Journal of Computational Neuroscience 6, 279–288 (1999)
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Neural Coding of Finger and Wrist Movements

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Received July 10, 1997; Revised October 15, 1998; Accepted November 10, 1998

Action Editor: Steve Redman

Abstract. Previous work (Schieber and Hibbard, 1993) has shown that single motor cortical neurons do not discharge specifically for a particular flexion-extension finger movement but instead are active with movements of different fingers. In addition, neuronal populations active with movements of different fingers overlap extensively in their spatial locations in the motor cortex. These data suggested that control of any finger movement utilizes a distributed population of neurons. In this study we applied the neuronal population vector analysis (Georgopoulos et al., 1983) to these same data to determine (1) whether single cells are tuned in an abstract, three-dimensional (3D) instructed finger and wrist movement space with hand-like geometry and (2) whether the neuronal population encodes specific finger movements. We found that the activity of 132/176 (75%) motor cortical neurons related to finger movements was indeed tuned in this space. Moreover, the population vector computed in this space predicted well the instructed finger movement. Thus, although single neurons may be related to several disparate finger movements, and neurons related to different finger movements are intermingled throughout the hand area of the motor cortex, the neuronal population activity does specify particular finger movements.

Keywords: finger movements, tuning, population vector

Introduction

Although somatotopic organization of the primary motor cortex has long been thought to provide a detailed map for controlling movement of different body parts, recent studies of motor cortical activity during individuated finger movements have shown that activity occurs throughout the motor cortex hand region irrespective of which finger the subject moves (Schieber and Hibbard, 1993; Sanes et al., 1995). Moreover, single motor cortical neurons do not discharge specifically for movements of a particular finger but instead are active with movements of several different fingers (Schieber and Hibbard, 1993). These observations suggest that control of each individuated finger or wrist movement is achieved not by activation of a specific territory of motor cortex but rather by the net activity of overlapping neuronal populations distributed throughout the hand region of the motor cortex. That these neuronal populations actually contain information specifying the finger movement to be performed, however, has not yet been demonstrated directly.

This problem is similar to the neural coding of the direction of reaching movements, for which it was shown (Georgopoulos et al., 1982; Schwartz et al., 1988) that single motor cortical cells are active with movements in different directions and are distributed throughout an area in the motor cortex (Georgopoulos et al., 1984). Single cells were found to be tuned with respect to the direction of the reaching movement and, therefore, could be assigned a “preferred direction” (Georgopoulos et al., 1982; Schwartz et al., 1988) for which cell activity is highest; preferred directions differ among cells and range throughout the directional continuum. It was also found that this directional tuning is broad and that cell activity can be expressed as a function of the direction cosines of the movement or, equivalently, as a function of the cosine of the angle between the preferred direction of the cell and the direction of a particular movement (Georgopoulos et al., 1982; Schwartz et al., 1988). The hypothesis was then proposed that the direction of a particular movement can be coded uniquely by a population of directionally tuned neurons and that this information could be extracted by taking the vector sum of the preferred directions weighted by a scalar that is a function of cell activity for that movement; this vector sum was called the “neuronal population vector” (Georgopoulos et al., 1983, 1984, 1986, 1988). Indeed, the direction of the population vector was found to predict accurately the direction of movement from the discharge of neurons in the motor cortex (Georgopoulos et al., 1983, 1986, 1988; Caminiti et al., 1991; Schwartz et al., 1994), the premotor cortex (Caminiti et al., 1991), area 5 of the parietal cortex (Kalaska et al., 1983), and the cerebellum (Fortier et al., 1989).

Although the case in which the population vector analysis was applied originally involved actual movements in space (Georgopoulos et al., 1983), this analysis can be generalized to other cases (Steinmetz et al., 1987) that can involve more abstract spaces (Young and Yamane, 1992; Ruiz et al., 1995). In one case (Young and Yamane, 1992), the “directional space” was an abstract one, the dimensions of which were generated by a multidimensional scaling of similarities among the faces employed as stimuli to elicit cell responses. Here we apply a population vector analysis to the problem of coding individuated finger and wrist movements to determine (1) whether single motor cortical neurons are tuned in an abstract instructed finger movement space and (2) whether the movement performed is specified by the neuronal population activity.

