Primary motor cortex and ventral premotor cortex neurons related to head movements

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Introduction

We trained monkeys on a task designed to examine interactions between lateralized choice of hand and target, and the influence of head direction on these choices. Two food wells were positioned to either side of the midline, and LEDs provided instructions on which hand to use (green), and to which target to reach (red), in order to get a reward. During these instruction cues, the monkeys were required to maintain both head and eyes fixed on a left, center, or right LED (Figure 1).

1. Behavioral task

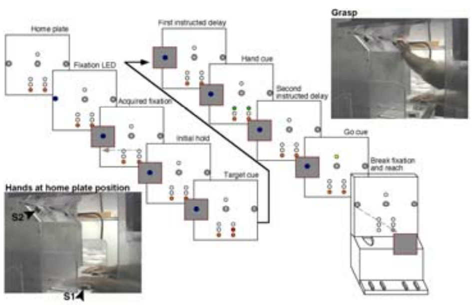

Figure 1. A series of panels illustrates the LED display viewed by the monkey during different periods of a single trial. To start a trial the monkey placed both hands in home plate positions (lower left photo). The monkey was informed of correct initial hand positioning (detected via infrared sensors, S1) by illumination of left and right orange LEDs at the bottom of the LED display (Home Plate panel). Then, one of three blue fixation-point LEDs was illuminated (Fixation LED) on the monkey's left (illustrated here as a blue filled circle), right, or at the center. The monkey directed both his head and eyes toward this fixation point in order to acquire fixation (Acquired Fixation panel, gray arrow and box). Then, the monkey went through a series of hold periods and cues that instructed him as to which target and which hand could be used to retrieve a small food reward. In this example the right LED came on (Target Cue panel), instructing the monkey that a food pellet would be dispensed only in the right food well, and then both green LEDs were illuminated (Hand Cue panel), instructing the monkey that he could choose either hand to use in reaching to the target. A yellow LED was lit as a GO cue (Go Cue panel). The monkey then was allowed to break fixation and reach for the food pellet (upper right photo). The behavioral apparatus generated event codes specifying the time of instructions provided to the monkey. In addition, movements were monitored through infrared sensors (S1 and S2). To monitor head and eyes movements, a head coil was mounted on a post implanted on the skull located approximately above the center of horizontal head rotation, and a scleral search coil was implanted in one eye. A single electrode drive was used to record single-units in both the primary motor cortex (M1) and the ventral premotor cortex (PMv). A total of 93 units were recorded from M1, and 127 from PMv in two pig tail macaques (Macaca nemestrina; Monkey J and Monkey O).

2. M1 neuron recording during successful trials

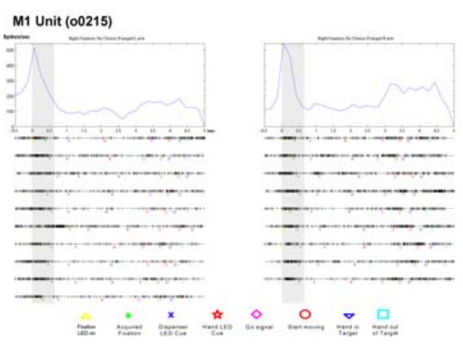

Figure 2. Example of data recorded during complete successful trials. This unit was recorded from M1 of the right hemisphere in Monkey O. This neuron discharged a burst as the monkey acquired fixation. The neuron's firing frequency also increased following the go signal during reaching and grasping with the right more than when the monkey used the left arm. The present analysis focuses on neuron discharge related to head movements as the monkey acquired fixation (i.e. in the **Acquiring-fixation period**, highlighted in gray).

3. Different types of single unit activity

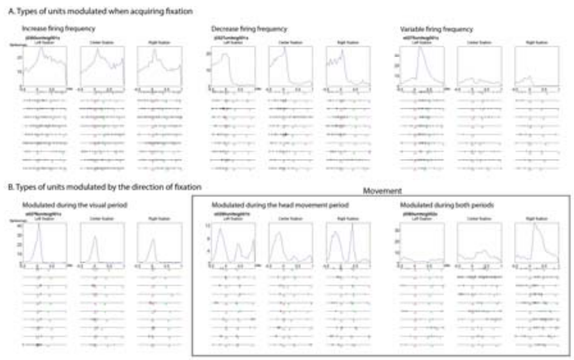

Figure 3. Examples of different types of single unit activity. All these units were selected from PMv, but units of each kind were also found in M1. A) We found units that increased firing frequency, and other units that decreased firing frequency, during the acquiring-fixation period. Still other units either increased or decreased firing frequency depending on the fixation direction (variable). To be considered an 'acquiring-fixation unit', a neuron had to be significantly modulated in at least one of the three gaze directions. B) In the 'acquiring fixation unit' population, some were modulated by gazes directions. In some units, the firing frequency during the early phase of the acquiring-fixation period only (<150ms; visual period) was modulated with gaze. For other units, the firing frequency modulation occurred later in the acquiring fixation period (>150ms; movement period) or during both the early and late periods. Only the later two types of units were considered to be potentially modulated in relation to head movement, and were further analyzed.

