Movement imitation depends on an abstract trajectory representation in dorsal premotor cortex

Aaron L. Wong[1†*], Steven A. Jax[1†], Louisa L. Smith[1], Laurel J. Buxbaum[1], John W. Krakauer[2,3]

1. Moss Rehabilitation Research Institute, Elkins Park, Pennsylvania, 19027
2. Department of Neurology, Johns Hopkins University School of Medicine, Baltimore, Maryland, 21205
3. Department of Neuroscience, Johns Hopkins University School of Medicine, Baltimore, Maryland, 21205

*Corresponding author: 50 Township Line Rd., Elkins Park, PA 19027, wongaaro@einstein.edu

†Co-first authors

Keywords: imitation; motor planning; movement trajectories; apraxia

ABSTRACT

Humans are particularly good at copying novel and meaningless gestures. The mechanistic and anatomical basis for this specialized imitation ability remains largely unknown. One idea is that imitation depends on a representation of the relative configurations of body parts (body schema). Here we propose an alternative route to imitation that depends on an abstract representation of the trajectory path of the end-effector. We studied a group of patients with strokes that encompassed the left premotor and posterior parietal cortices. We found that they were equally impaired at imitating movement trajectories using the ipsilateral limb (i.e., the non-paretic side) that were cued either by an actor using their whole arm or just by a cursor, suggesting that body configuration is not always critical for imitation and that a representation of abstract trajectory shape may suffice. In addition, imitation ability was uncorrelated to the ability to identify the trajectory shape, suggesting a dissociation between producing trajectory shapes and perceiving their paths. Finally, a lesion-symptom mapping analysis found that imitation deficits were associated with lesions in left dorsal premotor but not parietal cortex. Together, these findings suggest a novel body-independent route to imitation that relies on the ability to plan abstract movement paths within dorsal premotor cortex.

INTRODUCTION

Imitation, which is critical for learning to communicate through gesture, to use tools, and to acquire complex skills, has been the subject of much speculation and investigation since the start of the 20th century. What has become clear is that most non-human animals, including chimpanzees and other great apes, are very limited in their ability to copy gestures that are novel or meaningless (Whiten et al., 2004). Humans, in contrast, appear to possess a unique imitation-specific specialization: from a very young age we are very good at copying meaningless gestures that have no goal, semantic meaning, or desired outcome other than the action itself (Subiaul, 2016). The component processes that comprise this distinct imitation ability remain largely unknown.

Current views of imitation in humans emphasize the need for a representation of the body (Buxbaum et al., 2000; Goldenberg, 2009; Goldenberg, 2013). Evidence for this stems in large part from research into the curious condition of ideomotor apraxia, in which patients have normal movement ability – e.g., hand pre-shaping during prehension or arm kinematics during reach-to-grasp (Buxbaum et al., 2005; Ietswaart et al., 2006) – but impaired imitation ability (Buxbaum et al., 2014). Studies in these patients and in healthy controls have led to the theory that humans imitate meaningless actions by computing the set of transformations required to move or reposition this body-schema representation to match the actor; this facilitates the ability to recognize and copy static postures (Goldenberg, 1999) or dynamic actions (Schwoebel et al., 2004).

However, specifying the form of a gesture does not necessarily need to rely on a description of relative body configurations. Another important movement feature is the path

traced by the end-effector. For example, specification of the movement trajectory, rather than a transformation of the body schema, is likely the route by which actions such as writing are controlled; for example, writing the letter "S" only requires a representation of the sinuous shape along which the end-effector must move. Indeed, handwriting must have an effector-independent representation of trajectory path because kinematic characteristics are preserved regardless of the effector used to execute the action (Rijntjes et al., 1999; Wright, 1990) or the size scale at which it is performed (Kadmon Harpaz et al., 2014; van Galen and Teulings, 1983; Wing, 2000). Recently, we demonstrated that this ability to abstractly represent the desired trajectory path can be useful for planning complex actions, such as reaching around obstacles (Wong et al., 2016). Moreover, this ability to represent effector-independent movement trajectories is likely the means by which non-primates such as dolphins can imitate human actions (Harley et al., 1998; Xitco Jr et al., 1998), since dolphins don't have multi-segmented arms and are therefore unlikely to have an internal body-schema representation that affords imitation of human arm movements. We hypothesized, therefore, that if one carefully explores what it means to imitate, it is possible to identify a second route to imitation: one that does not involve processing body-part relationships and their changing positions, but is instead trajectory-based and body-independent.

If there are indeed two distinct routes to imitation, a reasonable follow-up question is to ask whether these routes are mediated by the same brain regions. Current evidence suggests that the ability to perform complex actions such as imitation becomes impaired when there is damage to the left inferior parietal and premotor cortex (i.e., Brodmann areas 40 and 6, among others) (Buxbaum et al., 2014; Caspers et al., 2010). Neural activity in both of these regions tends to be quite similar across a number of tasks, such as during action observation (Buccino et al., 2001; Buccino et al., 2004; Wheaton et al., 2004). However, given the flow of information from visual

cortex to motor cortex, there is likely a caudal-rostral gradient along which information processing progresses from being largely tied to perceptual information to being more reflective of motor planning. In line with this, the posterior parietal cortex has also been implicated in processes related to visual imagery and manipulation of the body schema, such as the ability to perform mental rotations of body parts (Bonda et al., 1995; Zacks, 2008) or distinguishing between mirror-reversed shapes (Davidoff and Warrington, 2001). In contrast, neural activity in dorsal premotor cortex modulates according to the trajectory path taken to reach a target (Hocherman and Wise, 1990, 1991; Pearce and Moran, 2012). Thus, we hypothesized that if there is a route to imitation that involves the representation of movement trajectory path, the neural substrates of such a representation are maintained in dorsal premotor cortex and not inferior parietal cortex.

To address our behavioral and anatomical hypotheses, we required healthy control participants and patients with left hemisphere strokes to imitate unfamiliar, meaningless movement trajectories. Imitation was tested using the left hand, which in patients corresponded to their ipsilateral limb (i.e., the unaffected side) Since the shape of the motion itself was the goal of the action, we could ascertain whether imitation of meaningless trajectories was intact in these patients. Critically, participants were cued by watching either a video of an actor or the motion of a cursor on a screen; if patients had equal difficulty with these two cuing conditions, this would call into question whether imitation deficits always stem from body-representation deficits and support our idea of an alternative, body-independent route to imitation. We recruited patients with heterogeneous lesion locations that, as a group, included the dorsal premotor and inferior parietal cortices, with the anticipation that patients might exhibit a range of imitation abilities depending on the exact location of their lesion. This enabled us to examine the relationship

between lesion location and imitation ability to test where movement-trajectory paths may be computed.

RESULTS

Twenty-one patients with left-hemisphere stroke (Fig. 1) and thirteen age-matched controls were asked to imitate meaningless trajectories after watching the movement of either an actor (body-cued stimulus) or a cursor (body-free stimulus). Trajectories were reasonably complex (Fig. 2) in that they were concatenations of multiple straight or curved movement segments that were executed in a smooth, continuous fashion. To provide a frame of reference (e.g., potential via points) for the stimulus trajectories, either one or five static landmarks were also displayed throughout the movement. After viewing a stimulus, participants were asked to either imitate the observed movement trajectory by moving their left (non-paretic, non-dominant) hand along a vertically mounted Plexiglass surface (Production task), or to report with a button

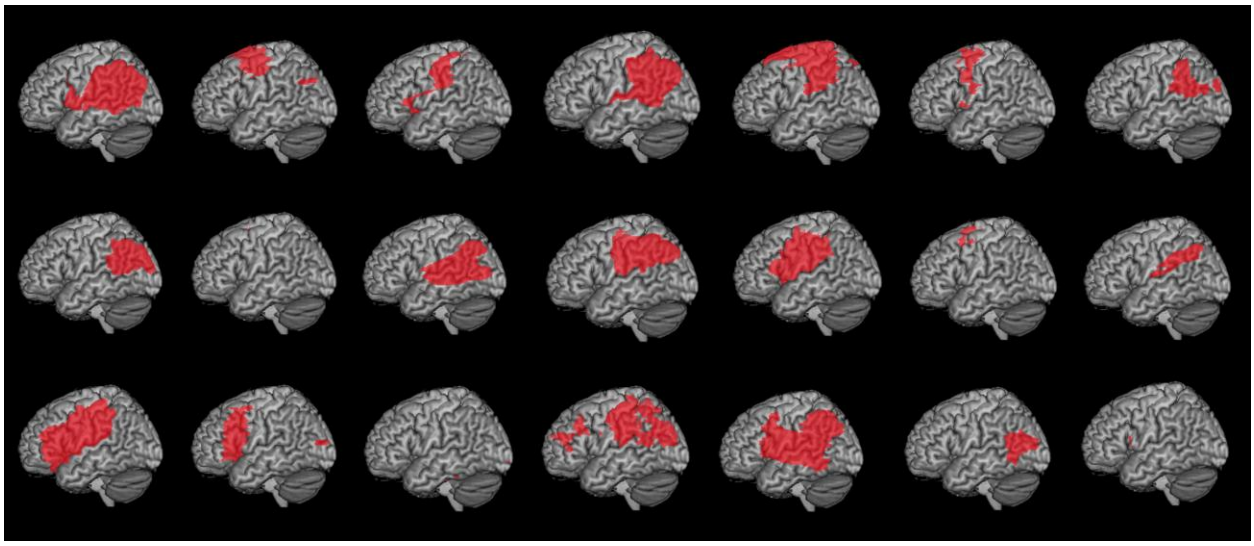

Figure 1. Cortical view of lesion maps for individual patients. Patients were selected to have a range of lesions spanning the left fronto-temporo-parietal cortex.

