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REVIEW

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Arm movements in monkeys: behavior and neurophysiology

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Abstract Reaching to objects of interest is very common in the behavioral repertoire of primates. Monkeys possess keen binocular vision and make graceful and accurate arm movements. This review focuses on behavioral and neurophysiological aspects of eye-hand coordination in behaving monkeys, including neural coding mechanisms at the single cell level and in neuronal populations. The results of these studies have converged to a common behavioral-neurophysiological ground and provided a springboard for studies of brain mechanisms underlying motor cognitive function.

Key words Monkey · Motor cortex · Neuronal populations · Directional tuning · Spinal Cord

Introduction

The behavioral goal of reaching is to bring the hand to a desired point in extrapersonal space. This is accomplished by well coordinated and tightly coupled motions about the shoulder and elbow joints (Soechting and Lacquaniti 1981). A reaching movement is a vector in space that can be fully described by its direction and amplitude, relative to the point of origin of the movement. Studies on the neural coding of these spatial aspects (i.e. direction and amplitude) of reaching movements were initiated in the early 1980's (Georgopoulos 1990). In 1982, the first systematic study of the relations of motor cortical cell activity to the direction of reaching was published (Georgopoulos et al. 1982). This study was complemented, eleven years later, by a comprehensive investigation of the relations of cell activity to the amplitude of movement (Fu et al. 1993).

With respect to the direction of reaching movements, we have investigated the following questions: How do animals learn to make movements in a desired direction? How does the brain specify the direction of a movement in space? How does a movement direction change when the target of the movement changes while the movement is planned, or while it is evolving? We investigated these question in rhesus monkeys. These animals, like other primates, possess keen vision and proficient visuomotor coordination; in fact, reaching movements towards visual objects of interest are very common within the monkey's behavioral repertoire. We chose the motor cortex as the area to study because it is intimately connected to the motor system on its output side (i.e. the brainstem and spinal motor structures), but it also receives a wealth of input from other cortical areas and from the thalamus. Finally, the behavioral devices we used were of two kinds: one allowed movements of a handle on a 2-dimensional (2D) planar working surface (Georgopoulos et al. 1981), whereas the other permitted free movements in 3D space; the former movements resembled drawing movements on a board, whereas the latter resembled natural pointing movements (Schwartz et al. 1988).

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I review below the results of studies of reaching movements by monkeys with respect to their behavioral organization and the neural mechanisms underlying their specification and control.

Visuomotor learning and transfer of skill

In our initial studies, we trained monkeys to move a handle on a planar working surface towards lighted targets (see Fig. 1 in Georgopoulos et al. 1981). Essentially, the monkey had to learn how to use an articulated manipulandum to capture lighted targets at different position on the working surface. A light was turned on first in the center and then at one of eight peripheral locations on an imaginary circle of 8 cm radius. The targets covered the whole circle, every 45°; therefore, the animal's movements were of the same origin and amplitude but of different directions. However, such "drawing" movements are not natural for monkeys. Therefore, it takes several weeks for an animal to be trained. The first step is to familiarize the animal with the apparatus so that it grasps the handle, moves it around on the plane and uses it as a tool to capture lighted targets, as they are turned on. In the beginning, the animal is rewarded with drops of apple juice for merely grasping the handle and moving it around. Fortunately, rhesus monkeys are very inquisitive animals and indeed they grasp and move the manipulandum around during almost all the training time (3–4 h a day). It is upon that continuous and apparently haphazard motion of the handle that the shaping of behavior is then applied. For example, to train the monkey to capture a visual target, the animal is rewarded through a computer program only when it moves the handle within a circular area centered around the lighted target. The size of this circular window is large at the beginning of training (e.g. 25 mm radius) and, as the training advances, progressively smaller circles are used, down to the 5 mm radius circle used in the neural recording experiments. At all times during the training period, the light appears first in the center and then in one of several peripheral locations. When the animal has learned to move the handle to the light that is on, the conditions of reward change so that there is no reward for holding at the center light, but only for moving from the center to the peripheral light and holding there for a period of time. Initially, the animal has to hold at the peripheral light for 20–40 ms, but ultimately holding periods of 0.5–2 s are used. Similarly, holding at the center before the peripheral light comes on is short, but at the final stages of training center hold times from 1.5 to 5 s are required.

Recording the movement trajectories during the training period provided an objective way to visualize and quantify the motor learning. The spatial variability of the trajectories decreased substantially with training, i.e. practice. This decrease was exponential, as is the case with other learning curves. In general, it takes 30–40 days for a monkey to become proficient in this task, although this period varies among animals.

The acquisition of this motor skill is rather specific for the hand that was trained in it. When the other hand is used, the spatial variability of the trajectories is initially high, similar to that exhibited during the beginning of the original training. This is in spite of the fact that the animal knows now the meaning of the lights as targets of the movement. However, the motor learning progresses very rapidly in this case, and low levels of trajectory variability are achieved with the new hand within a few days, compared to several weeks of training in the case of the original hand. This finding indicates that there are substantial savings in the motor learning by the new hand.