Methods

Neural Database

The present study analyses a population of 176 motor cortex neurons, the activity of which was shown previously to be widely distributed in overlapping territories during any of 12 instructed movements of the fingers and wrist (Schieber and Hibbard, 1993). Of these 176 neurons, 115 were recorded from one monkey (K), and 61 from another monkey (S).

The movements performed by these monkeys have been described in detail previously (Schieber, 1991). Briefly, each monkey sat in a primate chair and inserted its right hand into a pistol-grip manipulandum that separated each finger into a different slot. At the end of each slot, the fingertip came to lie between two microswitches, one of which the monkey closed by flexing the digit, the other by extending the digit. This manipulandum was mounted on a shaft coaxial with the wrist, such that the monkey could also flex and extend his wrist. A display of light-emitting diodes instructed the monkey to close one switch (or move the wrist) without closing any others for a water reward. Flexion and extension movements of each digit and of the wrist were performed in a pseudo-random rotation.

Although task performance depended only on switch closure, each digit’s flexion or extension motion was transduced continuously by strain gauges mounted on the microswitch lever arms. The flexion and extension strain gauges for each digit were configured as two arms of a bridge circuit, providing a single analog output representing the flexion or extension motion of the digit. Rotation of the wrist axis was transduced with a precision potentiometer. Analysis of the simultaneous motion of all five digits and the wrist showed that in each correctly performed (rewarded) movement the instructed digit moved more than any other digit. During some movements—thumb flexion, wrist flexion, and wrist extension—only the instructed digit (or wrist) moved. During other movements, however, noninstructed digits moved to some lesser degree along with the instructed digit (Schieber, 1991). In this respect the finger movements performed by these monkeys resembled those performed by normal human subjects when typing (Soechting and Flanders, 1997) or even when asked to move one finger at a time (Hayes and Schieber, 1996). Nevertheless, we refer to each finger movement as an instructed movement of a given digit in a particular direction. For brevity, we refer to each instructed movement by the number of the instructed digit (1 = thumb through 5 = little finger, and W = wrist) and the first letter of the direction (f = flexion, e = extension). Instructed extension of the index finger, for example, is denoted as "2e."

Trial-by-trial analysis of change in discharge frequency during the reaction or movement period, versus a control hold period, demonstrated that each of these 176 neurons was significantly and consistently related to the monkey's performance of at least one, and often several, of the 12 instructed movements (Schieber and Hibbard, 1993). Because most motor cortex neurons reached their peak discharge frequencies in the 100 ms immediately preceding the end of movement (switch closure), the present analyses were based on the discharge frequency of each neuron recorded during this interval in each correctly performed trial. Data from four to 19 such trials were available for each instructed movement for each neuron.

Instructed Hand Movement Space (IHMS)

We defined an abstract instructed movement space that recapitulated the geometric configuration of the hand (Fig. 1). In this 3D space, instructed movements of digits 1 (thumb) to 5 (little finger) are represented as points separated by 45° on a unit-length radius semicircle, centered on another point representing wrist movement. Flexion and extension movements are represented in two planes at equal, unit-length distances from a middle, neutral position plane; the Cartesian coordinates $[X, Y, Z]$ of each one of these points are given in Table 1. In this space, the direction $\boldsymbol{F}$ of a particular finger movement from the origin O in Fig. 1 is given by the set of direction cosines $[f_x, f_y, f_z]$, where $f_x = X/(X^2 + Y^2 + Z^2)^{1/2}$,

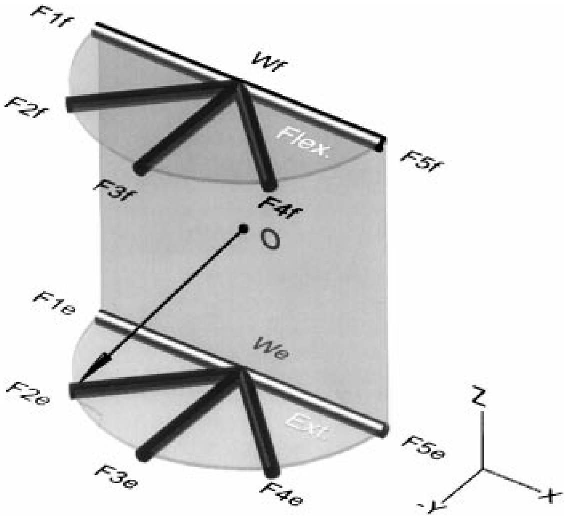

Figure 1. Representation of instructed flexion and extension movements of five fingers and wrist ($N = 12$ movements) in a three-dimensional space that recapitulates the geometry of the hand. Each instructed movement is denoted by the number of the instructed digit (1 = thumb through 5 = little finger, W = wrist) and the first letter of the instructed movement direction (f = flexion, e = extension). The arrow exemplifies a vector from the origin of the axes to one finger movement (F2e).

