ly charged air. Several clouds growing over the negative charge source developed extensive regions containing positive charge in their lower portions. An example is shown in Fig. 2. The measurements reported for 1985 were made with ground-based equipment because the instrumented airplane and balloon systems used in 1984 were not available.

It is conceivable that the abnormal polarity of electrification exhibited by these storms may have been an unusual natural occurrence that was not related to the artificial release of negative space charge during the growing period of the thundercloud. This is unlikely, however. Observations in this region of New Mexico over the past 20 years show that this polarity of electrification very rarely, if ever, occurs naturally in isolated clouds. Of the approximately 1000 thunderstorms whose electric fields have been observed, no isolated cloud above us has exhibited abnormal polarity. That three abnormal storms would have occurred by chance during a 2-week interval seems highly improbable.

The idea that the electrified wire powered by less than 100 W could influence the development of a thundercloud that produces 100 MW may at first strain credulity. However, if the electrification of a thundercloud is brought about by a feedback process similar to that acting in a laboratory influence machine, this growth of charge in the thundercloud can reasonably be expected. In describing his laboratory experiments, Kelvin (11, p. 69) wrote, "It is curious, after commencing with no electricity except a feeble charge in one of the jars, only discoverable by a delicate electrometer, to see in the course of a few minutes a somewhat rapid succession of sparks pass in some part of the apparatus . . . ." Just as his apparatus supplied with mechanical energy was capable of multiplying the "feeble charge in the jar" until it produced sparks, so the growing cloud supplied with energy from the atmosphere should be able, by electrostatic induction, to multiply either naturally occurring positive space charge or artificially introduced negative charge until the resultant electric field becomes sufficiently intense to produce lightning. The fine weather electrical process, which may usually initiate thunderstorm electrification, involves a current of only 1 μA and a power of <1 W for each square kilometer.

That the charge released from the wire could have influenced the polarity of the much larger charges forming later in the thundercloud indicates that the electrification process can be of the "feedback" or "influence" kind. It appears that on some occasions enough of the negative charge

from the wire is carried up into the cloud to overbalance the other factors that normally determine the electrical polarity of thunderclouds.

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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 where 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 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 midsagittal plane to allow the combination of right- and left-hand data. The average duration of movement was 0.435 ± 0.205 (SD) second. Some of the movement trajectories at the wrist were monitored with a 3-D sonic-tracking 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 studied 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 nondirectional, 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 χ, ψ, and ω 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 $m_x = \cos \chi$, $m_y = \cos \psi$, and $m_z = \cos \omega$, and where

$$(m_x^2 + m_y^2 + m_z^2)^{1/2} = 1$$

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

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

where $d(M)$ is the frequency of discharge of a particular neuron during movement in direction (m_x, m_y, m_z), and b, b_x, b_y, and b_z 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 observed 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

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

where θ_{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
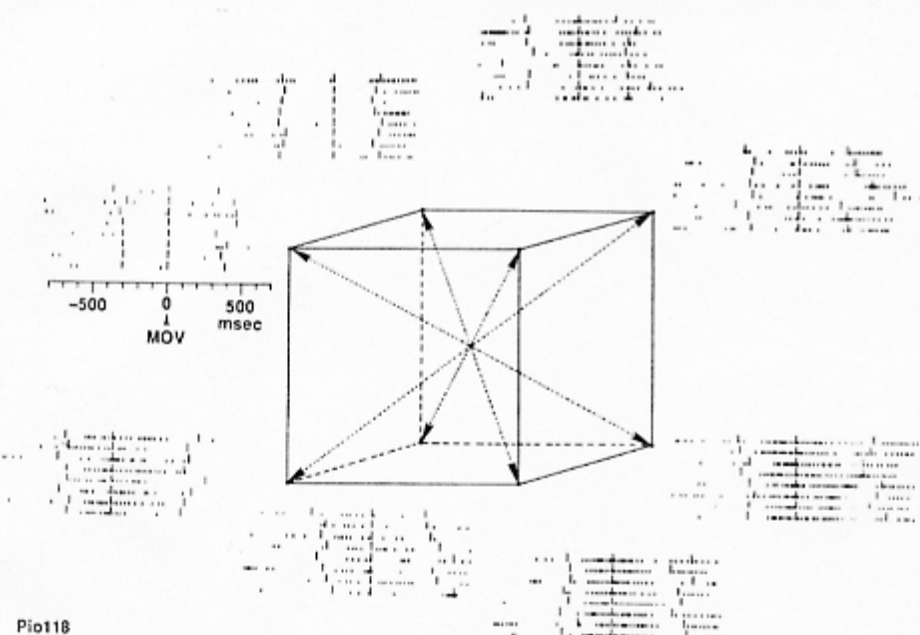
Pio118

