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Decoding intransitive actions in primary motor cortex using fMRI: toward a componential theory of 'action primitives' in motor cortex

Elizabeth A. Shay^a, Quanjing Chen^a, Frank E. Garcea^{a,b,c} and Bradford Z. Mahon^{a,c,d,e}

^aDepartment of Brain & Cognitive Sciences, University of Rochester, Rochester, NY, USA; ^bMoss Rehabilitation Research Institute, Elkins Park, PA, USA; ^cCenter for Visual Sciences, University of Rochester, Rochester, NY, USA; ^dDepartment of Neurosurgery, University of Rochester Medical Center, Rochester, NY, USA; ^eDepartment of Neurology, University of Rochester Medical Center, Rochester, NY, USA

ABSTRACT

Multivoxel pattern analysis (MVPA) over functional MRI data can distinguish neural representational states that do not differ in their overall amplitude of BOLD contrast. Here we used MVPA to test whether simple intransitive actions can be distinguished in primary motor cortex. Participants rotated and flexed each of their extremities (hands and feet) during fMRI scanning. The primary motor cortex for the hand/wrist was functionally defined in each hemisphere in each subject. Within those subject-specific ROIs, we found that the average amplitude of BOLD contrast for two different movements of the contralateral hand (rotation, flexion) were higher than for the ipsilateral hand, as well as movements by both feet; however, there was no difference in amplitude between the two different types of movements for the contralateral hand. Using multivoxel pattern analysis (linear correlation), we were able to distinguish the two movements for the contralateral hand. These findings demonstrate that simple intransitive actions can be distinguished in primary motor areas using multivoxel pattern analysis.

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fMRI; multivoxel pattern analysis; hand movements; intransitive actions, componential representations, apraxia

Introduction

The ability to use our arms, hands, and fingers in a dexterous and goal driven manner across a range of different contexts and environments represents an exceptionally well-developed cognitive capacity in humans. Understanding the neural bases of gesture and action representation in the human brain would inform theories of how semantic and goal representations interface with and are implemented in motor-based production processes. A core issue in this regard concerns the granularity of action representation in primary motor cortex, as discoverable with functional magnetic resonance imaging (fMRI). In this report, we take a step toward addressing this issue by using multivoxel pattern analysis over fMRI data in healthy adults who are performing simple intransitive actions with their hands and feet.

Multivoxel pattern analysis (MVPA) is a powerful technique for evaluating representational content of neural regions. While the technique has been widely used to probe representations in the visual domain (e.g., Haxby et al., 2001; Kriegeskorte et al., 2008), relatively less research has used multivoxel methods

in motor areas to probe the neural representational structure of first-person unseen actions. Some clues are offered by studies of the neural bases of manipulable objects, such as tools and utensils (e.g., Chao and Martin, 2000; Chen, Garcea, & Mahon, 2016, Chen, Garcea, Jacobs, & Mahon, *in press*), and studies of transitive actions, or actions that are directed toward objects. For instance, Chen et al. (*in press*) showed that, within the supramarginal gyrus of the inferior parietal lobule, a classifier trained to discriminate first person transitive pantomimes transfers to a task in which participants are performing a perceptual matching task over images of tools, indicating compulsory access to abstract representations of actions in the inferior parietal lobe even when participants are just identifying objects. In line with this, Gallivan, McLean, Valyear, and Culham (2013) showed that there are regions of frontoparietal cortex that have common representations for planned hand- and tool-related actions, unlike in the parietal and occipitotemporal regions where those two types of actions are dissociable (see also Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012; Wurm, Ariani, Greenlee, & Lingnau, 2016; Wurm, Caramazza,

& Lingnau, 2017). In another important prior study, Gallivan and colleagues (2011a) showed that the planning phase of transitive actions elicits decodable patterns of activation across the parieto-frontal motor network. Those patterns were not distinguishable based on signal amplitude differences, but were when using multivoxel pattern analyses (see Gallivan, McLean, Smith, & Culham, 2011b; Gallivan et al., 2013). Macuga & Frey 2012) looked at similar parieto-frontal regions during action observation (viewing an action being performed), motor imagery (imagining performing an action), and open-loop execution (first-person unseen actions), and found that there are dissociable patterns of activation, with some overlap in regions, across those three conditions.

