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Hypothetical joint-related coordinate systems in which populations of motor cortical neurons code direction of voluntary arm movements

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Abstract

Results of the recent electrophysiological experiments by Caminiti et al. suggest that populations of neurons of the motor areas code direction of voluntary arm movement in an intrinsic coordinate system. In this letter I propose a set of joint-related coordinate systems that rotate with the posture of the arm in which populations of motor cortical neurons code direction of the arm movement. In these frames of reference, the movement directions represented vary with the posture of the arm but the preferred directions of the motor cortical neurons do not rotate. It is suggested that the difference in the neuronal activity for different workspaces, which was observed by Caminiti et al., is due to the dependence of the movement direction, represented in one of the joint-related coordinate systems, on the posture of the arm.

Key words: Motor cortex; Voluntary movement; Movement direction; Population coding; Preferred direction; Extrapersonal coordinate system; Intrapersonal coordinate system

Results of a series of neurophysiological experiments show that kinematics and dynamics of voluntary arm movements are represented distributedly by populations of motor cortical neurons [4–11,13,14,17]. In their analyses of the coding, a population vector has been proposed, with which performance of the coding is quantified. It is remarkable that the upcoming movement of the arm is predicted to some extent by the time-varying population vector [4,5,11].

Recently, Caminiti et al. [1–3] reported that the discharge rates of both premotor and motor cortical neurons varied significantly with the static position of the arm in space. These positional effects were observed in 88.5% of premotor and 91.8% of motor cortical neurons [3]. This suggests that populations of neurons in the cortical arm areas code direction of voluntary arm movement in an intrinsic coordinate system [1]. Moreover, Soechting and his coworkers suggested from psychophysical experiments that the neuronal processing in visual reaching movements involves a series of sensorimotor transformation between extrinsic and intrinsic coordinates [18–22,26]. According to these suggestions, I propose a set of coordinate systems in which populations of motor cortical neurons code direction of voluntary arm movement. The coordinate systems rotate with the posture of the arm; the amounts of the rotation will be determined by the amounts of the rotations of the joint angles. Then the movement direction represented in any of these coordinate systems is no longer identical to that represented in the extrapersonal coordinate system. As a consequence, it is to be that the activity of the motor cortical neurons in the population is different for the movements with the same relative direction but different starting points in the extrapersonal space. That is what was actually observed in electrophysiological experiments [1–3].

Humphrey et al. [12], Thach [25], and Murphy et al. [16] suggested that there exist relations of the activity of motor cortical neurons with the rotation of the joints involved in arm movements. It is further suggested that 'neurons in the forelimb area of primate motor cortex are organized into populations which are functionally coupled to the peripheral musculature in such a way as

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to provide a major component of the control of position of limb parts about single, forelimb joints' [15]. Accordingly, it is assumed in the present model that the arm area has several populations, each of which have close relations to a different joint of the arm. A population employs its own intrapersonal (joint-related) coordinate system in which the activity of the population represents movement direction of the arm.

The analysis in the present letter will be restricted to two-dimensional movements of a model arm with two joints (see Fig. 1). The results of the series of electrophysiological experiments in which extracellular recordings from single motor cortical neurons in rhesus monkeys were obtained during the performance of visual reaching movements in three-dimensional as well as two-dimensional spaces show that most motor cortical neurons have a directionally selective activity [8,10,11,13,14,17]. They further showed that the directionally selective activity of the motor cortical neurons is appropriately described with a cosine function with the argument of the difference between the movement direction and the preferred direction of each neuron. In the two-dimensional case, therefore, the activity of the motor cortical neurons in the population is appropriately described by

$$a_{ji} = a_{0ji} + r_{ji}\cos(\varphi_j - \theta_{ji}) \tag{1}$$

where a_{ji} is the activity of the motor cortical neuron i in the population j, a_{0ji} is the non-directional component of the activity, r_{ji} is the parameter that describes the magnitude of the directionally selective response, φ_j is the movement direction represented in the intrapersonal coordinate system related to the joint j, and θ_{ji} is the preferred direction of the neuron. Both a_{0ji} and r_{ji} vary from