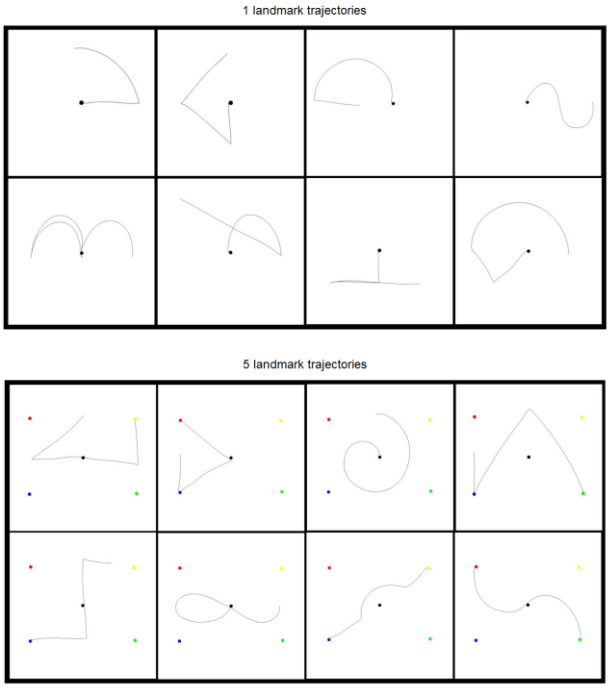

Figure 2. Reach trajectories employed in the Production and Perception tasks. Trajectories were cued by observing the movement of either an actor or a cursor, and were made with reference to either one (top panel) or five (bottom panel) landmarks. These static shapes were derived from motion trackers placed on the actor, and were displayed in the Perception task. In the one-landmark condition (top), motion always began at the central target; in the five-landmark condition (bottom), the starting location of the trajectory varied for each stimulus shape.

press whether a subsequently displayed static image had the same or different (mirror-inverted) shape compared to the stimulus trajectory (Perception task).

Patients and controls exhibited comparable point-to-point reach kinematics

We first analyzed the imitation of point-to-point reaches to confirm that the ability to reproduce straight movement paths was unimpaired in patients. Example point-to-point movements for a representative control, a patient with dorsal premotor but without inferior parietal lobe damage (patient 6 in Figure 1), and a patient with inferior parietal lobe damage but without dorsal premotor damage (patient 1 in Figure 1) are shown in Figure 3. As can be seen by

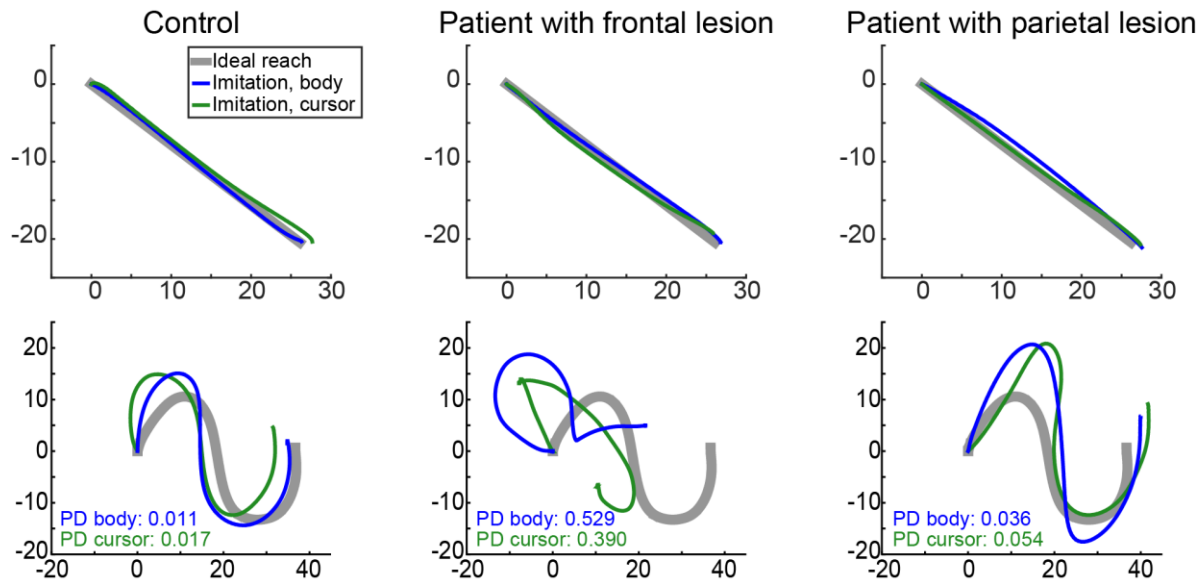

Figure 3. Examples of imitated trajectories from a single control participant (left column), a patient with dorsal premotor but without inferior partial damage (center column), and a patient with inferior parietal lobe damage but without dorsal premotor damage (right column). In all panels, imitation of a body stimulus is shown in blue and imitation of a cursor stimulus is in green; the thick gray line reflects the ideal movement as performed by the actor. Point-to-point trajectories were comparable across participants (top row). In contrast, imitation ability for complex paths (bottom row) was worse for the patient with dorsal premotor damage than the other two participants, for both the body and cursor conditions. Imitation ability was quantified using a shape dissimilarity (Procrustes distance, PD) metric, in which larger values indicate worse replication of the actor's movement.

comparing the three top panels of the figure, all three participants produced similar movements. This observation was confirmed in a group-level analysis focusing on the ability to generate reaches that were straight and aimed in the correct direction. Specifically, we measured the straightness of the movement path (maximum hand-path deviation from a straight line) and the initial reach direction error (deviation of the aiming direction of the hand 100 ms after movement initiation). The patient and control groups did not differ in either the straightness of the movement path (patients: 4.28 ± 2.91 mm; controls: 3.49 ± 1.72 mm; $\chi^2(2) = 3.26$, $p = 0.20$) or the initial direction error (patients: 3.48 ± 2.96° ; controls: 5.39 ± 1.79°; $\chi^2(2) = 0.25$, $p = 0.62$). Thus, patients and controls imitated point-to-point reaches with comparable accuracy, suggesting that the ability to perceive and reproduce simple goal-directed actions was unimpaired.

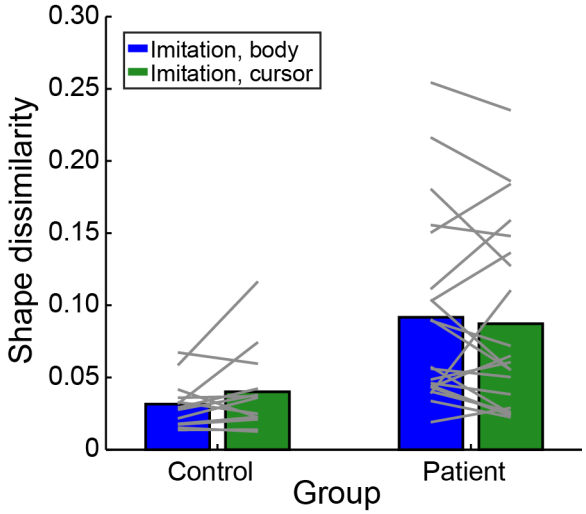

Figure 4. Mean shape dissimilarity (Procrustes distance) of imitated movements in the Production task. Group means (bars) and individual means (lines) are shown separately for the body-cued (blue) and cursor-cued (green) conditions.

Imitation of complex trajectories was impaired in patients with left hemisphere damage

Despite being able to produce straight point-to-point trajectories, at the group level patients with left hemisphere damage often exhibited deficits in the ability to reproduce the shapes of movement trajectories in the Production task (see Methods). Example trajectories are shown in the bottom panels of Figure 3. Shape imitation errors were quantified by calculating a dissimilarity score (Procrustes distance metric) (Goodall, 1991) between the movement of the actor/cursor displayed in the stimulus and the trajectory produced by the participant. Mean dissimilarity scores are shown in Figure 4 at both the group (bars) and participant (lines) level. Although patients exhibited a wide range of dissimilarity scores, as a group their scores were generally larger than those of the controls but similar between the body-cued or cursor-cued stimuli.

When shape dissimilarity scores were analyzed with a mixed-effects model, there was a main effect of group (patient versus control: $\chi^2(2) = 17.29$, $p = 0.0009$), in which stroke

participants reproduced the shape less accurately compared to controls. However, no significant main effect was observed for stimulus type (body-cued versus cursor-cued: $\chi^2(1) = 0.613$, $p = 0.434$), suggesting that regardless of whether or not the stimuli provided information about the relative positioning of limb segments during movement, participants performed equally well at imitating the required shape.