Taken together, those prior findings suggest, but have not directly tested whether, basic intransitive actions are distinguishable based on multivoxel patterns in primary motor cortex. If this were the case, it opens the door for the possibility that there could be a set of core ‘primitives’ or ‘motor morphemes’ that can be compositionally combined to build more complex actions. As a first step toward testing this larger question, we asked participants to execute two actions with each hand and each foot: rotation and flexion (see Figure 1 for schematic). We first tested whether the two actions could be distinguished using univariate methods. We then tested whether multivoxel pattern analyses (MVPA) could distinguish neural representations corresponding to the two movements. To anticipate our core finding, while the amplitude of neural

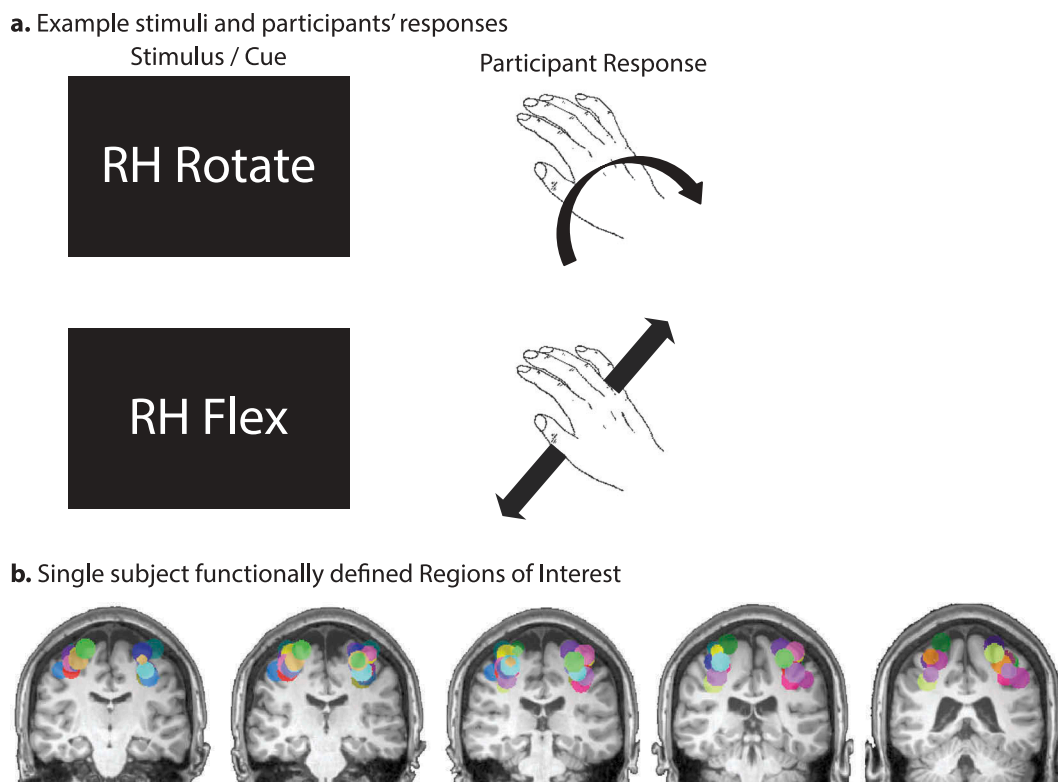


Figure 1. Example stimuli, participants' responses, and Regions of Interest. A. Example stimuli/cues and participant responses. Participants lay supine in the scanner, and a black screen with the cue, for instance 'RH Rotate', was presented (white font). The participant then rotated their right hand at the wrist. During flexion trials, participants were instructed to bring their hand or foot from a resting, inferior position, upwards, into an extended position, and then to smoothly return their hand/foot back (~0.5 oscillation per second). Likewise, during the rotation trials, the participants were instructed to comfortably rotate their hands or feet at the wrist or ankle, while minimizing elbow and hip movements, respectively (~0.5 oscillation per second). Participants were given explicit directions and practice with the cues before entering the scanner. B. Single subject Regions of Interest. The first functional run of hand and foot movements was used to define subject-specific regions of interest (ROIs) for the primary motor representation of the hand/wrist. The single subject ROIs are shown as spheres overlaid on reference anatomy in standard (Talairach) space. Mean coordinates ± 1 standard deviation (Talairach) were: left hemisphere: -32 ± 5 , -28 ± 7 , 51 ± 9 ; right hemisphere: 30 ± 5 , -28 ± 7 , 53 ± 8 .

responses (univariate approach) did not distinguish rotation from flexion, MVPA was able to decode the two types of actions, but only for those actions performed by the contralateral effector.

Methods

Participants

Twenty-three students from the University of Rochester participated in the study in exchange for payment (13 females; mean age, 21 years, standard deviation, 1.8 years). All participants were right-hand dominant, as assessed with the Edinburgh Handedness Questionnaire (Oldfield, 1971), had no history of neurological disorders, and had normal or corrected to normal vision. All participants gave written informed consent in accordance with the University of Rochester Research Subjects Review Board. The data from one participant were excluded from analysis because the participant fell asleep during the experiment.