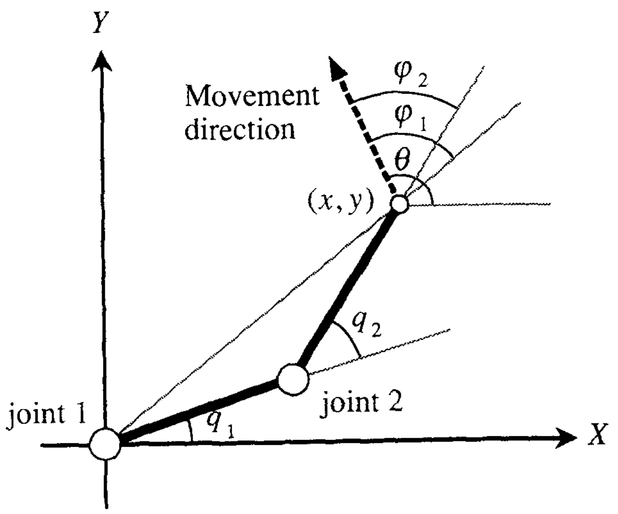

Fig. 1. Two-joint model arm and the coordinate systems. The position of the tip of the arm is represented by (x, y) in the extrapersonal coordinate system. The movement direction is represented by θ in the extrapersonal coordinate system, by φ_1 in the intrapersonal coordinate system related to the joint 1, and by j_2 in the intrapersonal coordinate system related to the joint 2. The angles q_1 and q_2 are the joint angles.

neuron to neuron as is observed experimentally [17] and is illustrated numerically [23,24]. Note that the movement direction is represented not in the extrapersonal frame of reference but in the intrapersonal ones.

In the two-joint model arm (Fig. 1), the x and y (extrapersonal) coordinates of the tip of the arm are related to the joint angles, q_1 and q_2, as

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} L_1\cos q_1 + L_2\cos(q_1 + q_2) \\ L_1\sin q_1 + L_2\sin(q_1 + q_2) \end{pmatrix} \tag{2}$$

where L_1 and L_2 are the lengths of the upper and lower arms. The amount of small displacement of the tip of the arm, $(\Delta x, \Delta y)$, which is represented also in the polar coordinates as $(\Delta\rho, \xi)$, is related to the amount of small rotation of the joints, $(\Delta q_1, \Delta q_2)$, as

$$\begin{aligned} \begin{pmatrix} \Delta x \\ \Delta y \end{pmatrix} &= \begin{pmatrix} \Delta\rho\cos\xi \\ \Delta\rho\sin\xi \end{pmatrix} \\ &= \begin{pmatrix} -L_1\sin q_1 - L_2\sin(q_1 + q_2) & -L_2\sin(q_1 + q_2) \\ L_1\cos q_1 + L_2\cos(q_1 + q_2) & L_2\cos(q_1 + q_2) \end{pmatrix} \begin{pmatrix} \Delta q_1 \\ \Delta q_2 \end{pmatrix} \end{aligned} \tag{3}$$

We here introduce the 'direction of joint action', which is defined as the movement direction of the tip of the arm when one of the joints rotates by a small amount. There are two directions of joint action in the present case because the model arm has two joints. The directions of joint action that are represented in the extrapersonal coordinate system, denoted by ξ_j $(j = 1, 2)$, are the solutions to Eq. (3) for small $\Delta q_j \neq 0$ and $\Delta q_k = 0$ $(k \neq j)$, which are obtained as

$$\begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix} = \begin{pmatrix} \tan^{-1}\left[\dfrac{L_1\sin q_1 + L_2\sin(q_1 + q_2)}{L_1\cos q_1 + L_2\cos(q_1 + q_2)}\right] + \dfrac{\pi}{2} \\ q_1 + q_2 + \dfrac{\pi}{2} \end{pmatrix} \tag{4}$$