Consistent with the lack of a main effect of stimulus type on imitation performance, participants that exhibited larger shape dissimilarity scores in the body condition also performed worse during the cursor condition. Regression analyses indicated that participants' average shape dissimilarity in the body task was highly correlated with their average shape dissimilarity in the cursor task, with a slope near 1 and intercept near 0 ($R^2 = 0.78$; slope = 0.902, intercept = 0.006). Similar results were obtained when considering only the stroke participants ($R^2 = 0.78$; slope = 0.88, intercept = 0.015). Thus, the ability to imitate trajectory paths was not different whether participants were given information about the configuration of the entire limb or saw only a body-independent representation of the end-effector.

Although we would not expect low-level motor impairments to impact the ability to imitate complex actions (despite the potential of mild motor deficits on the ipsilateral side (Krakauer and Carmichael, 2017)), our metric of imitation ability cannot strictly distinguish between poor imitation and poor motor control. To confirm this assertion, we examined correlations between the ability to generate point-to-point reaches and imitate complex gestures. As expected, we found no correlation between the performance of point-to-point reaches and shape dissimilarity in the Production task (maximum hand-path deviation: $R^2 = 0.035$, $p = 0.413$; initial direction error: $R^2 = 0.01$, $p = 0.53$); thus, measures of imitation impairments did not simply reflect problems with aiming or controlling the limb. Additionally, patient performance

could not be explained by a nonspecific cognitive effect of lesion volume, as there was no relationship between shape dissimilarity and total lesion volume ($R^2 = 0.001$, $p = 0.857$).

Trajectory perception was also impaired in patients with left-hemisphere damage

One potential concern was that imitation deficits could arise not because of problems in generating the desired action, but in simply being able to perceive the movement to be copied. Hence, to examine deficits in the ability to perceive rather than produce the shape of the trajectory path, participants were required to also complete a second task (Perception task) in which they observed a movement trajectory as in the Production task, but then simply had to make a binary choice (yes/no) as to whether a subsequently displayed static image had the same shape as the path of the viewed stimulus trajectory. As before, the stimuli could be cued either by an actor or a cursor.

Mean accuracy and reaction time (RT) in identifying a static shape as being the same or different from the observed movement are shown in the Figure 5A and 5B, respectively. As with the Production task, patients exhibited a wide range of performance, but were generally worse

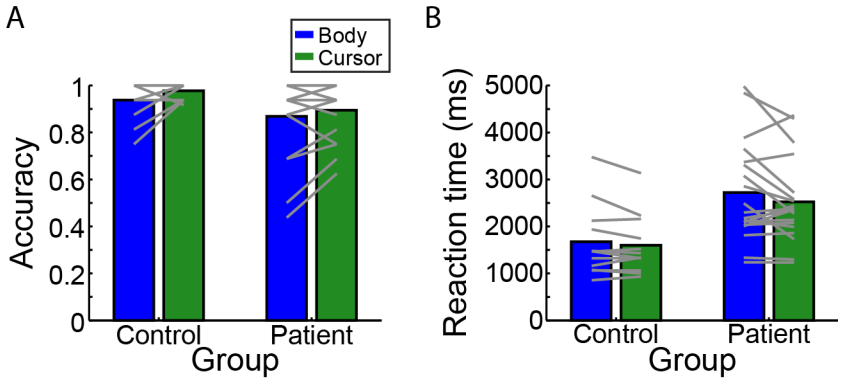

Figure 5. Mean performance in the Perception task was quantified using the complimentary measures of accuracy (A) and reaction time (B). Group means (bars) and individual means (lines) are shown separately for the body-cued (blue) and cursor-cued (green) conditions.

than controls (lower accuracy, higher RTs). Accuracy and RT measures were negatively correlated across participants ($r^2 = 0.25$, $p = 0.004$), suggesting that impairments in trajectory perception generally affected both measures similarly. However, since accuracy is informative about the likelihood of correctly reporting the observed trajectory whereas RT as a continuous measure provides a sense of uncertainty about that choice, both provide a complementary view of performance in this Perception task.

For response accuracy (Figure 5A), a mixed-effects model revealed no significant main effects; in particular, while there was a tendency for a difference between groups ($\chi^2(1) = 5.229$) and between stimulus types (body-cued versus cursor-cued: $\chi^2(1) = 3.951$), neither effect was significant after correcting for multiple comparisons ($p = 0.11$ and $p = 0.19$ respectively). No significant interaction was observed between group and stimulus type ($\chi^2(1) = 0.445$, $p = 0.45$).

For RT (Figure 5B), a mixed-effects model showed a significant main effect of group ($\chi^2(2) = 24.43$, $p = 0.0001$), with patients having longer RTs than controls (2623.7 ± 948.3 ms and 1638.4 ± 696.0 ms respectively). We also observed a significant interaction between group and testing order (whether the Production or Perception task was performed first; $\chi^2(1) = 3.867$, $p = 0.049$) that was not observed for the Production task or for Perception accuracy, but no main effect of testing order ($\chi^2(1) = 3.006$, $p = 0.083$). In this interaction, controls exhibited slower RTs when the Perception task followed the Production task; patients exhibited no effect of testing order. Importantly, we again observed no significant effect of stimulus type ($\chi^2(1) = 2.646$, $p = 0.208$) and no interaction between stimulus type and group ($\chi^2(1) = 2.056$, $p = 0.505$). Together, the accuracy and RT data suggest that patients in general exhibited disrupted performance on the Perception task compared to that of control participants, and performed similarly when the movement was cued by an actor or a cursor. Thus, as with the Production

task, availability of information about the relative positioning of the limb segments did not strongly influence the ability to accurately perceive and report the observed trajectory path.

Performance on the Production and Perception tasks were uncorrelated

The previous two sections indicate that left hemisphere damage disrupts performance on both the Production and Perception tasks. Since these analyses were performed at the group level, it is important to understand whether the same participants exhibited deficits on both tasks (indicating that both tasks potentially rely on the same underlying computational processes or that difficulties in the Perception task can account for impaired performance in the Production task), or whether the group-level deficits stemmed from different subgroups of patients that were impaired on only one of the two tasks (suggesting that separate processes may underlie performance of the Production and Perception tasks).

The relationships between shape dissimilarity in the Production task and performance (accuracy and RT) in the Perception task are shown in Figure 6. As can be seen in the figure, there was no clear relationship between performance on the two tasks. Interestingly, several

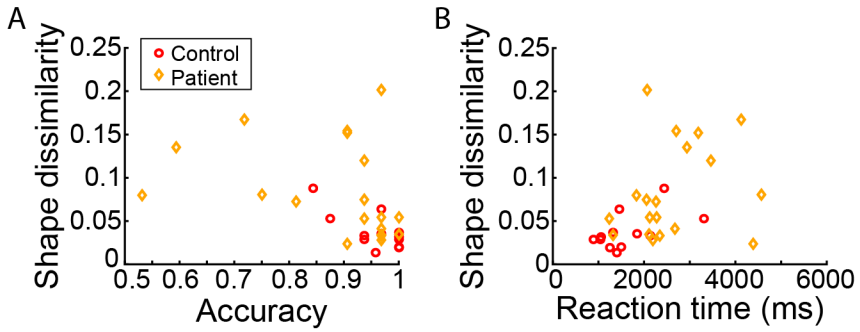

Figure 6. Relationship between Production (ordinate) and Perception (abscissa) tasks, shown separately for Perception task accuracy (A) and reaction time (B). Mean performance is shown for each patient (orange diamonds) and control (red circles).

patients exhibited relatively good performance in the Production task (low shape dissimilarity) but disrupted performance on the Perception task (low accuracy/high RT), while other patients exhibited the opposite trend.

To confirm these impressions, we used a mixed-effects model to predict Production-task shape dissimilarity using Perception-task accuracy and RT as well as the primary task factors (e.g., group and stimulus type). We observed a significant main effect of group on shape dissimilarity ($\chi^2(2) = 15.18$, $p = 0.004$), consistent with the findings reported above. However, there was no significant effect of Perception task accuracy ($\chi^2(2) = 0.543$, $p = 1.00$) or RT ($\chi^2(2) = 0.938$, $p = 1.00$) on shape dissimilarity, nor was there an interaction ($\chi^2(1) = 0.012$, $p = 1.00$), indicating that how well a given individual performed on the Production task was uncorrelated with their performance during the Perception task. This was also true when looking only at patients (effect of accuracy: $\chi^2(2) = 0.268$, $p = 1.00$; effect of RT: $\chi^2(2) = 0.475$, $p = 1.00$) or only at controls (effect of accuracy: $\chi^2(2) = 1.269$, $p = 0.53$; effect of RT: $\chi^2(2) = 3.745$, $p = 0.15$). Thus, across both groups we observed a dissociation between how participants performed on the Perception and Production tasks, which indicates that a subset of participants had difficulties specifically in the ability to imitate but not to simply report the shape of the desired movement.

