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 extremity representation of macaques may be viewed as having a central core of distal representation surrounded by a "horseshoe" of proximal representation. Neurons in the core and horseshoe each are considered to represent particular features of muscle activity and/or related movement kinematics and dynamics. To the extent that reach and grasp proceed in parallel, this model would predict that activation in the horseshoe related to reach location and activation in the core related to grasp shape would proceed in parallel.

Methods

Experimental Setup

We recorded spiking activity from primary motor cortex (M1) as two monkeys (*Macaca mulatta*), L and X, reached and grasped one of 4 Objects in up to 8 different Locations, then manipulated the object to close a switch.

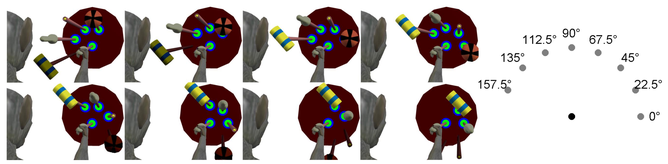

Figure 1. Reach-to-grasp task. For each block of trials, the objects were rotated as a group to one of eight zones. The eight possible locations for a given object were 157.5° (most left location), 135°, 112.5°, 90°, 67.5°, 45°, 22.5°, and 0° (right horizontal location). Objects not located at one of these locations for a given zone were not included in the task. (Illustration created with MSMS software courtesy of R. Davoodi and G. Loeb)

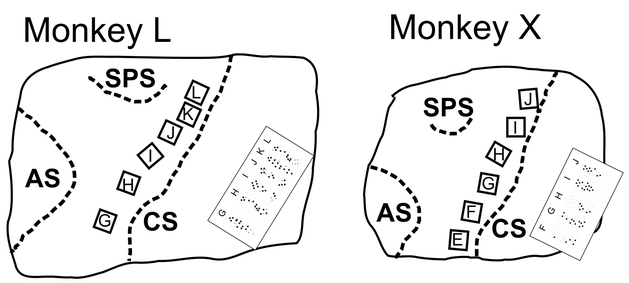

Figure 2. Recording array locations in M1. Six 16-electrode, chronic floating microelectrode arrays (MicroProbes, Inc.) were implanted in primary motor cortex in the left hemisphere of both animals. Top: medial, bottom: lateral, left: anterior. Insets at lower right in each frame illustrate the positions of electrode tips projected down the anterior bank of the central sulcus (CS), with larger dots indicating electrodes from which units were recorded. (AS, arculate sulcus; SPS, superior precentral sulcus)

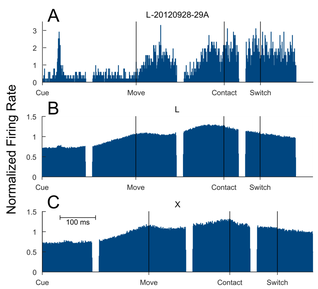

Figure 3. Spike histogram. Total number of spikes across all trials using 1 ms time bins aligned on cue, move, contact, and switch closure. Spike counts were normalized such that a constant firing rate with no task related modulation yields a value of one in each bin. A) Histogram for example unit. B & C) Histograms averaged across all recorded units for monkeys L & X, respectively.

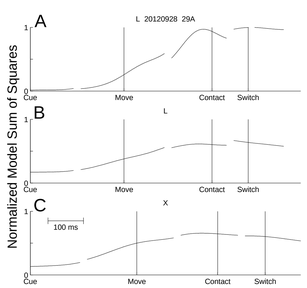

Figure 4. Total variance explained as a function of time. Sum of squares explained by model using the 24 different movements to the object/location combinations. Each unit was normalized by setting the time point with maximum variance explained to one. A) Normalized total variance explained for example unit. B & C) The mean calculated for each array for monkeys L and X, respectively.

