

NSL 05471

Do neurons in the motor cortex encode movement direction? An alternative hypothesis

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Key words: Motor cortex; Multi-joint movement; Preferred direction; Activation vector; Jacobian matrix; Muscle moment arm; Distribution; Fourier series

Previous investigations by Georgopoulos et al. of cell activities in the primate motor cortex during the execution of voluntary arm movements have shown that these cells are characterized by tuning properties related to the direction of hand trajectories. Here, it is demonstrated that these findings do not necessarily imply that cortical cells encode spatial features of hand movements and an alternative hypothesis is considered according to which cortical cells encode muscle state variables. It is shown that this hypothesis would lead both to the single-cell activities and to the population behaviors observed by Georgopoulos et al.

Recent investigations of multi-joint arm trajectories [1, 3, 4, 8] have suggested that the central nervous system plans and represents arm movements in terms of spatial coordinates associated with the hand rather than in terms of joint or muscle coordinates.

The physiological studies of Georgopoulos et al. [5, 6] point toward a similar conclusion on the basis of the single cell recordings from the primate motor cortex during the execution of planar hand movements. They found that the activities of these cells were characterized by 'tuning' curves of the form

$$v_i = v_{0,i} + \gamma_i \cos(\varphi_H - \varphi_{0,i})$$

where v_i is the firing rate of a cell, i , φ_H is the direction of the hand movement and $v_{0,i}$, γ_i , $\varphi_{0,i}$ is a triplet of parameters specifying, respectively, the overall mean firing rate, a gain and the 'preferred direction' of the cell. The preferred direction, $\varphi_{0,i}$, is defined as the direction corresponding to maximum firing rate. As a large cell population was examined, the values of $\varphi_{0,i}$ were found to be scattered throughout an angle of 2π radians. The firing behavior of individual cortical cells, characterized by broad

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maxima of cell activity around the preferred directions, was recently considered as evidence for ‘coarse coding’ of spatial features associated with movements [9]. According to coarse coding models, a population of neurons provides more accurate encoding of spatial features if each neuron is characterized by a broad, instead of a sharp, tuning curve [7].

Considering an ensemble of 241 cortical cells, Georgopoulos et al. [6] introduced a vector method to represent the overall population response. This method is summarized here as follows: for each cell preferred direction, $\varphi_{0,i}$, form a unit vector $\mathbf{e}_i = (\cos \varphi_{0,i}, \sin \varphi_{0,i})$ in the plane where movements occur. Then, for each hand movement (in a direction φ_H) and for each cell, i , define a vector, \mathbf{a}_i , with direction \mathbf{e}_i and with length equal to the change in cell discharge from the average level ($v_{0,i}$), i.e.

$$\mathbf{a}_i = \gamma_i \cos(\varphi_H - \varphi_{0,i}) \mathbf{e}_i \quad (2)$$

In the following, I will refer to \mathbf{a}_i as the cell *activation* vector. Georgopoulos et al. found that, for any movement of the hand, the vector sum of all the measured activation vectors \mathbf{a}_i was approximately colinear with movement direction. Hence, they concluded that ‘...the direction of movement might be encoded in the population discharge of directionally tuned motor cortical cells’.

Here, I demonstrate that the hypothesis according to which cells encode the direction of movements, is not necessarily implied by these experimental findings since *the same results could be obtained from cells whose activity is related to the action of single muscles*. To demonstrate the latter statement, I will consider the hypothesis that the activity of a cortical cell encodes linearly the planned muscle shortening velocity, l_i , i.e. that

$$v_i = v_{0,i} + \xi_i l_i \quad (3)$$

where ξ_i is a gain parameter of the cell. It is important to note that the velocities l_i do not refer to single skeletal muscles but rather to ‘equivalent muscles’ defined by the connections between cortical cells and motor units. For example, consider a cell operating on two muscles, m_1 and m_2 , with moment arms $M_{m_1,1}$ and $M_{m_2,1}$ with respect to the shoulder and $M_{m_1,2}$ and $M_{m_2,2}$ with respect to the elbow. Then, this cell defines a single equivalent muscle whose shortening rate, l , is related to the joint velocities, θ'_1, θ'_2 of the shoulder and the elbow as

