

# Spatial Coding of Movement: A Hypothesis Concerning the Coding of Movement Direction by Motor Cortical Populations

A.P. Georgopoulos, R. Caminiti, J.F. Kalaska, and J.T. Massey

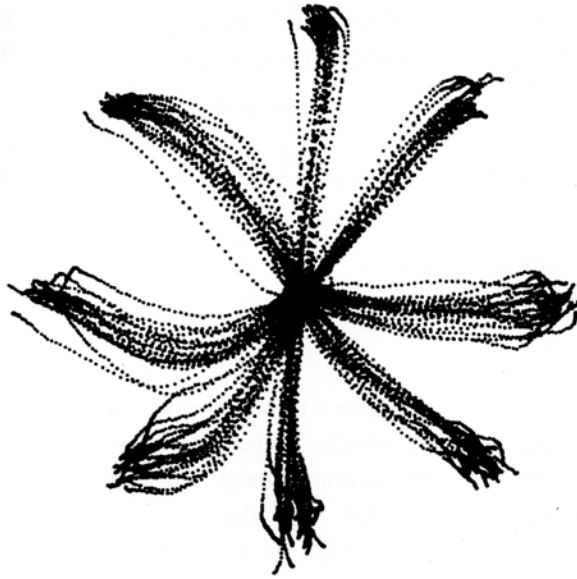
The Philip Bard Laboratories of Neurophysiology, Department of Neuroscience,  
The Johns Hopkins University, School of Medicine, Baltimore, MA 21205, USA

How are movements in a particular direction made? We studied this problem by recording the discharge of single neurons in the motor cortex of monkeys while the animals performed two-dimensional arm movements on a plane working surface. These movements started from the same point and were of the same amplitude, but their directions differed at intervals of  $45^\circ$ .

## Experimental procedure

An apparatus was used (GEORGOPOULOS et al., 1981) in which a light-weight handle could be moved freely and with low friction in the two (X-Y) dimensions across a plane working surface. Monkeys were trained to move the handle and capture (within a circle attached to it) lighted targets in a reaction-time task. Of 9 targets, one was at the center and 8 around it on a circle of 8 cm radius. In a typical trial, the animal first captured the center light and held there for a variable period of time (control period), then a peripheral light came on and the animal had to move the handle to capture that target to receive a liquid reward. Since the 8 targets were arranged equidistantly around the circumference of the circle, the directions of the movements made from the center to the target covered the whole circle at  $45^\circ$  intervals. Motor behavioral data concerning performance in this task have been described elsewhere (GEORGOPOULOS et al., 1981). Families of trajectories of movement made by a well trained animal are shown in Figure 1.

Glass-coated platinum-iridium microelectrodes were advanced through the dura into the cortex of rhesus monkeys. The action potentials of individual neurons were recorded extracellularly using standard electrophysiological techniques (GEORGOPOULOS et al., 1982). The experiment was controlled through a PDP 11/20 minicomputer. The XY position of the manipulandum was sampled at 100/sec. Neuronal data were collected as interspike intervals with a sampling density of  $10^4$ /sec and analyzed off-line using standard display and statisti-



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└ 10 mm

Fig. 1. Families of trajectories of movements made in 8 directions by a well trained monkey from the center of the plane to peripheral targets

cal techniques. Methods appropriate for the analysis of directional data were employed (MARDIA, 1972) where needed.

#### Single cell discharge and movement direction

Sixty nine penetrations were made into the proximal arm area (WOOLSEY et al., 1950) of the motor cortex of rhesus monkeys (area 4 and posterior strip of area 6, see WIESENDANGER, 1981). Three hundred and twenty three task-related cells were recorded (5 hemispheres, 4 monkeys). All of these cells discharged in association with movements of the contralateral arm at the shoulder and/or elbow.

