Representation of Multiple Kinematic Parameters of the Cat Hindlimb in Spinocerebellar Activity

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Bosco, G. and R. E. Poppele. Representation of multiple kinematic parameters of the cat hindlimb in spinocerebellar activity. J. Neurophysiol. 78: 1421–1432, 1997. Dorsal spinocerebellar tract (DSCT) neurons have been shown to transmit signals related to hindlimb position and movement direction in the anesthetized cat. Because both parameters may be encoded by single neurons, we examined the extent to which their representations might occur sequentially or simultaneously by recording unit activity while the hindlimb was moved passively in the sagittal plane by a robot arm. A center-out/out-center paradigm moved the foot 2 cm from a given position radially to eight positions located 45° apart, holding each position for 8 s. Another paradigm moved the foot along various paths to 20 positions distributed throughout most of the limb’s workspace. With each paradigm, we could assess the activity related to foot position and the direction of movement to each position. Modulation of unit activity evoked by center-out/out-center movements was determined for each 1-s postmovement interval by use of a cosine tuning model that specified modulation amplitude and preferred direction. Of 125 units tested, 82.4% were significantly modulated ($P < 0.05$) according to this model. We assessed the relative contributions of position and movement by taking advantage of the fact that directional modulation following center-out movements to a common position could only be related to the movement, whereas that following the center-out movements related to both position and movement. The results suggested a simultaneous modulation by these two parameters. Each cell could be characterized by a similar preferred direction for position or movement modulation and the distribution of preferred directions across cells clustered significantly along an axis close to the limb axis. When the limb axis was rotated, the unit preferred directions rotated similarly, on average. Unexpectedly, we found the activity of more than half the cells to be modulated for $\geq 8$ s after out-center movements, implying a persistent movement-related activity well after a movement is completed. These findings were confirmed and extended with the second paradigm by using a multivariate regression model that included terms for position, movement, and their multiplicative interaction. The activity of 81.3% of the 97 neurons tested fit the model ($R^2 > 0.4, P < .0001$); 31.6% were modulated exclusively by foot position, and 58.2% simultaneously by both position and movement, with significant interaction. We conclude from our results that DSCT neurons may be modulated simultaneously by limb position and movement, and their preferred directions tend to align with the limb axis. The modulation is interactive such that movement modulation amplitude depends on limb position, and many cells also retain a memory trace of recent movements. The results are discussed in terms of a possible role for the DSCT in encoding limb compliance.

INTRODUCTION

Early investigations of dorsal spinocerebellar tract (DSCT) neurons led to their characterization as transmitters of localized sensory receptor information to the cerebellum (see Bloedel and Courville 1981; Oscarsson 1965 for reviews). More recent studies have shown, however, that the activity of these cells correlates more consistently with whole limb kinematic variables than with single joint angles or the lengths of specific muscles (Bosco et al. 1996; Osborn and Poppele 1993). For example, the activity of a large number of DSCT neurons is broadly tuned with respect to directions of hindlimb displacements (Bosco and Poppele 1993), and the complex patterns of activity evoked by small amplitude perturbations of the hindlimb are also broadly tuned with respect to the direction of whole-limb perturbations (Bosco and Poppele 1996). From an analysis of population responses to a variety of limb movements and postures, we concluded that DSCT activity represents the movement and position of the foot relative to the most proximal joint, the hip. This is equivalent to a representation of the limb axis (an axis connecting the hip and the foot), which can be described in the polar coordinates of the axis length and orientation.

Our findings imply that individual DSCT neurons may encode at least two limb kinematic parameters in this framework, namely foot position and the direction of foot movements (Bosco et al. 1996). This raises the question of how such multiple parameter coding might be implemented by these cells. To address this question, we attempted to relate the DSCT representation of kinematic limb parameters to kinematic representations found in other parts of the CNS. As a basis for comparison, we cite two examples from brain areas involved in sensory-motor integration to illustrate different ways in which single neurons have been found to encode multiple kinematic parameters.

In the motor and premotor cortex of behaving monkeys, the activity of many neurons is found to be broadly tuned with respect to the direction of arm reaching movements (Georgopoulos et al. 1982). In addition, Fu et al. (1995) have shown that neurons recorded during a reaching task also may encode both target distance and position. Their data strongly suggested a strict temporal ordering in which activity related to movement direction (occurring $\sim 100$ ms before the movement onset), is followed sequentially by activity related to target position ($\sim 50$ ms after movement onset) and distance ($\sim 250$ ms after movement onset). According to the authors, this temporal parcellation of unit activity would prevent any ambiguity in interpreting the activity of a neuron that may encode different parameters.

