Mirror neurons reflect hidden state progressions during a reach, grasp, and manipulate task

Kevin A. Mazurek, Marc H. Schieber
Neurobiology and Anatomy, Neurology, Center for Visual Science
University of Rochester Medical Center, Rochester, NY

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Introduction

Mirror neurons (MNs) in the ventral premotor cortex (PMv) and primary motor cortex (M1) discharge during both execution and observation of grasping actions, but are not generally thought to represent other epochs of behavior. We used Hidden Markov Models (HMMs) to test the hypothesis that PMv and M1 MNs represent phases of behavior in addition to grasping actions.

Methods

Experimental Setup

We recorded spiking activity from primary motor cortex (M1) and ventral premotor cortex (PMv) as two rhesus macaques (L, X), reached, grasped, and manipulated one of 4 objects: sphere, push button, coaxial cylinder, and perpendicular cylinder.

- **Action Execution (AE)** trials: the monkey performed the task
- **Action Observation (AO)** trials: the monkey observed an experimenter perform the task

Neural activity was recorded through Floating Microelectrode Arrays (FMAs, MicroProbe Inc). The present recordings were obtained from 8 arrays (96 electrodes) spanning M1 and PMv in each of two monkeys.

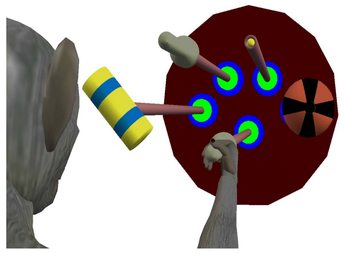


Figure 1. Reach, grasp, and manipulate task. Objects left to right: perpendicular cylinder, coaxial cylinder, push button, and sphere. Circles of blue LEDs around each object cue the monkey which object to grasp, and green LEDs indicate when an object is manipulated. (Illustration created with MSMS software courtesy of R. Davoodi and G. Loeb)

Single- and Multi-unit Analysis

Single- and Multi-unit activity (S/MUA) were sorted using the Plexon Offline Sorter (Plexon Inc.).

- Units were analyzed for firing rates which varied significantly from baseline
- **Significant units:**
  - Increased firing rate 3 standard deviations above baseline for 300ms or
  - Decreased firing rate 1 standard deviation below baseline for 600ms

Mirror Neurons (MNs): Units which significantly modulated for both execution (AE) and observation (AO) trials

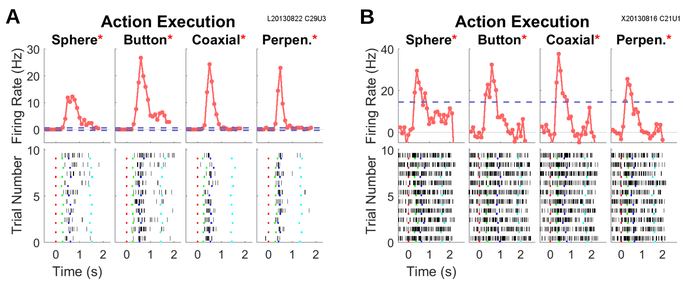


Figure 2. (**A**,**B**) Examples of two units which significantly modulate during the Action Execution (AE) trials. (**A**) Monkey L, (**B**) Monkey X. Dashed lines in firing rate plot (top) represent baseline standard deviation thresholds. Raster plots have colored markers indicating the time epochs for each trial: cue presentation (Red), onset of movement (Green), object contact (Blue), completion of final hold (Cyan). Firing rates binned in 100ms windows.

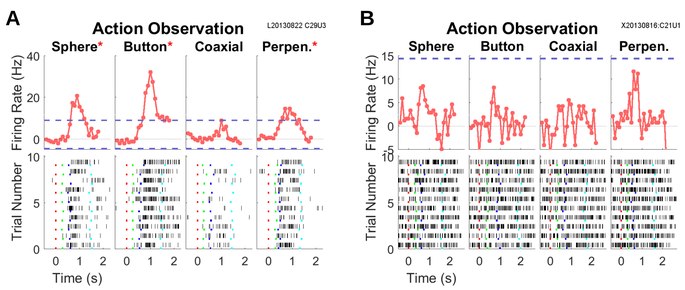


Figure 3. (**A**,**B**) Same units as in Figure 2 responding during Action Observation trials (AO). (**A**) Unit modulates significantly for 3 of the objects. (**B**) Unit does not modulate significantly for any of the objects.