On-line visuomotor control

In the experiments described above, the movements were directed to a stationary target. How would the movement be affected if its target were to change unpredictably during the reaction or movement time? Is the process that generates the aimed movement all-or-none, or is it modifiable? This is an important question, for often in nature the object of interest towards which a monkey directs its hand changes location, and therefore, it is interesting to know whether the motor system can follow the target and change the movement in mid-flight, or whether an appreciable lag exists between switching motor patterns. We investigated these problems as follows.

Two peripheral lights in opposite locations were used (e.g. at 12 and 6 o'clock). The monkey held the handle in the center for a variable period of time after which one of the two peripheral targets was turned on; it remained on for 50, 100, 150, 200, 250, 300 or 400 ms and then was turned off, and the other target was turned on. The animal was rewarded after holding at the 2nd light for 0.5 s. Trials in which the 1st light stayed on without changing location were interspersed among those in which the target location changed, so that the animal could not predict whether the target will change location in a given trial; moreover, the animal could not predict for how long the 1st target would stay on in the trials in which it changed location. We found consistently that the arm moved initially towards the 1st target, then changed direction and moved towards the 2nd target (Fig. 1). Quantitatively, the duration of the arm movement towards the 1st target was a linear function of the time for which the 1st target stayed on. This indicated a tight temporal coupling between the visual stimulus and the arm movement controlled by it.

A different question concerns the spatial characteristics of the trajectory of the first movement. In most cases tested, the two target lights were located along the

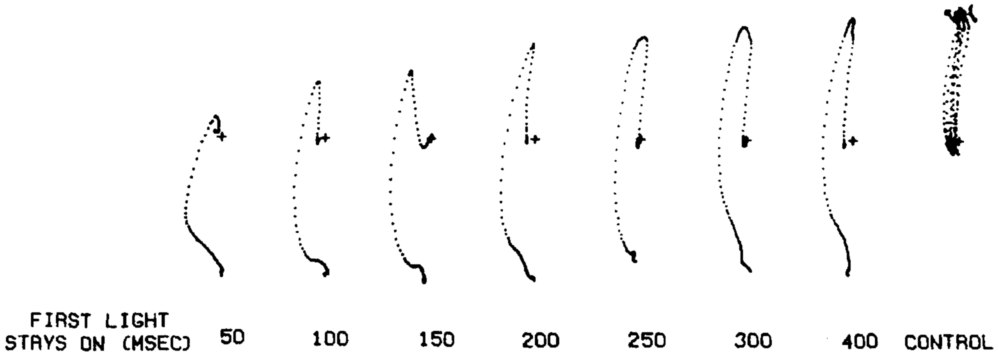

Fig. 1 Modification of hand movement trajectories in the target shift task. The first target light was at 12 o'clock; it stayed on for the time indicated and then changed location to 6 o'clock. Single trajectories are shown (X-Y data points were recorded every 10 ms). At the far right (*control*), seven trajectories to the target at 12 o'clock are superimposed. (Adapted from Georgopoulos et al. 1981)

same line, so that the first and second movements were in opposite directions. However, when the two target lights were arranged in such a way that the corresponding movements were not in opposite directions, a modification of the direction of the trajectory of the first movement was observed in some trials, in which the trajectory deviated towards the direction of the second target, the more so the shorter the interstimulus interval. These results indicate that the motor command for the direction of movement generated after the appearance of the first target can be modified by the second target, when the targets shift early in time.

Finally, it was interesting to examine the velocity characteristics of the trajectories of the movements towards the second target, after their reversal. In fact, these movements were much faster that those made towards the first target; the peak velocity of the movements towards the second target was approximately 3x that of the movement towards the first target. This was true even for the interstimulus interval of 50 ms, in which case the movement towards the first light was small, and, therefore, the amplitude of the second movement was very similar to that of the movement made directly to the second target in control trials. These results can be explained by the strategy that monkeys, and human subjects, used to solve the problems posed by this target-shift task. This strategy was revealed by an analysis of the forces exerted on the manipulandum during performance of the task (Massey et al. 1986). Briefly, subjects produced a large braking force in response to the second target that stopped the movement of the hand towards the first target and then moved it to the second target. This braking force was excessive for the short movements towards the first target but was effective for all cases and did not require individual adjustments for particular trials. Thus, a simple and mechanically effective, but energy-inefficient, strategy underlay the efficient eye-hand coordination in this task.

