in the movement and then calculating the average curvature (see MATERIALS AND METHODS for details). Ranked movements thus spanned a range from straight point-to-point reaches to curved S shapes.

For both groups, RT was found to modulate to only a small extent with trajectory complexity [T^{Plan} slope = 0.27 ms/complexity rank; T^{NoPlan} slope = 0.32 ms/complexity rank; effect of complexity, likelihood ratio test, $\chi^2(1) = 9.15$, $P = 0.003$; Fig. 2*B*]. However, the relationship between RT and complexity was independent of the presence of the path cue [*t*-test between slopes, $t(124) = -0.26$, $P = 0.80$; interaction

between group and complexity, likelihood ratio test, $\chi^2(1) = 0.79$, $P = 0.38$]; to the extent that the regression slopes were different between groups, RT appeared to modulate with complexity more strongly for the T^{NoPlan} group. This reveals that RT is only minimally influenced by the execution-complexity of the movement; instead, the RT primarily reflects a fixed cost for invoking a trajectory-representation planning stage regardless of the movement shape.

Point-to-Point Movements Had No Trajectory Planning Cost

Although the data presented suggest that a trajectory representation stage is invoked during motor planning, recent studies have argued that point-to-point movements can be generated via feedback control policies (optimal feedback control, OFC; Todorov and Jordan 2002) and do not require an overt representation of the desired movement trajectory. Surprisingly, however, data from *experiment 1*, in which one of the barrier configurations was a point-to-point (straight) movement, indicated that point-to-point reaches can exhibit an RT cost when performed in the context of uncued, intentionally curved movements (Fig. 3*A*, *left*). These results suggest that we may have introduced a contaminating influence of context in which subjects represented the trajectories of point-to-point movements even though it was not necessary.

To test whether point-to-point movements actually lack the trajectory representation cost noted for intentionally curved movements, we measured RTs when blocks of trials included only barriers oriented such that the resulting movements would be straight (point-to-point) reaches (*experiment 2*). As before, we tested for the inclusion of a trajectory representation stage during movement preparation by looking for a prolongation of the RT compared with movements whose trajectories were directly cued. The RTs of point-to-point reaches did not exhibit a change in RT depending on the presence of a path cue [Fig. 3*A*, *right*; RTs: point-to-point with planning and without a path cue (P^{Plan}), 308.32 ± 11.37 ms; point-to-point without planning and with a path cue (P^{NoPlan}), 311.02 ± 17.17 ms; *t*-test, $t(10) = 0.18$, $P = 0.86$]. In contrast, point-to-point movements performed alongside intentionally curved movements (i.e., in *experiment 1*) exhibited a large RT cost (significant interaction between presence of a path cue and context of intentionally curved movements, ANOVA, $F = 9.36$, $P = 0.0048$), suggestive of a context effect. Nevertheless, the lack of an RT cost for point-to-point movements performed in isolation is consistent with the assertion made by current models of motor control such as OFC (Nashed et al. 2012; Todorov and Jordan 2002) that endpoint-directed movements do not have a trajectory representation cost.

Since *experiment 2* provided an estimate of the RT required to produce point-to-point movements, we could compare this to the RT measured when producing intentionally curved movements. The RTs of point-to-point movements were about 81.00 ms shorter than those of curved movements generated by the same subjects (in the P^{Plan} group) in a different block of trials [paired *t*-test, $t(5) = 3.14$, $P = 0.03$]. The RT difference observed between the P^{Plan} group and the T^{NoPlan} group from *experiment 1* was smaller but was also significantly different [difference of 34.23 ms; *t*-test, $t(10) = 3.25$, $P = 0.01$]. However, this smaller RT difference between point-to-point reaches and cued-trajectory reaches could be attributable to

