Neuronal Population Coding of Movement Direction

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Although individual neurons in the arm area of the primate motor cortex are only broadly tuned to a particular direction in three-dimensional space, the animal can very precisely control the movement of its arm. The direction of movement was found to be uniquely predicted by the action of a population of motor cortical neurons. When individual cells were represented as vectors that make weighted contributions along the axis of their preferred direction (according to changes in their activity during the movement under consideration) the resulting vector sum of all cell vectors (population vector) was in a direction congruent with the direction of movement. This population vector can be monitored during various tasks, and similar measures in other neuronal populations could be of heuristic value wherever there is a neural representation of variables with vectorial attributes.

For many functions controlled by the brain or variables represented in the brain, the relevant unit is the neuronal population rather than the individual neuron. Elucidating the nature of this representation of information by a neuronal ensemble is a central problem of neuroscience (1). We have approached this problem by investigating the brain mechanisms subserving the direction of arm movement in three-dimensional (3-D) space in order to predict directed arm movements from the neural responses of populations of motor cortical neurons.

Rhesus monkeys were trained to reach out and push red buttons that had been lit. A center button was located directly in front of the animal at shoulder level. Eight target buttons were placed at equal distances (12.5 cm) from the center button so that the direction of movements made from the center to targets sampled the 3-D space at approximately equal angular intervals (Fig. 1). In a trial, the center light came on first, and the animal pushed it and held its hand on that button for at least 1 second. Then...

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the center light went off and one of the eight targets was turned on. The animal moved its hand toward this target and pushed it to get a liquid reward. In subsequent trials, different targets were lit so that all of the eight targets were presented in a random sequence. Eight complete sequences (or blocks) were obtained for most cells studied. Movements of the left arm were reflected with respect to the mid sagittal plane to allow the combination of right- and left-hand data. The average duration of movement was 0.485 ± 0.205 (SD) second. Some of the movement trajectories at the wrist were monitored with a 3-D sonotrack system (2) to obtain estimates of the direction of the movements aimed at the eight targets.

We used standard electrophysiological techniques (3) to record extracellularly the activity of single neurons during microelectrode penetrations into the motor cortex contralateral to the performing arm. We selected neurons that changed activity with spontaneous movements of the arm or with movements directed to food rewards offered to the animal by the experimenter. We then recorded quantitatively the relations between the activity of these arm-related cells and the direction of arm movement in 3-D space. We used the frequency of discharge (neural impulses per second) from the onset of the target illumination until the end of the movement as a measure of the neuronal activity. An analysis of variance (4) was performed to assess the statistical significance of the differences in neuronal activity associated with different movement directions. Of the 282 neurons studied, 41 (14.6%) were termed non directional, as they showed no statistically significant directional variation ($P < 0.05$, F test), and were not analyzed further. For the remaining neurons, a multiple regression was performed (5) (with parameters described in the next section). Neurons that had an activity pattern that was fit by the regression equation ($n = 224$ (79.4%), $P < 0.05$, F test in multiple regression) were considered directionally tuned and were used for the population analyses described below. Finally, data from 17 (6%) neurons were not fit by the regression equation (directionally nontuned) and were not analyzed further.

We used the following model to describe the relations between the activity of each directionally tuned neuron (Fig. 1) and the direction of movement in 3-D space. Let $x$, $y$, $z$ be the positive axes of a Cartesian coordinate system with center at the origin of the movement. Consider a movement vector $M$ of unit length that makes angles $\chi$, $\omega$, and $\psi$ with the $x$, $y$, and $z$ coordinate axes, respectively. The direction of vector $M$ in 3-D space is specified by its direction cosines ($m_x$, $m_y$, $m_z$) (6) where $m_x = \cos \chi$, $m_y = \cos \omega$, and $m_z = \cos \psi$, and where

$$m_x^2 + m_y^2 + m_z^2 = 1$$

We used the following model to relate cell activity to movement direction.

$$d(M) = b + b_x m_x + b_y m_y + b_z m_z$$  (1)

where $d(M)$ is the frequency of discharge of a particular neuron during movement in direction ($m_x$, $m_y$, $m_z$), and $b_x$, $b_y$, $b_z$, and $b$ are coefficients that vary from neuron to neuron. The values of these coefficients and their standard errors were estimated with multiple regression techniques (5).

