This process must be repeated at short time intervals during the motion.

Having said this much, one may hypothesize that a similar control problem must be solved by a vertebrate moving its arm, and thus one would expect to find neurons that fire at rates corresponding to required joint motion directions. Perhaps these neurons are also tuned broadly. Ratios of their weights $w_i(\mathbf{M})$ to the weights of neurons found in (*1*) might be related to entries in matrix *J*.

However, the problem is more complex because of the fact that vertebrates' muscles are not connected one-to-one to their joints. A matrix similar to *J* that describes such relationships would not be square and would be more complex than *J* for a typical robot arm. Moreover, there are numerous coordinate systems involved: **X**, corresponding to Cartesian coordinates; **Θ**, corresponding to arm joints; **A**, corresponding to the arm's actuators (muscles or motors); **E**, corresponding to eye movements; **H**, corresponding to head movements; and so forth.

One would expect there to be relevant Jacobian matrices relating Cartesian and joint, Cartesian and actuator, arm and actuator, and Cartesian and eye coordinates. For example, afferent information to the arm must be in actuator coordinates, but efferent information from the arm concerning its position is in joint coordinates.

The findings in (*1*) relate specifically to Cartesian coordinates. Given the above discussion, it is unlikely that the coding described in (*1*) relates to arm control. Rather, it is more likely that it relates to the "error vector" joining the hand's initial or current position and the desired one. This vector is perceived by means of eye movements and subsequent processing of visual information, and it influences the planning of the arm's motions. Such plans appear then to be abstract in the sense that they apparently are made in Cartesian space, when in fact they will be executed in actuator space and monitored in joint and eye space. One would thus expect to find many sites of neuronal activity with different codings, or to find within one site different groups of neurons with different codings corresponding to the coordinate system(s) they relate to.

The hypothesis that the direction vector identified in (*1*) is in fact the error vector defined above is consistent with the remark in reference 15 of (*1*) concerning arbitrariness of motion origin.

It would be interesting to see complete experimental results of the measurements taken with the sonic sensor attached to the monkey's hand. Typically hand motions are not straight lines in Cartesian space, so the error vector's length and direction will likely change during the motion. If this is true, then time variations in neuronal direction coding will be correlated with readings from the sonic sensor.

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Response: Whitney states lucidly the correspondence between the problems faced by the central nervous system (CNS) and by robotics in controlling movements of the arm. He also states clearly the sequence of steps and coordinate transformations involved in a mathematical solution of these problems. These steps may indeed be appropriate, or even necessary, for the solution of the problem in robotics, but it is unclear whether the CNS follows the same route. As Whitney points out, the situation with muscles and joints is much more complicated than that in robotic arms. It is possible that the implementation of a trajectory by the CNS involves "smart" solutions (*1*) that might employ specialized neural networks and might have been arrived at by a long evolutionary process of "trial-and-error" learning.

An example is provided by the spinal cord: the ongoing elucidation during the past two decades of anatomical and physiological substrates involved in the control of such biomechanically complicated acts as locomotion (*2*) and reaching (*3*) attests to the plausibility of the idea that ad hoc solutions rather than general purpose, step-by-step solutions of the inverse kinematics problem might be used by the CNS. The key elements in these spinal circuits are interneurons, and a common theme in the organization of the inputs and outputs of these interneurons is an appreciable degree of convergence and divergence. For example, propriospinal neurons involved in the implementation of reaching movements project to several motoneuronal pools that innervate muscles acting at several joints; these propriospinal neurons receive convergent inputs from several supraspinal structures and from limb afferents arising from many parts of the limb (*3*). Thus, the action of the propriospinal system seems to be exerted on the motor apparatus of the limb as a whole and, in a corresponding way, the supraspinal structures that address that system would seem to be addressing the limb as a whole. In fact, the principles of convergence and divergence of descending and peripheral inputs to spinal neurons is pervasive and extends to other classes of interneurons (*4*) and to the cells of origin of pathways that carry information from the spinal cord to supraspinal structures (*5*).

Stated another way, these findings indicate that motor spinal neural circuits do not relate to muscles or joints in a one-to-one fashion (*6*). It is also remarkable that supraspinal systems, including the corticospinal system arising from the motor cortex, address the spinal cord in a divergent fashion (*7*). The essence of the interactive, multijoint, multimuscle nature of spinal and supraspinal motor control of reaching movements involving the whole limb still evades us. Its elucidation may provide the answer to the question of how the CNS actually implements a desired movement trajectory (*8*).

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