Results

Analysis

Two-way ANOVA was performed with Location (8 categories) and Object (4 categories) used as factors, as well as an interaction term (Object x Location). To compare the effect size more accurately across time points, the effect size, η^2 , of each factor was normalized by using the maximum error variation at any time, rather than the error variation at each time point (Eqn. 1). Additionally, to quantify the relative effects of Location and Object, a Location/Object quotient (Q_m) was calculated (Eqn. 2).

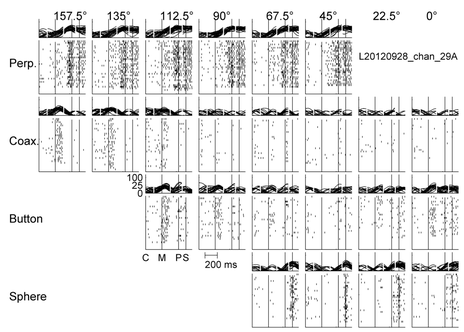

Figure 5. Example unit activity and η^2. Observed spikes are plotted for each set of trials for all of the object/location combinations. The estimated firing rate (in Hz) is plotted above the raster plot using a square root scale. For this unit, η^2 as a function of time is shown in panel A of Figure 7 (to the right). Note the early Location effect followed later by an Object effect.

$$Eqn.\ 1 \quad \eta_i^2(t) = \frac{SS_i(t)}{SS_{Obj}(t) + SS_{Loc}(t) + SS_{ObjxLoc}(t) + \max(SS_{Error})}$$

$$i = Obj, Loc, or\ Obj\ x\ Loc$$

$$Eqn.\ 2 \quad Q_m = \frac{SS_{Loc}(t)}{SS_{Obj}(t) + SS_{Loc}(t)}$$

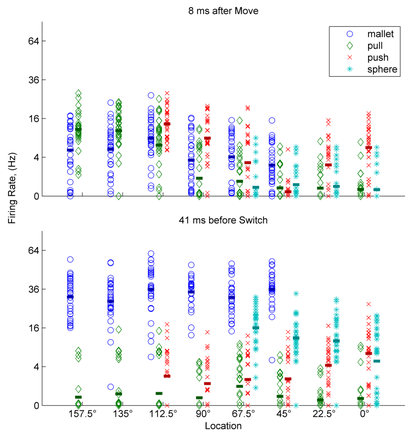

Figure 6. Example unit firing rate at two time points. The firing rate for the single unit illustrated in Fig. 5 is plotted at two time points: 1) 8 ms after the onset of movement, and 2) 41 ms before peripheral object switch closure. Note variation depending largely on Location at the former time, but variation depending largely on Object at the latter.

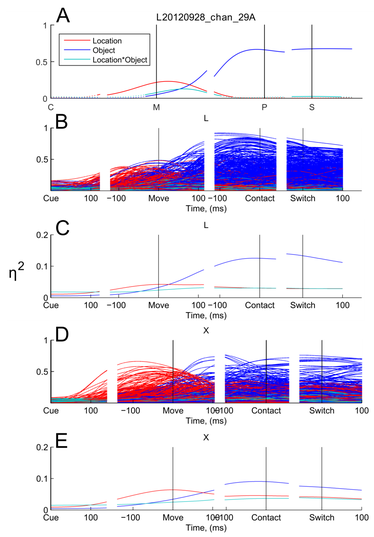

Figure 7. η^2 time-course. The η^2 from ANOVA model using Object, Location and their interaction (Object x Location) as factors. All data and analysis were aligned on four time points: cue, onset of movement, peripheral object contact, and switch closure. A) η^2 for the example single unit shown in Figure 5. B & D) η^2 plotted for all units recorded from monkeys L and X, respectively. C & E) Mean η^2 for data plotted in B & D for monkeys L and X.