The frequency of discharge of 241/323 (74.6%) of cells studied varied in an orderly fashion with the direction of the movement ("directionally tuned cells"). Almost all of these cells showed changes of activity in association with more than one, and commonly with all, movement directions. However, discharge was most intense with movements in a preferred direction and was

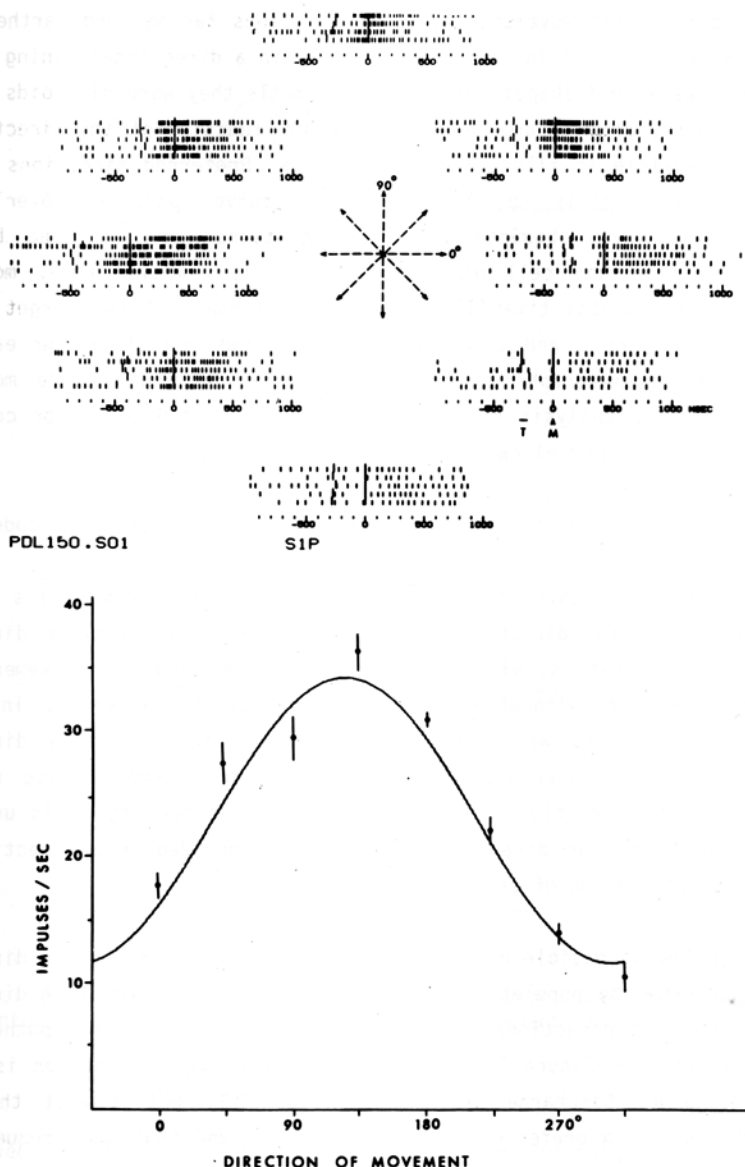


Fig. 2. Orderly variation in the frequency of discharge of a motor cortical cell with the direction of movement. Upper half: Rasters are oriented to movement onset, M, and show impulse activity during five movements in each of the 8 directions indicated by the center diagram. Longer vertical bars in the spike trains indicate the time of target (T) and movement onset for individual trials. Lower half: Directional tuning curve of the same cell. Discharge frequency is for "total experimental time", i.e. from the appearance of the target to the end of the movement (approximately 500 msec after movement onset). Data points are mean  $\pm$  SEM. The regression equation for the fitted sinusoidal curve is  $D = 23.37 + 9.27 \sin \theta - 6.88 \cos \theta$ , where  $D$  is the frequency of discharge and  $\theta$  the direction of movement; or, equivalently,  $D = 23.37 + 11.54 \cos (\theta - \theta_0)$ , where  $\theta_0$  is the preferred direction ( $\theta_0 = 126.6^\circ$ ).