Neural mechanisms of visuomotor coupling

When the location of visual stimuli changed in quick succession, the patterns of cell activity in the arm area of the motor cortex follow these changes with remarkable temporal fidelity (Georgopoulos et al. 1983a) and attest to the efficient engagement of this structure during eye-hand coordination. Specifically, the pattern of cell activity was initially the one associated with movement to the 1st target; this pattern lasted for a time proportional to the time for which the first target stayed on, and then became like the pattern of activity associated with movement to the 2nd target (Fig. 2). The temporal relations between the duration of presentation of the first target, the duration of change in cell activity associated with the presentation of the first target, and the duration of the hand movement towards that target were pairwise linear (Georgopoulos et al. 1983a). These results indicate that when a sequence of hand movements is generated towards targets that change location, the motor cortical activity follows well the changes in visual information and generates the appropriate motor commands without temporal smearing. This apparently underlies, at least in part, the efficient eye-hand coordination observed at the behavioral level.

Directional tuning of single cells

The experimental variable of interest in these studies was the direction of the movement trajectory in space. How does the activity of single cells in the motor cortex vary with respect to this variable? A clear answer to this question was obtained (Georgopoulos et al. 1982); cell activity varies in an orderly fashion with the direction of the movement. Specifically, cell discharge is highest with movements in a particular direction (i.e. the cell's *preferred direction*) and decreases progressively with movements made in directions farther and farther away from the preferred one. These changes in cell activity relate to the direction, and not the endpoint of the reaching movement (Georgopoulos et al. 1985). Quantitatively, cell activity is a linear function of the cosine of the angle between the preferred direction of the cell and the direction of a particular movement (Fig. 3), as follows:

$$d_i(M_l) = b_i + a_i \cos\theta_{C_iM_l} \quad (1)$$

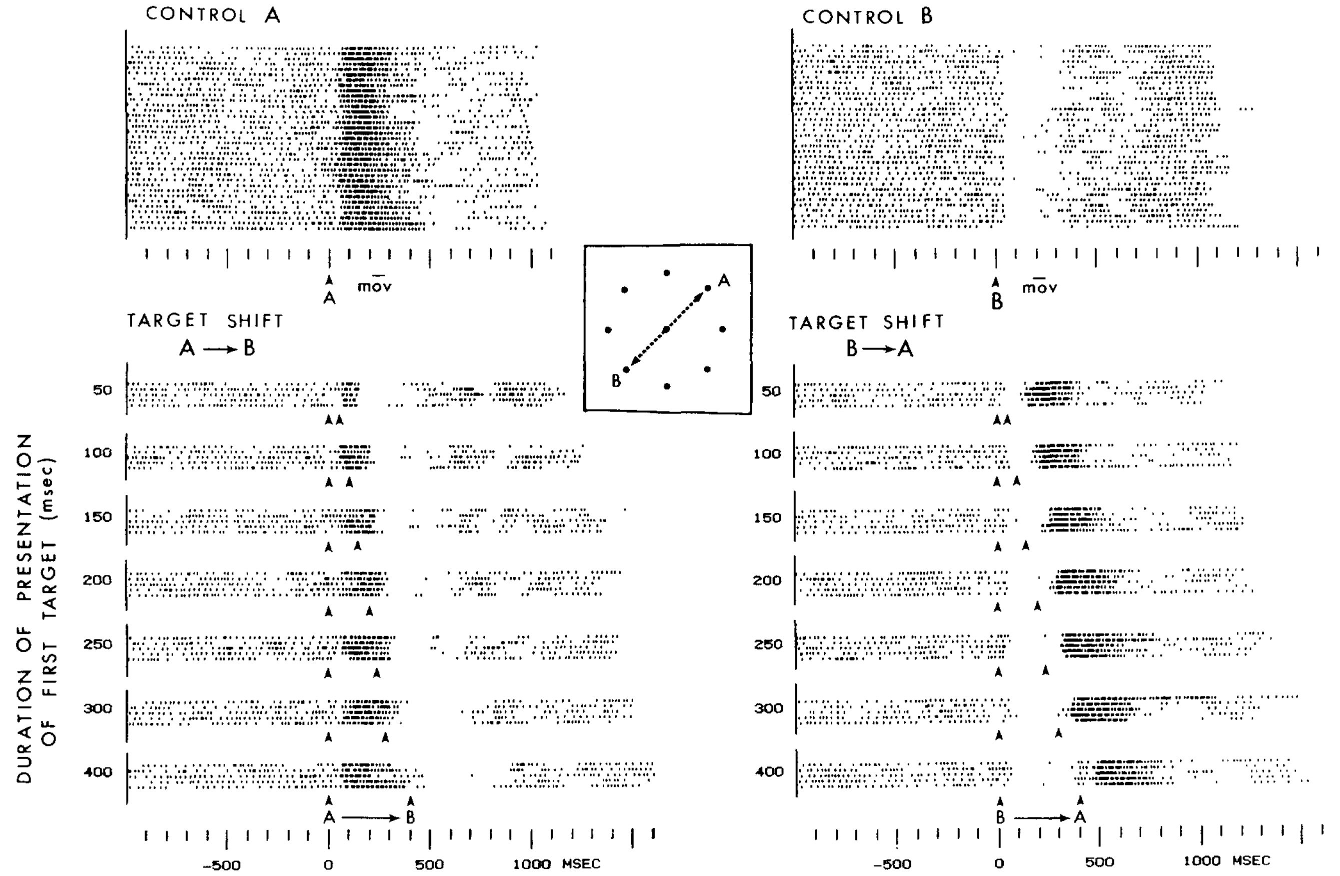

Fig. 2 Changes in discharge of a motor cortical cell in the target shift task. Beneath each control raster are seven groups of five trials each during which the target changed location after 50–400 ms, as indicated; the first target to appear in each trial was the same as that for the control trials plotted above it. The initial change of activity seen in the target shift trials was of the same sign as that during the corresponding control trials, i.e., an increase in cell activity on the left, and a decrease on the right. The initial pattern of activity did not continue as long as in control trials, however, for shortly after the target changed, it was replaced by a pattern of activity similar to that recorded during movement to the other target. Thus, the initial increase in activity during movements to target A was truncated by a complete suppression of activity similar to that seen in control trials during movements to target B, while the decrease in activity on the right side was terminated by a brisk increase in activity like that seen for movements to target *A*. This was true for all interstumulus intervals tested. The time at which the switch in the pattern of activity occurred was related to the time of the target shift (*second arrows*). The *horizontal bar labelled MOV* indicates the range of the times of movement onset. The 1st and 2nd *arrows* indicate the time of presentation of the first target and of the target shift, respectively. (From Georgopoulos et al. 1983a)

where $d_i(M_l)$ is the discharge rate of the ith cell with movement in direction M_l, b_i and a_i are regression coefficients, and θ is the angle formed between the cell's preferred direction C_i and the direction of movement M_l. Equation 1 holds both for 2D reaching movements performed on a plane (Georgopoulos et al. 1982) and for free 3D reaching movements (Schwartz et al. 1988). The preferred directions differ for different cells and are distributed in the whole 3D directional continuum (Schwartz et al. 1988). Finally, pairs of cells with similar preferred directions tend to show excitatory synaptic interactions whereas pairs of cells with opposite preferred directions tend to show inhibitory synaptic interactions (Georgopoulos et al. 1993).

It is obvious that the directional tuning is the result of orderly and delicate interplay of excitatory and inhibitory effects, as can be appreciated by inspecting published records (see, for example, Fig. 3). Given that single cortical neurons do not seem to receive more than a small percent of their inputs from any single source (Martin 1988), it is obvious that the directional tuning cannot be explained as the *exclusive* effect of any single factor. The diversity of these factors is attested by the fact that probably any motor cortical cell receives convergent inputs from many sources, including the thalamus, nearby cortical cells through intracortical connections and recurrent collaterals, neurons from a large number of other cortical sites (ipsilateral and contralateral frontal and parietal areas), monoaminergic inputs, etc. Functionally, it is attested by the rich variety of factors that influence motor cortical activity, including memory signals (Alexander and Crutcher 1990; Smyrnis et al. 1992; Ashe et al. 1993) and contextual, task-specific information (Muir and Lemon 1983).