Methods

Hidden Markov Modeling

Hidden Markov Models (HMMs) demonstrated a hidden state sequence during the execution and observation of the task

- Used spike times of population being modeled to create a vector of spiking IDs (2ms bin width)
- Trained 10 models at different initial conditions
- Selected the model with the greatest log-likelihood

Trained three different HMM conditions:

1. AE modulating Units – train on AE trials to demonstrate the hidden state sequence
2. MN modulating Units – train on AO trials to demonstrate a similar hidden state sequence
3. MN modulating Units – train on AE trials and decode on AO trials to show how the model translates between AE and AO trials for MNs

Selecting HMM States

Metric weighed the number of trained states with how consistent this state sequence occurred on an object by object basis

$$\underset{N_{states}}{\operatorname{argmax}}\left\{N^{*}_{states} \times \frac{mode(seq(N_{states}))}{N_{trials}}\right\}$$

Optimal N_{states} value varied per object and N^{*}_{states} is the number of unique states in the most consistent sequence (which usually is the number of trained states).

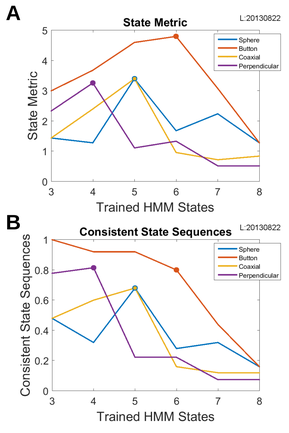
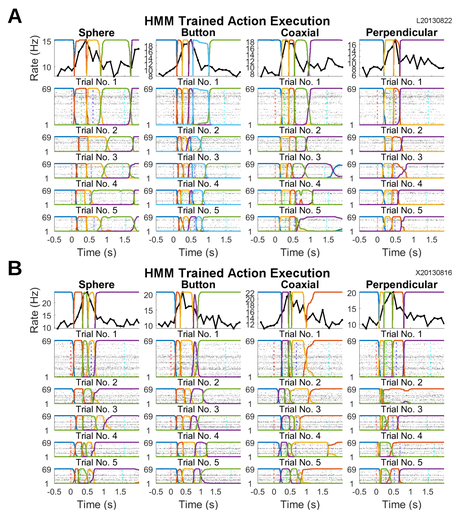
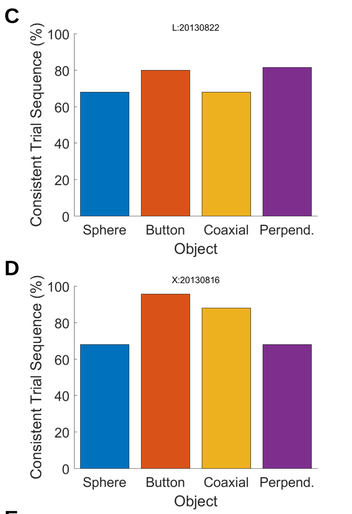


Figure 4. (**A**) State Metric and (**B**) Consistent State Measurements for Action Execution trials (AE). Circular marker indicates optimal HMM state.

Results





E

	L (20130822)	X (20130816)
AE Trials	102	98
AO Trials	84	89
AE Units	69	69
MN Units	9	16

Figure 5: (**A**,**B**) HMM Results for the AE trials for 4 objects. (**A**) Monkey L. (**B**) Monkey X. (**C**,**D**) Percentage of trials with the same HMM state sequence. (**C**) Object states for L: Sphere (5), Button (6), Coaxial cylinder (5), Perpendicular cylinder (4). (**D**) Object states for X: Sphere (5), Button (6), Coaxial cylinder (5), Perpendicular cylinder (5). (**E**) Trials and units for action execution (AE) and action observation (AO).