reduced gradually with movements made in directions farther and farther away from the preferred one (Fig. 2). This resulted in a directional tuning curve. These curves were bell-shaped, and in 75% of cells they were sinusoids ; that is, the frequency of discharge was a sinusoidal function of the direction of movement. An example is illustrated in Figure 2. Preferred directions differed for different cells so that the tuning curves partially overlapped. Similar results were obtained when the relations were analyzed between movement direction and cell discharge during the reaction time, movement time, total experimental time (TET, from the appearance of the target to the end of the movement), and also during the period preceding the earliest changes in electromyographic (EMG) activity (ca. 80 msec before movement onset). A detailed analysis of the directional properties of motor cortical cells has been described elsewhere (GEORGOPOULOS et al., 1982).

Coding for the direction of movement in motor cortex : a population code ?

A salient finding of this study was that although individual cells in the motor cortex possessed directional preference, they lacked extreme directional specificity ; that is, virtually no cells discharged during movement in a particular direction without also discharging during movements in other directions. Indeed, it was found that movements in a certain direction engaged neurons with overlapping directional tuning curves. These results indicate that the direction of movement is not subserved by cells uniquely related to a particular direction but is instead encoded in a directionally heterogeneous population of cells.

We discuss below a possible mechanism by which movements in a given direction could be generated by populations made up of cells possessing both directional preference and directional spread. We call it the "vector hypothesis" ; it is illustrated in Figure 3. In (A) the tuning curve of a neuron is shown as a polar plot. Discharge frequency is for TET. Notice that the cell discharged most in a preferred direction (at  $0^\circ$ ), and that the frequency of discharge was less for directions away from this preferred one. The circle indicates the average frequency of discharge during these movements. In (B), the first of two main assumptions underlying this hypothesis is illustrated. This assumption comprises the three following postulates. 1) For all movements, a cell exerts a directional influence (vector) which is along the axis of the cell's preferred direction (e.g. at  $0^\circ$  -  $180^\circ$  in Fig. 3); 2) the direction of this vector is in the cell's preferred direction (at  $0^\circ$ ) for an increase (+) of discharge above the average level, or in the opposite direction (at  $180^\circ$ ) for a decrease (-) in discharge (shaded area, Fig. 3A) ; and 3) the magnitude of

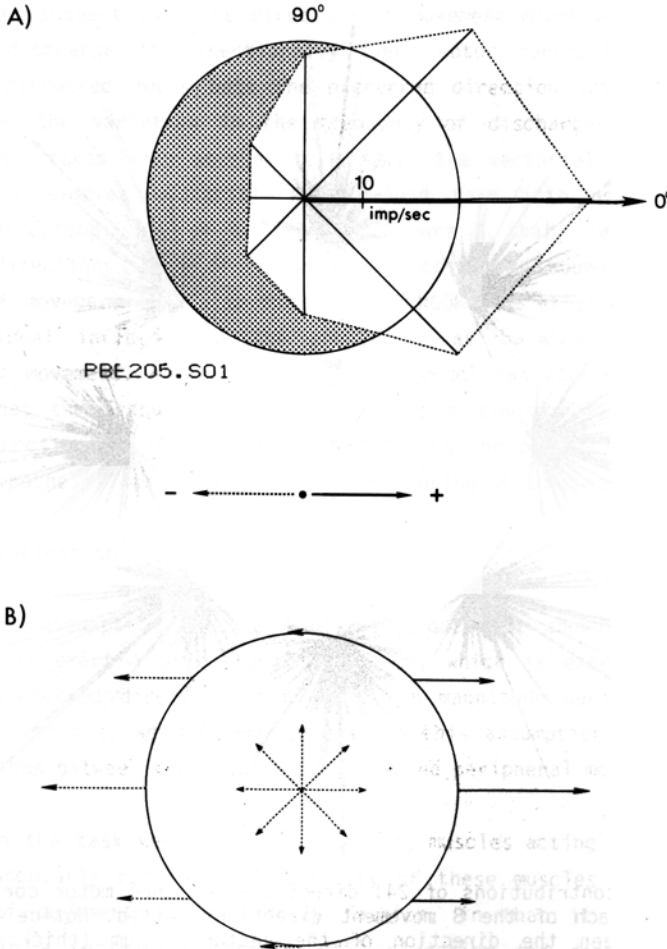


Fig. 3. Vector hypothesis. See text for explanation. The interrupted lines at the center in B indicate the 8 directions of movement tested

that vector is proportional to the change in discharge from the average level. The second assumption (not illustrated) is that for a given movement direction individual cell contributions as defined above are summed linearly as vectors.