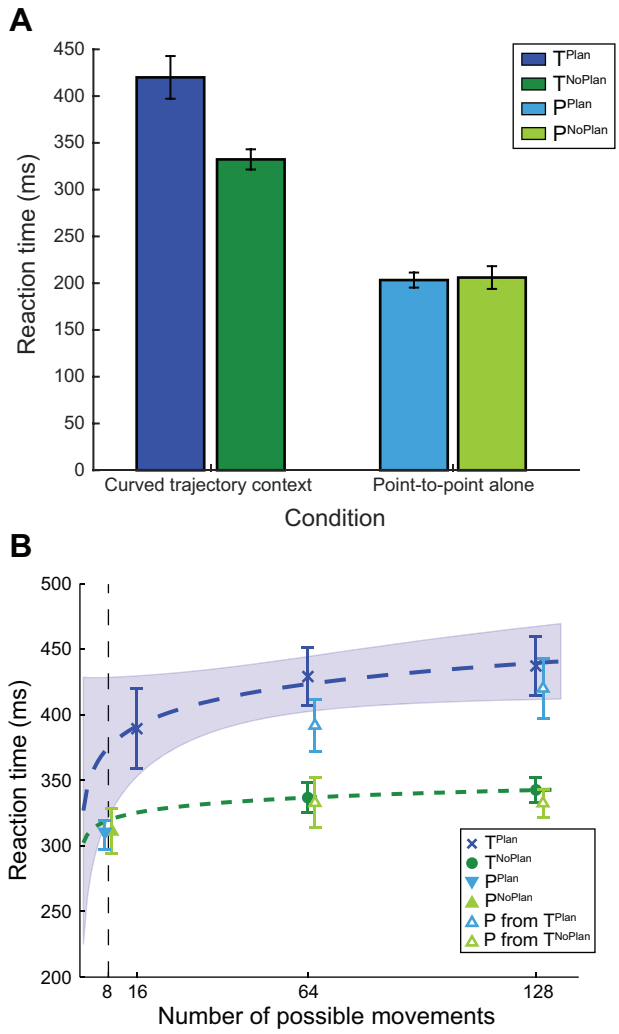

Fig. 3. Results from *experiment 2*. *A*: unlike point-to-point reaches generated in the context of curved movements (*left* bars), point-to-point RTs performed in isolation (*right* bars) were not modulated by the presence of a path cue [point-to-point with (P^{Plan}) or without (P^{NoPlan}) a path cue]. This finding is different from that noted in *experiment 1*, where an RT cost was observed for point-to-point movements. *B*: Hick's law curves for the Planning (blue) and No-Planning (green) conditions for different numbers of barrier configurations. Curve fits excluded the point-to-point movements performed in isolation (filled triangles). RTs of point-to-point movements generated in the context of curved reaches have been extracted for comparison (open triangles).

Hick's law (i.e., that RT is dependent on the number of possible movement alternatives available; Hick 1952) since there were only 8 possible point-to-point reaches but 128 possible curved reaches.

To confirm that Hick's law likely explained the RT difference between point-to-point and cued T^{NoPlan} reaches, it was necessary to estimate two Hick's law curves, one for cued curved movements and one for planned (uncued) curved movements (Fig. 3*B*). Additional groups of subjects completed blocks of trials in which a subset (64) of all the possible barrier configurations was present; as before, different groups were presented with either uncued ($T^{Plan}{}_{64}$) or cued trials ($T^{NoPlan}{}_{64}$). Furthermore, we included in this analysis the block of trials in which a small number (16) of uncued, curved-trajectory barrier configurations were presented to the P^{Plan} group ($T^{Plan}{}_{16}$). A Hick's law curve (logarithmic fit) was then fit to the data from

individual subjects for the three trajectory-planning conditions (T^{Plan}_{16}, T^{Plan}_{64}, and the T^{Plan} group from *experiment 1* that experienced 128 possible barrier configurations), as well as to the individual subject data from the two cued-trajectory groups (T^{NoPlan}_{64} and the T^{NoPlan} group from *experiment 1*; Fig. 3*B*). Interestingly, RTs of point-to-point movements fell outside the 95% confidence interval of the Hick's law curve for movements requiring trajectory planning and fell close to the Hick's law fit for movements executed without trajectory planning. This is consistent with the hypothesis that point-to-point movements and path-cued curved movements are similar in their lack of a requirement for a trajectory representation during motor planning.

Evaluating Alternative Explanations for the Observed RT Cost of Planning

Two additional control analyses were conducted to examine whether the observed RT cost for trajectory representation might instead be attributed to differences in perceptual processing or decision making that arose because of the presentation of a path cue. The results of these analyses are presented below.

RT cost could not be attributed to differences in perception. The RT cost exhibited by the T^{Plan} group could alternatively arise because the path cue provided the T^{NoPlan} group with a perceptual advantage; e.g., it may have allowed subjects to avoid having to perceive and discriminate the orientations of the barriers. That is, there is a perception-related decision-making time associated with identification of the particular stimulus on each trial; the T^{NoPlan} group may have avoided making this discrimination by simply accepting the solution provided by the cue and ignoring the rest of the stimulus display. If this is true, however, then subjects should produce a movement that entirely follows the cued path regardless of whether it is appropriate for the presented barriers. To test this, subjects in *experiment 3* performed the T^{NoPlan}_{64} task, except in 12.5% of all trials they were presented with a path cue that was incorrect: the cue led to the back of the goal barrier, 180° opposite to the actual barrier opening (Fig. 1*C*). As before, all visual feedback was removed once the reaching movement began, so any online corrections during the movement could only arise from information perceived before movement onset.

