

Motor Cortical Activity During Sinusoidal Tracing

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Abstract

Single cell activity recorded from the proximal arm area of motor cortex during the performance of arm reaching tasks can be related to the direction of movement. This was found for single straight movements made directly to a target and for movements in which direction changed continually. Responses from a population of 226 directionally-sensitive cells were combined to form neural images of the trajectory. The construction of these images suggests that trajectory-related information in the motor cortex is generated incrementally throughout the task and is coded in an instantaneous coordinate system.

The motor cortex historically has been considered important in controlling volitional behavior. This is interesting because the recording of cellular activity from the motor cortex during volitional movement has taken place only within the last 20 years. This region of cerebral cortex was implicated in volitional control many years before the first recordings in experiments that used lesions or electrical stimulation in anesthetized animals. In primates, lesions of primary motor cortex result in minor movement deficits, mostly confined to the distal extremities (deficit in precision grip). Electrical activation of motor cortex results in movements that at best produce compound muscle contractions at one or two joints. Most of the time, such activation results in twitch-like contractions in one or several muscles. Beginning in the late 1960s studies comparing motor cortical activity to volitional movements were designed to examine movement about a single joint. Animals were rewarded for flexing or extending the elbow or wrist. These studies showed that single cell activity was related to the force used to accomplish the task in a certain direction (flexion or extension).

In the late 1970s and early 1980s, motor cortical physiologists began to look at unrestrained, multi-joint movements. One of these studies, (2) used a task in which the animal moved a freely movable handle over a surface. The animals were rewarded for moving the handle from a target in the center of the surface to one of eight radially-oriented targets. These trajectories were relatively straight, so the movements were made in eight equally spaced directions. Many cells recorded in the proximal arm area of motor cortex were found to have discharge rates related to the direction of movement. The discharge rate was averaged over each trial from the time the radial target was presented (go) to the time the

animal completed the movement. Therefore, one number, average discharge rate, could be compared to the direction of movement to each of the eight targets. When these two parameters, average discharge rate and direction, were compared it was found that a cosine tuning function spanning the entire directional domain (0, 360 degrees) could describe much of the data. Each cell seems to code for movements made in any direction. The movement direction which elicits the maximum discharge rate for a particular cell is considered that cell's "preferred direction." The range of preferred directions for a population substantially covers the directional domain in a homogeneous manner.

All cells of the directionally-sensitive neuronal population are coding for movement direction simultaneously. This suggests the population vector hypothesis: each cell in the population is represented by a vector in the cell's preferred direction. The magnitude of this cell vector is adjusted by the discharge rate of the cell. The resultant population vector formed by the vector sum of all the cell vectors of the recorded population, points in the direction of movement. This has been confirmed for reaching movements in two- and three-dimensional space (3,4,5,7).

In summary, proximal-arm single motor cortical cells have been found to code (by their average rate of discharge) any direction of arm movement made. Each cell has a preferred direction of movement to which it fires maximally. Knowing each cell's preferred direction and its rate of discharge during a reaching movement makes it possible to combine responses of a population of motor cortical cells to generate an accurate prediction of the direction of the upcoming movement. Originally this work focused on movements that involved single directions (movements directly to a target). The observation that these trajectories were essentially straight made it possible to use a single number (average rate) to describe each neuron's activity over the entire movement.

Recent studies have begun to examine movement-related neuronal processes that involve changes in direction. One experiment of this type (1) was designed to examine the neuronal processes taking place in motor cortex as an animal selected a direction to move relative to a stimulus. The task again used a radial arrangement of eight targets. As the animal holds at a center target in the middle of the array, one of the eight radial targets appeared. Instead of moving directly to the target, the animal was rewarded for moving 90 degrees counterclockwise to the lit target. A similar task performed on human subjects found that as the angle between the target cue and the calculated target was varied, the subject's reaction time increased linearly with the calculated angle. These results and those from experiments in which subjects were asked to identify rotated objects suggested that the subjects are doing a "mental rotation" in the task. This was

substantiated in the primate recording experiments. Populations of neurons were again recorded from the proximal arm area of motor cortex. Population vectors were constructed from these cells every two milliseconds beginning at the time of the cue presentation. The population vector initially pointed to the cue, then changed direction until it was pointing at a position 90 degrees counterclockwise from the cue.