Table 1. Cartesian coordinates of points in the unit length space depicted in Fig. 1.

	X	Y	Z
F1f	-1	0	1
F2f	$-\sqrt{2}$	$-\sqrt{2}$	1
F3f	0	-1	1
F4f	$\sqrt{2}$	$-\sqrt{2}$	1
F5f	1	0	1
Wf	0	0	1
F1e	-1	0	-1
F2e	$-\sqrt{2}$	$-\sqrt{2}$	-1
F3e	0	-1	-1
F4e	$\sqrt{2}$	$-\sqrt{2}$	-1
F5e	1	0	-1
We	0	0	-1

Table 2. Direction cosines corresponding to the Cartesian coordinates shown in Table 1.

	f_x	f_y	f_z
F1f	$-\sqrt{2}$	0	$\sqrt{2}$
F2f	-0.5	-0.5	$\sqrt{2}$
F3f	0	$-\sqrt{2}$	$\sqrt{2}$
F4f	0.5	-0.5	$\sqrt{2}$
F5f	$\sqrt{2}$	0	$\sqrt{2}$
Wf	0	0	1
F1e	$-\sqrt{2}$	0	$-\sqrt{2}$
F2e	-0.5	-0.5	$-\sqrt{2}$
F3e	0	$-\sqrt{2}$	$-\sqrt{2}$
F4e	0.5	-0.5	$-\sqrt{2}$
F5e	$\sqrt{2}$	0	$-\sqrt{2}$
We	0	0	-1

$f_y = Y/(X^2 + Y^2 + Z^2)^{1/2}$, and $f_z = Z/(X^2 + Y^2 + Z^2)^{1/2}$. These direction cosines for each finger movement are given in Table 2.

Tuning of Neurons in IHMS

We first tested the hypothesis that single neurons were broadly tuned in the 3D IHMS described above. For this purpose, we performed a multiple linear regression of the neuron's discharge frequency d during the 100 ms prior to the end of movement against the 12 instructed movement unit vectors [$\boldsymbol{F}$ with components f_x, f_y, f_z] (Schwartz et al., 1988). This analysis provided least squares, best-fit regression coefficients, b_0, b_x, b_y, b_z, for the equation

$$d(\boldsymbol{F}) = b_0 + b_x f_x + b_y f_y + b_z f_z + e. \qquad (1)$$

The statistical significance of this model was assessed by evaluating the F-statistic. We used a probability level of $P < 0.01$ to reject the null hypothesis that the association in Eq. (1) was due to chance. We adopted this more conservative (than the traditional $P < 0.05$) probability level to test the presence of tuning with a higher degree of certainty.

For a statistically significant regression model, we calculated the neuron's "preferred direction" $\boldsymbol{C}$ as the unit vector, $[c_x, c_y, c_z]$, where

$$c_x = b_x/k \qquad (2)$$

$$c_y = b_y/k \qquad (3)$$

$$c_z = b_z/k, \qquad (4)$$

where

$$k = \left(b_x^2 + b_y^2 + b_z^2\right)^{1/2}. \qquad (5)$$

Equation (1) is equivalent to the tuning equation

$$d(\boldsymbol{F}) = b_0 + k \cos(\theta_{CF}), \qquad (6)$$

where b_0 and k are defined above, and θ_{CF} is the angle in instructed-movement space between the cell's preferred direction $\boldsymbol{C}$ and the direction of the instructed-movement vector $\boldsymbol{F}$. This angle was calculated from the dot product relationship between $\boldsymbol{C}$ and $\boldsymbol{F}$ using the following equations:

$$\cos(\theta_{CF}) = c_x f_x + c_y f_y + c_z f_z \qquad (7)$$

and

$$\theta_{CF} = \cos^{-1}(c_x f_x + c_y f_y + c_z f_z). \qquad (8)$$

Since there are 12 movement vectors (Fig. 1), 12 θ_{CF} were computed for each cell.