Lesion analyses

Given the heterogeneity of patient performance in both the Production and Perception tasks, our final set of analyses focused on understanding this variability based on lesion location. We utilized two complementary lesion-analysis approaches. First, we performed Support Vector Regression-Lesion Symptom Mapping (SVR-LSM) analyses (Zhang et al., 2014) to examine the

voxel-level relationship between performance in the behavioral tasks (shape dissimilarity for the Production task and both the accuracy and RT measures for the Perception task) and the patients' lesion locations. Second, we performed a Region of Interest (ROI) analysis (Buxbaum et al., 2014) to examine the contributions of specific brain areas (defined on the lesion maps according to Brodmann areas) that we hypothesized to be involved in imitation based on prior research; this included dorsal premotor cortex (Brodmann area 6) (Caspers et al., 2010; Hocherman and Wise, 1990; Pearce and Moran, 2012), and inferior parietal cortex (Brodmann areas 39 and 40) (Buxbaum et al., 2014; Kadmon Harpaz et al., 2014). The ROI analyses allowed us to identify larger neural *regions* correlated with behavioral impairments that might be missed with a voxel-level analysis like SVR-LSM, particularly if there is inter-subject variability in the individual voxels associated with the task. Importantly, the results of both lesion analysis approaches were found to be consistent; we report the outcomes of both approaches below.

The SVR-LSM analysis of lesions associated with shape dissimilarity in the Production task (averaging across stimulus type; voxel-wise $p < 0.005$ and controlling for multiple comparisons using a $p < 0.05$ cluster-level correction) is shown in Figure 7A. The lesions contributing most highly to increased shape dissimilarity were located in the dorsal premotor and primary motor cortices. These regions were highly overlapping for the body and cursor conditions when analyzed separately (Figure 7B; voxel-wise $p < 0.05$ and controlling for multiple comparisons using a $p < 0.05$ cluster-level correction). This large region of overlap corresponds nicely to the lack of significant effect of stimulus type in the behavioral data, as will be discussed below.

In contrast, although the SVR-LSM analyses for the Perception task failed to reach statistical significance after correction for multiple comparisons, Perception accuracy and RT

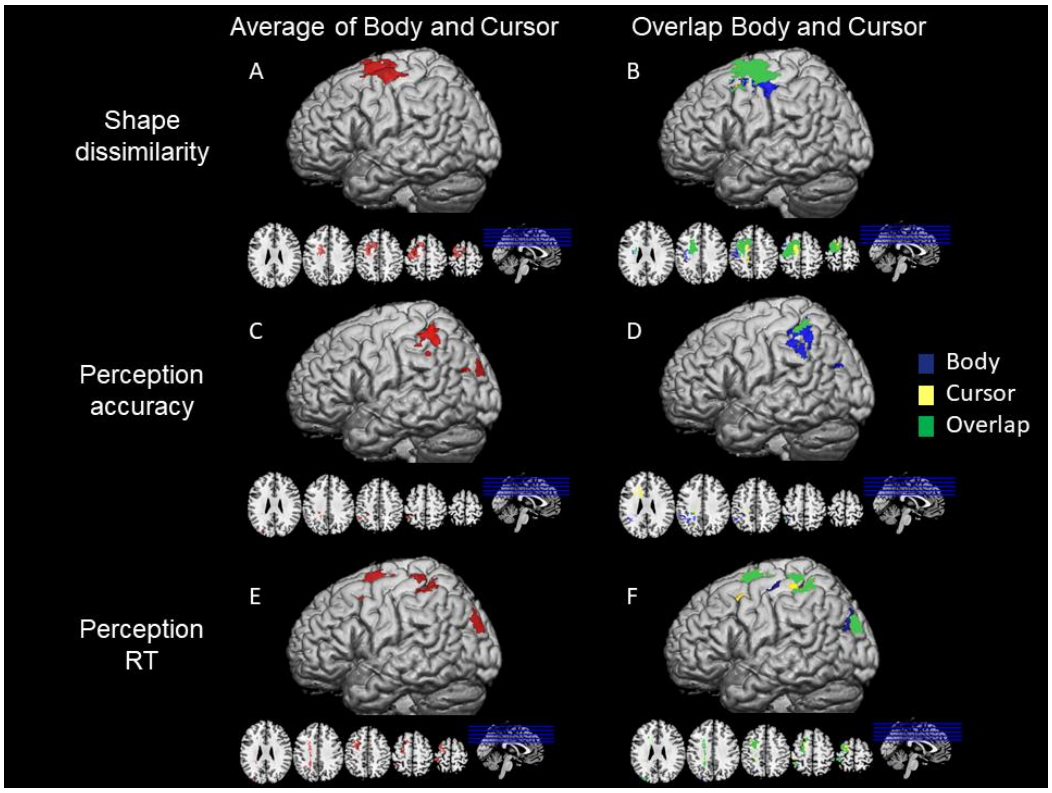

Figure 7. Results of the SVR-LSM analyses of shape dissimilarity in the Production task (top row), Perception task accuracy (middle row), and Perception task RT (bottom row). Results are presented for both the average data collapsing across the body and cursor stimuli (left column), as well as displaying the body and cursor results separately (right column).

were associated with damage to the parietal lobe when examined at a reduced statistical threshold (voxel-wise $p < 0.05$; Figures 7C,E). Perception task accuracy and RT were most strongly associated with damage to the superior portions of the supramarginal gyrus and posterior portions of the angular gyrus. Perception task RT was also associated with damage to the portion of the dorsal premotor cortex associated with shape dissimilarity in the Production task, as well as damage to middle occipital gyrus. For the Perception task, regions associated with the body and cursor conditions remained similar but with slightly less overlap than in the Production task (Figures 7D,F). Nevertheless, in general the findings from the SVR-LSM analysis suggest that lesions to different regions of the brain are associated with performance in the Production and Perception tasks respectively, with the former largely correlated with lesions

in dorsal premotor cortex and the latter correlated with lesions in inferior parietal lobule and middle occipital gyrus. In contrast, lesions generally overlapped when responses in either task were cued with a body-based or body-free stimulus.

Findings from the ROI analyses were consistent with the results from the SVR-LSM analysis. Specifically, for the Production task, the proportion of damage to Brodmann area 6 (premotor cortex) significantly predicted shape dissimilarity ($\chi^2(1) = 6.22$, $p = 0.050$). In contrast, for the Perception task, there was a significant correlation between accuracy and proportion damage to Brodmann area 40 (supramarginal gyrus) ($\chi^2(1) = 6.67$, $p = 0.039$). No other regions were found to correlate with any of the performance metrics from the Production or Perception tasks, and there was no significant effect of stimulus type in any cases.

Taken together, the results of the two lesion-analysis approaches, along with the lack of correlation in performance across patients for the Production and Perception tasks, suggest a dissociation between the brain regions required to perform the Production and Perception tasks.

DISCUSSION

Although imitation is widely recognized as an important aspect of learning, communicating, and using tools, the mechanisms by which imitation occur are not well understood. Here we demonstrated that individuals imitate meaningless actions by representing and reproducing the kinematic shape of the end-effector's movement in space (i.e., trajectory path). This path representation, and hence the ability to imitate moving trajectories, is disrupted by a stroke in the left dorsal premotor cortex. Critically, this disruption cannot be attributed to

general impairments due to the stroke, particularly as it manifests in the non-paretic arm and there is no impairment when imitating straight point-to-point gestures. Moreover, cueing trajectories by an actor or a cursor yield similar performance accuracy in patients, supporting the body-independent nature of this representation in contrast to the possibility of copying movement dynamics in a body-dependent manner using a body-schema representation (Schwoebel et al., 2004). These results thus reveal a novel route to imitation in humans that relies on an abstract trajectory representation. Finally, behavioral and anatomic dissociations between the imitation of movement trajectories and the ability to identifying their static shapes suggest distinct roles for parietal and premotor cortices in imitation.

Imitation can occur by forming a representation of the trajectory path

Our findings reveal that individuals can imitate by using a representation of the trajectory path to guide the mimicked movement. In our task, participants imitated trajectories generated by an actor, which provided full information about the relative positioning of the body segments, or a cursor, which provided only information about movement of the end-effector. Despite the difference in body-postural information, imitation of cursors and actors (cursor or body conditions, respectively) was not noticeably different for either the patient group or for the control group. This is consistent with research suggesting that participants attend only to the effector that is most relevant for imitation of the action (Matarića and Pomplunb, 1998). Moreover, a trajectory-based route for imitation can explain how species such as dolphins or parrots are able to successfully imitate humans (Harley et al., 1998; Moore, 1992; Xitco Jr et al., 1998), despite having bodies that do not afford a one-to-one replication of limb and joint

positions. Thus, our data support the hypothesis of a route to imitation via a body-independent representation of trajectory path.

Our prior research suggests that neurologically-intact individuals do form such trajectory-path representations when planning more complex actions such as reaches around obstacles (Wong et al., 2016). Interestingly, the variance of the hand during reaching movements tends to be smaller than the variance of the elbow and shoulder joints (Sergio and Scott, 1998; Tseng et al., 2002), supporting the hypothesis that movement planning involves the specification of the motion of the end-effector in space. These representations therefore likely describe not only the desired path of the movement trajectory, but additional kinematic information necessary to plan the movement along that path; hence, forming trajectory representations is likely an important stage of motor planning (Wong et al., 2015). Such trajectory representations might be useful for anticipating the movement of an observed object by extrapolating its future motion (2017), or for overcoming unexpected perturbations of the limb when the spatiotemporal properties of the hand motion, such as the time at which the hand must be at the target, are instructed by the task (Cluff and Scott, 2015). Furthermore, trajectory representations are useful when writing, and can explain the observed kinematic invariance across movement effectors (Rijntjes et al., 1999; Wright, 1990) or letter size (Kadmon Harpaz et al., 2014; van Galen and Teulings, 1983; Wing, 2000). Indeed, the abstract nature of trajectory representations is consistent with the finding that movements are similar when cued verbally or through imitation, and similar deficits across both tasks are observed bilaterally with a unilateral left-hemisphere stroke (Weiss et al., 2001).

