Changes in Motor Cortex Activity During Reaching Movements With Similar Hand Paths but Different Arm Postures

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SUMMARY AND CONCLUSIONS

1. Neuronal activity was recorded in the motor cortex of a monkey that performed reaching movements with the use of two different arm postures. In the first posture (control), the monkey used its natural arm orientation, approximately in the sagittal plane. In the second posture (abducted), the monkey had to abduct its elbow nearly to shoulder level to grasp the handle. The path of the hand between targets was similar in both arm postures, but the joint kinematics and kinetics were different.

2. In both postures, the activity of single cells was often broadly tuned with movement direction and static arm posture over the targets. In a large proportion of cells, either the level of tonic activity, the directional tuning, or both, varied between the two postures during the movement and target hold periods.

3. For most directions of movement, there was a statistically significant difference in the direction of the population vector for the two arm postures. Furthermore, whereas the population vector tended to point in the direction of movement for the control posture, there was a poorer correspondence between the direction of movement and the population vector for the abducted posture. These observed changes are inconsistent with the notion that the motor cortex encodes purely hand trajectory in space.

INTRODUCTION

The activity of shoulder-related neurons in motor cortex during whole-arm reaching movements covaries with the direction of movement, typically in the form of broad symmetrical tuning curves centered on a preferred direction (Georgopoulos et al. 1988; Kalaska et al. 1989). With the use of a population vector model, the activity of these cells has been interpreted as defining a coordinate system that encodes the trajectory of the hand in space (Caminiti et al. 1990; Georgopoulos et al. 1988; Schwartz 1993, 1994). However, the interpretation of these data can be ambiguous because of the stereotypical coupling between extrinsic (i.e., hand trajectory) and intrinsic (i.e., joint angles or muscle activity) attributes of reaching movements (Mussa-Ivaldi 1988).

Caminiti et al. (1990) addressed this question by training monkeys to make reaching movements with parallel hand paths from starting positions in different parts of the work space. The directional tuning of single cells in the motor cortex tended to rotate with the starting shoulder angle. This showed that single cells did not uniquely code the direction of movement of the hand from its present position toward that of the target. However, because the parallel hand paths in their task were in different parts of the work space, uncertainty remains about how to interpret the modulation of single cell activity with starting arm posture. It could signify processing of an extrinsic parameter, hand path in space that varies with starting arm position, or it could reflect intrinsic parameters of the movement. Nevertheless, even though single cells showed a rotation of their directional tuning with starting shoulder angle, the population vector was described as remaining aligned with the direction of hand movement throughout the work space.

The present paper reports observations on the response properties of motor cortical cells in a monkey during reaching movements along similar hand paths to the same target locations, with the use of two different arm postures. This more fully dissociates the extrinsic and intrinsic attributes of the reaching movements. A majority of cells showed significant changes in their activity between the two arm postures, and there were significant differences in the directional signal generated by the cell population in the two postures.

METHODS

A juvenile male rhesus monkey (Macaca mulatta; 4 kg) was trained to move a pendulum-like handle with its right arm from a central starting position to eight equally spaced light-emitting diode (LED) targets. The apparatus and task have been described elsewhere (Kalaska et al. 1989). However, for this experiment, the position of the handle grasped by the monkey on the manipulandum was at shoulder height. The monkey was trained to hold the manipulandum over the central target for a variable period of time (1–3 s), then to move it to one of eight peripheral targets and to hold it at the target for 2 s. The eight target lights were presented five times in a randomized-block design.

The monkey performed the task with the use of two different arm postures. In the first posture (control), the monkey was allowed to perform the task in its preferred natural arm orientation (largely in the sagittal plane with the elbow suspended vertically below the level of the hand and shoulder). In the second posture (abducted), a barrier was attached to the manipulandum immediately below the handle, so that the monkey had to abduct its arm ~80° into the horizontal plane above the barrier to grasp and move the handle. Therefore the position and trajectory of the hand in external space were similar in both experimental conditions. In contrast, the intrinsic kinematics and kinetics of the movement were dramatically different.

