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Acknowledgements
It is our pleasure to thank our colleagues at the Max-Planck-Institute for Brain Research and at The Neurosciences Institute for valuable discussions, and William Newsome for helpful comments on an earlier version of the manuscript.

LETTERS TO THE EDITOR

Directional motor control

The recent review by Georgopoulos¹ highlights the prodigious output of the small army of researchers who have taken to summarizing the activity of motor-cortical units as a population vector in coordinates of polar extrapersonal space. In order to treat this paradigm as a hypothesis, as claimed, the author must clarify what the hypothesis actually states.

Georgopoulos does provide some necessary conditions for any population vector to describe a set of reaching movements, but these actually hold equally well for population vectors in myriad co-ordinate systems, including those based on intrinsic co-ordinates of the limb (for example, muscle and joint velocities) with no components related directly to the end point of the limb. Mussa-Ivaldi² has already provided a formal statement of the necessary conditions and a general proof that the cortical activity that actually represents muscle-based co-ordinates can be used to construct accurate population vectors in extrapersonal space.

The proponents of the population-vector hypothesis are really inviting the reader to infer the truth of another, more interesting, hypothesis, namely that the activity of individual neurons and columns of the motor cortex is invariantly related to the direction of movement of the end point of the limb, as represented in an extrinsic co-ordinate frame, that is, extrapersonal space. The problem is that this hypothesis has been tested and shown to be false. If the motor cortex is actually organized in extrapersonal space co-ordinates, then making the same set of movements of the hand in different postures of the arm should not change the

tuning vectors of individual motor-cortical cells, but it does³. Dismissing this finding by recomputing population vectors (Fig. 1 in Georgopoulos¹) is simply a retreat into the uninteresting hypothesis. Stating that the 'preferred direction [of individual units]...can change...when the posture of the arm change[s]' reduces the 'hypothesis' to curve fitting.

There is no question that somewhere between the eyes and the limb muscles, there must be a transformation between the visually encoded targets in extrapersonal space and the motoneuronal recruitment to reach such targets. The problem is to identify the actual steps in the transformation and where and how they are computed. What do we actually know about this?

As Georgopoulos points out, motor cortex does not appear to compute the control signals to individual muscles. This is hardly surprising, given the fact that almost all of the pyramidal-tract activity is filtered through a phalanx of spinal interneurons before reaching any motoneurons. These interneurons are remarkably divergent in their output projections and convergent in their inputs from somatosensory afferents and extrapyramidal descending systems⁴. On the other hand, the organization of sensorimotor-cortical areas might reflect more of the organization inherent in the sensory feedback that is shared with the spinal cord. This information is necessarily closely related to the topology of the musculoskeletal apparatus and skin; there is little possibility or reason for it to be transformed into extrapersonal space co-ordinates en route through the dorsal column and thalamic nuclei⁵. The most

salient sensory feedback for unobstructed reaching would be kinesthesia, which appears to be derived largely from muscle-spindle primary endings that have precisely the sorts of direction and velocity tuning that have been found in motor-cortical cells⁶. These signals have an orderly relationship to hand movement because of the mechanical linkage imposed by the musculoskeletal apparatus of the arm. More importantly, in a kinematically redundant system, the preferred direction in extrapersonal space of the individual signals might rotate with the origin and posture of the movement, whereas extrapersonal-space vectors based on the end point of the movement should not. Furthermore, there is at least the possibility that a co-ordinate frame constructed from intrinsic sensors might produce an orderly topical map for motor cortex, which is conspicuously lacking in population-vector theories.

This is not to say that motor cortex computes in a reference frame that is defined by muscle spindles, but is rather to show how little can be said about this computational problem by creating and displaying population vectors in any arbitrary co-ordinate frame. The 'top-down theory of computation' approach to the visual system is useful because the hypotheses that are derived from a theory about perception can be tested psychophysically. A 'top-down' theory of sensorimotor control must be integrated 'bottom-up' with musculoskeletal mechanics and spinal circuitry in order to understand whether any particular hypothesis actually offers a test of the theory or simply the inevitable consequences of trigonometry and newtonian mechanics.