Despite the occasional inappropriateness of the path cue, subjects initiated their movements at low RTs, comparable to the RTs of subjects performing the original T^{NoPlan} version of the task [$\chi^2(1) = 0.64$, $P = 0.42$]. No significant differences were found within subjects between the RTs for trials in which the presented path cue was incorrect compared with those when it was correct [correct-cue trials: 366.37 ± 1.68 ms; incorrect-cue trials: 373.67 ± 5.15 ms; $\chi^2(1) = 0.56$, $P = 0.46$]. Although movements were launched at low RTs, subjects were surprisingly good at recognizing trials in which the path did not lead to the opening of the goal barrier and making an appropriate online correction during the movement to avoid the barrier (Fig. 4). These midflight updates occurred within the first third of the movement; a classification analysis (see MATERIALS AND METHODS) revealed that, on average, the time between movement initiation and when a change of mind occurred was about 246.64 ms (range of median change-of-mind times across the 8 barrier configurations: 107.69 to 492.31 ms). All but two subjects made two or fewer mistakes (i.e., blindly following the path cue with no correction, out of a total possible 48 incorrect trials); nevertheless, these two subjects still made only a small number of errors (4 and 6 errors, respectively). Hence, although subjects initiated all of their movements at low RTs, indicative of a lack of formulation of a trajectory representation and use instead of the supplied cue shape on all trials, they were still capable of updating their movements midflight. Thus the reduction in RT associated with the path cue was unlikely to arise because subjects were not perceiving the orientations of the barriers at all; otherwise, they would not have had the information available to recognize a mistake and correct their movements appropriately. It could be argued that processing the barrier orientation was simply not completed until after movement onset in the path-cued condition and thus could not influence the executed movement until some time later. This would be surprising, though, since completion of perceptual processing was unable to exert an influence earlier than 250 ms into the movement whereas the observed RT cost was less than half that time.

In further support of the notion that the RT cost did not reflect time for stimulus perception, in an alternative version of the task subjects were informed that the barrier around the goal target would always appear in a fixed orientation (these groups comprised the 64-barrier configuration data set used to estimate Hick's law). Hence, the only barrier whose orientation had to be discriminated was the one around the start target, located where subjects were presumably already attending when the trial started. This reduction in perceptual processing requirements should have affected the T^{Plan} group more than the T^{NoPlan} group if subjects in the T^{NoPlan} group were relying on the path cue to avoid perceptual processing. Despite fixing the orientation of the goal barrier, however, subjects in these fixed-barrier groups did not exhibit any differences in RT compared with the respective conditions (i.e., with or without the path cue) in *experiment 1*, in which the barrier orientation was allowed to vary [mixed-effects models; T^{Plan}, effect of fixing the barrier: $\chi^2(1) = 0.12$, $P = 0.73$; T^{NoPlan}, effect of fixing the barrier: $\chi^2(1) = 0.008$, $P = 0.93$; Fig. 5*A*]. Furthermore, despite fixing the goal-barrier orientation, an RT cost of 92.21 ms was still observed depending on whether or not a path cue was presented [fixed-barrier orientation: T^{Plan}, 429.02 ± 38.70 ms; T^{NoPlan}, 336.81 ± 20.33 ms; mixed-effects model, $\chi^2(1) = 14.62$, $P < 0.001$], which is quite similar to the original estimate of a 94.61-ms RT cost [mixed-effects model, interaction between fixing the barrier and presence of the path cue: $\chi^2(1) = 0.33$, $P = 0.57$]. If stimulus perception did influence the RT cost associated with trajectory representation, fixing the goal-barrier orientation such that it was always known in advance (i.e., it would not need to be perceived) should have reduced that cost to some extent; however, the data indicate that no such RT advantage occurred.

Finally, we examined whether the path cue was providing a perceptual advantage by showing subjects the location of the start-barrier opening, allowing subjects to rapidly initiate their movement and then complete the remainder of the movement while in flight. To examine this, in *experiment 4*, two additional groups of subjects completed the same task as in *experiment 1*, except that the barrier around the starting position appeared, on average, 1,100 ms before the onset of the target

