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Motor Cortical Encoding of Hand Orientation in a 3-D Reach-to-grasp Task

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Abstract— **The activity of 979 motor cortical cells was recorded in a monkey trained to reach and grasp one of two targets oriented at various angles. 568 cells were found to be task-related and further classified. Among them, 24% correlated only with target orientations which determined hand orientation, 18% correlated only with target location (movement direction), 24% correlated with both target orientations and locations. Thus, hand orientation is an important control parameter during reach-to-grasp task. The data showed that in the motor cortex a portion of neurons could code hand orientation independent of movement direction. At the same time, cells encoding hand orientations and cells encoding movement directions coexist in the same region of the motor cortex, which indicates there probably exists a common pathway in M1 that controls both parameters.**

I. Introduction

Prehension movements involve three components: transport, manipulation, and hand orientation. Ever since Jeannerod's famous visuo-motor channel hypothesis that prehension movements are controlled by two separate channels for reaching and grasping [1], researchers have been focused on the problem of control coordination of prehension movements. Jeannerod proposed that the planning of reaching movements is based on the extrinsic properties (direction, distance, etc) of an object, while grasping is solely concerned with object's intrinsic properties (shape, size, etc) [1, 2, 3]. If the channel hypothesis is true, the transport should be independent of the object's shape or size. However, the observation that both transport time and peak velocity can be affected by object size [4] hints at how interrelated these independent processes might be.

From the temporal coordination aspect, Jeannerod suggested a temporal constraint that the time of maximum grasp aperture (MGA) and the onset of the low-velocity portion of the transport component were synchronous [2]. However, only a weak correlation between the timing of MGA and the onset of low-velocity movement was found [5]. An alternative suggestion is that a strategy based on a simple spatial amplitude ratio determines the relative duration of digit opening and closing in grasping [6]. This strategy preserves the idea that prehension is treated by the central nervous system (CNS) as two separable, yet coordinated components. The mechanical component of the coupling between transport and manipulation is the control of hand orientation by wrist and forearm. Hand orientation for grasping is known to depend on the shape [7] and orientation of objects [8, 9], leading some to introduce hand orientation as a third component of reach-to-grasp [10]. Our previous studies on human subjects have shown that hand orientation is controlled as an individual channel of prehension movements [10]. However, study performed by Desmerget et al. [11] showed that arm transport and hand orientation did not constitute independent visuomotor channels. To address the controversy on the kinematic studies, we designed an experiment to investigate from the upper command level how the CNS controls hand orientation during prehension movements.

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II. METHODOLOGY

A. Experimental Apparatus and Design

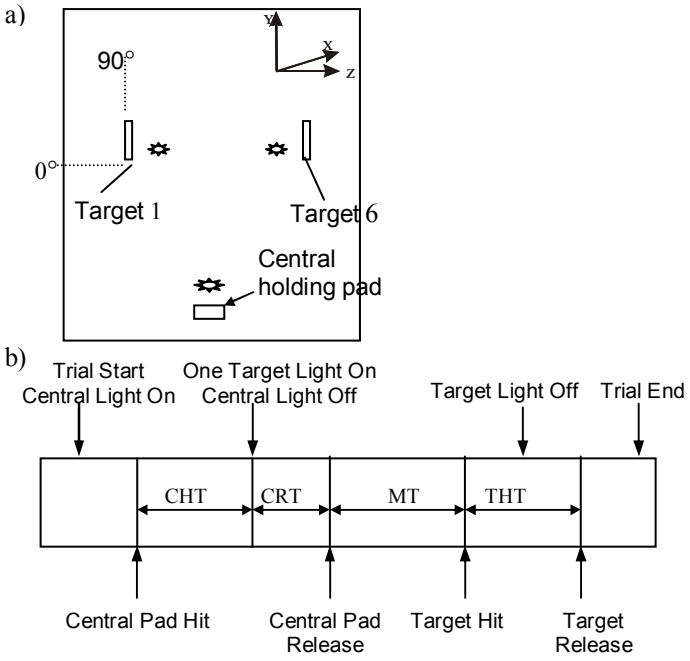

Fig.1. **Experimental setup**. **a**) The front view of the apparatus and the target orientation definition. **b**) The sequence of events for the reach-to-grasp task and the trial epochs. The cue reaction time (CRT) was defined as the time from target light on to central pad release; the movement time (MT) was defined as the time from central pad release to target hit; the target holding time (THT) was defined as the time from target hit to target release.

