Location then object representations sequentially predominate in the widely distributed activation of the primary motor cortex during reach to grasp

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Introduction
The primary motor cortex (M1) upper arm representation of macaques may be viewed as having a central core of distal representation surrounded by a "horizon" of proximal representation. Neurons in the core and horizon each are considered to express particular features of reach activity and/or related movement kinematics and dynamics. To the extent that such core and horizon predominate in parallel, this model would predict that activation in the horizon would be related to reach location and activation in the core related to grasp shape would be predominant.

Methods
Experimental Setup
We recorded spiking activity from primary motor cortex (M1) in two monkeys (Macaca mulatta). One (L) and one (X) reached and grasped sizes of 0-9 Objects in a set of 8 different locations. Thus, manipulated the object to choose a switch.

Monkey L

Figure 1. Reach-to-grasp task. For each block of trials, the stimuli were arranged in a group-to-one of eight zones. The eight possible locations for a given object were 175° (front left location), 355°, 112.5°, 90°, 67.5°, 45°, 22.5°, and 0° (right horizontal location). (Objects not located at one of these locations for a given zone were not included in the task. Illustration created with OpenPIV software by R. Marsden and G. Latham.)

Figure 2. Example of activity and movement. Observed spikes are plotted for each set of trials for all of the object-location combinations. The estimated firing rate (in Hz) is plotted above the raster plot using a square root scale. For this set of trials, the function of time is shown in panel A of Figure 5 (to the right). Note the early Location effect followed by an Object effect.

Figure 3. Spikes. Number of spikes across all trials using a 50 ms time bins aligned on cue, move, contact, and relax phases. Spikes contain more normalized such that a constant firing rate with no task related modulation yields a value of 1 in each bin. A: Histograms for example units. B & C: Histograms averaged across all recorded units for monkeys L & X, respectively.

Figure 4. Example of activity and movement. Observed spikes are plotted for each set of trials for all of the object-location combinations. The estimated firing rate (in Hz) is plotted above the raster plot using a square root scale. For this set of trials, the function of time is shown in panel A of Figure 5 (to the right). Note the early Location effect followed by an Object effect.

Figure 5. Example of activity and movement. Observed spikes are plotted for each set of trials for all of the object-location combinations. The estimated firing rate (in Hz) is plotted above the raster plot using a square root scale. For this set of trials, the function of time is shown in panel A of Figure 5 (to the right). Note the early Location effect followed by an Object effect.

Figure 6. Example of activity and movement. Observed spikes are plotted for each set of trials for all of the object-location combinations. The estimated firing rate (in Hz) is plotted above the raster plot using a square root scale. For this set of trials, the function of time is shown in panel A of Figure 5 (to the right). Note the early Location effect followed by an Object effect.

Results

Discussion

• Neuronal activity, like kinematics and EMG activity shown previously, appeared to be active in two, largely sequential phases: 1) Early activity preceding movement onset was predominantly Location-tuned, with lower firing rates and smaller depth of modulation. 2) Later activity preceding object contact was predominantly Object-tuned, with higher firing rates with larger depth of modulation.

• A fixed model that segregates neurons by spatial location or by reaching versus grasping is inadequate to describe M1 encoding of reach-to-grasp.

• Segregation into a central core of Object (distal) representation surrounded by a horseshoe of Location (proximal) representation was minimal.

Acknowledgments
This work was supported by NIH NS01-NS078644.