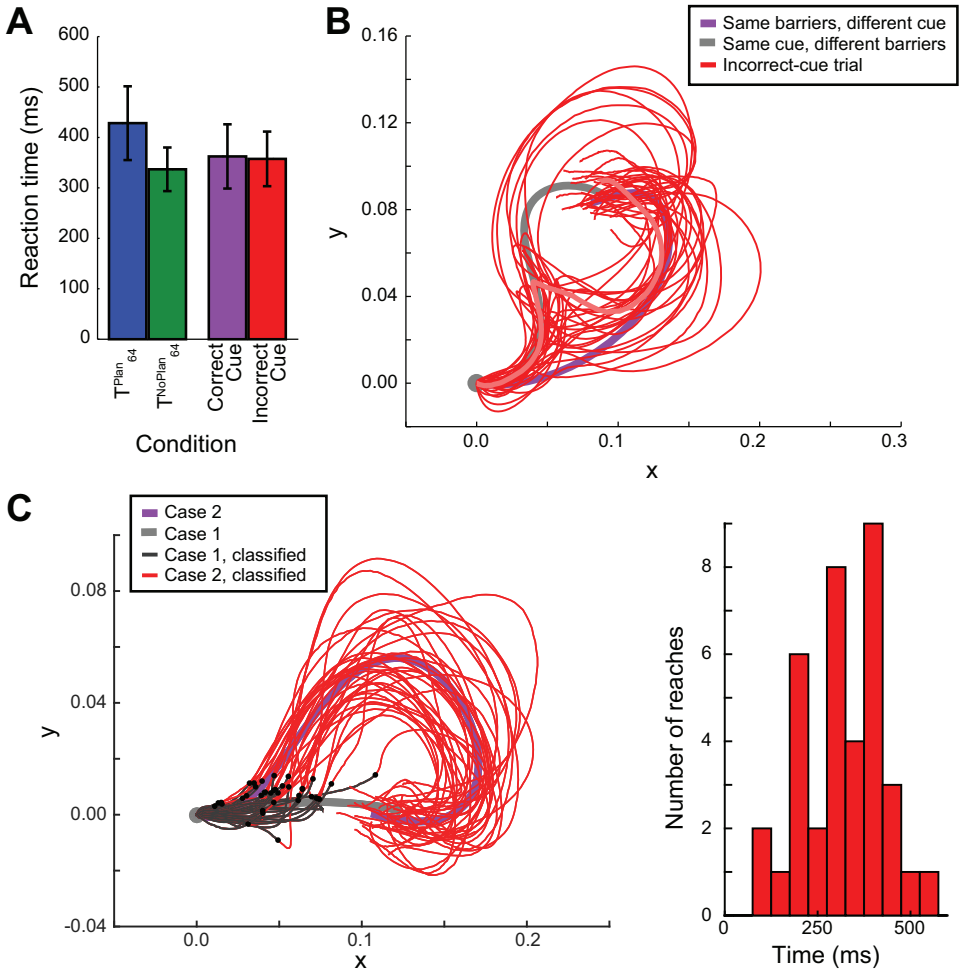

Fig. 4. Results from *experiment 3*. *A*: average RTs for trials in which the path cue was correct (purple) or incorrect (red) compared with RTs for the T^{Plan}_{64} (blue) and T^{NoPlan}_{64} (green) groups. RTs were comparable to those of the T^{NoPlan}_{64} group [$\chi^2(1) = 0.64$, $P = 0.42$] and did not differ between correct-cue and incorrect-cue trials. *B*: incorrect-cue trajectories for one barrier configuration compared with the average reach trajectories made under *case 1* (same path cue, different barriers; gray) and *case 2* (same barriers, different path cue; purple). Dramatic changes of mind occurred midflight (example trajectory, light red). On average, subjects failed to update their motor plans on only 1.60 ± 0.64 of 48 possible trials. *C*: incorrect-cue trajectories from another example barrier configuration, with change-of-mind points identified by black dots (*left*). The distribution of change-of-mind times is also shown for this example trajectory (histogram at *right*).

and target barrier. This allowed subjects more than sufficient time to identify the opening of the start barrier before moving (Fig. 5*B*). Subjects who could observe the start-barrier orientation in advance exhibited a significant RT advantage of 61.32 ms [mixed-effects model, $\chi^2(1) = 13.80$, $P < 0.001$]. This is consistent with the 49.25-ms RT advantage observed for a point-to-point reach that is cued by the orientation of the start barrier when the barrier is presented early as opposed to synchronously with the go cue [*t*-test, $t(11) = 272.43$, $P < 0.01$].

However, this perceptual advantage did not affect the RT difference provided by the path cue. The availability of the path cue still resulted in a significant decrease in RT of 76.83 ms [mixed-effects model, $\chi^2(1) = 5.10$, $P = 0.02$], comparable