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Reply

The population-vector coding hypothesis (PVCH) has been stated previously, as well as in my *TINS* article¹; namely, that the weighted vector sum of directionally tuned cells yields a population vector that points in the direction of the movement. The procedure for deriving the population vector has also been clearly explicated; that is (1) the direction space is sampled by movements in different directions while the discharge rate of a given cell is recorded; (2) the presence of directional tuning is determined using standard statistical methods; and (3) the population vector is calculated as the vector sum of single-cell vectors weighted by the change in cell discharge. The PVCH has been applied successfully to the coding of movement direction in several motor structures (see Ref. 2), extended to visual space³ and generalized to abstract spaces⁴.

An important aspect of the PVCH is that no special assumptions are required as to how the directional tuning arises. The directional tuning is defined operationally by the procedures above and is, conceptually, at the same level as, for example, the orientation tuning in the striate cortex, the orientation, direction and speed tuning in the middle temporal visual area⁵, and the directional saccadic tuning in frontal-eye fields⁶: these are all experimental facts. In none of these cases has the concept of tuning been challenged on the basis of understanding (or lack thereof) of all the events leading from the retina to the visual-cortical circuitry, or from the frontal cortex to the eye muscles.

Loeb, Brown and Scott propose a specific hypothesis concerning the mechanism of directional tuning of single-cell activity; namely, that 'the activity of individual neurons and columns of the motor cortex is invariantly related to the direction of the movement of the end point of the limb, as represented in an extrinsic co-ordinate frame'. This is a straw hypothesis that the authors put up and then pull down themselves. Fortunately, it is their hypothesis, not mine, and obviously has nothing to do with the PVCH, which does not rely on any particular explanation as to how the directional tuning arises.

The success of the PVCH under conditions using an altered arm posture⁷ (see also Fig. 1 in Ref. 1) has demonstrated the robustness of this hypothesis. The computation of the population vector under these conditions not only does not dismiss but, on the contrary, takes explicitly into account the current state of affairs with respect to the preferred directions and discharge rates obtained under the new conditions to which the motor system has been adapted.

The omission by the authors of the direct feed-forward corticomotoneuronal projections (see Ref. 8), as well as the lack of any discussion of the relationship of motor-cortical activity to isometric force, are understandable given the apparent novel hypothesis advanced by the authors that 'a co-ordinate frame constructed from intrinsic sensors might produce an orderly topical map for motor cortex'. Indeed, since the authors treat the motor cortex as a sensory area, there is no room left for motor functions!

Finally, the potential role of muscle afferents in shaping motor-cortical discharge has been discussed in my *TINS* article¹. However, it is obvious that the motor cortex is not just a glorified spindle-discharge processor, and movement-related patterns of motor-cortical activity are essentially unchanged after deafferentation⁹ or section of the dorsal

columns¹⁰. If one takes into account the experimental findings reviewed elsewhere¹², the motor cortex emerges as a processor of complex, multidimensional, polymodal information in motor control, and our challenge is to elucidate this complex function rather than try to force it to fit on an arbitrary procrustean bed.

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The Flybrain Project

Editorial changes to our article 'The Flybrain Project' (Ref. 1) might have conveyed an impression that the authors were jointly responsible for Flybrain, an on-line atlas and database of the nervous system of *Drosophila*. The article was in fact intended merely as a report of the Göttingen workshop 'A Computerized Atlas of the *Drosophila* Brain', for which MH and KK were the organizers. Flybrain itself is co-ordinated by three principal investigators (Karl-Friedrich Fischbach, Kim Kaiser, and Nick Strausfeld; for further information see Ref. 2). We apologize if any misunderstandings have been caused. The omitted Flybrain accession numbers for the two figures in the *TINS* article are AA00015 (Fig. 1) and AA00030 (Fig. 2).

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