Population Vector Coding of Instructed Finger and Wrist Movements

The population vector was calculated as

$$\boldsymbol{P}_j = \sum_{i=1}^{N} w_{ij} \boldsymbol{C}_i, \qquad (9)$$

where $\boldsymbol{P}_j$ is the population vector for the jth finger or wrist movement, $\boldsymbol{C}_i$ is the preferred direction of the ith cell, and w_{ij} is a weighting function:

$$w_{ij} = d_{ij} - \bar{d}_i, \qquad (10)$$

where

$$\bar{d}_i = \frac{1}{M} \sum_{j=1}^{M} d_{ij} \qquad (11)$$

and $M = 12$ instructed finger movements.

Optimal Linear Estimator

The calculation of the population vector above was based on the algorithm used previously (Georgopoulos et al., 1983). However, a method has been developed recently (Salinas and Abbott, 1994)—namely, the optimal linear estimator (OLE)—that provides a more efficient algorithm for the calculation of the population vector. Specifically, one of the assumptions of the vector method described above is that the population of preferred directions is uniformly distributed (Georgopoulos et al., 1988). However, when the number of cells sampled is small, it is likely that the distribution is not uniform even if the total population has a uniform distribution. The OLE method corrects for bias and nonorthogonality of the preferred directions (Salinas and Abbott, 1994). The direction of the population vector obtained with the OLE method is equivalent to the one obtained with the vector method only if the population of preferred directions is uniformly distributed and the tuning curves are symmetric. We have implemented the method described by Salinas and Abbott (1994) to calculate the population vector $\boldsymbol{P}'_j$ for each condition j:

$$\boldsymbol{P}'_j = \sum_{i=1}^{N} w_{ij}\, \boldsymbol{D}_i. \tag{12}$$

The weighting function w_{ij} represents the response of cell i in condition j and was calculated as shown in Eq. (10) above.

The OLE method determines a set of vectors $\boldsymbol{D}_i$ that minimizes on average the squared distance between the estimated-population vectors $\boldsymbol{P}'_j$ and the instructed-movement vectors $\boldsymbol{F}_j$. Therefore, the vectors $\boldsymbol{D}_i$ are not generally in the same direction than the preferred directions $\boldsymbol{C}_i$. The vectors $\boldsymbol{D}_i$ are defined by

$$\boldsymbol{D}_i = \sum_{k=1}^{N} Q_{ik}^{-1} \boldsymbol{L}_k, \tag{13}$$

where Q_{ik} is the correlation of the firing responses of neurons i and k defined by

$$Q_{ik} = \delta_{ik} s_i^2 + \frac{1}{M} \sum_{j=1}^{M} w_{ij} w_{kj}, \quad \delta_{ik} = \begin{cases} 1 & \text{if } i = k \\ 0 & \text{if } i \neq k. \end{cases} \tag{14}$$

The variance of neuronal response s_i^2 is added to the diagonal of the matrix Q to ensure that it can be inverted; $\boldsymbol{L}_k$ represents the "center of mass" of the response curve of neuron k:

$$\boldsymbol{L}_k = \frac{1}{M} \sum_{j=1}^{M} \boldsymbol{F}_j w_{kj}. \tag{15}$$

We applied this method (1) to find out how well the population vector could predict finger movements under optimal linear estimation and (2) to determine the dependence of this prediction on the sample size—that is, the number of cells involved.

Bootstrappings

We used bootstrapping techniques (Efron and Tibshirani, 1993) to test several null hypotheses (see Results) and determine the level at which they could be rejected.

Results

Tuning of Single-Cell Activity in IHMS

The activity of a large percentage of cells (132/176; 75%) was significantly tuned ($P < 0.01$, F-test; Eq. (1)) within the IHMS shown in Fig. 1. An example is illustrated in Fig. 2. In this figure, the ordinate represents the activity (±SD) of a single cell and the abscissa is the cosine of the angle θ_{CF} formed between the preferred direction of the cell and the direction of movement, calculated as shown in Eq. (7). There are 12 points plotted, one for each of the 12 movement directions. Although the maximum range of $\cos(\theta_{CF})$ is from -1 to $+1$, both the range and the actual location of these 12 points in the abscissa may vary from cell to cell given their different preferred directions and, therefore, different θ_{CF}. Finally, the line fitted in Fig. 2 is the least square estimate of Eq. (6).