In fact, this abstract quality of a trajectory representation implies that actions such as imitated gestures can be represented in a fairly compact manner. That is, rather than calculating the motion of every joint of the limb, specifying a movement would only require a representation

of the path of the desired trajectory of the end-effector – making the description of any given gesture more computationally tractable (Billard et al., 2004; Ijspeert et al., 2001). Because this trajectory representation is not directly tied to the details of movement execution (e.g., controlling particular muscles), it would not need to be represented bilaterally; this provides one potential explanation for how a unilateral lesion in the left hemisphere can disrupt movement imitation bilaterally.

We propose that the ability to represent desired movement trajectories is useful more broadly for praxis (e.g., imitating gestures or pantomiming the use of tools). Tool use, for example, may be supported by the successful translation of an abstract trajectory-path representation of the tool's effector into a movement produced with one's body; thus, the ability to represent abstract trajectories may provide insight into an important route not only for imitation but also for pantomime and tool use. Reliance on such a trajectory representation is consistent with some previous descriptions of apraxia positing that imitation and tool-use abilities depend upon representations of "time-space-form pictures" of movements that precede the encoding of "innervatory patterns" required for moving a specific limb (Geschwind, 1975; Liepmann, 1905; Mack et al., 1993).

Dissociation between production and perceptual reporting

In addition to deficits in producing trajectories by imitation, stroke participants had difficulties reporting the shapes of trajectories that they simply observed. Curiously, individuals who had difficulty actually producing trajectory paths were often not the same individuals who had difficulties reporting the observed trajectory shapes. This dissociation was evident

behaviorally, in that performance of the two tasks was uncorrelated, with some patients performing significantly worse than controls in only one of the two tasks.

Although it seems surprising that participants would be impaired at only the perceptual task, this could arise for a few reasons. For one, the Perceptual task requires recognition in comparing the stimulus motion with the provided static shape, whereas the Production task requires recall of the model's action. Thus, consistent with the previous literature suggesting that recognition and recall arise from distinct processes (Anderson and Bower, 1972; Hollingworth, 1913; Kintsch, 1970; Tulving, 1976); tasks invoking recognition versus recall may be uncorrelated. Additionally, the Perception and Production tasks likely possess distinct, unshared processing stages. For example, the Perceptual task likely requires visual imagery to think about the observed movement, a transformation from a dynamic movement to a static image (Korneev and Kurgansky, 2014), and cognitive processes such as distinguishing between mirror-reversed shapes – an ability that is known to be impaired in patients with lesions in the parietal lobe (Davidoff and Warrington, 2001) – that facilitate the comparison between the two paths. These additional processes are unlikely to be required in the Production task. Thus, there may not be a deficit in perception of the movement per se, but on the operations that need to be applied to that perception that distinguish performance in the two tasks. For these reasons, performance on the Production and Perceptual tasks may dissociate.

Additionally, the Production and Perception tasks were dissociated not only at the behavioral level, but also neurally. Deficits in the Production task were correlated with lesions in dorsal premotor cortex (PMd, Brodmann area 6) whereas deficits in the Perception task were correlated with lesions in a portion of inferior parietal lobule (supramarginal gyrus, Brodmann area 40). This distinction is consistent with a long-recognized posterior-to-anterior gradient in

the brain regions required for perception versus production (Liepmann, 1905), and implicates the dorsal premotor cortex as being particularly relevant for representing abstract trajectories for planning upcoming movements. In particular, whereas the Production task requires the representation of an abstract trajectory as part of motor planning, the Perception task may require alternative processes such as mental rotations to reconstruct the correct relative positioning of the limb segments, or recognizing that two actions are similar – computations of a more perceptual flavor that have previously been associated with posterior parietal cortex (Bonda et al., 1995; Kable et al., 2005; Zacks, 2008).

Although we observe a neural dissociation between dorsal premotor cortex and posterior parietal cortex in our data, previous research has suggested that neurons in both of these regions modulate their firing rate according to the path that monkeys take to reach a particular goal (Hatsopoulos et al., 2007; Hocherman and Wise, 1990, 1991; Pearce and Moran, 2012; Schwartz, 1994; Torres et al., 2013). However, in such studies, it is unclear that non-human primates are actually planning the trajectories of their movements; the complex actions produced in these tasks are typically elicited through tracing (Moran and Schwartz, 1999) or by operantly conditioning a series of small movement segments (Averbeck et al., 2006). Moreover, non-human primates are generally thought to be poor imitators relative to children (Subiaul, 2016); to the extent that they do imitate, it is done either by reproducing the action goal rather than the kinematics of the movement itself (Subiaul, 2016; Whiten et al., 2004), or by attending to the joint angles of the entire limb rather than the motion of the end-effector (Kumashiro et al., 2003). Hence, non-human primates may not be planning actions in the same way that humans do, and thus these studies may not be informative regarding the manner in which humans represent movement trajectories.

Two routes to imitation

That the imitation of actions – particularly body configurations – is challenging is attested to by the admiration we have for mime artists. One possible source of the difficulty in imitating bodies is that copying the entire limb requires replication of the positioning of each limb segment. A trajectory-representation approach might require planning a distinct trajectory per limb segment (Ijspeert et al., 2001); however, humans have difficulty planning multiple trajectories simultaneously (Albert and Ivry, 2009). Alternatively, it may be possible to copy an entire body configuration, which suggests the existence of an internal representation of the body to which appropriate transformations could be specified. Our data hint at the possibility of a difference between reporting the motion of bodies versus cursors in both the behavioral and neural measures in the Perception task. Furthermore, previous research has shown that in imitation, kinematic errors during the movement can dissociate from postural errors at the end of the movement (Hermsdorfer et al., 1996). This suggests that imitation could be carried out in two ways: either by copying a movement trajectory or a body-part-relationship goal.

In fact, previous research has focused on the idea that imitation relies upon a specialized representation of the body that describes the relative positioning and motion of body parts – i.e., a body schema representation (Goldenberg, 2013). This body-dependent route to imitation is based on prior studies that have, in large part, required imitation of an actor by moving their own bodies or a surrogate such as a manikin (Goldenberg, 1995; Goldenberg and Hagmann, 1997; Harrington and Haaland, 1997), and scored imitation ability according to the successful positioning of the body segments (e.g., upper arm, forearm, and hand) throughout the action

(Tarhan et al., 2015). Thus these studies have claimed the existence of a body-specific representation for imitation (Buxbaum et al., 2000; Goldenberg, 1999; Goldenberg, 2013; Schwoebel et al., 2004), recognizing the importance of observing the entire limb and its joints while imitating actions (Kumashiro et al., 2003).

However, much of the research regarding this route to imitation have relied on the ability to perceive and mimic static postures; hence, the imitation of dynamic gestures need not specify movement kinematics, but could instead be performed by linking together a series of static postures to be attained. This suggests that body-schema representations are likely more perceptual-flavored and directly informed by cognitive processes as action recognition or mental rotation, rather than being a motor-planning stage; consistent with this idea, previous work has suggested that body-schema representations reside in parietal cortex (Chaminade et al., 2005). In contrast, we propose that trajectory representations are much more "motor" flavored in that they contain information regarding the kinematics of the trajectory motion along with its path. Hence, we conjecture that the functional distinction between the inferior parietal lobe and dorsal premotor cortex that we observed across our two tasks may parallel these two distinct routes to imitation.

It remains to be seen under what circumstances an abstract trajectory or body-schema representation is employed to support imitation. For example, deficits associated with relative positioning of the individual body segments are frequently observed in the imitation of both dynamic movements (Buxbaum et al., 2014) and static postures (Goldenberg and Hagmann, 1997). These deficits could potentially be observed if the task instructions (or individual strategy) favors mimicry of the motion and positioning of the entire body rather than only the end-effector. Our task places a strong emphasis on copying of the endpoint trajectory, hence it is

perhaps unsurprising that we did not observe body-dependence for imitation. Other tasks examining imitation have reported that measures of hand-posture configuration accuracy, rather than kinematic features (i.e., amplitude and timing), may be more sensitive measure of imitation deficits (Buxbaum et al., 2007). This suggests that if individuals take imitation to mean more than just copying of the motion of the endpoint, they may utilize body-dependent processing routes (Schwoebel et al., 2004). Thus, while our data suggest that dynamic movements can be imitated by simply representing the trajectory path in a body-independent manner, future work is required to determine whether such representations are used for imitation more broadly.

Conclusions

This study sought to examine imitation, particularly that specialized human ability to copy gestures that are novel or meaningless. Specifically, we tested the hypothesis, based on our prior research, that our ability to represent trajectory paths can be employed to copy meaningless actions, and sought to identify where in the praxis network spanning the left fronto-parietal cortex such a trajectory-path representation exists. Our findings confirm the importance of an abstract (body-independent) trajectory-path representation for planning and executing complex actions such as copying gestures, which can be dissociated behaviorally and neurally from the ability to accurately report the shape of the observed action. Furthermore, we provide strong evidence that damage to dorsal premotor cortex disrupts this ability to represent trajectory shapes, giving rise to deficits in the ability to imitate meaningless actions.