Fig. 1. Impulse activity of a single cell with movements in eight different directions indicated in the center drawing. Each line represents activity in one trial; eight trials for each movement direction are shown. Short bars indicate the occurrence of a spike; longer bars in each trial indicate, from left to right, the onset of target, the beginning of movement (MOV, aligned at zero time), and the end of the movement. (The discharge after the end of the movement was not analyzed.) In the analysis of variance, the differences in activity among the eight movement directions were statistically significant ($P < 0.0001$, F test). Each set of eight trials corresponds to the movement direction that points to it in the center diagram. The multiple regression for Eq. 1 was statistically significant ($P < 0.009$, F test; $r^2 = 0.929$) and yielded the following equation: $d(M) = 17.37 + 6.99m_x + 8.83m_y - 13.07m_z$. The standard errors of the coefficients b, b_x, b_y, and b_z were 0.598, 1.265, 0.964, and 0.981, respectively. The parameter k was 17.25.
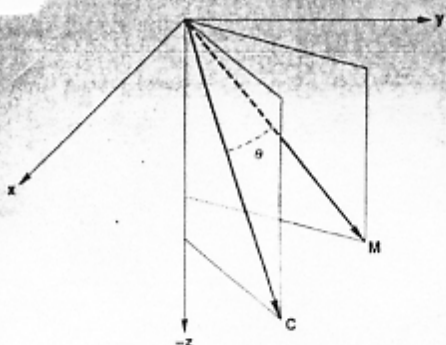
Fig. 2. Schematic diagram to show the preferred direction (C) of the cell illustrated in Fig. 1. The direction cosines of the preferred direction were $c_x = 0.41$, $c_y = 0.51$, $c_z = -0.76$. Also shown are a movement vector M with coordinates $m_x = 0.23$, $m_y = 0.78$, $m_z = -0.58$, and the angle θ 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 ith 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 ith cell for movement in direction M. From assumptions (i) and (ii), it follows that the weighted vectorial contribution of the ith cell is

$$N_i(M) = w_i(M) C_i$$

The vector $N_i(M)$ will point toward the ith 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 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