General procedure

The scanning session began with a T1 anatomical scan, and then proceeded with either four 7-minute functional runs (nine subjects) or two 7-minute functional runs (13 subjects; see below for details). Some subjects also participated in functional scans for a category localizer experiment, a 6-minute resting state functional MRI scan, and a 15-minute diffusion tensor imaging (DTI) scan (data not analyzed herein; for analysis of those data, see Garcea, Chen, Vargas, Narayan, & Mahon, *in press*).

During fMRI, participants were prompted to rotate or flex their left or right hand or foot when presented with a visual cue (see Figure 1). One of the eight actions (left|right*rotate|flex*hand|foot) was cued for each mini-block of 12 seconds, interspersed by 12-second fixation periods. Each action was cued two times per run, in random order, with the constraint that a cell of the design did not repeat on two successive presentations. Because participants lay supine in the scanner, all actions were performed out of participants' view.

MRI parameters

Whole-brain imaging was conducted on a 3-T Siemens MAGNETOM Trio scanner with a 32-channel

head coil located at the Rochester Center for Brain Imaging. High-resolution structural T1 contrast images were acquired using a magnetization prepared rapid gradient echo (MP-RAGE) pulse sequence at the start of each participant's scanning session (TR = 2530 ms, TE = 3.44 ms, flip angle = 7°, FOV = 256 mm, matrix = 256 × 256, 1 × 1 × 1 mm³ sagittal left-to-right slices). For 13 of the participants (including all with four functional runs and four with two functional runs), the following parameters were used for T2* contrast: TR = 2000 ms, TE = 30 ms, flip angle = 90°, FOV = 256 × 1256 mm², matrix = 64 × 64, 30 sagittal left-to-right slices, voxel size = 4 × 4 × 4 mm³). For the remaining nine participants, the following T2* contrast parameters were used: TR = 2200 ms, TE = 30 ms, flip angle = 90°. FOV = 384 × 384 mm, matrix = 64 × 64, 33 sagittal left-to-right slices, voxel size = 4 × 4 × 4 mm³). The change in parameters was implemented for broader reasons having to do with accommodating subjects with larger heads in the field of view. The total run time for both T2* collection processes was the same, with the increased TR allowing more slices to be collected. All data were analyzed in the same manner regardless of which scanning parameters were used. The first six volumes of each run were discarded to allow for signal equilibration (four volumes at data acquisition and two volumes at preprocessing).