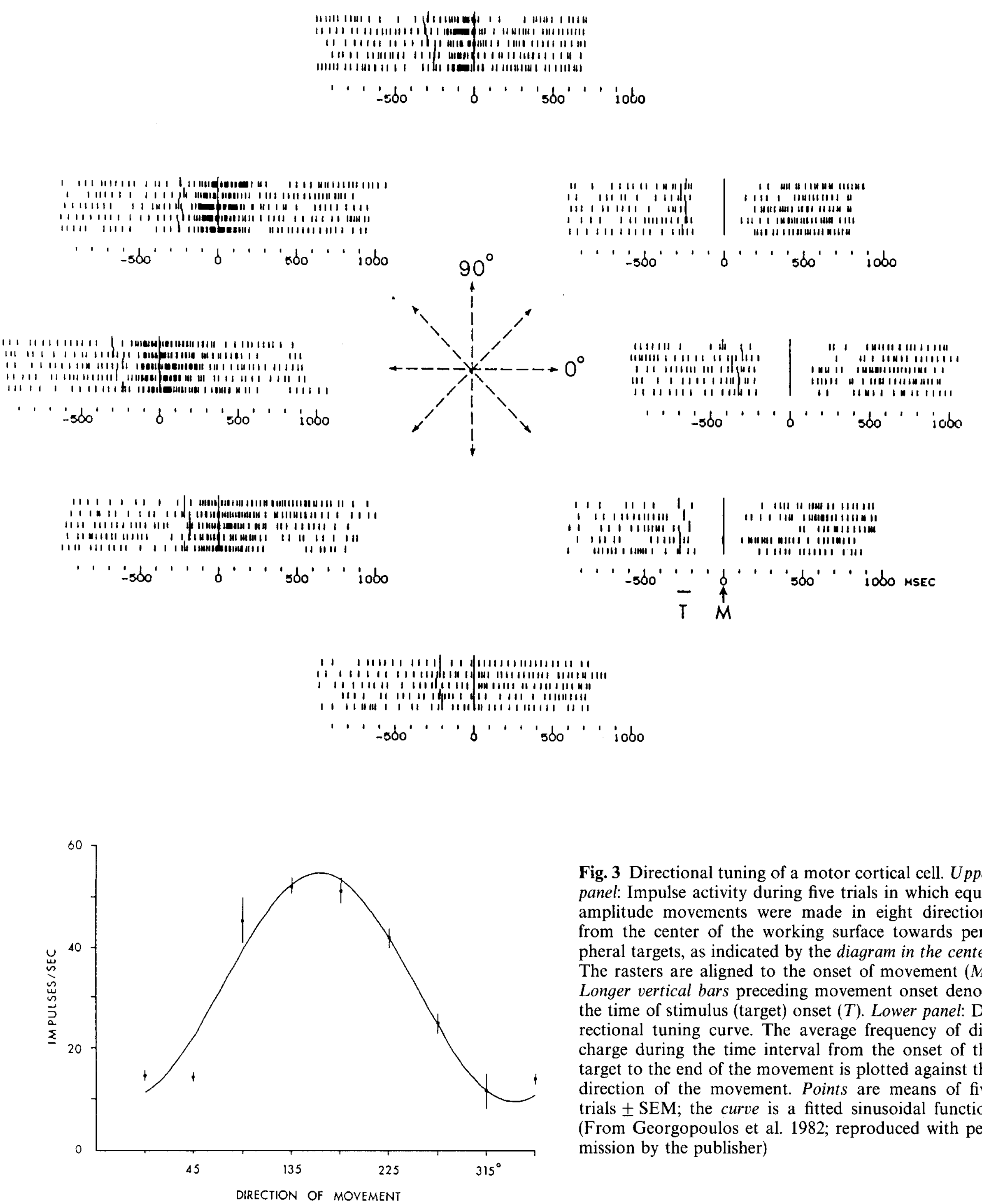

Fig. 3 Directional tuning of a motor cortical cell. *Upper panel*: Impulse activity during five trials in which equal amplitude movements were made in eight directions from the center of the working surface towards peripheral targets, as indicated by the *diagram in the center*. The rasters are aligned to the onset of movement (*M*). *Longer vertical bars* preceding movement onset denote the time of stimulus (target) onset (*T*). *Lower panel*: Directional tuning curve. The average frequency of discharge during the time interval from the onset of the target to the end of the movement is plotted against the direction of the movement. *Points* are means of five trials ± SEM; the *curve* is a fitted sinusoidal function (From Georgopoulos et al. 1982; reproduced with permission by the publisher)

Directional coding by neuronal populations

The broad directional tuning indicates that a given cell participates in movements of various directions, and that, conversely, a movement in a particular direction will engage a whole population of cells. Therefore, a unique signal for the direction of movement could reside in the activity of the neuronal ensemble. We proposed a vectorial code for the recovery of this signal from the neuronal ensemble (Georgopoulos et al.

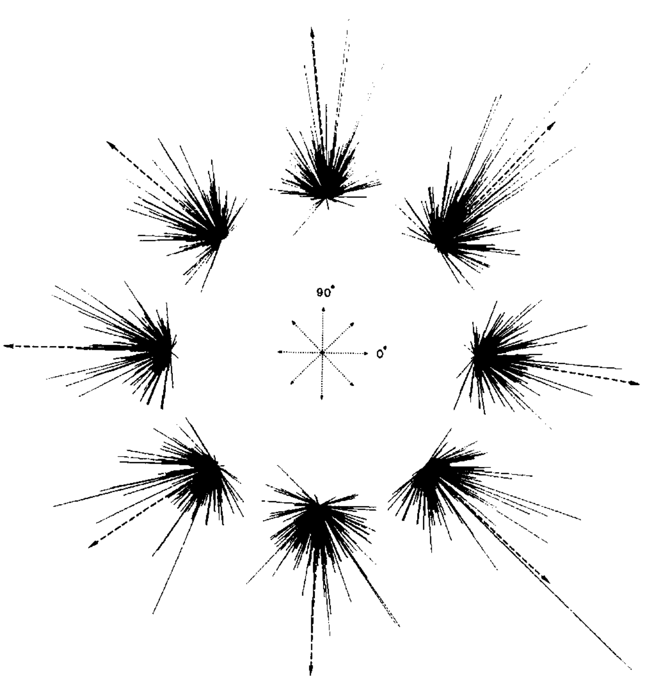

Fig. 4 Population vectors (*interrupted arrows*) for eight movement directions in 2D space. Each cluster represents the directional contributions of 241 directionally tuned cells. The movement directions are shown in the *diagram in the center*. The population vector points approximately in the direction of the movement. (From Georgopoulos et al. 1983b)

1983b, 1986, 1988), as follows: (a) a cell is represented as a vector that points in the cell's preferred direction C_i; (b) the length of a cell's vector, w_{il}, for a given arm movement, represents the change in the cell's activity during that particular movement; and (c) the sum of these vectors (i.e. the population vector $\boldsymbol{P}_l$) provides the unique outcome of the ensemble coding operation. This operation can be expressed as follows:

$$\boldsymbol{P}_l = \sum_i^N w_{il} \boldsymbol{C}_i \tag{2}$$

It was found that the population vector points in the direction of the movement (Fig. 4; Georgopoulos et al. 1983b, 1986, 1988).