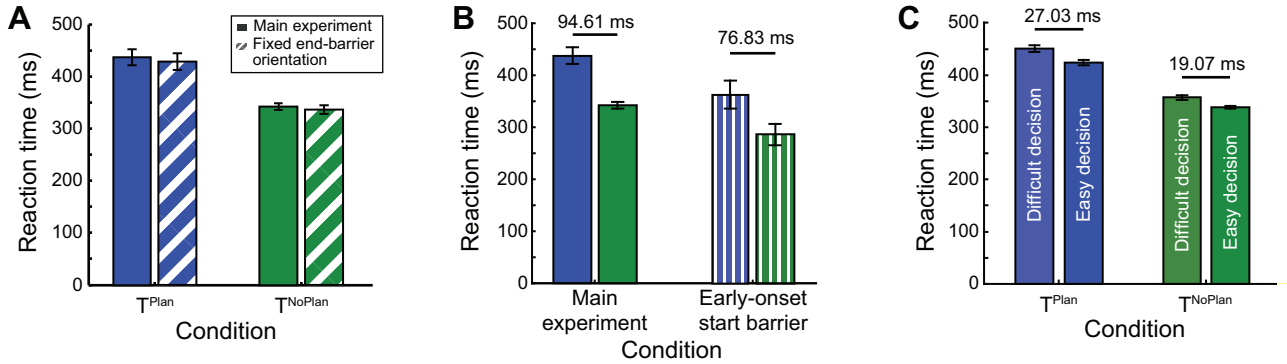

Fig. 5. Data from additional control analyses. *A*: first control for stimulus perception. Despite fixing the goal-barrier orientation, no measureable RT difference was observed for either the T^{Plan} or the T^{NoPlan} condition, and there was no significant change in the RT difference between the T^{Plan} and T^{NoPlan} conditions when the goal-barrier orientation was fixed (difference in RT cost of 2.4 ms). *B*: second control for stimulus perception. Presentation of the start barrier in advance of target onset reduced RTs similarly for both the T^{Plan} and T^{NoPlan} conditions but did not influence the path-cue RT advantage. C: control for decision-making time. Trajectories in the T^{Plan} group were categorized according to the frequency with which subjects opted to take different paths to the target, reflecting the difficulty of the decision regarding how to initiate the movement. Although the RT was significantly longer for "difficult-decision" compared with "easy-decision" trajectories in the T^{Plan} group, the RT difference for those same barrier configurations in the T^{NoPlan} group was comparable (difference of 8 ms).

to the RT difference observed in *experiment 1* [nonsignificant interaction between whether the path cue was present and when the start barrier was presented; mixed-effects model, $\chi^2(1) = 0.35$, $P = 0.55$]. Thus the path cue provided important information regarding the shape of the upcoming movement that was independent of merely informing subjects how to direct their initial reach direction.

RT cost did not depend on deciding the initial movement direction. Another possible interpretation for the observed RT cost is that it could reflect the time required to determine the best way to initiate the reach to acquire the target, i.e., a decision-making cost associated with selecting how best to navigate around the start barrier. Pearce and Moran (2012) demonstrated that neural activity in the delay period preceding the go cue modulates with the direction of movement initiation regardless of the location of the endpoint goal. Once subjects successfully exited the start barrier, they could then use online feedback corrections to guide the hand the remainder of the way to the target location. Hence, the observed RT cost could reflect a path decision-making time to resolve whether subjects should move up or down upon exiting the start barrier, rather than creating a representation of the shape of the movement trajectory in its entirety. To estimate the RT associated with deciding about the initial movement direction, we examined those barrier configurations in which subjects in the T^{Plan} group often chose different routes to get to the target (i.e., on at least 25% of all trials for that barrier configuration subjects opted to take a different path to navigate around the barriers). These alternative routes reflected the ambiguous nature of the barrier configuration, suggesting that the choice to select the initial path direction was more difficult on those trials. We compared the RTs on these difficult-decision configurations with the RTs when the choice of the movement path was easy (i.e., all subjects in the T^{Plan} group chose to execute the same canonical path).

A significant RT difference was observed between difficult- and easy-decision sets of barrier configurations for the T^{Plan} group [difficult-decision configurations: RT = 450.73 ± 23.61 ms, $n = 15$ configurations; easy-decision configurations: RT = 423.70 ± 21.08 ms, $n = 15$ configurations; difference of 27.03 ms; *t*-test, $t(28) = 3.31$, $P = 0.003$]. However, a difference of similar magnitude was observed between the RTs of the same sets of barrier configurations in the T^{NoPlan} group even though no decision about the movement path was required because subjects were asked to just follow the cue [difficult-decision configurations: RT = 357.05 ± 15.98 ms, $n = 15$ configurations; easy-decision configurations: RT = 337.98 ± 10.85 ms, $n = 15$ configurations; difference of 19.07 ms; *t*-test, $t(28) = 3.82$, $P < 0.001$]. RT differences between difficult- and easy-decision configurations across subjects were not significantly different for cued and uncued reaches [$t(18) = 1.29$, $P = 0.21$]. Hence, only about 8 ms of the 27-ms difference between difficult- and easy-decision trials could be directly attributed to decisions about the direction of the movement path; the remainder reflected execution-related differences in RT shared across the T^{Plan} and T^{NoPlan} groups (Fig. 5*C*).