fMRI data analysis

fMRI data were analyzed using the BrainVoyager software package (Version 2.8) and in-house scripts drawing on the BVQX toolbox written in MATLAB. Functional data preprocessing included, in the following order, slice scan time correction (sinc interpolation), motion correction with respect to the first volume of the first functional run, and linear trend removal in the temporal domain (cutoff: two cycles within the run). The functional data were registered (after contrast inversion of the first volume) to high-resolution deskulled anatomy on a participant-by-participant basis in native space. For each participant, echo-planar and anatomical volumes were transformed into standardized space (Talairach & Tournoux, 1988). The functional data were interpolated to 3 mm³. The data were not spatially smoothed. The general linear model was used to fit beta estimates to individual trials. Experimental

events were modeled with a box-car function that was convolved with a standard 2-gamma hemodynamic response function; the onsets and offsets of the box-car function were aligned to onsets and offsets of each miniblock. The first derivatives of 3D motion correction from each run were added to the model as regressors of no interest to attract variance attributable to head movement.

ROI definition: Primary motor representation for each hand

To ensure uniformity across participants, the first run of each participant was used to define participant-specific primary motor regions for each hand (see [Figure 1](#) for details). There is no reason to suppose that the *a priori* decision to use the first run for ROI definition would impact any of the outcomes of the study. The data from the second (or subsequent) run(s) was then used for hypothesis testing, in the context of both univariate and multivoxel analyses. In this way, our analytic pipeline maintained strict independence of the data that was used to define the regions of interest (ROIs) and the data used for statistical analysis (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). Spheres (9 mm radius) were centered on each participant's peak voxel in the pre-central gyrus that exhibited stronger BOLD contrast for contralateral hand movements than contralateral foot movements, collapsing across action type. Note that due to the particular movements being performed, these motor regions correspond more to primary motor cortex for the wrist, rather than the fingers, resulting in more dorsal locations for the ROIs. ROIs were defined in both the left and right hemispheres.

Univariate analyses

Using data from the runs not used for ROI-definition, the average BOLD contrast, averaging over all voxels in the subject-specific ROIs, was computed for each movement type (rotation and flexion) and for each extremity (both hands and feet). Average BOLD contrast (% signal change, as estimated by regression coefficients (betas) from the general linear model) was compared between movement types within each extremity. Significant differences between the two movement types within an extremity would indicate

that those movements are distinguishable using univariate methods. Additionally, we would expect the average BOLD contrast level for the two movements in the contralateral hand for each ROI to be significantly higher than the average BOLD contrast for the other extremities. We tested these hypotheses using a series of planned t-tests. Because these constituted *a priori* planned tests, an alpha level (uncorrected for multiple comparisons) of .05 was used.

Multivoxel analyses

Linear correlation-based MVPA was used to test whether there was greater similarity in neural representations for the same movement type (within an extremity) than between the two different movement types (within an extremity). The key step in linear correlation MVPA is to correlate the voxel vectors of BOLD contrast (from an ROI) between two instances of the same condition (e.g., flexion of left hand with flexion of left hand) and two instances of different conditions (e.g., flexion of the left hand with rotation of the left hand; for review and discussion, see Haxby et al., 2001; Norman, Polyn, Detre, & Haxby, 2006; Spiridon & Kanwisher, 2002). If the correlation between two instances of the same condition is higher than the correlation between instances of different conditions then linear correlation MVPA can be said to discriminate the conditions (in this case, the flexion and rotation actions). Due to our interest in understanding the ability of these methods to discriminate movements within the hand/wrist ROIs of the motor cortex, analyses were restricted to comparing within and between the two different movement types for hand actions (i.e., excluding foot movements). Analyses were conducted using custom scripts drawing on the BVQX toolbox for MATLAB. Multivoxel linear correlations were always compared within- and between-movements, performed by the same effector. In addition, all linear correlation MVPA, for both within- and between-condition correlations, were carried out using data from the same run. By always comparing data within a run, the analysis accounts for autocorrelation, which should equally affect the within- and between-condition correlations (see Mumford, Davis, & Poldrack, 2014

for a discussion). For participants with more than two runs, the analysis was carried out for each run, and the results (correlation values) were first averaged over runs, before moving on to group-level analyses. In this way, each subject contributed the same number of average MVPA correlations to the group-level analyses, regardless of how many runs were completed. All correlation coefficients were Fisher z-transformed before computing group-level statistics, which consisted of paired t-tests (two-tailed). Because there is no principled reason to treat the two movement types (rotation and flexion) separately in this analysis, the data from both movement types are collapsed. Specifically, we average the within-condition correlation, for instance for left hand rotate with left hand rotate, with the within-condition correlation for left hand flexion with left hand flexion. This is because the key test is whether within-movement-type multivoxel patterns have higher correlations than between-movement-type multivoxel patterns, regardless of the actual movement type.