$$l = \mu_1 \theta'_1 + \mu_2 \theta'_2$$

where the parameters μ_1 and μ_2 are equivalent moment arms obtained from linear combinations of the moment arms, $M_{i,j}$, of the actual skeletal muscles influenced by the cell. I will show that the hypothesis of Eqn. 3 yields the same results obtained by Georgopoulos et al., thus demonstrating that spatial tuning of single cells and directional responses of cell populations can be obtained from units encoding muscle states instead of spatial directions. While a rigorous demonstration is provided here for a specific coding rule (Eqn. 3), it is not intended that cortical populations may not encode muscle-related variables other than shortening rates. For example, taking into account the muscle viscoelastic properties, a desired change of muscle length can

be expressed, equivalently, by a change of muscle rest-length or by a change of muscle steady-state tension. Accordingly, the arguments presented here are expected to hold, with some modifications, if cortical neurons encode muscle tensions.

For two-joint planar hand movements, the joint velocity vector, $\theta' = (\theta'_1, \theta'_2)$, is related to the hand velocity vector $\mathbf{r}'_H = (x'_H, y'_H)$, by the jacobian matrix*, $\mathbf{J}(\theta)$, i.e.

$$\theta' = \mathbf{J}(\theta)^{-1} \mathbf{r}'_H \quad (4)$$

Furthermore, the muscle velocity vector, $\mathbf{l}' = (l'_1, l'_2, \dots, l'_N)$, is obtained from the joint velocity vector by multiplication with the matrix of moment arms $\mu(\theta)$,

$$\mathbf{l}' = \mu(\theta) \theta' \quad (5)$$

Combining (4) with (5), we obtain

$$\mathbf{l}' = \mathbf{C}(\theta) \mathbf{r}'_H \quad (6)$$

with $\mathbf{C}(\theta) = \mu(\theta) \mathbf{J}(\theta)^{-1}$. The matrix \mathbf{C} has N rows (N = number of cortical cells and equivalent muscles) and 2 columns and is a function of joint configuration. In Georgopoulos' experiments, movements had different directions but a common starting location. Hence, the initial value of \mathbf{C} was the same for different trajectories.

The rate of shortening of muscle i is simply given by

$$l'_i = C_{i,1} x'_H + C_{i,2} y'_H \quad (7)$$

According to our hypothesis (Eqn. 3), the firing rate of the cortical neuron associated with this muscle is

$$v_i = v_{0,i} + \xi_i (C_{i,1} x'_H + C_{i,2} y'_H) \quad (8)$$

If the hand velocity is expressed in polar coordinate we have that

$$x'_H = v_H \cos \varphi_H \quad (9)$$

$$y'_H = v_H \sin \varphi_H$$

where φ_H is the direction of the movement and v_H is the speed. Then, Eqn. 8 reduces to Eqn. 1 with

$$\gamma_i = \xi_i v_H, \text{ and}$$

$$\varphi_{0,i} = \arctan(C_{i,2}, C_{i,1}) \text{ (the 'preferred direction')}$$

Note that, since we included in the definition of \mathbf{C} both the joint jacobian \mathbf{J} and the matrix of moment arms, μ , of equivalent muscles which contains several linear combinations of muscle moment arms, the preferred directions can, a priori, assume any value within an angle of 2π . This demonstrates that 'spatial tuning' of single cells can be a side-effect of coding muscle-related variables.

*For simplicity we consider a non-redundant situation where the number of joints is equal to the number of free hand-coordinates. However, the demonstration holds for any locally linear relation from hand to joint velocity, e.g. for any pseudoinverse of the jacobian matrix.