Another task utilizing directional changes has also shown that the motor cortex may be important in generating volitional aspects of movement. Monkeys were trained to trace sinusoids on the surface of a touch-screen monitor. Initially a target circle would appear on the left or right edge of the screen. The animal would touch and hold its finger in the circle. After a random interval, a sine wave would appear on the screen and the animal would trace the shape across the screen with its finger. Five sinusoids were traced, with peak to peak amplitudes ranging from three to 12 centimeters and with spatial frequencies of one to three cycles per 23 centimeter screen. Each sinusoid was traced from left to right and back again. The monkeys (two rhesus males) performed these tasks smoothly with their index fingers. Each cell was recorded in the following manner: The monkey worked continually performing the center-out task (center start position, eight radial targets). When a cell was isolated, (platinum-iridium, glass-coated electrodes for extracellular recording, 1.5 to 4 megohms), activity was recorded as the monkey repeatedly moved to each of eight targets, five times (random block design). The average interspike interval for trials to each target was calculated. The inverse of this measure or average instantaneous rate was regressed to a cosine tuning function. This function relates firing frequency to movement direction. Cells (n=226) recorded from four hemispheres of the two monkeys were found to have a significant fit ($r^2 > .7$) to the cosine tuning function.

When the center-out task was completed, the activity of the same cell was recorded as the animal performed the sinusoidal task. The question could then be asked: Does the relation between discharge rate found in the center-out task (movements made in a single direction) remain valid in the sinusoidal task where direction changes continually during the movement? To answer this, a predicted discharge rate was calculated for each cell. This was accomplished by calculating (at 20 msec intervals) the direction of the monkey's arm movement using the coordinates of its finger position on the touch screen. The predicted discharge rate was found by using the tuning function:

$D = B_0 + A * \cos(\text{movement direction} - \text{preferred direction})$. B_0 , A and the preferred direction were derived from the center-out task. This analysis showed that the predicted and actual discharge rate (calculated from the fractional interspike interval) covaried with the predicted rate, lagging as

determined by cross-correlation, the actual rate by approximately 120 milliseconds. This suggests that the cells' directionally-related firing patterns lead the corresponding movement by that interval.

Population vectors were also constructed in this task. Each sinusoidal trial was normalized to 100 bins starting 120 milliseconds before the animal began its movement. The instantaneous rate calculated from the average fractional interval in a particular bin was used to weight each cell's contribution (cell vector in the cell's preferred direction) to the population. This resulted in a series of 100 population vectors for each sinusoidal trajectory. The vectors were combined tip-to-tail and formed a neural image of the trajectory which closely approximated the actual sinusoidal trajectory.

Vectors have both direction and magnitude. If a trajectory is broken into segments, each segment would be pointing in an instantaneous direction and have a length proportional to instantaneous tangential velocity. The finding that population vectors can be used to create an image of the trajectory suggests that they represent instantaneous velocity as well as direction. This was examined by plotting population vector magnitude versus instantaneous velocity. The two were highly correlated (Fig. 1). The issue could also be examined by constructing hybrid vectors that have direction specified by the population, but with a magnitude equal to instantaneous directional velocity. Hybrid trajectories constructed from these vectors are very similar to trajectories constructed from population vectors suggesting that instantaneous velocity and population vector magnitude are equivalent.

This work is all based on the simple finding that many cells in motor cortex encode movement direction in a way that can be modeled with a cosine function. This is very similar to work done with neural networks in which the activity of an artificial neuron is related to the cosine of the angle between an input vector (represented in an N dimensional signal space) and the orientation of an N dimensional vector representing "transmittances" or sensitivity of the artificial neuron. As the two vectors become more similar, the cosine of the angle between them approaches one (6). Although direction of movement is at best three-dimensional, it may account for a large portion of the signal space to which neurons in this region of motor cortex are sensitive. These experiments show that this cosine relation is valid incrementally over a movement. Adding population vectors tip-to-tail indicates that the coordinate system in the motor cortex is instantaneous. (Supported by NIH grant NS26375).