The population vector approach has proved useful not only in studies of motor cortex (Georgopoulos et al. 1983b; Georgopoulos 1988; Kalaska et al. 1989; Caminiti et al. 1990) but also in studies of other brain areas, including the cerebellum (Fortier et al. 1989), the premotor cortex (Caminiti et al. 1991), area 5 (Kalaska et al. 1983), and area 7 (Steinmetz et al. 1987).

Three aspects of the population vector analysis are remarkable, namely its *simplicity*, its *robustness*, and its *spatial outcome*. With respect to *simplicity*, the ongoing calculation of the population vector is a simple procedure, for it (i) rests on the directional selectivity of single cells, which is apparent, (ii) involves weighting of vectorial contributions by single cells on the basis of the change in cell activity, which is reasonable, and (iii) relies on the vectorial summation of these contributions, which is practically the simplest procedure to obtain a unique outcome. In fact, an important aspect of the population vector analysis is that it relies on the directional tuning as defined operationally by the procedures above; no special assumptions are made or required as to how this tuning comes about.

With respect to *robustness*, the population vector is a distributed code, and as such does not depend exclusively on any particular cell. Its robustness is evidenced by the fact that it can convey a good directional signal with only a small number of cells (Georgopoulos et al. 1988; Salinas and Abbott 1994). It also remains as unbiased predictor of the direction of movement when the posture of the arm changes (Kettner et al. 1988; Caminiti et al. 1991; see also Fig. 1 in Georgopoulos 1995), even when the preferred directions of individual cells may change with different movement origins (Caminiti et al. 1990).

Finally, the population vector's *spatial outcome* is isomorphic to the direction of movement in space. Indeed, this population analysis transforms aggregates of purely temporal spike trains into a directional signal.

Translation of cortical commands to muscle activations

How are directional motor commands translated into multi-muscle activations to generate a directed force (and initial movement) in space? In general, the neural signals from the motor cortex do not activate muscles directly but ultimately influence the activity of motoneurons through the spinal cord. In certain cases, the corticospinal axons terminate within the motor nuclei, as is the case, for example, for the motoneurons innervating distal muscles of the limb in adult primates (Porter and Lemon 1993). However, in the vast majority of cases, the influence on the motoneuronal pools is exerted through intercalated interneurons. Some clues as to the possible organization of spinal interneuronal populations involved in motor control have been provided by recent studies on the spinal cord of the frog (Bizzi et al. 1991; Giszter et al. 1993; Mussa-Ivaldi et al. 1994). These studies have revealed possible substrates for the operation of directionally tuned motor cortical activity to produce an appropriately directed motor output by the limb.

In these experiments, the technique of microstimulation was used to determine the effects of interneuronal populations on the direction and magnitude of the force in space developed by the limb of the spinalized frog. There were three major findings of these studies. First, microstimulation at a particular interneuronal zone in the spinal cord elicited the development of force by the limb, the direction and magnitude of which differed depending on the position of the limb in space.

The set of these forces define a "force field". In the absence of microstimulation, there were passive forces due to the resistance to stretch of the tissues of the limb; during microstimulation, active forces were developed which, added to the passive ones, resulted in the total force exerted by the limb. In the experiment, the total and the passive forces were measured, and the passive subtracted from the total to obtain the "active" force field. It was found that microstimulation in a given area resulted in an active force field in which the force vectors converged on a particular point in space at which the force developed was zero; this was called the "equilibrium point" of that field. In many cases, the force field predicted the limb motion when the limb was allowed to move; therefore, these fields can be regarded as underlying movement primitives (Giszter et al. 1993). The second finding was that only a few (3–4) clusters of equilibrium points were found by a detailed and systematic microstimulation of extensive areas of the spinal cord; each equilibrium point was represented at different locations in the spinal cord. Finally, concomitant microstimulation at any two sites produced a new force field which was the result of a point-by-point linear summation of the force field produced at each of the two stimulation sites; thus new equilibrium points were created (Mussa-Ivaldi et al. 1994).

These findings suggest possible mechanisms by which supraspinal commands could be translated into motor action as follows. First, since microstimulation will activate an appreciable number of neurons (Phillips and Porter 1977), these intrinsic spinal motor mechanisms involve populations of neurons and summation of influences from potentially separate neuronal ensembles. Second, it is likely that these ensembles are the targets of supraspinal influences. For example, a common characteristic of pyramidal tract axons is their appreciable divergence in the spinal cord with collaterals to various spinal segments.