The next step is to find under which conditions Georgopoulos' results on population averages, namely the fact that the sum of the activation vectors is colinear with the direction of the hand movement, can be considered as a direct consequence of the definition [2] of the activation vectors. This will indicate under which conditions our hypothesis can account not only for single cell behavior but also for the overall population properties. I will show that, in fact, Georgopoulos et al.'s results are a direct consequence of the activation vector definition if and only if the distribution of the principal directions over an angle of 2π satisfies a moderately restrictive condition, i.e. that it is continuous over the whole range of angles and that it does not contain second harmonics (i.e. bimodal components). The conditions seem to be met by the histogram presented in Georgopoulos et al. which indicates a unimodal distribution of principal direction, with a maximum at 45° and a minimum at 225° . Kalaska (1988, personal communication) has found a more uniform distribution which also satisfies these conditions.

As a large number of cells is considered within a cortical population, I will discuss the problem in the domain of continuous variables. This requires a change in the notation for the direction vectors: for each angle, φ , in the (closed) interval $[-\pi, \pi]$ a preferred direction vector, $\mathbf{e}(\varphi)$ is defined as

$$\mathbf{e}(\varphi) = (\cos\varphi, \sin\varphi) \quad (10)$$

Similarly, given a hand movement in the direction φ_H , the activation vector associated with a cell having preferred direction φ and gain ξ is defined as

$$\mathbf{a}(\varphi) = \gamma \cos(\varphi_H - \varphi) \mathbf{e}(\varphi) = \xi \langle \mathbf{r}'_H \mathbf{e}(\varphi) \rangle \mathbf{e}(\varphi) \quad (11)$$

where \mathbf{r}'_H is the hand velocity (Eqn. 2) and the acute brackets $\langle \rangle$ indicate the scalar product operation. In order to relate these direction and activation vectors to experimental findings a distribution, $f(\varphi)$, must be given defining the probability, P , of finding a cell preferred direction within φ and $\varphi + d\varphi$ as

$$P = f(\varphi) d\varphi \quad (12)$$

The expected value, \mathbf{u}_{exp} of a vector function of φ , $\mathbf{u}(\varphi)$ is given by the expression

$$\mathbf{u}_{\text{exp}} = \int_{-\infty}^{+\infty} \mathbf{u}(\varphi) f(\varphi) d\varphi$$

Since $f(\varphi)$ is, by hypothesis, continuous in $[-\pi, \pi]$, it can be expanded in a Fourier series as

$$f(\varphi) = a_0 + \sum_{k=1}^{\infty} [a_k \cos(k\varphi) + b_k \sin(k\varphi)] \quad (13)$$

with $a_0 = 1/2\pi$. This corresponds to expressing a generic distribution as a sum of harmonics, each one having a number of maxima given by the index, k . Essentially, a generic distribution is obtained from a uniform distribution (a_0) plus a unimodal component (terms with coefficients a_1 and b_1), a bimodal component (terms with components a_2 and b_2) and so on.

The following theorem defines the constraints on the distribution that are implied by Georgopoulos' results on the population vectors:

if (and only if) the distribution $f(\varphi)$ has no second harmonics (i.e. if $a_2=b_2=0$) then the expected value of the sum \mathbf{A} of the activation vectors, \mathbf{a}_i , is colinear with the direction of the hand movement, i.e.

$$\mathbf{A}_{\text{exp}} = N \int_{-\pi}^{\pi} \langle \mathbf{r}'_H \mathbf{e}(\varphi) \rangle \mathbf{e}(\varphi) f(\varphi) d\varphi = c \mathbf{r}'_H \quad (14)$$

where N is the number of cells in the population and c , on the right hand side, is a scalar constant.