The model of Eq. 1 implies that there is a particular movement vector $C$ for which the cell's activity will be highest. The direction of this vector is the cell's preferred direction, which can be determined by estimating the direction cosines $c_x$, $c_y$, and $c_z$ of the vector $C$ from Eq. 1 as follows.

$$c_x = b_x/k$$

$$c_y = b_y/k$$

$$c_z = b_z/k$$

where

$$k = (b_x^2 + b_y^2 + b_z^2)^{1/2}$$

The preferred directions indicated for the 224 neurons that fit the model ranged over the whole 3-D directional continuum about the origin of the movement.

An equivalent expression of the model of Eq. 1 is

$$d(M) = b + k \cos \theta_{CM}$$  (2)

where $\theta_{CM}$ is the angle formed by the cell's preferred direction $C$ and the direction of a particular movement $M$ (Fig. 2) (7). It follows that the discharge rate, $d(M)$, will be highest with movements in the cell's preferred direction, that is, when $C$ and $M$ coincide ($\theta_{CM} = 0$ degrees, $\cos \theta_{CM} = 1$); lowest with movements in the opposite direction ($\theta_{CM} = 180$ degrees, $\cos \theta_{CM} = -1$); and in between with movements in intermediate directions ($0 < \theta_{CM} < 180$ degrees, $1 > \cos \theta_{CM} > -1$) (8).

Equation 2 indicates that motor cortical cells are broadly tuned in the sense that they change their activity with movements in any direction. In contrast, sharply tuned neurons, which might have changed activity with only one or two adjacent movement directions, were not observed.

The broad directional tuning of single neurons suggested that the direction of movement is not coded by individual cells that respond only with movements in a specific direction. Instead, the direction of movement may be coded in a unique fashion.
Fig. 2. Schematic diagram to show the preferred direction (C) of the cell illustrated in Fig. 1. The direction cosines of the preferred direction were \( c_x = 0.41, c_y = 0.51, c_z = -0.76 \). Also shown is a movement vector M with coordinates \( m_x = 0.23, m_y = 0.78, m_z = -0.58 \), and the angle \( \theta \) formed between the cell's preferred direction C and the direction of movement M.

by the neuronal ensemble. Consider a movement in an arbitrary direction M. We want to find a way by which the neuronal population of the 224 directionally tuned cells will yield information about the direction of movement M. For that purpose we made three assumptions. (i) Each cell (indexed by \( i \)) makes a vectorial contribution along its preferred direction, \( C_i \). (ii) The magnitude of the contribution (or length of the vector) \( w_i(M) \) of the \( i \)th cell is a function of the movement direction and is taken to be equal to the change in cell activity from an offset level.

\[
w_i(M) = d_i(M) - b_i
\]

where, from Eq. 2, \( b_i \) is a constant and \( d_i(M) \) is the frequency of discharge of the \( i \)th cell for movement in direction M. From assumptions (i) and (ii), it follows that the weighted vectorial contribution of the \( i \)th cell is

\[
N_i(M) = w_i(M) C_i
\]

The vector \( N_i(M) \) will point toward the \( i \)th cell's preferred direction if the weight \( w_i(M) \) is positive or in the opposite direction if the weight is negative (9). (iii) Finally, we sum vectorially these cell vectors to obtain the neuronal population vector \( P(M) \) corresponding to movement direction M.

\[
P(M) = \sum_{i=1}^{224} N_i(M)
\]

The outcome for one of the movement directions tested is shown in Fig. 3. The yellow line indicates the movement direction M. The cluster of light purple lines represents the 224 cell vectors (that is, the vectors \( N_i(M), i = 1 \) to 224) for movement direction M. The direction of the population vector \( P(M) \) yielded by the vectorial summation of these cell vectors is orange. The direction of the population vector is very close to the direction of the movement vector (Fig. 4) (10). Therefore, the population vector predicts accurately the direction of the movement (11, 12).