DISCUSSION

The findings presented in this study, along with previous data on motor equivalence (Kadmon Harpaz et al. 2014; Rijntjes et al. 1999; van Galen and Teulings 1983; Wright 1990), bimanual interference (Albert and Ivry 2009; Diedrichsen et al. 2001), and priming (Griffiths and Tipper 2009, 2012; Jax and Rosenbaum 2007), suggest that when the particular path of a movement is a relevant part of the motor goal (explicitly or implicitly), a significant portion of the RT is spent generating a representation of the shape of the upcoming movement trajectory.

Movement Trajectories are Explicitly Represented During Planning

About 90 ms of RT appear to be related to the preparation of a representation of the desired movement trajectory. This time is not related to the preparation of motor commands for execution, because it is not observed when subjects are presented with a cue indicating the shape of the movement they should produce, and is it not significantly influenced by the complexity of the movement to be executed. Additionally, this RT cost is unlikely to be attributable solely to perceptual factors, such as the time required to perceive and discriminate the orientations of the barriers or to decide on the initial movement direction away from the start target. Instead, we propose that this RT is associated with a distinct motor planning stage in which the shape of the desired movement trajectory is represented.

This trajectory representation is likely more than a static visual image of the trajectory path; it also may include an understanding of how to generate a movement with that particular shape. Returning to the example of drawing a numeral 8, we propose that the trajectory representation includes both the shape of the 8 and some information about the manner in which it is to be drawn, i.e., as a continuous sinuous line or a pair of ovals. Thus we propose that the nature of this trajectory representation is more akin to motor imagery than to visual imagery (Kosslyn et al. 2001), because the representation itself contains information about the movement that will be generated to achieve the motor goal. On the other hand, this representation, as implied by the phenomenon of kinematic motor equivalence in handwriting, seems to exist at a fairly abstract level that precedes choices of the size scale (van Galen and Teulings 1983; Wing 2000) or effector (Rijntjes et al. 1999; Wright 1990), choices that are often implied as part of motor imagery. Hence, trajectory representation may exist somewhere between what is classically considered to be visual imagery and motor imagery (e.g., "visual-motor memory"; Waterman et al. 2015) and could facilitate the transformation from visual movement goals to motor commands for execution.

Point-to-Point Reaches Do Not Require a Trajectory Representation

A trajectory representation stage appears to be optional for endpoint-directed movements. When placed in the context of a task that requires subjects to plan the trajectories of their movements, point-to-point reaches can be made to incur an RT cost for planning, presumably because subjects are spending time unnecessarily representing the trajectories of these movements. Since it has previously been shown that kinematically identical point-to-point movements can be elicited at RTs much lower than typically observed when the go cue is paired

with a startling stimulus (Carlsen et al. 2004; Valls-Sole et al. 1999), when encouraged to move at lower RTs (Haith et al. 2016), or during reaching to intercept a rapidly moving object (Perfiliev et al. 2010), it seems unlikely that this absence of an RT cost for point-to-point reaches occurred because of a floor effect (i.e., subjects simply could not initiate their movement at a lower RT).

Under typical circumstances, subjects do not spend time imagining the shape of point-to-point movements because simply specifying the movement endpoint is enough. Indeed, corrective feedback responses for point-to-point reaches return the hand to a straight-line path following a perturbation only when the movement trajectory is defined as part of the task goal (Cluff and Scott 2015). In fact, feedback control policies are thought to be sufficient to give rise to quite complex curved movements that can appropriately avoid obstacles to reach a desired endpoint in the absence of the need for an overt trajectory representation (Liu and Todorov 2007; Nashed et al. 2012). In contrast, control policies for intentionally curved movements (e.g., drawing the numeral 8) would likely require that the intended movement shape be included as a cost-function constraint (Scott 2012), but these theories do not explain where this shape representation comes from to begin with to be included within the cost function. Thus the representational capacity we presently propose seems important primarily for movements wherein the trajectory shape is task relevant (e.g., for either intentionally curved or intentionally straight reaches) and could serve as the source of the shape representation that a control policy would require in such cases. More importantly, however, the ability to represent trajectory shapes could form the basis for generating the very broad repertoire of intentionally curved actions that humans possess, such as when making gestures and using tools.

Implications for the Neural Representations of Planning Intentionally Curved Reaches

If an overt representation of a movement trajectory exists as part of a motor plan, then a neural correlate for it should be identifiable. Neural recordings from the posterior parietal cortex in monkeys hint that some neurons may respond differently depending on whether the hand must avoid an obstacle en route to the target goal (Torres et al. 2013). Additionally, premovement neural activity in premotor and primary motor cortex during a delay period modulates with the path that will be taken to reach a target (Hocherman and Wise 1990, 1991; Pearce and Moran 2012), although whether this is merely a downstream transformation of an upstream trajectory representation into the appropriate motor commands for action is unclear.