METHODS

Contact for resource sharing

Further information and requests for resources should be directed to and will be fulfilled by the Corresponding Author, Aaron Wong (wongaaro@einstein.edu).

Experimental Model and Subject Details

Twenty-one chronic stroke survivors with lesions confined to the left hemisphere (8 female) and thirteen neurologically intact controls (7 female) completed the experiment. The stroke group was marginally younger than the control group (57.4 ± 10.1 years vs. 64.2 ± 11.1 years, $p = 0.086$), thus any detrimental effects of aging on performance would be reflected more heavily in the control group than the patient group. All participants provided written consent to participate in the study in accordance with the guidelines of the Einstein Medical Center Institutional Review Board and were compensated for their participation.

Method Details

All participants completed two tasks as part of this experiment: the Production task and the Perception task (details below). Each task consisted of two trial phases. The first phase was a practice block in which participants were provided with instructions on how to complete the task, were shown how to perform the task, and then allowed to rehearse three example trials in which they were given feedback regarding their performance. Following this, participants completed a

test phase during which they received no further reminders of task instructions or feedback regarding their accuracy in performing the task. Participants received different stimuli during the practice and test blocks.

Trajectory production task

In the Production task, participants executed two dimensional movements by sliding their fingertip along the surface of a vertically mounted sheet of clear Plexiglass. The left arm was used for all participants so that the stroke group would produce movements with the ipsilesional limb. Stimulus trajectories varied in size, but all were contained within a 38 cm x 56 cm area at the center of the board. Participants sat at a distance that allowed them to comfortably perform movements, approximately 50 cm from the Plexiglass with their hand resting in their lap (i.e., the "home" position). Instructions about the movements to perform were presented via a laptop computer placed approximately 30 cm behind the Plexiglass. Each video clip, which ranged in length from 4.5 to 6.4 seconds, was played twice with a 1 second delay between clips. Following the second video, there was a 1 second delay before a tone sounded to inform participants they should begin their movement. The movement consisted of reaching out and upward to contact the Plexiglass surface, generating the required trajectory in the vertical plane by sliding the hand along the Plexiglass, and then returning the hand to the home position in their lap. Participants were given the instructions to "use you left finger to trace the same path the dot or person made. Make sure your path looks exactly like the video's. It's very important that you be as precise as possible." If participants began to move before the end of the video, they were reminded to wait for the tone. The position of each participant's left index finger was continuously recorded using

an Ascension TrakSTAR motion tracking system (Ascension Technology, Shelburne, VT) at 150 Hz.

Participants produced 16 trajectories (Figure 2) grouped into 2 presentation conditions. We manipulated task difficulty by providing a differing number of visible landmarks (2 cm diameter circular dots placed on the Plexiglass) under the hypothesis that landmarks could potentially be used as reference points to subdivide a complex action into simpler point-to-point reaches, thus reducing the trajectory planning requirements. Stimuli were thus cued with reference to either a single central landmark or with four additional landmarks bounding a rectangular workspace. However, in general we found that varying the number of landmarks did not significantly impact performance; thus while we include a landmark factor in our statistical models for completeness (see Quantification and Statistical Analysis below), for conciseness we do not report the outcomes of statistical tests of this factor in the Results.

More importantly, each trajectory was reproduced under two levels of stimulus type (body or cursor). As described in the Introduction, this stimulus-type manipulation was included to test whether imitation is dependent upon the ability to observe and represent the relative positions of limb segments during the action, or if imitation instead can be performed more abstractly by replicating only the kinematics of the end-effector. Video stimuli for the body condition consisted of a seated actor producing trajectories on a Plexiglass board identical to the one in front of the participant (i.e., with the same number of landmarks). The actor was shown facing the participant and moving his right arm so that the experimenter's arm mirrored the participant's left arm. Participants were trained to imitate the mirrored version of the actor; no mirror-inversion mistakes were observed for either the patients or the controls during this task. Video stimuli for the cursor condition consisted of a single black cursor moving over a white

background, with landmarks visible as appropriate. Cursor trajectories were created from motion tracking data collected during filming of the body stimuli, resulting in identical end-effector movement trajectories for the two stimulus types. Participants completed two blocks of trials; the two levels of the landmark factor (1 or 5) were manipulated between-blocks, while the two levels of the stimulus type factor (body or cursor) were intermixed within blocks.

The experiment also included a third stimulus-type condition that was intended to test whether any potential disruption of performance in the body condition (relative to the cursor condition) would occur for jointed non-body stimuli. Like the cursor condition, stimuli in this "stick" condition were derived from the body condition kinematic data, but used the location of the elbow and shoulder from the actor in addition to the fingertip location. The three points on the body were used to create a two-segment stick-figure arm that ended at a cursor which represented the fingertip position (identical to the cursor in the cursor condition). Data from this condition were not included because participants found this condition to be confusing, due to the high overlap caused by projection of the 3D line segment motion into a 2D plane, as confirmed by reliably worse performance compared to the other conditions across all participants and tasks. Since performance in this stick condition did not offer meaningful insight into trajectory imitation per se, it was excluded from further analysis.

As part of this task, we also examined the ability of patients and controls to imitate simple point-to-point reaches by evaluating the ability to imitate the initial segment of one of the more complex movement trajectories (see below for details). Analysis of point-to-point movements allows us to control for whether observed imitation deficits could be attributed to deficits in accurately producing components of the complex trajectories.

Trajectory perception task

Deficits in imitating trajectories could be attributed to one of two possible causes: impairment in the ability to plan the necessary trajectory shape, or difficulty with perceiving and/or recalling the required shape after the delay period (i.e., a perceptual or working-memory problem). To distinguish between these possibilities, participants were additionally required to complete a Perception task. In this task, participants were exposed to the identical video stimuli as in the Production task, but were asked to simply make a decision about the path they had observed rather than producing the actual movement. That is, stimuli consisted of two presentations of the same videos used in the Production task followed by a 1 second delay before the presentation of a static image of a trajectory shape. Participants were instructed to indicate "if the path in the picture is the same as the movement made in the video." The shape either matched the exact trajectory produced in the video or was a mirror image of the trajectory that was reflected about the vertical or horizontal axis; there were no significant differences in performance errors made for reflections about these two axes. The shape remained on the screen until participants indicated a match or non-match by pressing one of two buttons on a computer keyboard with their left hand. Task accuracy and reaction time were measured, although due to technical difficulties reaction time data at the trial level were unavailable for 1 control and 2 stroke participants, and thus these individuals could not be included in analyses involving mixed-effects models (see Quantification and Statistical Analysis below).

As with the Production task, participants in the Perception task completed two blocks of trials; the two levels of the landmark factor (1 or 5) were manipulated between-blocks, and the two levels of the stimulus type factor (body or cursor) were intermixed within blocks. The order

of the Production and Perception tasks were counterbalanced across participants.

Stroke group auditory comprehension

Patients with strokes completed the auditory comprehension subsection of the Western Aphasia Battery (Kertesz, 1982), which quantifies capacity to understand verbal instructions. Scores on the WAB were high (9.06 ± 1.32 out of 10 possible points). Thus, we felt confident that any group differences in performance could not be explained by differences in instruction comprehension.

Quantification and Statistical Analysis

Production Task

Response trajectories were recorded and analyzed offline using custom software written in Matlab (The MathWorks, Natick, MA). Fingertip velocity was calculated by smoothing the recorded fingertip position using a second-order Savitzky-Golay filter with a frame size of 19 samples, then taking the derivative. Movement start and end were identified as the time when the fore/aft reach velocity became minimal (< 0.03 m/s), reflecting the time when the participants contacted the Plexiglass surface and their primary axis of motion was along this surface. Each start and end time was verified by visual inspection. All motion produced between the identified start and end times was labeled as the complete imitated movement generated by the participant. The three-dimensional data returned by the motion tracking system were projected into the plane

of the Plexiglass surface to account for any small angular mismatch between the Plexiglass (on which the reference landmarks were positioned) and the vertical plane of the tracker axes. Movements were smoothed and time-normalized using a b-spline fit with 200 points. Finally, the shape of the generated response was compared to the ideal template (the normalized and smoothed trajectory produced by the actor in the stimulus video) by performing a Procrustes distance analysis (Goodall, 1991). The Procrustes distance analysis estimates the best translation, rotation, and scaling parameters that match the sample reach to the template, and returns a dissimilarity measure for the resulting transformed response trajectory shape (normalized between 0 and 1, with 0 being identical and 1 being completely dissimilar).

Data were analyzed using mixed-effects models including fixed effects of Group (patient or control), Stimulus type (body-cued or cursor-cued), Landmark (1-dot or 5-dot), Task order (Production first or Perception first), and random effects of Subject and Stimulus shape. Models were fit using the *glmmTMB* package in R (Magnusson et al., 2017). Since the response outcome (Procrustes distance) did not follow a Gaussian distribution (being bounded between 0 and 1) a logarithmic link function was used in the model. Significant main effects were evaluated using likelihood ratio tests comparing a model with the effect of interest against a model without the effect of interest, with step-down Bonferroni-Holm corrections applied to address multiple comparisons.