The apparatus consists of a central holding pad and two rectangular targets (Fig. 1a). The two targets are fitted with touch sensors on both sides of each target. A successful trial is produced by grasping the target firmly using a power grip, making contact with both sensors.

The monkey was trained to reach and grasp one of two targets (left, right) at various orientations (45º, 90º, 135º). The sequence of events for the reach-to-grasp task is shown in Fig. 1b. Each trial started with central light on, cueing the monkey to place its hand on the central holding pad. After a random center holding time (CHT), a target light came on, cueing the monkey to reach for the indicated target and make a whole hand grasp. The target light would go off after a minimum target hold period. The monkey would return the hand to the central pad and wait for the next trial (Fig. 1b). The Institutional Animal Care and Use Committee approved the behavioral paradigm, surgical procedures and animal care.

B. *Data Collection*

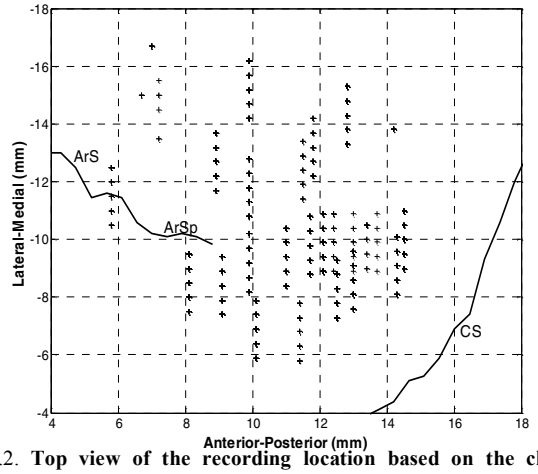

Fig.2. **Top view of the recording location based on the chamber's coordinates**. Each cross represents an electrode penetration. The recording location in the chamber's coordinates was recorded everyday before cortical signal recording. The chamber location in the stereotaxic coordinates was measured during the surgery. The rotation matrix from the stereotaxic coordinates to the chamber's coordinates was calculated. Then we converted the coordinates of the major landmarks (ArS, ArSp, and CS) in the stereotaxic coordinates into that in the chamber's coordinates. ArS: arcuate sulcus, ArSp: arcuate sulcus spar, CS: central sulcus.

A recording chamber was placed on the contralateral hemisphere. The electrical activity of single motor cortical neurons was recorded with five independently driven microelectrodes (ThomasRecording). Fig. 2 shows the locations of the recorded neurons. The penetrations covered the hand representation area of M1, and some of PMd and PMv. Each electrode made one penetation a day, and we changed the recording depth after every 108 successful trials (18 trials to each target condition) to record from different cells. All isolated neurons were recorded, and the activity of 979 motor cortical cells was recorded totally.

C. *Data Analysis*

A two-way analysis of variance (ANOVA) was used to evaluate whether changes in the average cell discharge were significantly modulated by target orientation, or movement direction, or their interaction effect ($P < 0.05$). The firing rates during CHT were considered as the baseline firing rates. For 105 out of 979 (10.7%) neurons, their neuronal discharge frequencies within CHT were significantly altered by target orientation. During CHT, the monkey's hand was resting on the central holding pad, the target was not presented and movement had not started. There were two reasons that could account for the changes: one was the visual input of different target orientations, the other was movement preparation. We also found 22 (2.3%) sensory cells in the motor cortex. These cells showed significant higher firing frequency during the CHT, CRT and THT when the monkey's hand was either touching the central holding pad or holding the target, but lower firing frequency during MT when there was no cutaneous sensory input. The next step was to find task-related cells. We define a cell as task-related if its average firing rates within any of the last three epochs was at least 2SDs greater than its baseline firing rate. Another 284 neurons (29%) showed no significant increase of discharge frequency during any of the last three epochs. The remaining 568 out of 979 neurons (58%) were found to be task-related and were further classified.