Lesions of the left frontoparietal cortex in humans following stroke result in the cognitive-motor deficit of apraxia, in which patients have great difficulties in executing complex movements such as the imitation of meaningless gestures (Hermsdorfer et al. 1996; Goldenberg and Hagmann 1997) or the pantomime of tool-use actions (Buxbaum and Saffran 2002; Buxbaum et al. 2014; Goldenberg and Hagmann 1998) but are still able to perform simple point-to-point reaching movements with little to no impairment (Botvinick et al. 2009; Buxbaum et al. 2005; Hermsdorfer et al. 1996; Ietswaart et al. 2006). Thus there is a clear divide between the production of simple point-to-point movements and more complex actions. We conjecture, on the basis of this dissociation between types of movements and in light of the present findings, that imitation and tool use may both rely in part on a trajectory representation stage that supports the production of these intentionally curved movements. Such a stage may span a pathway from parietal to premotor cortex and guide the production of such actions. Performance impairments in patients with apraxia may therefore at least partially reflect an impaired ability to represent the trajectories of upcoming actions (Heilman 1979; Liepmann 1905).

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.L.W. and J.W.K. conception and design of research; A.L.W. performed experiments; A.L.W. and J.G. analyzed data; A.L.W., J.G., and J.W.K. interpreted results of experiments; A.L.W. and J.G. prepared figures; A.L.W. drafted manuscript; A.L.W., J.G., and J.W.K. edited and revised manuscript; A.L.W., J.G., and J.W.K. approved final version of manuscript.

REFERENCES

Albert NB, Ivry RB. The persistence of spatial interference after extended training in a bimanual drawing task. *Cortex* 45: 377–385, 2009.

Bates D, Maechler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67: 1–48, 2015.

Botvinick MM, Buxbaum LJ, Bylsma LM, Jax SA. Toward an integrated account of object and action selection: a computational analysis and empirical findings from reaching-to-grasp and tool-use. *Neuropsychologia* 47: 671–683, 2009.

Brown SH, Cooke JD. Movement-related phasic muscle activation. I. Relations with temporal profile of movement. *J Neurophysiol* 63: 455–464, 1990.

Buxbaum LJ, Saffran EM. Knowledge of object manipulation and object function: dissociations in apraxic and nonapraxic subjects. *Brain Lang* 82: 179–199, 2002.

Buxbaum LJ, Johnson-Frey SH, Bartlett-Williams M. Deficient internal models for planning hand-object interactions in apraxia. *Neuropsychologia* 43: 917–929, 2005.

Buxbaum LJ, Shapiro AD, Coslett HB. Critical brain regions for tool-related and imitative actions: a componential analysis. *Brain* 137: 1971–1985, 2014.

Carlsen A, Chua R, Inglis JT, Sanderson DJ, Franks IM. Prepared movements are elicited early by startle. *J Mot Behav* 36: 253–264, 2004.

Cluff T, Scott SH. Apparent and actual trajectory control depend on the behavioral context in upper limb motor tasks. *J Neurosci* 35: 12465–12476, 2015.

Cooke JD, Brown SH. Movement-related phasic muscle activation. II. Generation and functional role of the triphasic pattern. *J Neurophysiol* 63: 465–472, 1990.

Diedrichsen J, Hazeltine E, Kennerley S, Ivry RB. Moving to directly cued locations abolishes spatial interference during bimanual actions. *Psychol Sci* 12: 493–498, 2001.

Glencross DJ. Latency and response complexity. *J Mot Behav* 4: 251–256, 1972.

Goldenberg G, Hagmann S. The meaning of meaningless gestures: a study of visuo-imitative apraxia. *Neuropsychologia* 35: 333–341, 1997.

