this ancient river valley contained a continuous sequence of 3 m thick calcareous diatomite with radiocarbon ages of 7780 ± 90 years at the base and 3805 ± 65 years at the top (Hv 14446 and Hv 14441). This inner Saharan archipelago of brackish to freshwater lakes was possibly linked to the Mourdi depression (*10*).

At Nukheila, only 40 km east of this Holocene river, rhinoceros bones were found in lacustrine marls (*11*). The lake marl terrace here is located 6 m above the present level of the hypersaline ground water fed–lake. The pollen-bearing algal muds of the Oyo complex (*12*) also belong to this archipelago of early to mid-Holocene lakes and correspond to those at El Atrun and Selima. The latter existed between about 9200 and 4500 years ago (*13*). Finally, the fossiliferous lake chalk sequences 80 km northwest of Laqiya Arbain dated between 7500 and 6500 years ago fit into this picture (*14*).

It is now clear that there is substantial evidence of a rainfall regime supporting an early Holocene ground-water recharge and that this evidence culminates in the lower Wadi Howar (18°N). It was surrounded by the early Holocene Sahel zone, which stretched about 500 km further north than today. Since the number of paleoclimatic indicators decreases northward of Wadi Howar, we conclude that rainfall was due to tropical influences from the south. These findings show parallels to paleoclimatic evidence from the central and western Sahara. Lake Chad (14°N) as well as the Mali lakes (21°N) record high levels and humid phases between 9500 and 4500 years ago (*15, 16*).

The extreme summer aridity (*17*) of the Sahara was suspended in early Holocene time. At present it is due to the sinking air masses in the delta of the tropical easterly jet stream, which in turn is caused by high summer temperatures in the central Asian mountains. Should the proposal of a persistent glaciation in the Tibetan mountains during the early Holocene prove correct (*18*), summer paleorainfall in the eastern Sahara could be explained by a continuing weakening of the easterly jet stream.

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1. This Holocene wadi flowed across Serir Tibesti in southern Libya (present rainfall, 2 mm/year) into Serir Calanscio (present rainfall, 20 mm/year) (Fig. 1b). Along its course calcitic lake deposits, radiocarbon dated to 8800 to 5000 years ago, were formed in freshwater lakes. In Egypt's Western Desert however (1 to 2 mm of annual rainfall), silty clayey semi-lacustrine sediments prevail in deflation hollows at numerous sites, mainly at the base of escarpments, during the period between 10,000 and 4,000 years ago; this reflects a west to east decrease in rainfall at a latitude of 23°N in the early Holocene. See H.-J. Pachur, *Berl. Geogr. Abh.* **17**, 62 (1974); C. V. Haynes, in *Desert Landforms of Southwest Egypt: A Basis for Comparison with Mars*, F. El-Baz, T. A. Maxwell, Eds. (NASA CR-3611, Washington, DC, 1982), p. 91.
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3. D. Newbold, *Sudan Notes Rec.* 7, 43 (1924); R. Said [in *The Geological Evolution of the River Nile* (Springer, New York, 1981)] does not even preclude the Wadi Howar as a possible source of the late Pliocene Paleonile about 2 to 4 million years ago.
4. Geological Map of the Sudan 1:2,000,000 (BRGM, Orléans, 1981); B. Meissner and H.-J. Schmitz, *Berl. geowiss. Abh.* (*A*) **47**, 87 (1983). The region under discussion here was not covered by the Columbia Shuttle Imaging Radar (SIR-A) which revealed subsurface valleys in the Selima Sand Sheet about 400 km further north [J. F. McCauley *et al.*, *Science* **218**, 1004 (1982)].
5. The capital of the Early Christian kingdom of Makouria about A.D. 550. On the south bank of Wadi Howar, 150 km west of the Nile, there is a hitherto unknown rectangular fortress about 150 m in diameter with stone walls more than 5 m thick, discovered in 1984 by an archeological expedition from the University of Cologne. We could fix the location by satellite Doppler positioning at 17°48′24″N, 29°59′18″E (Fig. 1a, locality 6). The locations of the capital and this fortification indicate the importance of the lower Wadi Howar as a transit route to Chad as late as the sixth century A.D.
6. It must be emphasized that some of the skeletons found were not buried, but embedded in the completely undisturbed sediment. For that reason death may have been accidental, possibly due to drowning.
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8. Charophyta were identified by I. Soulié-Märsche, Montpellier.
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10. The Ptolemaic world map (about A.D. 150) shows marshes inhabited by tortoises in this region. Actually we found tortoise and giraffe remains in calcareous mud deposits reaching thicknesses of about 3 m and containing freshwater Mollusca and Ostracoda. C. V. Haynes [*Natl. Geogr. Res.* **16**, 269 (1985)] refers to part of this abandoned valley calling it "Wadi Mahgour."
11. H.-J. Pachur and H.-P. Röper, *Berl. geowiss. Abh.* (*A*) **50**, 249 (1984).
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13. The early Holocene lake at Selima was 14 m deep and occupied an area of more than 11.5 km^2. There is a complete sedimentary sequence ranging from lake sands, algal mud, freshwater chalk, rhythmites, aragonitic lake chalk, and diatomite to sulfatic, highly saline sediments.
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Technical Comments