Significant tuning in the IHMS suggests that the discharge of many motor cortex cells carried broadly tuned information related to the spatial geometry of the hand. Such tuning often was not apparent on inspection of raster and histogram displays, however, indicating that much of the discharge variability was not systematically related to the IHMS.

Statistical Significance of IHMS

The IHMS shown in Fig. 1 was constructed to conform to certain constraints of hand geometry, with the addition of two parallel planes representing flexion and extension movements. Within IHMS, the 12 directions are specific in that they represent directions from a neutral (with respect to flexion and extension) position, which indicates absence of movement. We used the bootstrap (Efron and Tibshirani, 1993) to test various null hypotheses concerning this particular IHMS representation for the tuning of neural activity. First, we determined the probability that the observed proportion of 132/176 (75%) tuned cells could be obtained by chance. For that purpose, we assigned the 12 instructed

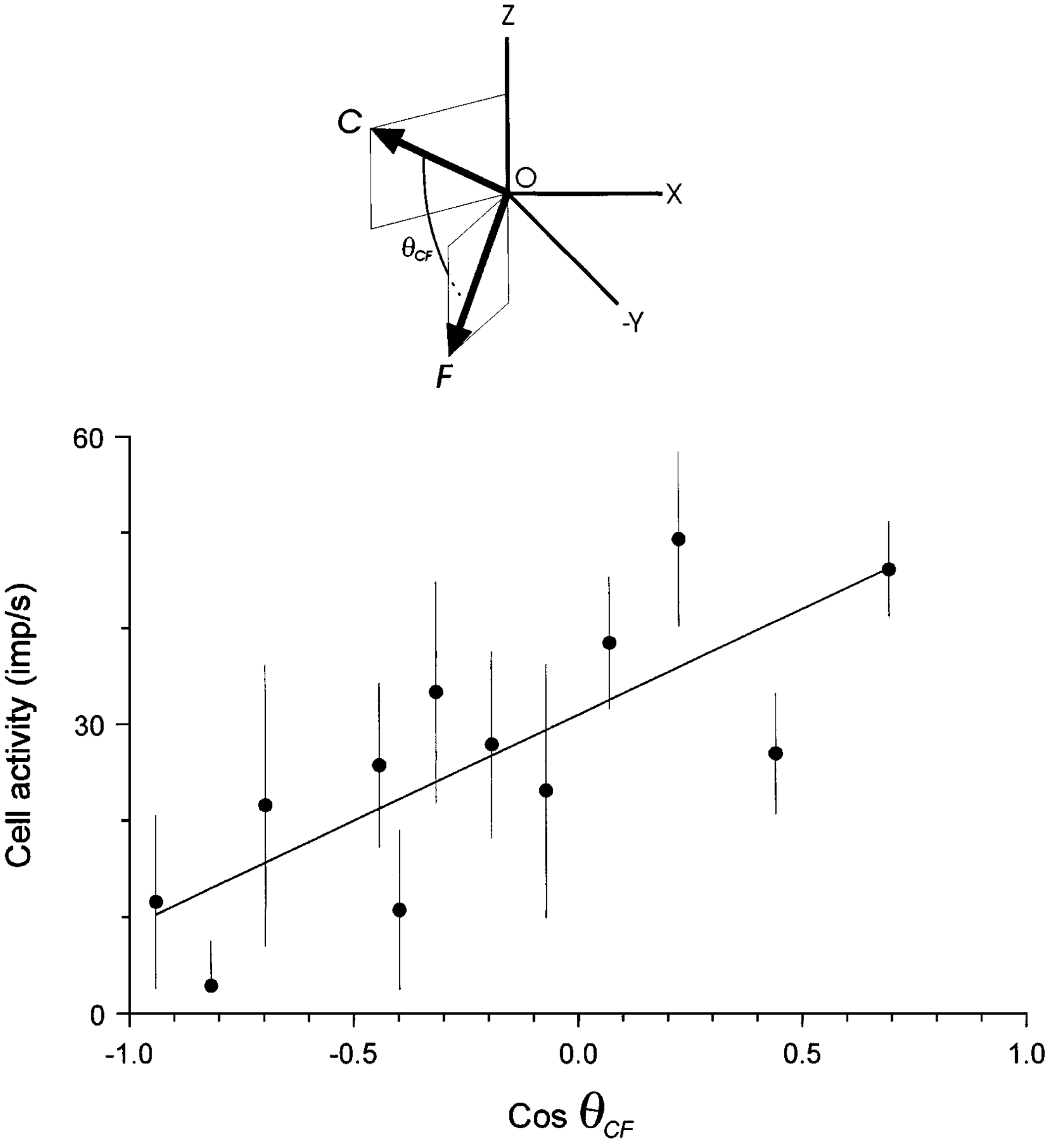

Figure 2. The frequency of discharge of a single cell (mean ± SD) during each of the 12 instructed finger and wrist movements ($N = 160$ total trials) is plotted against the cosine of the angle θ_{CF} between the preferred direction ***C*** of the cell and each of the 12 instructed finger movement vectors ***F*** in the space depicted in Fig. 1. The insert illustrates the angle θ_{CF} for a particular case.

movements to 12 randomly chosen vectors, and then we used the same 12 vectors for all 176 neurons to regress their activity against the cosines of the 12 directions. In 10,000 bootstraps, the number of cases in which 75% or more of the 176 neurons showed a regression significant at $P < 0.01$ was 437. We therefore can reject the null hypothesis that the population of neurons is tuned to 12 randomly chosen 3D vectors at the (437/10,000)—that is, $P < 0.05$ level. Nevertheless, we further examined these 437 randomly chosen instructed movement spaces that did provide significant regressions for 132 or more cells to determine whether any of these alternative "good-fit" direction sets might be closely related to the original IHMS. We reasoned that possibly some of these sets might have been similar to the IHMS of Fig. 1—that is, the randomly chosen direction sets might also have been hand-like. To examine