III. RESULTS

A. *Hand Kinematics*

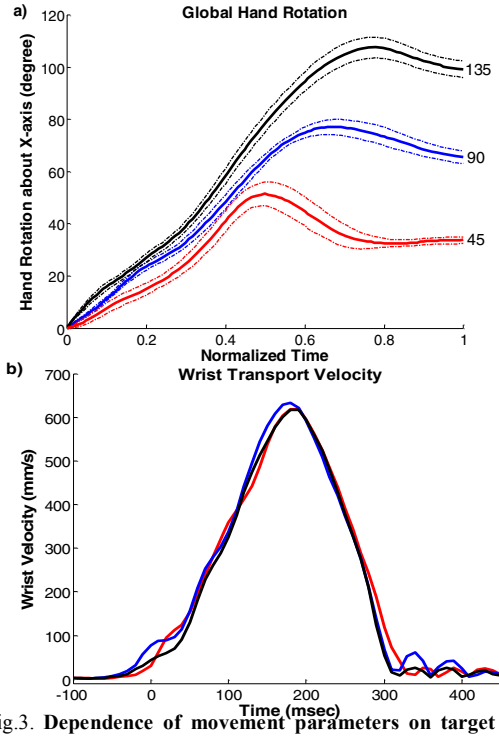

Fig.3. **Dependence of movement parameters on target orientation**. **a**) Averaged hand rotation trajectories (solid) +/- SDs (dashed) during movements to targets oriented at 45° (red), 90° (blue), 135° (black). Each solid curve is averaged from all trials of movements to the same target fixed at the same orientation in one day. **b**) Averaged wrist transport velocity profiles to different orientations. The color index is the same as plot a. Time zero is aligned at central pad release.

The features of the experiment paradigm are that hand orientation is determined by the target orientation (Fig. 3a); movement direction is determined by the left/right target; transport velocity profiles show no dependence on target orientation (Fig. 3b).

B. *General Nature of Orientation-related-only Cells*

Fig.4 shows perievent histograms of an exemplary motor cortical neuron. The left column shows the cell's activity during movements to the left target; the right column shows the cell's activity during movements to the right target. The

three rows correspond to three levels of target orientations. Each raster illustrates the firing pattern of the cell during 18 trials of movements to the same target condition. The neuron began to fire approximately 100msec before movement onset. The effect of target orientation caused a significant change in the overall level of cell activity before, during and after movements (ANOVA, $P<0.05$). The changes in firing activity caused by target orientation were consistently observed among movements to the two targets, and no clear difference was observed between firing patterns to the two targets.

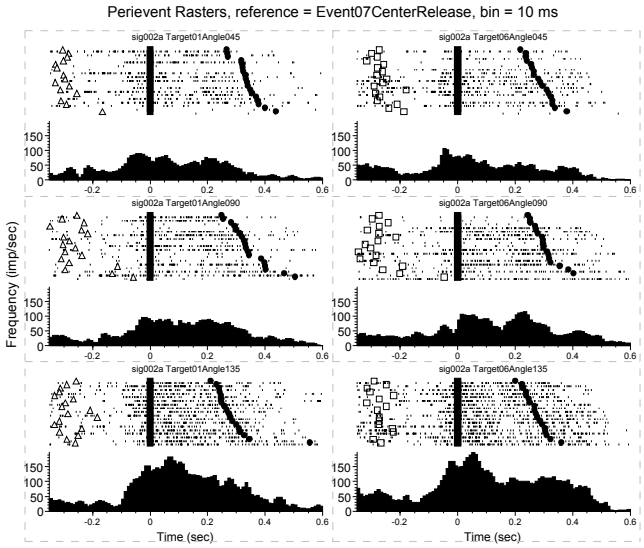

Fig.4. **Perievent histogram of a motor cortical cell encoding hand orientation during reaching and grasping the targets oriented at three different angles.** Time zero is alligned at central pad release (movement onset). The empty triangles represent left target light on; the empty squares represent right target light on; the solid diamonds represent target hit. The raster are ordered by ascending movement duration. The histograms were calculated with the bin of 10 msec and smoothed using a Gaussian filter with filter width of 3 bins.