Trajectory production control: point-to-point reaches

Although patients were tested on their non-paretic side, we wanted to confirm that errors made during trajectory production could not be explained by more elementary deficits in

producing straight movements. Thus, we isolated point-to-point reaches from the initial movement segment of one of the 5-landmark stimuli for both the body and cursor conditions. This particular stimulus was chosen because it afforded a reasonably long initial movement segment that started and ended on visible landmarks, thus providing clearly identified movement start and end positions that defined the desired movement. The movement segment of interest was identified using a velocity threshold (tangential velocity > 0.05 m/s), and was verified by visual inspection. To evaluate the quality of reproducing the point-to-point movement, we calculated the maximal reach deviation as the greatest absolute perpendicular deviation of the finger from the straight line between the initial and final fingertip position of the point-to-point reach. We also calculated the initial reach direction of the velocity vector 100 ms after movement onset, and the initial direction error as the signed difference between the initial reach direction of the participant and the ideal (actor) reach direction.

Data were analyzed with mixed-effects models with main effects of Group and Stimulus type (body-cued or cursor-cued), and random effect of Subject regressing against maximal reach deviation from a straight line or initial direction error. Models were fit using the *lme4* package in R (Bates et al., 2015). Significant effects were evaluated using likelihood ratio tests.

Perception Task

Reaction time (RT) was measured as the time between the onset of the static trajectory and initiation of a button-press response (reporting “same” or “different”). Accuracy and RT were analyzed with mixed-effects models with main effects of Group, Stimulus type (body-cued or cursor-cued), Landmark (1-dot or 5-dot), and Task order (Production first or Perception first),

and random effects of Subject and Stimulus shape. The logarithm of the RT (logRT) was taken to reduce outliers and address the long-tail distribution. Models were fit using the *glmmTMB* package in R (Magnusson et al., 2017), using a Gaussian link function in the case of logRT or a binomial family in the case of Accuracy. Significant main effects were evaluated using likelihood ratio tests comparing a model with the effect of interest against a model without the effect of interest; step-down Bonferroni-Holm corrections were applied to address multiple comparisons.

Correlations in performance between the Perception and Production tasks were tested by examining the relationship between Procrustes distance and accuracy or RT using mixed-effects models that also included fixed effects of Group (patient, control), Stimulus type (body-cued or cursor-cued), and Landmark (1-dot or 5-dot), and random effects of Subject and Stimulus shape. Models were fit using the *glmmTMB* package in R (Magnusson et al., 2017), using a logarithmic link function. Significant main effects were evaluated using likelihood ratio tests comparing a model with the effect of interest against a model without the effect of interest, with step-down Bonferroni-Holm corrections applied to address multiple comparisons.

Lesion location identification

T1-weighted MRI brain scans (15 patients) or CT scans without contrast if MRI was contraindicated (6 patients) were used to identify lesion locations. Lesions were segmented under the supervision of a neurologist (H. Branch Coslett) who was blind to all behavioral data. Details of the lesion location identification procedure can be found in Kalénine et al. (2010). Individual lesion locations for all stroke participants are shown in Figure 1. Total lesion volume for each

individual patient was then calculated (71,850 ± 34,488 mm^3) and used as a control for overall stroke severity (see below).

Support vector regression lesion-symptom mapping

Support vector regression lesion-symptom mapping (SVR-LSM) (Zhang et al., 2014) uses machine learning techniques for multiple regression to train a model to predict behavioral scores using the full lesion maps of all participants. SVR-LSM is a significant improvement over earlier techniques such as voxel-based lesion-symptom mapping (VLSM) (Bates et al., 2003), which perform all analyses at the individual voxel level and then aggregate across voxels to create a full-brain map. By predicting behavioral scores using all voxels simultaneously, SVR-LSM has the capability to avoid vasculature-related biases that can systematically distort lesion-symptom maps (Mah et al., 2014).

The SVR-LSM analyses were performed using software provided by Zhang and colleagues (Zhang et al., 2014; https://cfn.upenn.edu/~zewang/) and modified to include a cluster-wise correction for multiple comparisons (P. Turkeltaub, personal communication). All analyses were run using Matlab R2017a. Statistical significance was determined using both voxel-wise and cluster-wise corrections for multiple comparisons. First, a beta-map of the observed data was computed. This beta-map regressed out the effects of total lesion volume in both the behavioral and lesion data to avoid identifying spurious voxels whose lesion status correlates with lesion volume. Only voxels damaged in at least three participants (15% of the stroke group) were included in the analyses. The observed beta-map was compared to beta-maps derived from 1,000 Monte-Carlo style permutations, where behavioral scores were randomly

paired with lesion maps. These permutations were used to derive a voxel-wise p-map. The SVR-LSM analysis of the Production task data averaging across the body and cursor conditions (Figure 7A) was thresholded using the most stringent criteria; $p < 0.005$ for the voxel-wise map and then subjected to a $p < 0.05$ permutation-derived cluster-level correction for multiple comparisons (the standard method of correcting for multiple comparisons in neuroimaging studies (Woo et al., 2014). For analyses that failed to produce results at this threshold, reduced statistical thresholds were used as noted in the main text. For analyses of the Production task data that separately examined performance in the body and cursor conditions (Figure 7B), a $p < 0.05$ voxel-wise and $p < 0.05$ cluster-level correction for multiple comparisons was used. For all analyses of the Perception task data (Figure 7C-F), a $p < 0.05$ voxel-wise threshold without correction for multiple comparisons was used.

We additionally performed region of interest (ROI) analyses to confirm whether there was any relationship between performance in either the Production or Perception task and the percentage of lesioned voxels within three ROIs selected *a priori*: Brodmann area 6 (premotor cortex), Brodmann areas 39 (angular gyrus), and Brodmann area 40 (supramarginal gyrus). Mixed effects models were run using the *glmmTMB* package in R (Magnusson et al., 2017) and included fixed effects of Total Lesion Volume, Stimulus type (body or cursor), and Landmark (1-dot or 5-dot). Models also included random effects of Subject and Stimulus shape. Significant main effects were evaluated using likelihood ratio tests comparing a model with the effect of interest against a model without the effect of interest, with step-down Bonferroni-Holm corrections applied to address multiple comparisons.

ACKNOWLEDGEMENTS

This work was supported by NSF Grant BCS-1358756 to JWK and NIH Grant R01-NS065049 to LJB. The authors would like to thank H. Branch Coslett for his assistance with lesion identification, Stephanie Shaia for her assistance in running the SVR-LSM analysis, and Peter Turkeltaub and Andrew DeMarco for sharing their SVR-LSM software. The authors declare no competing financial interests.

REFERENCES

Albert, N.B., and Ivry, R.B. (2009). The persistence of spatial interference after extended training in a bimanual drawing task. Cortex 45, 377-385.

Anderson, J.R., and Bower, G.H. (1972). Recognition and retrieval processesin free recall. Psychol Rev 79, 97-123.

Averbeck, B.B., Sohn, J.W., and Lee, D. (2006). Activity in prefrontal cortex during dynamic selection of action sequences. Nat Neurosci 9, 276-282.

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

Bates, E., Wilson, S.M., Saygin, A.P., Dick, F., Sereno, M.I., Knight, R.T., and Dronkers, N.F. (2003). Voxel-based lesion-symptom mapping. Nat Neurosci 6, 448-450.

Billard, A., Epars, Y., Calinon, S., Schaal, S., and Cheng, G. (2004). Discovering optimal imitation strategies. Rob Auton Syst 47, 69-77.

Bonda, E., Petrides, M., Frey, S., and Evans, A. (1995). Neural correlates of mental transformations of the body-in-space. Proc Natl Acad Sci U S A 92, 11180-11184.

Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G., and Freund, H.J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur J Neurosci 13, 400-404.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C.A., and Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: an FMRI study. J Cogn Neurosci 16, 114-126.

Buxbaum, L.J., Giovannetti, T., and Libon, D. (2000). The role of the dynamic body schema in praxis: evidence from primary progressive apraxia. Brain Cogn 44, 166-191.

Buxbaum, L.J., Johnson-Frey, S.H., and Bartlett-Williams, M. (2005). Deficient internal models for planning hand-object interactions in apraxia. Neuropsychologia 43, 917-929.

Buxbaum, L.J., Kyle, K., Grossman, M., and Coslett, H.B. (2007). Left inferior parietal representations for skilled hand-object interactions: evidence from stroke and corticobasal degeneration. Cortex 43, 411-423.

Buxbaum, L.J., Shapiro, A.D., and Coslett, H.B. (2014). Critical brain regions for tool-related and imitative actions: a componential analysis. Brain 137, 1971-1985.

Caspers, S., Zilles, K., Laird, A.R., and Eickhoff, S.B. (2010). ALE meta-analysis of action observation and imitation in the human brain. Neuroimage 50, 1148-1167.

Chaminade, T., Meltzoff, A.N., and Decety, J. (2005). An fMRI study of imitation: action representation and body schema. Neuropsychologia 43, 115-127.

Cluff, T., and Scott, S.H. (2015). Apparent and actual trajectory control depend on the behavioral context in upper limb motor tasks. J Neurosci 35, 12465-12476.

Davidoff, J., and Warrington, E.K. (2001). A particular difficulty in discriminating between mirror images. Neuropsychologia 39, 1022-1036.

de Wit, M.M., and Buxbaum, L.J. (2017). Critical Motor Involvement in Prediction of Human and Non-biological Motion Trajectories. J Int Neuropsychol Soc 23, 171-184.