Neuronal Coding and Robotics

Apostolos P. Georgopoulos *et al.* (*1*) present a study of neuronal coding of direction of arm movements in monkeys. They show that a group of neurons exist in the motor cortex which have firing rates that can be combined vectorially to predict the direction of arm movement.

In robotics, an analogous problem exists, called kinematic inversion (*2*). The issue is to decide how to drive the motors of a robot arm so as to drive the hand in a particular direction in Cartesian coordinates. The problem is interesting because the individual joint actuators do not contribute uniquely to any one Cartesian direction. Instead, their contributions are "broad" in the sense of (*1*): several motors contribute to motion along a single Cartesian direction. Furthermore, each motor must, in general, vary its contribution during a motion because the geometric relations between single motor contributions and ultimate hand direction vary as the arm moves and changes shape.

To be more precise, the problem in (*1*) is called the velocity control problem in robotics, wherein the controller must choose velocities for the joint actuators in order to obtain a velocity vector for the hand in Cartesian coordinates. This Cartesian velocity vector corresponds to vector **M** in (*1*). This problem was solved (*3*), as follows: Let X represent a position and V a velocity, respectively, in Cartesian space. Let Θ represent a vector of arm joint positions and Ω a vector of arm joint velocities. We say that Θ and Ω exist in joint coordinates. Then V and Ω are related by

$$V = J(\Theta)\,\Omega \tag{1}$$

where J is called the Jacobian matrix of the arm and consists of partial derivatives of Cartesian axis motions with respect to joint axis motions. In general, J is 6 × 6 because Cartesian motions comprise three translations and three rotations, and arms able to make such motions must have at least six joints. The velocity control problem is solved by writing

$$\Omega = J^{-1}(\Theta)\,V \tag{2}$$

The robot's control computer takes in V commands, reads Θ, calculates J and J^{-1}, and finally calculates Ω and sends it to the motors as individual command velocities.

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: $\mathbf{X}$, corresponding to Cartesian coordinates; $\boldsymbol{\Theta}$, corresponding to arm joints; $\mathbf{A}$, corresponding to the arm's actuators (muscles or motors); $\mathbf{E}$, corresponding to eye movements; $\mathbf{H}$, 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.

DANIEL E. WHITNEY
Charles Stark Draper Laboratory, Inc.,
555 Technology Square,
Cambridge, MA 02139

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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*).

APOSTOLOS P. GEORGOPOULOS
ANDREW B. SCHWARTZ
RONALD E. KETTNER
Philip Bard Laboratories of Neurophysiology,
Department of Neuroscience,
Johns Hopkins University,
School of Medicine,
725 North Wolfe Street,
Baltimore, MD 21205

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