this possibility, for each of the 437 spaces we computed the angle δ between each movement direction in a random set and the corresponding instructed movement direction in the original IHMS and then averaged all 12 angles for each randomly chosen direction set to compute the mean δ. If the randomly assigned directions were close to those in IHMS of Fig. 1, then the mean δ should be close to 0°. We found that the mean ± SEM δ was $90.1 \pm 0.586^\circ$ ($N = 437$), which is very close to the 90° angle expected from the distribution of angles formed by two random directions in the unit sphere. Moreover, in none of the 437 randomly chosen direction sets the mean δ was less than 50°. These results mean that none of these 437 configurations was close to the IHMS.

Another possibility is that the 437 good-fit configurations above were rotations of the IHMS. To test this hypothesis, we calculated the spherical correlation coefficient ρ (Fisher and Lee, 1986) between the hand-like space and each of the 437 good-fit spaces. The average unsigned ρ was 0.061. However, 40/437 (9.1%) correlations were statistically significant ($P < 0.05$); the maximum ρ was 0.4373. Therefore, some of these 437 good-fit configurations resembled rotated IHMS configurations, but overall they differed from it substantially.

Finally, we determined the probability that the original IHMS could be obtained randomly. For that purpose, we generated 100,000 random 3D direction sets (each consisting of 12 direction cosines) and calculated the average angle between the corresponding 12 directions of a random set and the IHMS. We found only 15 cases that had an average δ of 50° or less, and none had an average δ of 20° or less; therefore, the probability of finding random set configurations close (that is, up to 20° on the average) to IHMS is $P < 10^{-5}$.

Population Vector Analysis

The direction of the population vector (Eq. (9)) agreed well with the direction of the appropriate finger or wrist movement in the IHMS: the average angle between the direction of the population vector and the direction of finger movement was $30.6 \pm 6.4^\circ$ (mean ± SEM, $N = 12$ finger movements). By repeated calculation of the population vector using randomly chosen preferred directions for each cell ($N = 100{,}000$ bootstraps), we rejected the null hypothesis that this degree of agreement could occur by chance alone at the $P < 10^{-5}$ significance level.