Figure 4 shows the result of the application of this hypothesis to data obtained for movements in the 8 directions tested. For each direction of movement (indicated by interrupted lines at the center of the figure) the vector contributions of each of the 241 directionally tuned cells are displayed. Each line represents a vector which denotes the directional

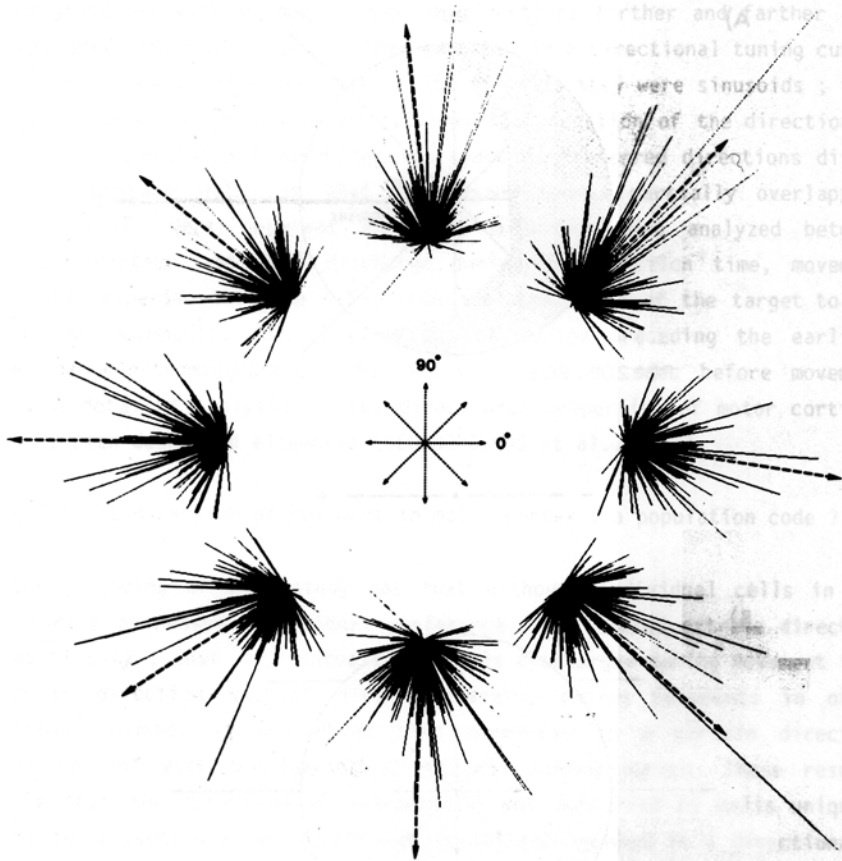


Fig. 4. Vector contributions of 241 directionally tuned motor cortical cells are shown for each of the 8 movement directions tested. Notice the spatial congruence between the direction of the vectorial sum (thick interrupted lines in each plot) and the direction of movement (thin interrupted lines at center). See text for explanation

influence of a cell along the axis of its preferred direction, according to the assumption described above. All cell-vectors are directed from center outward. The length of each vector is proportional to the percent change in cell discharge from the average frequency of discharge observed during the 8 movement directions. These vectors were then summed linearly. The direction of the vectorial sum is indicated by an interrupted line (long bars) for each direction of movement. It can be seen that this direction was very close (within  $11^\circ$ ) to the actual direction of movement. This range was within the variability of the directions of the actual movement trajectories observed in well trained animals.