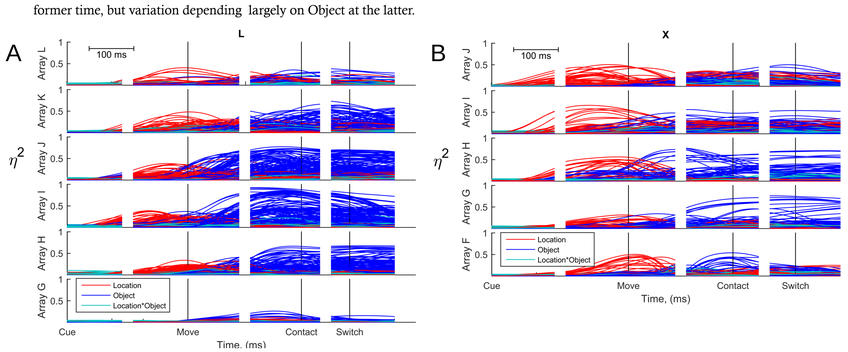

Figure 8. η^2 as a function of time. The η^2 for Location, Object, and their interaction (Location x Object) is plotted aligned on four time points: cue, move, contact, and switch. All units are plotted in a separate display for each array in the two monkeys A) L and B) X.

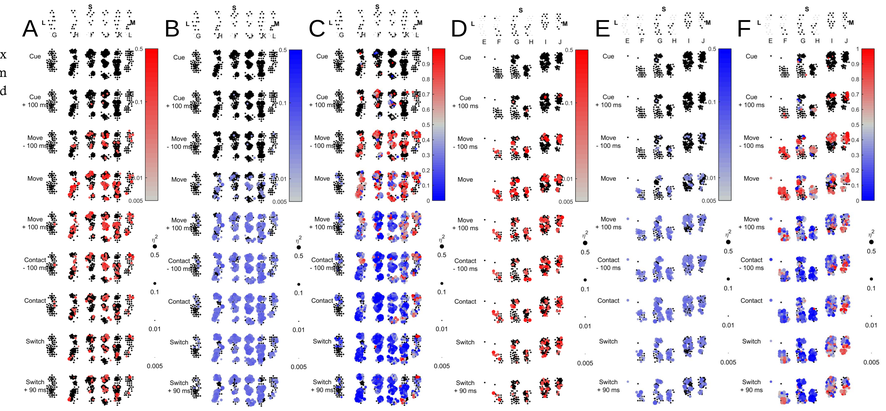

Figure 9. Spatial distribution of tuning to Object and Location at 8 time points (rows). Black dots indicate the spatial position of electrode tips in the anterior bank of the central sulcus (as in Fig. 2, insets). Each unit is presented by a colored circle.. All units from all days combined are shown for monkey L (A-C) and for monkey X (D-F). A&D) η^2 for Location, circle size and color both are scaled with η^2. B&E) η^2 for Object, circle size and color both are scaled with η^2. C&F) Location/Object quotient (Q_m) using a color scale ranging from blue (0, all Object effect) to red (1, all Location effect). Size is scaled with the total explained η^2.

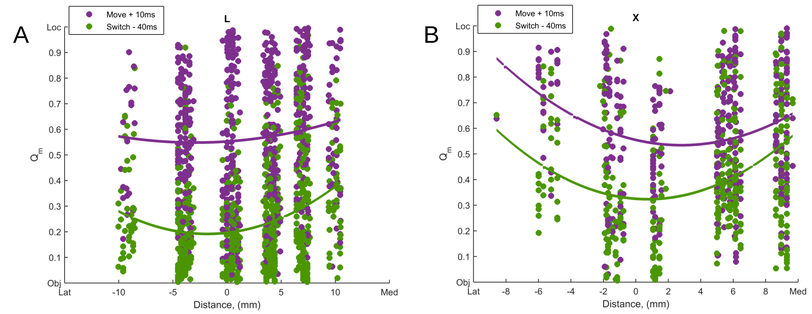

Figure 10. Object/Location quotient (Q_m) in medial/lateral dimension. The quotient of the η^2 values are plotted as a function of the calculated location of each electrode in the medial (+) / lateral (-) dimension along the central sulcus for monkey L (A) and X (B). A ratio of one corresponds to all location effect while zero corresponds to all object effect. Regression line was created with a quadratic model that included distance, distance^2, and intercept terms.

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

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