C. *Direction-related-only Cells*

We also found some direction-related-only cells. For these neurons, the discharge frequency during movement to one of the target was significantly higher (ANOVA, effect of movement direction, $P<0.05$) than that to the other target. And the difference in the neuronal discharge patterns caused by movement direction was consistently observed across movements to the three different target orientations.

D. *Orientation-direction-interaction Cells*

Another type of cells was found to have significant orientation-direction-interaction effect ($P<0.05$). Fig.5. shows perievent histograms of an illustrative cell. We noticed that most orientation-direction-interaction cells better encode target hit than central pad release, so we aligned the raster at target hit. A significant orientation-direction interaction effect indicates that the orientation effect was not uniform between both targets. There might be a shift in the orientation preference between two movement directions. Note that in the illustrative cell (Fig.5), for the left target, the neuron's discharge frequencies during movements to 90º and 135º target are higher than that during movements to 45º target; while for the right target, it is the firing during movements to the 45º target that has the greatest discharge frequency.

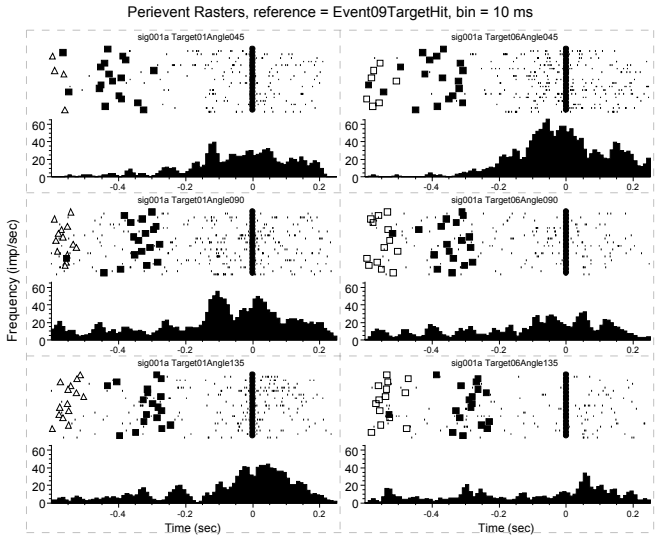

Fig.5. **Perievent histogram of a motor cortical cell encoding orientation-direction-interaction during reach-to-grasp**. The raster were grouped in the same way as we did in Fig.4. Time zero is aligned at target hit. The empty triangles represent left target light on; the empty squares represent right target light on; the solid squares represent central pad release. The raster are ordered by the trial sequence.

E. *Distribution of Task-related Neurons*

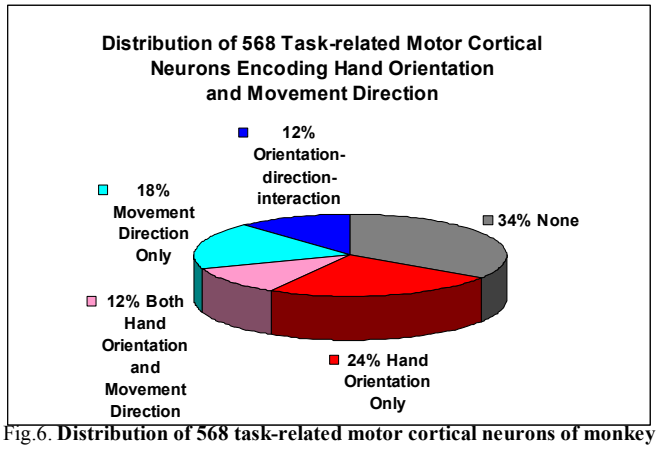

Fig.6. **Distribution of 568 task-related motor cortical neurons of monkey R encoding hand orientation and movement direction during three epochs** (from target light on to target off).