Results

Univariate analysis

We compared BOLD contrast amplitude between the two movement types for each extremity (left and right hands and feet) in each hemisphere (see Figure 2). In the right hemisphere ROI, there were stronger neural responses for the left hand than: **i)** right hand actions ($t(21) = 15.6, p < 0.001$), **ii)** left foot actions ($t(21) = 14.2, p < 0.001$) and **iii)** right foot actions ($t(21) = 13.5, p < 0.001$). There were no significant differences in amplitude between the rotation and flexion movements for any of the four extremities (left hand: $t(21) = 1.0, p = 0.33$; right hand: $t(21) < 1$; left foot $t(21) < 1$; right foot $t(21) < 1$). The same pattern was observed in the left hemisphere: stronger BOLD contrast for right hand movements than: **i)** left hand movements ($t(21) = 11.0, p < 0.001$), **ii)** left foot movements ($t(21) = 13.5, p < 0.001$) and **iii)** right foot movements ($t(21) = 13.5, p < 0.001$), with no difference between rotation and flexion movements for any

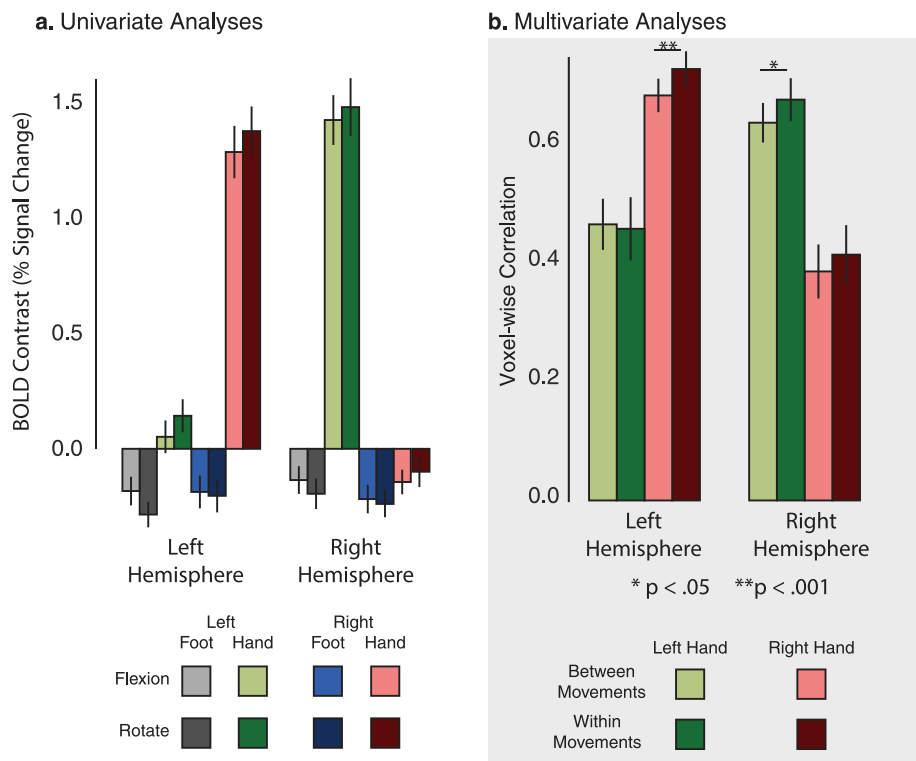


Figure 2. Univariate and multivoxel ROI analyses. A. Univariate Analyses. Average amplitude for each of the eight conditions (left|right*hand|foot*rotate|flexion) in each hemisphere. Error bars are between participant. While there is a clear bias for the amplitude to be greater for the contralateral hand, there is no difference between the two types of movements. B. Multivoxel Analyses. Voxel-wise correlations within each movement type and between the two movement types were computed for hand actions. Error bars are between participant. There is a significant difference between within-condition correlations and between-condition correlations for the contralateral hand in each hemisphere.

of the four extremities (left hand: $t(21) = 1.52$, $p = 0.14$; right hand: $t(21) = 1.35$, $p = 0.19$; left foot: $t(21) = 1.67$, $p = 0.11$; right foot: $t(21) < 1$).