Hand trajectories to each target for the control and abducted tasks were recorded to verify that they were similar. Each movement was divided into 20 equidistant points along its trajectory. The mean and standard deviation of each point along the trajectory were computed across all trials for each posture.

Conventional single unit recording techniques were used to record the activity of single cells in the motor cortex during the motor
results

The activity of 144 proximal arm-related cells was recorded in the anterior bank of the central sulcus in the left (contralateral) motor cortex. Each cell had to be related to movements of the proximal arm (shoulder or elbow) and had to be directionally tuned during either movement (RT+MT) or posture (THT) in at least one of the two arm postures to be included in the cell sample.

Many cells demonstrated significant differences in their response properties for reaching movements performed with the use of different arm postures, even though both hand paths and target endpoints were similar. In total, 130 (90.3%) and 131 (91.0%) cells studied showed differences in their activity (tonic activity or directional tuning, see below) between the 2 tasks during the RT+MT or THT epochs, respectively (F-test, $P < 0.05$).

The most common effect of arm posture was a change in tonic firing rate before, during, and after the reaching movements (Fig. 1). For instance, during CHT, 115 (79.9%) cells showed a change in tonic activity between the 2 tasks (average absolute change in firing rate was 8.2 spikes/s). Approximately equal numbers of cells showed higher tonic firing rate in either control or abducted postures, so that the mean tonic rate of the total population during CHT in the two postures was not significantly different (16.3 ± 10.2 spikes/s for control and 15.5 ± 11.4 spikes/s for abducted, mean ± SD; $P > 0.10$, paired t-test). Similar changes in overall activity level were seen during movement (RT+MT) and during posture (THT).

The change in arm posture could have three possible effects on the directionality of cell discharge. Cells could be directionally tuned in both postures and have the same directional preference. Alternatively, their preferred direction could change between the two postures. Finally, the cell could be directionally tuned in one posture but not in the other. We found many examples of all three possible outcomes. For instance, during the RT+MT epoch, 49 cells (34.0%) were unimodally tuned during movement in one posture but not the other (Rayleigh test, $P < 0.05$), with similar probability for selective directional tuning only in the control (28 cells) or abducted (21 cells) posture. Eighty cells (55.5%) were directionally tuned in both postures (the remaining 15 cells were not unimodally tuned in either posture during RT+MT but were tuned during THT in at least 1 of the 2 postures). Of these unimodally tuned cells, 40/80 (50%) showed a significant change in directional tuning between the 2 postures (Watson-Williams test, $P < 0.05$, Fig. 1). Therefore the change in arm posture had a strong impact on the directionality of movement-related activity of 89/129 tuned cells (69.0%), whereas only 40/129 cells (31.0%) showed no significant change in direction between arm postures. Similar results were found for the tonic activity related to holding the arm over the target endpoints after movement (THT epoch).

The magnitude and direction of the change in preferred direction varied considerably from cell to cell, and there was no consistent trend for a rotation in one direction or the other (clockwise or counterclockwise). For cells unimodally tuned in both postures, whether or not they showed a significant change in directionality, the absolute mean difference in preferred direction during RT+MT was 27.8°, but the arithmetic mean change in preferred direction for the entire sample between abducted and control postures was only $-2.3°$ (positive rotation is counterclockwise). Similarly, during THT, the absolute mean difference was 30.9°, and the arithmetic mean change in the preferred direction for the entire sample was only $-2.2°$.

Because the effect of arm posture on cell discharge was tested sequentially in two separate data blocks, random temporal variability in cell responsiveness could have contributed to the observed changes. To evaluate the stability of cell activity, a second pair of data blocks were collected from nine cells. The responses of the cell in the duplicate data blocks in the same posture could then be compared. There was a significant change in tonic activity during CHT in only 2/18 (11.1%) replicated files. Furthermore, the absolute change in tonic activity between original and repeat blocks across all 18 pairs of files was only 1.8 spikes/s, far smaller than the observed mean change in tonic activity between postures (8.2 spikes/s, see above). Of the 15 replicated pairs of files that could be tested with the use of the Watson-Williams test, none showed a significant difference (i.e., $P < 0.05$) in directional tuning between the original and duplicated files. Therefore the observed changes in tonic activity and directionality of the cells between the control...
and abducted postures cannot be explained simply by random variations in cell discharge between blocks of data.