Fig. 3. Cluster of 224 single cell vectorial contributions (light purple lines) for one movement direction (yellow). The population vector is orange.
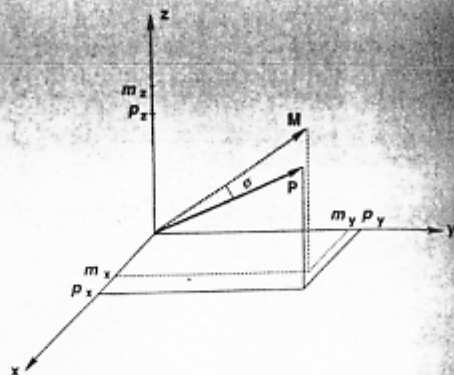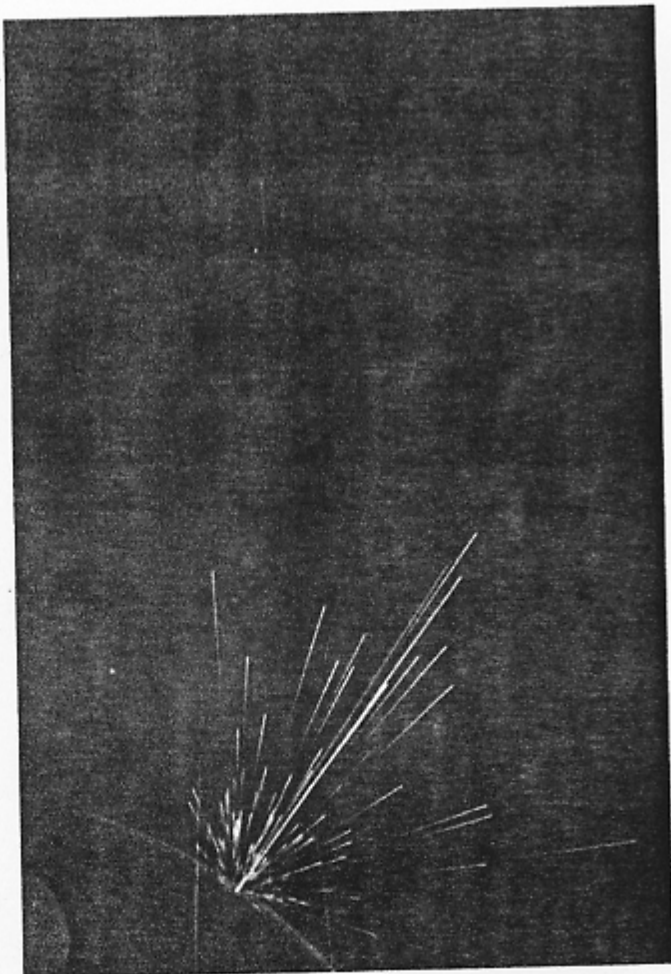

Fig. 4. Schematic diagram to show the directions of the population (P) and movement (M) vectors for the data in Fig. 3. For illustration purposes, the population vector has been normalized so that both P and M are of unit length. Therefore, the direction cosines of these vectors equal their projections onto coordinate axes x, y, and z. These projections are shown as p_x, p_y, p_z and m_x, m_y, m_z, for P and M, respectively. Also shown is the angle ϕ formed between the two vectors.

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 (14) (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
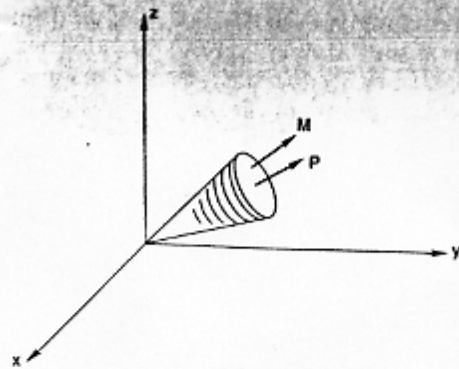
Fig. 5. Schematic diagram showing a 95% confidence cone around the population vector **P** illustrated in Fig. 3. The direction of the movement vector (**M**) falls within the cone.

(18), it will be important to know whether the representation of movement direction in these other structures is also expressed in terms of neuronal populations, or, for example, in terms of sharply tuned cells that would discharge only with movements in a specific direction (19).

The population vector can also be used as a probe to visualize and monitor the processing of directional information by neuronal populations over time. For example, we observed that, in 2-D space (20), if the population vector is calculated every 20 msec during the reaction time, that is, from the onset of a lighted target until the onset of movement toward it, the population vector can predict well the direction of the upcoming movement (21). Moreover, when an animal is trained to withhold movement for 0.5 to 3 seconds until the lighted target dims, the population vector computed for the motor cortex during the waiting period is in a direction congruent with that of the upcoming movement (22). This suggests that the population vector can serve to monitor brain events during the spatial planning of movement in space, in the absence of overt movement.