Similar results were obtained for the other movement directions (see cover). The resulting clusters have been placed, for illustrative purposes, on the surface of a hypothetical sphere where the respective movement vector, arising from the center of the sphere, crosses the surface. (The remaining two clusters are behind the sphere and cannot be seen.) The directions of the movement and the corresponding population vector were again similar (13). In general, the direction of movement fell within a 95% confidence cone constructed around the direction of the population vector (4) (Fig. 5). In preliminary work we have found that this result also occurs when the origin of the movement is changed (15).

These findings generalize to 3-D space previous results obtained in two-dimensional (2-D) space (3, 16) concerning the directional properties of single motor cortical cells and the predictive power of the neuronal population vector. These results indicate that single cells are broadly, rather than sharply, tuned to the direction of movement (17), and that the movement direction can be uniquely coded by a directionally heterogeneous neuronal population. Assuming that other brain structures are also involved in the control of the direction of movement.
in some cases the general cosine function of Eq. 2 has provided a good fit to the data (23, 26). The relevant directional variables in these other studies may be uniquely coded by neuronal populations according to principles outlined in our experiments. In fact, this was found to be the case in the coding of the direction of a visual stimulus by neuronal populations of the posterior parietal cortex of the monkey (28). Single cells were broadband tuned to the direction of the stimulus in the visual field but the population vector predicted accurately the direction of the stimulus. This result suggests that the population coding of motion direction proposed in our study may be of general significance to the problem of how directional information might be uniquely coded by neuronal ensembles (29).

REFERENCES AND NOTES


6. We adopt the notation that a vector (capitalized and in boldface) is a 3 by 1 matrix that contains the three components of the vector.

7. We use this convention throughout all of the text.

8. Angle $\theta$ is calculated from the dot product relationship: $\mathbf{C \cdot M}$ = $\mathbf{C} \cdot \mathbf{M}$ = $\cos \theta$, $\mathbf{c}_m = \frac{c_m}{\sqrt{c_m^2 + m^2}}$, $\mathbf{c} = \frac{c}{\sqrt{c^2 + m^2}}$, where $\mathbf{C}$ and $\mathbf{M}$ are the vectors of length $l$.

9. Equation 2 can potentially have $k > 1$ field negative values for the discharge rate $r$, and it can only take one positive value. This happened only rarely in our sample; in those cases, $k$ was set to zero.

10. This follows from the null hypothesis of a vector being a random vector.

11. In this case $M = 0.230, 0.180, 0.582, P(M) = 0.318, 0.822, 0.473$ between the values of $M$ and $P(M)$.


13. The average angle between the movement and population vectors for the eight directions tested was 18.8 degrees with a range from 7.2 to 21.9 degrees. The same analysis was performed on a different sample obtained from the second animal of 17 cells studied (12) from the model of Eq. 1. The average angle was 21.0 degrees for the population vectors calculated from these 12 cells and the direction of the movement was 18.4 degrees. The increase in that angle is probably due to the small sample size.

14. When population vectors were computed from 12 cells selected at random from the population of 224 cells obtained from the first animal, the average space angle between the direction of the vector and the direction of the movement was 20.7 degrees. This value is close to the angle of 20.4 degrees obtained from the second animal for the same sample size.

15. We constructed confidence cones for the direction of the population vector at the 95% probability level in order to account for trial-to-trial variability in cell discharge and applying statistical bootstrapping techniques [P. Diaconis and B. Efron, Am. Stat. 48, 110 (May 1988)]).


17. Forty-one (14.6%) neurons in our sample did not show significant changes in activity with the direction of the movement. The changes in these cells could reflect a general nonspecific action of the motor cortex, or they could relate to the control of other, multidirectional aspects of movement such as arm posture and hand position. Lack of data to support these or other possible functions for this subset of neurons. A smaller number of cells (n = 7.6%) showed directional changes but did not fit the unimodal model of Eq. 2. These cells could relate to the direction of movement in a more complex way.


19. The same principles hold for area 5 of the posterior parietal cortex (Fig. 2A) of the monkey (Fig. 5A). A. P. Georgopoulos, Exp. Brain Res. 51, 247 (1983).


21. This finding has now been confirmed in 3-D space (21).


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