The effect of arm posture on the behavior of the ensemble of cells was evaluated with the use of the population vector method (Georgopoulos et al. 1988). There was a change in the direction of the population vectors for movements performed in the two arm postures (Fig. 2, A and B). For the control posture, the vectors were of similar length and were distributed uniformly and oriented approximately in the direction of hand movement. In contrast, for the abducted...
Fig. 2. Mean population vectors calculated from the activity of the motor cortex cells for movements to 8 targets for the control (A) and abducted (B) postures (RT+MT epoch). The base of the vectors are at the center, whereas the tips of the vectors are joined together to form an 8-sided polygon. Below the polygons are the hand trajectories to each target for the control (A) and abducted (B) postures. The center of each cross denotes the mean position of the hand computed from all trials recorded in this study. The length of each arm in the cross denotes 1 standard deviation of the mean in the horizontal and vertical directions. C: comparison of the distribution of 100 population vector estimates for movements at 45°, generated with the use of statistical bootstrapping techniques (see text). Short vectors are the individual vector estimates, and long vectors (with arrows) are their mean for the control (— — —) and abducted (— — ) postures.

The trajectory of the hand was similar when the task was performed with the use of either arm posture (Fig. 2). The variability in the trajectory of the hand to a target for the control task overlapped extensively with the trajectories for the abducted task, with the least overlap of trajectories occurring for movements at 135 and 225°. Qualitative comparison suggests that the small differences in hand trajectory between control and abducted postures cannot explain the shifts in the mean population vectors. For instance, the population vector for movements at 0° is significantly rotated clockwise in the abducted posture compared with the control posture (Fig. 2, A and B), whereas the hand paths show the opposite direction of curvature in the two postures. In contrast at 135°, the change in the direction of the initial hand path and population vector from control to abducted postures are in the same directions. More definitive analysis awaits comparison of the instantaneous movement and neural-population vectors during movement. However, similar significant differences were likewise found between the mean population vectors calculated from the activity during the THT epoch (data not shown). This cannot be explained by any variation in the position of the hand, because the hand was being held stationary over the same target locations in the two arm postures (Fig. 2).

**Discussion**

The present study analyzed the activity of cells in the motor cortex during reaching movements along similar hand trajectories with the use of two different arm postures, to dissociate intrinsic from extrinsic attributes of movement. The results demonstrate that cell activity in the motor cortex is highly sensitive to changes in arm posture even though hand trajectory remained similar. Many cells in this same part of the motor cortex are also strongly modulated by the presence of external loads during reaching movements along the same spatial hand paths (Kalaska et al. 1989). Both these findings are consistent with the notion that single cells in that part of the motor cortex encode the direction of displacement of the hand through space.

Previous studies have suggested that, independent of the behavior of single neurons, the population activity of cells within motor cortex encodes the trajectory of the hand in space (Caminiti et al. 1990; Georgopoulos et al. 1988; Schwartz 1993). This hypothesis predicts that the population vector should remain constant for arm movements with identical hand paths but different arm geometries. However, we found statistically significant changes in the direction of the
population vector under these conditions. As well, in the abducted posture, several population vectors did not accurately predict the direction of movement. Although there was a slight variation in the hand paths when the monkey moved to a given target with the use of different arm postures, such variations do not appear to account for the observed shifts in the population vectors. A population analysis in this part of motor cortex has shown previously that the length and direction of the population vector was also altered by external loads and did not necessarily correspond with the path of the hand (Kalaska et al. 1989, 1990). Both of these findings are likewise inconsistent with the notion that the total population activity in that part of the motor cortex explicitly encodes the spatial kinematics of reaching trajectories in a hand-centered coordinate frame (Schwartz 1993, 1994).

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