Multivoxel analyses

The core goal of this investigation was to evaluate whether a multivoxel approach allows for actions to be discriminated when those actions are not discriminable using traditional univariate methods based on the average BOLD contrast amplitude across all voxels in an ROI. We thus compared the within-movement correlations with the between-movement correlations in each hemisphere, and for each hand (see Figure 2). For the right-hemisphere, the within-condition correlations were significantly higher than the between-condition correlations for the left hand ($t(21) = 2.0$, $p < 0.041$), while the same comparison was not significant for the right hand ($t(21) = 1.0$, $p = 0.29$). In the left-hemisphere, the within-condition correlations were higher than the between-condition correlations for the right hand ($t(21) = 3.7$, $p < 0.001$), while again, there was no difference for the same comparison for the left hand ($t(21) < 1$). These findings indicate that intransitive and unseen movements of the contralateral hand/wrist are distinguishable based on the multivoxel pattern that is elicited in primary motor cortex.

General discussion

Understanding the neural code for simple intransitive actions is a critical first step toward testing whether there is a componential inventory of 'action primitives' in motor cortex. Here we found that while univariate analyses revealed no difference between simple flexion and rotation movements of the contralateral hand in primary motor cortex, multivoxel analyses indicated that the voxel patterns were more similar for instances of the same movement of the contralateral hand than instances of different movements. The MVPA analyses allowed us to look at the patterns of voxel activation within each ROI in a way that is not possible with univariate analyses based on overall BOLD contrast amplitude. Each type of analysis is sensitive to different sources of variance (for discussion, see Davis et al., 2014; Jimura & Poldrack, 2012). Our findings indicate that it is possible to use

MVPA techniques to decode simple intransitive motor actions in the motor cortex, building on the results of prior studies (e.g., Gallivan et al., 2011b).

To this point we have used 'neural representation' to refer to a (voxel) pattern of BOLD signal in a given brain region. There is ongoing discussion about whether these 'neural representations' are coextensive with mental representations, and certainly there are a number of bridging assumptions that need to be carefully explored before assuming such a direct correspondence (for discussion, see Ritchie, Kaplan, & Klein, 2017). While we remain agnostic on the deeper theoretical issues about the correspondence or mapping between 'neural representations' and 'mental representations', we would suggest a direction for future work that operationalizes that mapping in a relatively simple-minded manner could prove fruitful. For instance, an important and open empirical question is whether basic intransitive actions can be combined, perhaps together with information given by visual processing, to yield neural representations of more complex actions, including transitive actions directed toward objects. Take the example of picking up a glass of water—that complex action, if decomposed, involves motor representations of movements of the shoulder, arm, wrist, hand and fingers—and all of those motor actions are informed by visual analysis of the volumetric properties of the object, its location in space in effector-relevant coordinate frames, as well as information processed by ventral extrastriate regions about the surface-texture and material properties of the target of the action. All of those processes are further subsumed within a goal state (take a drink of water), which presumably is itself quite divorced from the specifics of what is physically involved to take a drink from *this particular glass* and given the current state of the body. An interesting direction in which to apply this framework would be in patients with upper limb apraxia and impairments for transitive actions (e.g., Rumiati, Zanini, Vorano, & Shallice, 2001; Garcea, Dombovy, & Mahon, 2013; for review see Binkofski & Buxbaum, 2013). Specifically, an interesting possibility is that such patients exhibit heterogeneity in which aspects of 'action space' may be disrupted, with the dimensions of that action space understandable through a decomposition of complex actions into their component primitives.

Disclosure statement

No potential conflict of interest was reported by the authors.

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