In general, our investigation of the neural mechanisms subserving the direction of arm movement in space resembles studies in other fields that deal with the neural mechanisms subserving other directional variables. Examples include the neural coding of the direction of saccadic eye movements in the pontine reticular formation (23), the coding of the direction of head tilt in vestibular neurons (24), the coding of the direction of body motion relative to the neck, or of the head motion relative to the body, in spinal interneurons (25, 26), and the coding of the direction of motion of a visual stimulus in the middle temporal visual area of the cerebral cortex (27). In all of these studies, broadly tuned cells have been identified and

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 broadly 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).

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6. We adopt the notation that a vector (capitalized and in boldface) is a 3 by 1 matrix that contains the three direction cosines. For example, $\mathbf{M} = (m_x, m_y, m_z)$.
7. Angle θ is calculated from the dot product relationship: $\mathbf{C} \cdot \mathbf{M} = |\mathbf{C}| |\mathbf{M}| \cos \theta_{CM} = c_x m_x + c_y m_y + c_z m_z$, where $|\mathbf{C}|$ and $|\mathbf{M}|$ are the lengths of vectors $\mathbf{C}$ and $\mathbf{M}$, respectively; here both $|\mathbf{C}|$ and $|\mathbf{M}|$ equal 1 because $\mathbf{C}$ and $\mathbf{M}$ are vectors of unit length.
8. Equation 2 can potentially when $b < k$ yield negative values for the discharge rate d, which in reality can take only positive values. This happened only rarely in our sample; in those cases, d was set to zero.
9. This follows from the rule of multiplication of a vector by a negative scalar.
10. In this case $\mathbf{M} = (0.230, 0.780, -0.582)$, $\mathbf{P} \cdot \mathbf{M} = (0.318, 0.822, 0.473)$, and the angle between vectors $\mathbf{M}$ and $\mathbf{P}(M) = 8.3$ degrees.
11. The direction of the population vector was a consistent and robust measure, because it varied little when recalculated from a random sample of 224 cell vectors drawn with replacement from the original population, or when the number of cells contributing to the population was randomly reduced (12).
12. A. B. Schwartz, R. E. Kettner, A. P. Georgopoulos, *Soc. Neurosci. Abstr.*, in press.
13. The average angle between the movement and population vectors for the eight directions tested was 15.8 degrees with a range from 7.2 to 21.9 degrees. The same analysis was performed on a smaller sample obtained from a second animal. Of 17 cells studied 12 (70.6%) fit the model of Eq. 1. The average angle formed between the population vectors calculated from these 12 cells and the direction of the movement was 30.4 degrees. The increase in that angle is probably due to the small sample size.

When population vectors were computed from 12 cells selected at random from the population of 224 cells obtained from the first animal, the average angle between the direction of these vectors and the direction of the movement was 29.7 degrees. This value is close to the angle of 30.4 degrees obtained from the second animal for the same sample size.
14. We constructed confidence cones for the direction of the population vector at the 95% probability level by taking into account the trial-to-trial variability in cell discharge and applying statistical bootstrapping techniques [P. Diaconis and B. Efron, *Sci. Am.* 248, 116 (May 1983)].
15. In our experiments the origin of the movement was the same in all trials. In a preliminary study we tested the hypothesis that the population vector could predict the direction of movements made from different starting points and in new directions (R. E. Kettner, A. B. Schwartz, A. P. Georgopoulos, *Soc. Neurosci. Abstr.*, in press). For that purpose we used a task that utilized the same apparatus as in this study but the animals were required to move their arm between adjacent lights located at the corners of a square in front of the animal and close to the frontoparallel plane. Thus four different starting points and eight new movement directions were used. We studied 88 directionally tuned neurons in both the new task and the task described in the present experiments. We found that the population vector calculated from the 88 neurons for each of the new eight directions tested predicted well the direction of the corresponding movement. This result indicates that the population code for movement direction we have proposed holds for movements that are initiated from several different points in front of the animal, and that are made in directions that were not previously tested in these experiments.
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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 activation of the motor cortex, or they could relate to the control of other, nondirectional aspects of movement such as amplitude or speed. We lack data to support these or other possible functions for this subset of neurons. A smaller number of cells ($n = 17$, 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.
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