Although spinal microstimulation studies have not been performed in primates, it is reasonable to hypothesize a similar plan of spinal organization. Then this divergence of the pyramidal tract axons would enable central motor commands to address concomitantly a number of the spinal populations associated with different force fields, that is with different movement primitives. Finally, this organization could provide the background for the translation of the motor cortical command, as understood at the single cell and neuronal population level, to motoneuronal activation (Georgopoulos 1988, 1996; Lukashin et al. 1996).

The time-varying neuronal population vector as key for understanding dynamic directional processes

In the following analyses the population vector was calculated at short successive intervals (e.g. every 10 or 20 ms) as a time-varying signal and its relation to an ongoing or a planned movement was assessed.

Continuous, tracing movements

In these experiments (Schwartz 1993, 1994) monkeys were trained to trace smoothly with their index finger sinusoids or spirals displayed on a screen, from one end to the other. The direction of the population vectors, calculated successively in time along the trajectory, changed throughout the movement, closely matching the smoothly changing direction of the finger path.

Reaction time

When a movement is elicited in response to a visual stimulus, the reaction time (~ 300 ms) is defined as the time period from the onset of the stimulus until the beginning of the movement. For the case of reaching movements, the changes in cell activity in the motor cortex precede the onset of movement by approximately 160–180 ms, on the average (Georgopoulos et al. 1982). These changes are directionally selective and yield a time-varying population vector the direction of which points in the direction of the upcoming movement (Georgopoulos et al. 1984, 1988).

Instructed and memorized delay tasks

In these studies, a delay period is interposed between the onset of a the visual stimulus and the beginning of the movement. For that purpose, monkeys are trained to withhold the movement for a period of time after the onset of a visual cue signal, and to move later in response to a "go" signal. The target could stay on or be turned off during the delay period ("instructed" and "memorized" delay task, respectively). During both kinds of tasks, the time-varying population vector in the motor cortex, computed every 20 ms, predicts well the direction of the instructed movement (Georgopoulos et al. 1989b; Smyrnis et al. 1992).

Mental rotation

This task required a transformation of an intended movement direction. In these studies we first carried out psychological experiments in human subjects. Then we trained monkeys to perform the same task and recorded the activity of single cells in the brain of these animals during performance of the task. Finally, we tried to connect the neural results with those of the human studies and interpret the latter on the basis of the former. The objective was to get as close as possible in relating neurophysiology and cognitive psychology.

The task required subjects to move a handle at an angle relative to a reference direction that was defined by a visual stimulus on a plane. Since the reference direction was varied from trial to trial, the direction of the movement varied too, according to the instructed angle. In the psychological studies in human subjects (Georgopoulos and Massey 1987), seven angles (5–140°) were used. The basic finding was that the time to initiate a movement (reaction time) increased as a linear fashion with the angle. The most parsimonious hypothesis to explain these results is that subjects arrive at the correct direction of movement by shifting their motor intention from the reference direction to the movement direction, traveling through the intermediate angular space. This idea is very similar to the mental rotation hypothesis of Shepard and Cooper (1982) advanced to explain the monotonic increase of the reaction time with orientation angle when a judgment has to be made whether a visual image is normal or mirror-reversed. In both cases a mental rotation is postulated. In fact, the mean rates of rotation and their range among subjects were very similar in the perceptual (Shepard and Cooper 1982) and motor (Georgopoulos and Massey 1987) studies. Moreover, when the same subjects performed both perceptual and motor rotation tasks, their processing rates were positively correlated (Pellizzer and Georgopoulos 1993), which indicates similar processing constraints for both tasks.

In the *neurophysiological studies* (Georgopoulos et al. 1989a; Lurito et al. 1991), two rhesus monkeys were trained to move the handle 90° and counterclockwise from the reference direction. We recorded single cell activity in the motor cortex and then calculated the time-varying population vector. We found that during the reaction time the population vector rotated from the stimulus (reference) to the movement direction through the counterclockwise angle. (Fig. 5) These trials were intermixed with others in which the animals moved in the direction of the target. In these case, the population vector did not rotate but pointed all along in the direction of the stimulus (Fig. 5). It is remarkable that the population vector rotated at all, and also that it rotated through the smaller, 90° counterclockwise angle. These results showed clearly that the cognitive process in this task truly involved a rotation of an analog signal. The occurrence of a true rotation was further documented by showing that there was a transient increase during the middle of the reaction time in the recruitment of cells with preferred directions in-between the stimulus and movement directions: this indicated that the rotation of the population vector was not the result of varying activation of just two cell groups, one with preferred directions centered on the stimulus and another in the movement direction. Therefore, this rotation process, "sweeping" through the directionally tuned ensemble, provided for the first time a direct visualization of a dynamic cognitive process. In this respect, it is noteworthy that the