These results suggest that the direction of movement might be encoded in the population discharge of directionally tuned motor cortical cells. In the hypothesis discussed above both the preferred direction (direction of cell vectors) and the variation in the frequency of discharge (length of cell vectors) were taken into account to compute the vectorial sum(s) shown in Figure 4. A simpler vectorial model would take into account only the preferred direction. It can be seen in Figure 4 that, in general, these preferred directions were distributed symmetrically around any particular direction of movement (see also Fig. 8 in GEORGOPOULOS et al., 1982), so that the directional influence of the population as a whole was towards that direction of movement. Although this simpler model can account for the data, the fact that the frequency of discharge was a sinusoidal function of the movement direction in 75% of the cells supports the original version of the vectorial hypothesis, as described in the beginning of this section.

#### Possible relations to muscle events

An important assumption of the hypothesis outlined above is that motor cortical cells exert a directional influence, which is exerted on the same axis (the preferred direction) but varies in magnitude during movements in different directions. We wish now to examine this assumption in the light of known relations between motor cortical cells and peripheral motor structures.

Movements in the task were produced mainly by muscles acting on the shoulder. The intramuscularly recorded EMG activity of these muscles varied with the direction of movement in an orderly fashion, in that it was high during movements in a particular ("preferred") direction and decreased gradually with movements made in directions farther and farther away from the preferred one (MASSEY et al., 1981).

It could be regarded that this orderly variation in EMG activity is associated with similar variation in force exerted by the muscle, since force is related to surface EMG (BOUISSET, 1973), and surface EMG to intramuscular EMG (BOUISSET and MATON, 1972). Although some of these relations are non-linear (BOUISSET, 1973), it is likely that the essence of the tuning curve, i.e., directionality with spread, will be also observed in the force domain. The question then becomes one of interpreting the variation in the force exerted by an individual muscles during movements in different directions. In this context, it is reasonable to assume that the force developed by individual muscles is exerted in a direction determined by the anatomical relations between muscles and bones under specified positions of the skeleton. It is



likely that this preferred direction of muscle action will be similar during movements of various directions. For example, the pectoralis major exerts force in a roughly horizontal dimension, so that the upper arm is deviated medially. Accordingly, the "preferred" direction of pectoralis, as determined in our studies, was at  $180^\circ$  (right arm). Nevertheless this muscle was also active, but at a lower intensity, during movements at  $135^\circ$ , i.e. movements that deviated  $45^\circ$  from the muscle's preferred direction toward forward extension of the upper arm. It is reasonable to assume that during this latter movement at  $135^\circ$  the action of pectoralis was still at  $180^\circ$ , although the magnitude of its activation was lower; and similarly, for other directions. The same sort of analysis could be applied regarding other muscles. A generalization could then be made, namely that the direction of an increase in force exerted by individual muscles is approximately the same during movements in different directions, assuming that the relative position of other parts of the limb does not alter this relation. Another generalization could be made for a decrease in muscle activity, namely that a decrease in the force exerted by a muscle contributes, in fact, a force in a direction opposite to the muscle's preferred direction of action.

The considerations discussed above provide the background for an interpretation of the vector hypothesis, proposed above for motor cortical cells, as follows. For those cells that may relate to individual muscles, cell vectors could have an interpretation along the lines discussed for individual muscles above. However, a divergence exists in the corticospinal projection (ASANUMA et al., 1979; JANKOWSKA et al., 1975; SHINODA et al., 1981) so that a motor cortical cell might influence cells in several motoneuronal pools. A functional interpretation of this divergence could be that these motor cortical cells control muscle synergies (EVARTS, 1967). Muscle synergies, in turn, will produce force in a certain direction. This direction will differ depending upon the muscular composition of the synergy and the relative strength of activation of component muscles. An analysis similar to that described above for individual muscles could then be performed for these "synergistic" forces as well. Therefore, the vector hypothesis would apply whether motor cortical cells are regarded as controlling individual muscles or muscle synergies. Finally, it is crucial in this hypothesis that there be a summation point of the individual cell vectors, so that a vectorial sum of the population can be produced. Assuming that these vectors are related to forces produced by muscles or muscle synergies, a summation point could ultimately be the joint; more specifically for the task used in the present study, the shoulder joint.