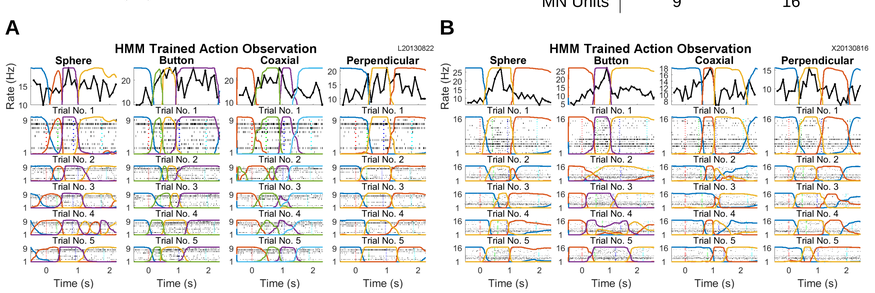


Figure 6: (**A**,**B**) HMM results for AO trials for 4 objects. (**A**) Monkey L Object states: Sphere (4), Button (5), Coaxial cylinder (6), Perpendicular cylinder(3). (**B**) Monkey X Object states: Sphere (3), Button (4), Coaxial cylinder (3), Perpendicular cylinder (3).

Results

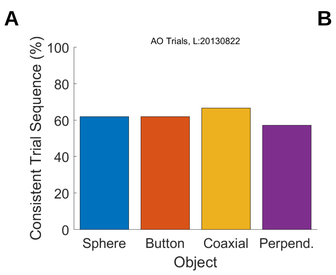


Figure 7 (**A**,**B**) Consistent state sequences for HMMS trained on Action Observation trials. (**A**) Monkey L, (**B**) Monkey X.

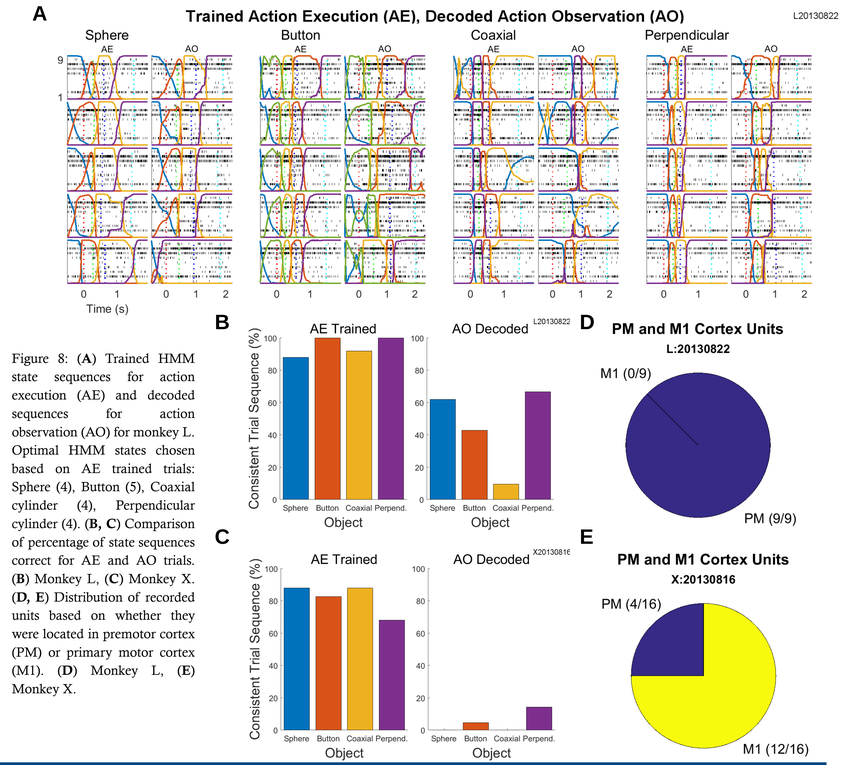


Figure 8: (**A**) Trained HMM state sequences for action execution (AE) and decoded sequences for action observation (AO) for monkey L. Optimal HMM states chosen based on AE trained trials: Sphere (4), Button (5), Coaxial cylinder (4), Perpendicular cylinder (4). (**B, C**) Comparison of percentage of state sequences correct for AE and AO trials. (**B**) Monkey L, (**C**) Monkey X. (**D, E**) Distribution of recorded units based on whether they were located in premotor cortex (PM) or primary motor cortex (M1). (**D**) Monkey L, (**E**) Monkey X.

Discussion

- Hidden Markov Models detect sequences of hidden states corresponding to time epochs in the behavioral trial
- Action Execution states reflect population activity that modulates during different epochs
- Action Observation trials with Mirror Neurons shows similar state sequences
- Decoding observation trials with the HMM trained on execution trials shows similar state progressions during AO and AE
- Populations of Mirror Neurons may represent the temporal sequence of the underlying state transitions across entire behavioral trials

Acknowledgments

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