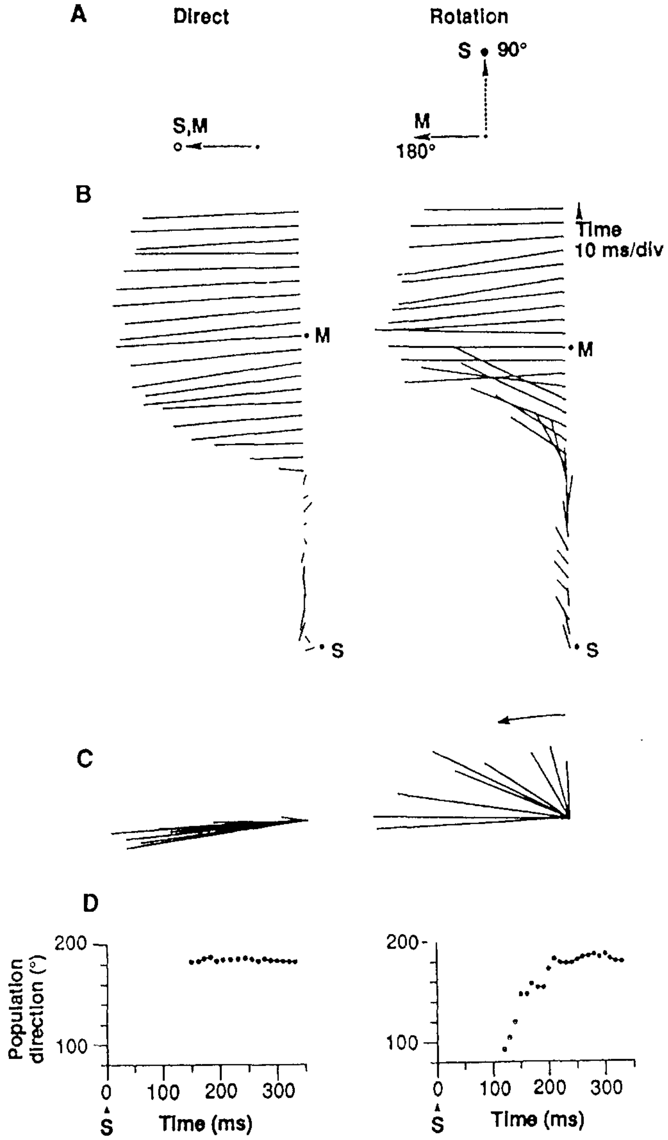

Fig. 5A–D Mental rotation of the population vector. *Left panel*: **A** Direction of required movement (*M*) was in the direction of the dim stimulus (*S*, *open circle*). Direction is indicated in polar angles. **B** Neuronal population vectors calculated every 10 ms from stimulus onset (*S*) points in the direction of upcoming movement (180°) which started at *M*. **C** Population vectors during the reaction time from the moment it is lengthening until the onset of movement. **D** Direction of population vectors identified in **C**, above, is plotted against time elapsed from stimulus onset. (Direction is in polar angles.) *Right panel*: **A** Direction of required movement (*M*) was in a direction perpendicular and counterclockwise form the direction of the bright stimulus (*S*, *filled circle*). **B** Neuronal population vector points initially in the direction of the stimulus (90°) and then rotates gradually counterclockwise and stabilizes, pointing in the direction of the upcoming movement (180°). **C** Population vectors during the reaction time from the moment it is lengthening until the onset of movement. Notice the counterclockwise rotation. **D** Direction of population vectors identified in **C**, above, is plotted against time elapsed from stimulus onset. (From Georgopoulos et al. 1989; reproduced with permission of the publisher, copyright by AAAS) population vector is, in essence, a measure that can take continuous values in direction.

In summary, the results of these studies provide the neural correlates of a dynamic cognitive representation (Freyd 1987). The essential contribution of this work is in the neural identification and visualization of the time-varying, dynamic representation of direction in the motor cortex when a transformation of this direction is required and achieved. Interestingly, the mean rotation rate and the range of rates observed for different reference directions were very similar to those obtained in the human studies.

Concluding remarks

The topics reviewed above have demonstrated the richness of neurophysiological and psychological studies of the direction of movement in space and have underlined the heuristic value and power of the neuronal population vector analysis in deciphering directional neuronal operations. A scheme for the possible translation of motor cortical directional commands to muscle activations via spinal interneuronal systems has been proposed (Georgopoulos 1988, 1996) and modeled (Lukashin et al. 1996). Finally, the biophysical mechanisms underlying population vector operations are currently being investigated in the cockroach (Levi and Camhi 1994).

Of course, the population vector analysis is quite general and need not be confined to physical space but can be generalized to arbitrary spaces and dimensions. Indeed, such an application has been made successfully to the coding of faces in the inferotemporal cortex of the monkey (Young and Yamane 1992) and another one has been suggested with respect to the coding of finger movements (Georgopoulos et al. 1993).

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