Proof. It will be sufficient to consider the case in which the movement occurs at 0° , e.g. $\mathbf{r}'_H = \mathbf{e}(0)$, and to show that the corresponding y component of \mathbf{A}_{exp} is zero if and only if $b_2 = 0$:

$$A_{\text{exp},y} = N \int_{-\pi}^{\pi} \cos(\varphi) \sin(\varphi) f(\varphi) d\varphi = 0 \quad (15)$$

In fact, to prove statement 14 for a movement in any direction φ_H it is sufficient to prove it at 0° with a rotation $-\varphi_H$ of the distribution function $f(x)$. Introducing the Fourier expression for $f(\varphi)$ (13) in Eqn. 15 and commuting sums with integrals we obtain

$$A_{\text{exp},y} = N(I_1 + I_2 + I_3) \quad (16)$$

$$I_1 = a_0 \int_{-\pi}^{\pi} \cos(\varphi) \sin(\varphi) d\varphi$$

$$I_2 = \frac{1}{2} \sum_{k=1}^{\infty} \int_{-\pi}^{\pi} a_k \cos(k\varphi) \sin(2\varphi) d\varphi$$

$$I_3 = \frac{1}{2} \sum_{k=1}^{\infty} \int_{-\pi}^{\pi} b_k \sin(k\varphi) \sin(2\varphi) d\varphi$$

The first two terms, I_1 and I_2 , are clearly zero whereas for the third we have

$$I_3 = \frac{1}{2} \int_{-\pi}^{\pi} b_2 \sin(2\varphi)^2 d\varphi = \frac{b_2 \pi}{2}$$

Hence $A_{\text{exp},y} = NI_3 = 0$ if and only if $b_2 = 0$. In order to apply this result to any direction of movement it is necessary to require that not only b_2 but also a_2 , is zero, i.e. that the distribution $f(\varphi)$ of principal directions has no bimodal components whatsoever. (End of proof.)

This theorem indicates an important limit at which the vector method used by Georgopoulos et al. would cease to provide an accurate estimate of the direction of hand movements. The data presented so far indicate that bimodal components in the distribution of cell preferred directions are negligible and, accordingly, that the sum of activation vectors over a whole population of cells is expected to be colinear with hand movement direction *regardless of the process which is responsible for the tuning*

characteristics of individual cells. The lack of bimodal components in the distribution of preferred directions within a portion of motor cortex has a specific relevance if cell activities are associated with muscle variables, as suggested in this paper. In fact, according to this hypothesis, a bimodal distribution component would be expected in a region where cells associated with antagonistic muscles operating on a single joint were significantly predominant*. Within such a region the population vector method would fail to correlate with movement direction. Hence, the data presented by Georgopoulos et al. are consistent with previous findings indicating that neurons in the motor cortex are often related to groups of muscles operating on different joints [2].

In summary, I have shown that spatial tuning of cells in the motor cortex does not necessarily imply that these cells encode the planning of multi-joint arm movements in terms of the desired hand direction. In fact, it is possible to interpret Georgopoulos et al.'s results by assuming that cortical cells encode the desired rate of shortening of muscles. Furthermore I demonstrated that the tuning behavior of individual cells directly implies that the population vector A is a good estimate of hand movement direction under a moderate but very specific restriction on the distribution of cell preferred directions. If motor cortical cells encode muscle-related variables, this restriction is a constraint that must be satisfied by the connections between cortical cells and muscle motor units.

I wish to thank Emilio Bizzi, Simon Giszter and Neville Hogan for discussing the issues presented in this paper. This work was partially supported by National Institute of Neurological Disease and Stroke Research Grant NS09343.

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*In fact, for a single-joint muscle the preferred direction, $\arctan(C_{i,2}, C_{i,1})$, depends only on the configuration of the arm and on the sign of the moment arm but not on its value. A single-joint flexor and a single-joint extensor of the same joint are, then, associated with two opposite preferred directions.

ERRATA

At p. 108, Equation (5)

Instead of: $f'(\mu(\theta))\theta'$

Read : $f'(\mu(\theta))\theta'$

At p. 108. line 25

The term "Eqn 1" refers to the first equation of this paper which appears unnumbered at p. 106.

At p. 109

Instead of : $u_{exp} = \int_{-\pi}^{+\pi} u(\phi) f(\phi) d\phi$

Read : $u_{exp} = \int_{-\pi}^{+\pi} u(\phi) f(\phi) d\phi$