When the joints are at the angles of $q_1 = q_2 = 0$, both of the directions of joint action, represented in the extrapersonal coordinate system, are $\pi/2$ as the above equation shows. The directions rotate as one or both joints rotate; the angles $\Delta\xi_j = \xi_j - \pi/2$ $(j = 1, 2)$ describe the net rotation of the directions of joint action. It is hypothesized that the joint-related coordinate systems also rotate with the rotation of the joint angles by $\Delta\xi_j$. Therefore, the movement directions represented in the joint-related coordinate systems, φ_j $(j = 1, 2)$, are related to the movement direction represented in the extrapersonal coordinate system, θ, by (Fig. 1)

$$\varphi_j = \theta - \Delta\xi_j \tag{5}$$

It should be noted that, although each population has a close relation to one of the joints, the relation is not exclusive: actually, the amount of the rotation of the corresponding joint-related coordinate system is a function of both joint angles. In the case of $L_1 = L_2$, the movement directions represented in these coordinate systems are simplified as

$$\begin{pmatrix}\varphi_1\\ \varphi_2\end{pmatrix} = \begin{pmatrix}\theta - q_1 - \dfrac{q_2}{2}\\ \theta - q_1 - q_2\end{pmatrix} \tag{6}$$

Caminiti et al. [1–3] reported that the preferred directions of the cortical neurons rotate when the static arm position changes. That is because the preferred directions are represented in the extrapersonal coordinate system. The preferred direction in the present model, θ_{ji} in Eq. (1), is constant because the movement direction is represented in an intrapersonal, joint-related coordinate system. This is, however, perfectly compatible with the report by Caminit et al. [1–3]. Actually, when the movement direction is represented in the extrapersonal coordinate system in the present model, the argument of the cosine function in Eq. (1) is written by $\theta - (\theta_{ji} + \Delta\xi_j)$. In this case, the term $\theta_{ji} + \Delta\xi_j$ should be regarded as the preferred direction. Then the preferred directions vary with the posture of the arm when they are represented in the extrapersonal coordinate system.

The rotation of the preferred directions can be further argued quantitatively to some extent. The rotation of the preferred directions reported by Caminiti et al. [1–3] corresponds, in the present model, to $\Delta\xi_j$. The typical amounts of the rotation reported by Caminiti et al. [3] are 17° (between the left-center work space), 18° (between the center-right work space) and 42° (between the left-right work space). The task employed in their experiments requires rotation of the joint angles by the amounts of the order of 10°. Then $\Delta\xi_j$ becomes also of the order of 10°. That is compatible with the results reported by Caminiti et al. [3], although the model arm is too simplified to compare the results quantitatively enough. It should also be noted that the amounts of the rotation of the preferred direction distribute widely [3]. That has not been taken into account in the present analysis.

The population vector proposed and analyzed by Georgopoulos et al. [4,5,11] is utilized as a measure of performance of the population coding of the movement direction. In the present model, each population represents movement in its own joint-related coordinate system. Then each population has its own population vector. In the limit of the infinite size of the population, it is obtained from Eq. (1) as

$$\mathbf{P}_j = \langle a_{ji}\mathbf{e}_{ji}\rangle = r_j\mathbf{e}_j \tag{7}$$

where $\mathbf{e}_{ji}$ is the unit vector in the preferred direction of the neuron i in the population j (i.e. the direction θ_{ji} in Eq. (1)), $\mathbf{e}_j$ is the unit vector in the movement direction of arm in the joint-related coordinate system (i.e. the direction φ_j in Eq. (1)), $\langle\ \rangle$ denotes the ensemble average over the neurons in the population, and $r_j = \langle r_{ji}\rangle$. It has been used the experimental observation that the preferred directions are distributed randomly in an approximately uniform fashion [11, 17]. The above equation shows that the population can code the movement direction successfully in the frame of reference for the corresponding joint.

In conclusion, direction of voluntary arm movement can be represented in the joint-related coordinate systems proposed in the present letter. Each joint-related coordinate system rotates differently by an amount given by a function of the rotations of the joint angles. In these frames of reference, the movement directions represented vary with the posture of the arm but the preferred directions of the cortical neurons do not rotate. It is suggested that the difference in the neuronal activity for different workspaces, which was observed by Caminiti et al. [1–3], is due to the dependence of the movement direction, represented in one of the joint-related coordinate systems, on the posture of the arm.

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