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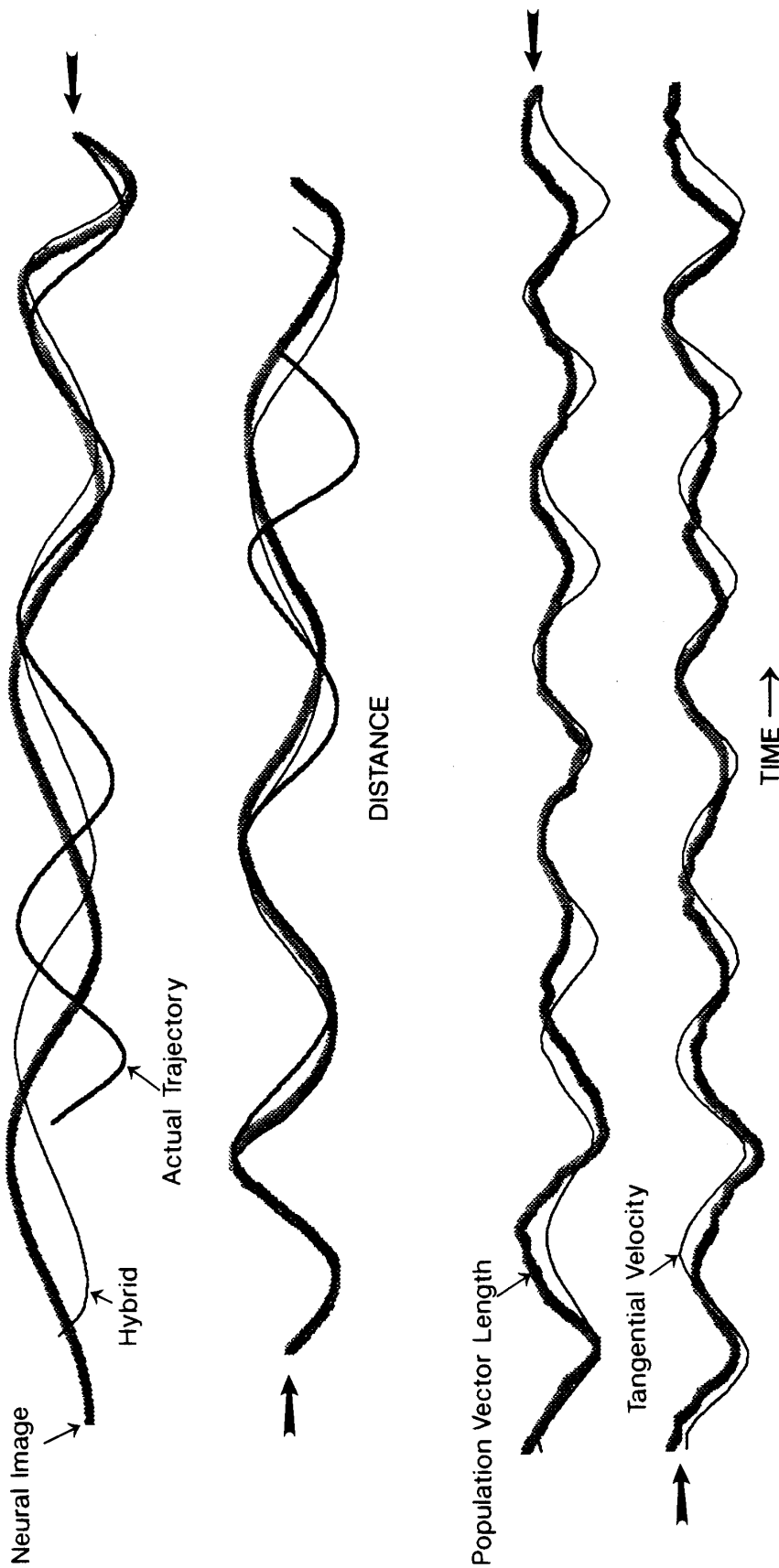


Figure 1.

A. Neural images were constructed by adding 100 population vectors tip-to-tail. The population vectors were converted from units of spike frequency to distance by multiplying Δx and Δy by a constant N , where $N = \text{maximum instantaneous velocity} / \text{maximum population vector length}$. Hybrid trajectories were calculated by adjusting the magnitude of each population vector to match that of the instantaneous tangential velocity at that point in the trajectory. This sinusoid was 6 cm peak-to-peak and 23 cm long. It was traced from left to right and back again (indicated by the arrow in the figure). Ordinate and abscissa are in units of arbitrary distance.

B. Instantaneous velocities compared with population vector length from the data presented in A. The two traces in each direction (specified by arrow) are again normalized by their maxima. The ordinate is in units of arbitrary velocity and spikes/second. The abscissa is in normalized time units.