4. Summary of units modulated during the acquiring-fixation period and influenced by gaze direction

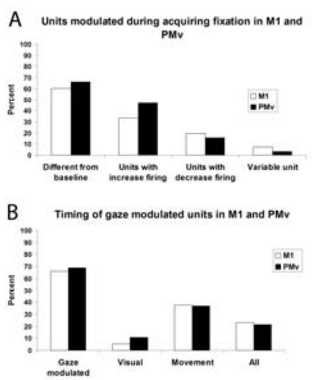

Figure 4. A) For each gaze direction (left, center, right), we compared the firing frequency of the neuron in the 100 ms prior to illumination of the fixation LED (baseline) to its frequency during the acquiring-fixation period (from illumination to acquisition of the fixation LED). A relatively high proportion of recorded units were modulated during the acquiring-fixation period. In both M1 and PMv, units with increased firing frequency were most common. Less than a quarter of units decreased their firing frequency and only few units showed an increase versus decrease depending on gaze direction. B) We examined whether the discharge of acquiring-fixation units was modulated depending on the different gaze directions. We separately compared the early phase of acquiring-fixation (visual) and the late phase (movement) for each unit. A high proportion of the acquiring-fixation units were gaze modulated. Few were modulated only during the visual phase. The majority were modulated during the movement phase only. We also found several units that were modulated during both the visual and movement periods.

5. Onset and offset of head movement

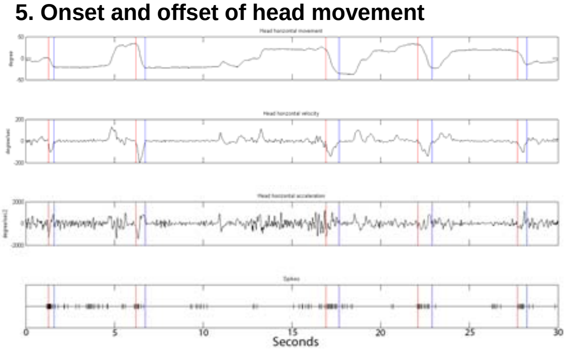

Figure 5. Example of recording of a right hemisphere PMv unit. From the top down, different traces show i) horizontal head position, ii) velocity, iii) acceleration and iv) neuron spikes. Red and blue lines mark the onsets and offsets, respectively, of head movements detected between illumination of the fixation LED and the subsequent target cues (which followed acquiring fixation) of successful trials. For gaze modulated units classified as potentially head movement-related, we identified head movements to investigate whether the neuron's firing frequency during these bursts correlated with final position, displacement, maximum velocity, and/or maximum acceleration.

6. Correlation of movement-related firing with parameters of head movement

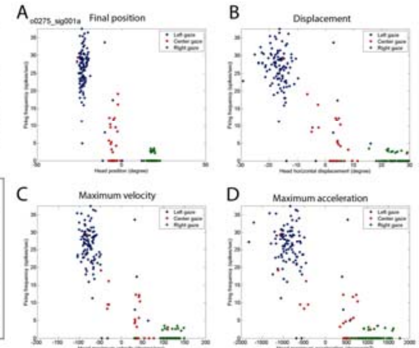

Figure 6. A head-movement related PMv neuron. In these scatter-plots, blue dots represent trials in which left fixation was required, red dots are trials requiring center fixation; and green dots are right fixation trials. This unit had a high firing frequency when the monkey turned his head to the left. Firing frequency was correlated with head final position (A), displacement (B), maximum velocity (C) and maximum acceleration (D). Units correlated significantly with one or more of these head movements parameters were classified as "head-movement" units.

7. Summary of head-movement units in M1 and PMv

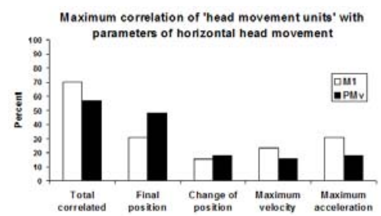

Figure 7. Many head-movement units were correlated significantly with one or more parameters of horizontal head movements. Interestingly, the highest correlation was found most often with head final position in both M1 and PMv neurons.

8. Cortical location of head-movement units

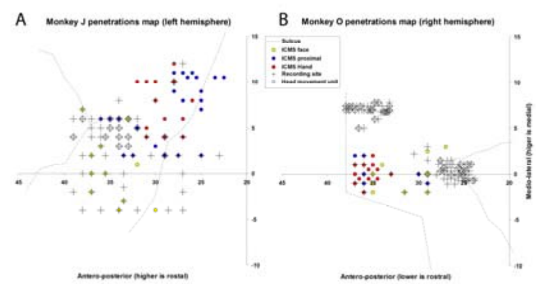

Figure 8. Location head-movement units. Sulcus locations are approximated based on structural MRI data. Intracortical microstimulation (ICMS) was performed at sites marked with colored circles. Neurons were recorded in penetrations marked with "+". A) Monkey J, penetrations in the left hemisphere. B. Monkey O, penetrations in the right hemisphere. Scales are in mm.

Conclusions

We found many units in M1 and PMv that were modulated during the acquiring-fixation period of our task. The majority of these units increased firing frequency in comparison to baseline. Furthermore, many were modulated differentially depending on whether the monkey looked to the left, center or right. We found some units with activity that was modulated by gaze only in the early phase of the acquiring-fixation period ('visual'). However, many more units were either modulated only in the late phase of the acquiring-fixation period or in both the early and late phases (potential 'movement-related'). A subset of these 'movement-related' units were correlated with parameters of head movements, most often the final position of the head. We found minor differences between the populations recorded in M1 and PMv. In both these cortical areas, head-movement units were relatively common, intermixed in the medial aspect of the arm representation. These units could play a role in the control of head movements, and in the coordination of head and arm movements.

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