## Concluding remarks

A "vectorial hypothesis" was proposed by which motor cortical cells possessing directional preference and directional spread could, as populations, generate movements in particular directions. The main assumptions of this hypothesis are that (a) cells exert a directional influence (vector) along the axis of their preferred direction, (b) this directional influence is on the same axis for all directions of movement, but (c) it is exerted toward the cell's preferred direction when there is an increase above the average discharge level, or toward the opposite direction when there is a decrease in discharge; and (d) for a particular movement direction, the vectorial components of individual cells sum linearly. Given these assumptions, the population vectorial sum was determined for each of the 8 directions of movement tested using experimentally observed data from 241 directionally tuned motor cortical cells. The direction of this population vector was within  $11^\circ$  from the straight-line movement direction. This was within the range of the directions of the movement trajectories produced by well trained animals. Possible relations between motor cortical cells and individual muscles or muscle synergies were discussed with respect to the hypothesis above. It was argued that the hypothesis would hold under either assumption, i.e. whether motor cortical cells are thought as controlling muscles or muscle synergies, assuming that no changes in the position of parts of the limb occur that would alter fundamentally the directions in which muscles exert their actions.

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## REFERENCES

- ASANUMA H, ZARZECKI P, JANKOWSKA E, HONGO T, MARCUS S (1979) Projection of individual pyramidal tract neurons to lumbar motor nuclei of the monkey. *Exp Brain Res* 34:73-89
- BOUISSET S (1973) EMG and muscle force in normal motor activities. In: DESMEDT JE (ed) *New developments in electromyography and clinical neurophysiology*. Karger, Basel, p 547-583
- BOUISSET S, MATON B (1972) The quantitative relation between surface and intramuscular electromyographic activities for voluntary movement. *Amer J Phys Med* 51:285-295
- EVARTS EV (1967) Representation of movements and muscles by pyramidal tract neurons of the precentral motor cortex. In: YAHR MD, PURPURA DP (eds)

Neurophysiological basis of normal and abnormal motor activities. Raven, New York, p 215-251

GEORGOPOULOS AP, KALASKA JF, MASSEY JT (1981) Spatial trajectories and reaction times of aimed movements: effect of practice, uncertainty, and change in target location. *J Neurophysiol* 46:725-743

GEORGOPOULOS AP, KALASKA JF, CAMINITI R, MASSEY JT (1982) On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J Neurosci* 2:1527-1537

JANKOWSKA E, PADEL Y, TANAKA R (1975) Projections of pyramidal tract cells to alpha-motoneurons innervating hind-limb muscles in the monkey. *J Physiol (Lond)* 249:637-667

MARDIA KV (1972) Statistics of directional data. Academic Press, New York

MASSEY JT, CAMINITI R, KALASKA JF, GEORGOPOULOS AP (1981) Cortical mechanisms of two-dimensional aimed arm movements. VI. Electromyographic analysis. *Soc Neurosci Abstr* 7:563

SHINODA Y, YOKOTA JI, FUTAMI T (1981) Divergent projection of corticospinal motoneurons of multiple muscles in the monkey. *Neurosci Lett* 23:7-13

WIESENDANGER M (1981) Organization of secondary motor areas of cerebral cortex. In: *Handbook of Physiology. The Nervous System*. Bethesda, Md. Amer Physiol Soc, Sect 1, Vol II, Part 2, p 1121-1148

WOOLSEY CN, SETTLAGE PH, MEYER DR, SPENCER W, HAMUY P, TRAVIS AM (1950) Patterns of localization in the precentral and "supplementary" motor areas and their relation to the concept of a premotor area. *Res Publ Assoc Res Nerv Ment Dis* 30:238-264