Goldenberg G, Hagmann S. Tool use and mechanical problem solving in apraxia. *Neuropsychologia* 36: 581–589, 1998.
Goldsmith J, Kitago T. Assessing systematic effects of stroke on motor control using hierarchical function-on-scalar regression. *J R Stat Soc Ser C Appl Stat* 65: 215–236, 2016.
Griffiths D, Tipper SP. Priming of reach trajectory when observing actions: hand-centred effects. *Q J Exp Psychol (Hove)* 62: 2450–2470, 2009.
Griffiths D, Tipper SP. When far becomes near: shared environments activate action simulation. *Q J Exp Psychol (Hove)* 65: 1241–1249, 2012.
Haith AM, Pakpoor J, Krakauer JW. Independence of movement preparation and movement initiation. *J Neurosci* 36: 3007–3015, 2016.
Heilman KM. Apraxia. In: *Clinical Neuropsychology*, edited by Heilman KM and Valenstein E. New York: Oxford University Press, 1979, p 159–185.
Henry FM, Rogers DE. Increased response latency for complicated movements and a memory drum theory of neuromotor reaction. *Res Q* 31: 448–458, 1960.
Hermsdorfer J, Mai N, Spatt J, Marquardt C, Veltkamp R, Goldenberg G. Kinematic analysis of movement imitation in apraxia. *Brain* 119: 1575–1586, 1996.
Hick WE. On the rate of gain of information. *Q J Exp Psychol* 4: 11–26, 1952.
Hocherman S, Wise SP. Trajectory-selective neuronal activity in the motor cortex of rhesus monkeys (*Macaca mulatta*). *Behav Neurosci* 104: 495–499, 1990.
Hocherman S, Wise SP. Effects of hand movement path on motor cortical activity in awake, behaving rhesus monkeys. *Exp Brain Res* 83: 285–302, 1990.
Ietswaart M, Carey DP, Della Sala S. Tapping, grasping and aiming in ideomotor apraxia. *Neuropsychologia* 44: 1175–1184, 2006.
Jax SA, Rosenbaum DA. Hand path priming in manual obstacle avoidance: evidence that the dorsal stream does not only control visually guided actions in real time. *J Exp Psychol Hum Percept Perform* 33: 425–441, 2007.
Kadmon Harpaz N, Flash T, Dinstein I. Scale-invariant movement encoding in the human motor system. *Neuron* 81: 452–462, 2014.
Khan MA, Mourton S, Buckolz E, Franks IM. The influence of advance information on the response complexity effect in manual aiming movements. *Acta Psychol (Amst)* 127: 154–162, 2008.
Kosslyn SM, Ganis G, Thompson WL. Neural foundations of imagery. *Nat Rev Neurosci* 2: 635–642, 2001.
Liepmann H. *The Left Hemisphere and Action*. London, ON, Canada: University of Western Ontario, 1905.
Liu D, Todorov E. Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. *J Neurosci* 27: 9354–9368, 2007.
Nashed JY, Crevecoeur F, Scott SH. Influence of the behavioral goal and environmental obstacles on rapid feedback responses. *J Neurophysiol* 108: 999–1009, 2012.
Pearce TM, Moran DW. Strategy-dependent encoding of planned arm movements in the dorsal premotor cortex. *Science* 337: 984–988, 2012.
Perfiliev S, Isa T, Johnels B, Steg G, Wessberg J. Reflexive limb selection and control of reach direction to moving targets in cats, monkeys, and humans. *J Neurophysiol* 104: 2423–2432, 2010.
Rijntjes M, Dettmers C, Buchel C, Kiebel S, Frackowiak RS, Weiller C. A blueprint for movement: functional and anatomical representations in the human motor system. *J Neurosci* 19: 8043–8048, 1999.
Scott SH. The computational and neural basis of voluntary motor control and planning. *Trends Cogn Sci* 16: 541–549, 2012.
Todorov E, Jordan MI. Optimal feedback control as a theory of motor coordination. *Nat Neurosci* 5: 1226–1235, 2002.
Torres EB, Quian Quiroga R, Cui H, Buneo CA. Neural correlates of learning and trajectory planning in the posterior parietal cortex. *Front Integr Neurosci* 7: 39, 2013.
Valls-Sole J, Rothwell JC, Goulart F, Cossu G, Munoz E. Patterned ballistic movements triggered by a startle in healthy humans. *J Physiol* 516: 931–938, 1999.
van der Wel RP, Fleckenstein RM, Jax SA, Rosenbaum DA. Hand path priming in manual obstacle avoidance: evidence for abstract spatiotemporal forms in human motor control. *J Exp Psychol Hum Percept Perform* 33: 1117–1126, 2007.
van Galen GP, Teulings HL. The independent monitoring of form and scale factors in handwriting. *Acta Psychol (Amst)* 54: 9–22, 1983.
van Mier H, Hulstijn W. The effects of motor complexity and practice on initiation time in writing and drawing. *Acta Psychol (Amst)* 84: 231–251, 1993.
Waterman AH, Havelka J, Culmer PR, Hill LJ, Mon-Williams M. The ontogeny of visual-motor memory and its importance in handwriting and reading: a developing construct. *Proc Biol Sci* 282: 20140896, 2015.
Wing AM. Motor control: mechanisms of motor equivalence in handwriting. *Curr Biol* 10: R245–R248, 2000.
Wong AL, Haith AM, Krakauer JW. Motor planning. *Neuroscientist* 21: 385–398, 2014.
Wright CE. Generalized motor programs: reexamining claims of effector independence in writing. In: *Attention and Performance XIII: Motor Representation and Control*, edited by Jeannerod M. Hillsdale, NJ: Erlbaum, 1990, p. 294–320.