These population vector computations used the preferred direction calculated for each cell in the IHMS. Because the instructed finger and wrist movements here were classified into 12 discrete categories, we also performed a second analysis in which we collapsed the preferred direction of each cell to the closest instructed movement vector—that is, to the one with which the angle of the cell's actual preferred direction was smallest. We then recalculated the population vector as above (Eq. (9)). The direction of the population vector thus calculated was also close to the direction of the instructed finger or wrist movement in the IHMS; the average angle between the direction of the population vector and the direction of instructed movement was $27.1 \pm 5.1^\circ$ (mean ± SEM, $N = 12$ finger movements). This angle did not differ significantly from that yielded by the population vector calculated using preferred directions in a continuous IHMS space (paired t-test, $P = 0.44$).

OLE Population Vector Analysis

Let $\boldsymbol{P}'$ be the population vector calculated using the OLE method. To evaluate the efficacy of the neuronal population vector to code for instructed finger and wrist movements, we calculated $\boldsymbol{P}'$ using different number of cells for each one of the 12 finger and wrist movements—namely, with various sample sizes K up to the total sample size of $K = 132$ cells (Fig. 3). For each $K < 132$, the cells were selected randomly with replacement from the set of the 132 tuned cells, conforming to the theory of bootstrapping. The procedure was repeated 100 times for each combination of K sample size and 12 finger movements in order to obtain a representative outcome. Figure 3 plots the average angle φ between the instructed finger movement vector $\boldsymbol{F}$ and the corresponding population vectors $\boldsymbol{P}$ and $\boldsymbol{P}'$ calculated using the original vector method (open circles) and the OLE method (filled circles). It can be seen that φ tends to an asymptote above $K = 25$. The value for $K = 132$ was calculated from the actually observed set of cells. This was $\varphi = 16.6 \pm 0.7^\circ$ (mean ± SEM, $N = 12$ finger movements), as compared to $\varphi = 30.6 \pm 6.4^\circ$ obtained using the original vector method.

Discussion

Tuning of Single-Cell Activity in IHMS

A salient finding of the present study was that the activity of a large percentage (75%) of motor cortical