Average firing rates during the interval from target light on to target release were calculated for each trial, then tested with ANOVA. Fig.6. shows the distribution of cortical encoding of 568 task-related motor cortical neurons. 24% of the cells (137 out of 568) are hand-orientation-related-only cells, 18% (104 of 568) are movement-direction-related-only cells, 12% (65 of 568) are orientation-and-direction-related cells, 12% (68 of 568) are orientation-direction-interaction cells, 34% (194 of 568) show no significant encoding of neither parameters.

To map the cortical distribution of orientation-related-only cells and direction-related-only cells, we compared the density contours of these two types of cells (Fig. 7). The density was calculated for each penetration as the number of cells related to orientation/direction divided by the total

number of cells recorded under that penetration. Then the densities for all the penetrations were smoothed by a median filter, and the density contour for these two types of cells were plotted. The hottest color indicates the highest density. Fig.7 shows that both orientation-related-only cells and direction-related-only cells have a common hot area in the primary motor cortex. This result indicates that there probably exists a common pathway within M1 that controls both hand orientation and movement direction.

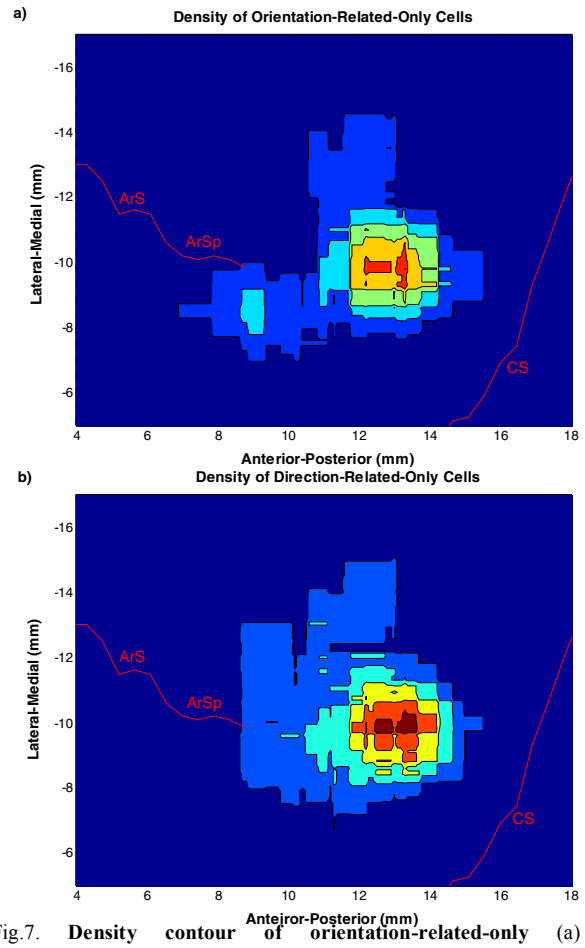

Fig.7. **Density contour of orientation-related-only** (a) **and direction-related-only** (b) **cells based on the chamber's coordinates.**

IV. Discussion

The present study was conducted to examine the motor cortical control of hand orientation during reach-to-grasp. We fixed initial hand position and target locations to keep the movement directions fixed, and investigated reach-to-grasp movements to targets oriented at various angles. We found single motor cortical neurons contributed to the control of hand orientation. Changes in hand orientation altered the discharge activity of motor cortical neurons before, during and after reach-to-grasp movements.

The present findings reveal that the discharge of a lot of single motor cortical neurons co-varied only with hand orientation independent of movement direction during reach-to-grasp movements. This is in contradiction to the suggestion that the position and orientation of the hand in space are unlikely to be controlled through separate independent neural pathways [12]. Our result shows that hand orientation constitutes an important control parameter of 3-D prehension movements, and any hypothesis proposed for prehension movement that does not take into account hand orientation as a constraint is inadequate. At the same time, we found significant amount of orientation-direction-interaction cells, and there is also a motor cortical area in which we found both cells encode only hand orientation and cells encode only movement direction, which indicate there probably exists a common pathway in M1 that controls both parameters.

Acknowledgment

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