Geschwind, N. (1975). The apraxias: neural mechanisms of disorders of learned movement. Am Sci 63, 188-195.

Goldenberg, G. (1995). Imitating gestures and manipulating a mannikin--the representation of the human body in ideomotor apraxia. Neuropsychologia 33, 63-72.

Goldenberg, G. (1999). Matching and imitation of hand and finger postures in patients with damage in the left or right hemispheres. Neuropsychologia 37, 559-566.

Goldenberg, G. (2009). How the mind moves the body: lessons from apraxia. In Oxford handbook of human action, E. Morsella, B.J. A., and P.M. Gollwitzer, eds. (Oxford: Oxford University Press).
Goldenberg, G. (2013). Apraxia : the cognitive side of motor control, 1st edn (Oxford: Oxford University Press).
Goldenberg, G., and Hagmann, S. (1997). The meaning of meaningless gestures: a study of visuo-imitative apraxia. Neuropsychologia 35, 333-341.
Goodall, C. (1991). Procrustes methods in the statistical-analysis of shape. J R Stat Soc Ser B 53, 285-339.
Harley, H.E., Xitco Jr, M.J., Roitblat, H.L., and Herman, L.M. (1998). Imitation of human models by bottlenose dolphins. In Napoli Social Learning Conference (Naples, Italy).
Harrington, D.L., and Haaland, K.Y. (1997). Representations of actions in ideomotor limb apraxia: clues from motor programming and control. In Apraxia: the neuropsychology of action, L.J. Rothi, and K.M. Heilman, eds. (London: Psychology Press), pp. 111-147.
Hatsopoulos, N.G., Xu, Q., and Amit, Y. (2007). Encoding of movement fragments in the motor cortex. J Neurosci 27, 5105-5114.
Hermsdorfer, J., Mai, N., Spatt, J., Marquardt, C., Veltkamp, R., and Goldenberg, G. (1996). Kinematic analysis of movement imitation in apraxia. Brain 119 (Pt 5), 1575-1586.
Hocherman, S., and Wise, S.P. (1990). Trajectory-selective neuronal activity in the motor cortex of rhesus monkeys (Macaca mulatta). Behav Neurosci 104, 495-499.
Hocherman, S., and Wise, S.P. (1991). Effects of hand movement path on motor cortical activity in awake, behaving rhesus monkeys. Exp Brain Res 83, 285-302.
Hollingworth, H.L. (1913). Characteristic differences between recall and recognition. Am J Psychol 24, 532-544.
Ietswaart, M., Carey, D.P., and Della Sala, S. (2006). Tapping, grasping and aiming in ideomotor apraxia. Neuropsychologia 44, 1175-1184.
Ijspeert, A.J., Nakanishi, J., and Schaal, S. (2001). Trajectory formation for imitation with nonlinear dynamical systems. In IEEE/RSJ International Conference on Intelligent Robots and Systems (Maui, HI, USA).
Kable, J.W., Kan, I.P., Wilson, A., Thompson-Schill, S.L., and Chatterjee, A. (2005). Conceptual representations of action in the lateral temporal cortex. J Cogn Neurosci 17, 1855-1870.
Kadmon Harpaz, N., Flash, T., and Dinstein, I. (2014). Scale-invariant movement encoding in the human motor system. Neuron 81, 452-462.
Kalenine, S., Buxbaum, L.J., and Coslett, H.B. (2010). Critical brain regions for action recognition: lesion symptom mapping in left hemisphere stroke. Brain 133, 3269-3280.
Kertesz, A. (1982). Western Aphasia Battery (New York: Grune & Stratton).
Kintsch, W. (1970). Models for free recall and recognition. In Models of human memory, D.A. Norman, ed. (New York: Academic Press), pp. 331-373.
Korneev, A.A., and Kurgansky, A.V. (2014). Internal representation of movement sequences on reproduction of static drawings and the trajectories of moving objects. Neuroscience and Behavioral Physiology 44, 892-901.
Krakauer, J.W., and Carmichael, S.T. (2017). Broken Movement: The Neurobiology of Motor Recovery After Stroke (Cambridge, MA: MIT Press).
Kumashiro, M., Ishibashi, H., Uchiyama, Y., Itakura, S., Murata, A., and Iriki, A. (2003). Natural imitation induced by joint attention in Japanese monkeys. Int J Psychophysiol 50, 81-99.

Liepmann, H. (1905). The left hemisphere and action (London, Ontario: University of Western Ontario).
Mack, L., Rothi, L.J.G., and Heilman, K.M. (1993). Hemispheric-specialization for handwriting in right-handers. Brain Cognition 21, 80-86.
Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., and Brooks, M. (2017). glmmTMB: Generalized linear mixed models using template model builder. R package version 013, https://github.com/glmmTMB.
Mah, Y.H., Husain, M., Rees, G., and Nachev, P. (2014). Human brain lesion-deficit inference remapped. Brain 137, 2522-2531.
Matarića, M.J., and Pomplunb, M. (1998). Fixation behavior in observation and imitation of human movement. Cogn Brain Res 7, 191-202.
Moore, B.R. (1992). Avian movement imitation and a new form of mimicry - tracing the evolution of a complex form of learning. Behaviour 122, 231-263.
Moran, D.W., and Schwartz, A.B. (1999). Motor cortical activity during drawing movements: population representation during spiral tracing. J Neurophysiol 82, 2693-2704.
Pearce, T.M., and Moran, D.W. (2012). Strategy-dependent encoding of planned arm movements in the dorsal premotor cortex. Science 337, 984-988.
Rijntjes, M., Dettmers, C., Buchel, C., Kiebel, S., Frackowiak, R.S., and Weiller, C. (1999). A blueprint for movement: functional and anatomical representations in the human motor system. J Neurosci 19, 8043-8048.
Schwartz, A.B. (1994). Direct cortical representation of drawing. Science 265, 540-542.
Schwoebel, J., Buxbaum, L.J., and Coslett, H.B. (2004). Representations of the human body in the production and imitation of complex movements. Cogn Neuropsychol 21, 285-298.
Sergio, L.E., and Scott, S.H. (1998). Hand and joint paths during reaching movements with and without vision. Exp Brain Res 122, 157-164.
Subiaul, F. (2016). What's special about human imitation? A comparison with enculturated apes. Behav Sci 6.
Tarhan, L.Y., Watson, C.E., and Buxbaum, L.J. (2015). Shared and distinct neuroanatomic regions critical for tool-related action production and recognition: Evidence from 131 left-hemisphere stroke patients. J Cogn Neurosci 27, 2491-2511.
Torres, E.B., Quian Quiroga, R., Cui, H., and Buneo, C.A. (2013). Neural correlates of learning and trajectory planning in the posterior parietal cortex. Front Integr Neurosci 7, 39.
Tseng, Y., Scholz, J.P., and Schoner, G. (2002). Goal-equivalent joint coordination in pointing: affect of vision and arm dominance. Motor Control 6, 183-207.
Tulving, E. (1976). Ecphoric processes in recall and recognition. In Recall and recognition, J. Brown, ed. (London: Wiley), pp. 37-74.
van Galen, G.P., and Teulings, H.L. (1983). The independent monitoring of form and scale factors in handwriting. Acta Psychol (Amst) 54, 9-22.
Weiss, P.H., Dohle, C., Binkofski, F., Schnitzler, A., Freund, H.J., and Hefter, H. (2001). Motor impairment in patients with parietal lesions: disturbances of meaningless arm movement sequences. Neuropsychologia 39, 397-405.
Wheaton, K.J., Thompson, J.C., Syngeniotis, A., Abbott, D.F., and Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. Neuroimage 22, 277-288.
Whiten, A., Horner, I., Litchfield, C.A., and Marshall-Pescini, S. (2004). How do apes ape? Learn Behav 32, 36-52.

Wing, A.M. (2000). Motor control: Mechanisms of motor equivalence in handwriting. Curr Biol 10, R245-248.
Wong, A.L., Goldsmith, J., and Krakauer, J.W. (2016). A motor planning stage represents the shape of upcoming movement trajectories. J Neurophysiol 116, 296-305.
Wong, A.L., Haith, A.M., and Krakauer, J.W. (2015). Motor Planning. Neuroscientist 21, 385-398.
Woo, C.W., Krishnan, A., and Wager, T.D. (2014). Cluster-extent based thresholding in fMRI analyses: pitfalls and recommendations. Neuroimage 91, 412-419.
Wright, C.E. (1990). Generalized motor programs: reexamining claims of effector independence in writing. In Attention and Performance XIII, M. Jeannerod, ed. (Erlbaum: Hillsdale), pp. 294–320.
Xitco Jr, M.J., Harley, H.E., and Brill, R.L. (1998). Action level imitation by bottlenose dolphins. In Napoli Social Learning Conference (Naples, Italy).
Zacks, J.M. (2008). Neuroimaging studies of mental rotation: a meta-analysis and review. J Cogn Neurosci 20, 1-19.
Zhang, Y., Kimberg, D.Y., Coslett, H.B., Schwartz, M.F., and Wang, Z. (2014). Multivariate lesion-symptom mapping using support vector regression. Hum Brain Mapp 35, 5861-5876.