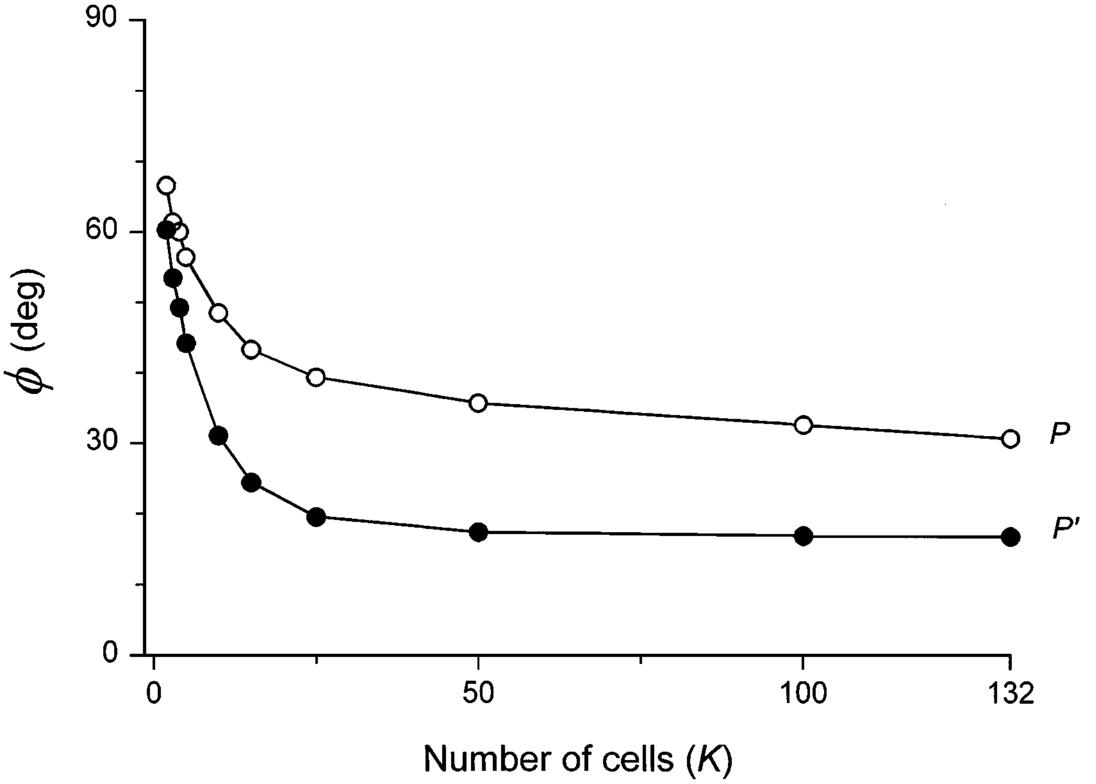

Figure 3. The average angle φ in deg ($N = 100$ bootstraps) between the instructed finger movement vector $\boldsymbol{F}$ and the corresponding population vectors $\boldsymbol{P}$ and $\boldsymbol{P}'$ calculated using the original vector method and the OLE method, respectively, is plotted against the number of cells (sample size $K = 2, 3, 4, 5, 10, 15, 25, 50, 100, 132$). The values for $K = 132$ were calculated from the actually observed set of cells and, therefore, are unique values.

neurons was tuned within the IHMS shown in Fig. 1. The null hypothesis that this percentage of tuned cells could be obtained by chance was rejected ($P < 0.05$). These findings mean that this IHMS is a meaningful configuration within which variation in cell activity can be expressed in an orderly fashion and that apparently captures an important feature of cell activity—namely, that single cells are active with several finger and wrist movements (Schieber and Hibbard, 1993). Indeed, the present analysis quantifies this previous qualitative observation.

The essential aspects of this IHMS rest on two assumptions—namely, the geometrical configuration of the hand and the opposite flexion or extension movements. Concerning the former, the IHMS preserves the basic geometric relationships in the hand, in that (1) instructed movements of adjacent fingers are equidistant from each other, (2) instructed movements of digits 1 and 5 are opposite one another, and (3) instructed movements of the wrist are equidistant from those of all fingers. With regard to the movements, flexion and extension instructed movements are represented as parallel planes. However, this configuration should not be construed as an absolute representation of the physical movements because most of the instructed movements represented in this abstract space included some lesser movements of noninstructed digits that commonly occur concomitantly with movement of the instructed digit (Schieber, 1991). Thus, the IHMS should be regarded as a truly *instructed movement* space and possibly one of several configurations of orderly arrangements of finger and wrist movements. Given this qualification, we can conclude that the discharge of motor cortex neurons related to individuated finger movements does contain information representing the spatial geometry of the hand embedded within the flexion and extension movement domain. Finally, spaces in qualitatively different domains (such as joints or muscles) could also be important for cell activity. In fact, the 25% of cells not tuned in IHMS could relate to such other variables. This problem remains to be investigated.

Population Vector Analysis

The population vector analysis was used in this study to extract information encoded in a population of motor cortical neurons recorded during performance of individuated finger and wrist movements. The results obtained showed that the direction of the population vector was a good predictor of the direction of the finger or wrist movements used in the IHMS. These findings demonstrate that although single neurons may discharge during several different instructed movements and although the neurons discharging during any instructed finger or wrist movement are distributed throughout the motor cortex hand region, the activity of these neurons does contain information adequate to specify the movement performed. By design of the IHMS, this information is a composite of the geometry of the hand and the kind of movement (flexion or extension) involved. In fact, this composite IHMS proved adequate both for describing the variation in cell activity and for extracting unique motor information from the ensemble. This information contained in the population could not have been identified by directly examining the discharge patterns of single neurons, which show extensive variations that confound attempts to classify neurons into similar groups. The population vector therefore may provide a tool for decoding and monitoring ensemble activity controlling the fingers over time, across different tasks, and through different cortical areas. Finally, it should be noted that the neural data we modeled come from single movements and therefore that the predictions above properly apply to single movements.

OLE Method

The OLE method for calculating the population vector yielded a more accurate estimate of the finger movement at all sample sizes tested (Fig. 3). This is in accord with previous results in arm movements (Salinas and Abbott, 1994). It should be pointed out that the OLE method requires a continuous distribution of preferred directions and, therefore, cannot be used when the preferred direction space is a discrete one. For example, the latter was the case when the preferred directions calculated were collapsed to the closest instructed movement vector—that is, to the one with which the angle of the cell's actual preferred direction was smallest (see above). In this case, only the original vector method can be used.

Acknowledgments

Supported by USPHS grants NS17413 (A.P.G.), NS27686 (M.H.S.), a VA Merit Review Grant (G.P.), the U.S. Department of Veterans Affairs, and the American Legion Brain Sciences Chair.

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