A different mechanism for encoding multiple parameters may be used in the posterior parietal cortex to encode the location of a visual target. Andersen et al. (1985) have shown that the response to target position in retinotopic coor-
dinates may be modulated by the position of the eyeball in the orbit or, more generally, by the direction of gaze (Brotchie et al. 1995). In this case, the two signals, one representing target direction and the other gaze direction, are not segregated but rather interact in a multiplicative way to form gain fields of activity whereby the magnitude of the response to a given target is modulated by gaze direction. The interpretation given to this finding came from neural network modeling experiments in which units having gain fields were found to encode an intermediate step in the process of transforming the representation of a visual target from retinotopic to head- or body-centered coordinates (Zipser and Andersen 1988). Gain fields are not unique to posterior parietal neurons because place cells in the hippocampus (Markus et al. 1995; Muller et al. 1994) and neurons in the ventral premotor and prearcuate cortex (Boussaoud et al. 1993) and in the superior colliculus show similar encoding properties (Van Hopstal et al. 1995).

These examples illustrate that information about several parameters may be expressed in the discharge of a single neuron simultaneously by means of some interaction between inputs or in temporally distinct modules. Within this framework, we analyzed the activity of DSCT neurons during passive movement and for various positions of the hindfoot to determine the extent to which coding of movement direction and foot position may correspond to one of these examples.

**METHODS**

We recorded extracellularly from the axons of DSCT neurons in the dorsolateral funiculus at the T10–T11 level of the spinal cord using insulated tungsten electrodes (5 MΩ, FHC, Brunswick, MN). Experiments were performed with 11 cats anesthetized by an intraperitoneal injection of barbiturate (Nembutal, Abbott Pharmaceuticals; 35 mg/kg ip initial dose followed by periodic intravenous administration to maintain deep surgical anesthesia throughout the entire course of the experiments). The units were identified as spinocerebellar by their responses to activation of the inferior cerebellar peduncle and/or the white matter of the anterior lobe, as described previously (Osborn and Poppele 1989).

**Experimental paradigms**

The animals were mounted in a frame which allowed the left hindlimb to move freely about the hip, knee, and ankle joints. The hip was fixed in position by pins in the iliac crests, and the foot pad was attached to a small platform (1.5 × 1.5 cm) with velcro (see also Bosco et al. 1996). A small robot (Microbot Alpha II, Questech) held the platform with the foot attached and moved it to various positions distributed in the sagittal plane within the limb’s workspace (see Fig. 1). Each movement was made at the same speed and completed by the robot in <400 ms. Once a position was reached, the foot was held still for 8 s before moving to the next location.

We recorded the movements and positions of the hindlimb with a video camera (Javelin Model 7242 CCD camera). For this purpose, we placed markers on the skin over bony landmarks at the hip, knee, ankle, and foot and positioned the camera normal to the plane of the hip and knee joints. In spite of the inherent unreliability of this technique, we found that markers at the foot, ankle, and hip were stable for the movements we used in their relation to the respective joints (Shen and Poppele 1995). Video images from the CCD camera were stored on conventional video tape and subsequently digitized using the Motion Analysis System (Model VD 110) (see Bosco et al. 1996; Shen and Poppele 1995 for additional analysis detail).

In this study, we used two stimulus paradigms, both of which have been described in other reports (Bosco and Poppele 1993; Bosco et al. 1996). The first paradigm, described in Fig. 1, was very similar to a task first described by Georgopoulos et al. (1982) and extensively used to study the relation of cortical neuron discharge to movement direction in behaving monkeys. In summary, the foot was displaced radially from a center position by 2 cm to eight positions located 45° apart in the sagittal plane. The foot was held in the radial position for 8 s and then returned along the same radius to the center position, where it was held for 8 s before moving to the next radial position in the counterclockwise direction. For analysis purposes, we separated all the trials in which the foot was moved outward (center-out, CO) from those in which foot paths converged to the center position (out-center, OC). Note that the CO movements place the foot in eight different positions, whereas the OC movements all place the foot in the same position (Fig. 1B).

In a second paradigm, also depicted in Fig. 1A, the hindfoot was moved to 20 positions covering a larger fraction of the limb’s sagittal workspace. Movements were made between adjacent positions along the paths indicated by lines in Fig. 1A, and each position was held for 8 s. The sequence of movements was such that the six positions in the center of the workspace (●) were each approached from four different directions but in no particular order. This arrangement allowed us to study the directional sensitivity of DSCT neurons in different areas of the workspace. The 10 positions along the edges (○) were approached from three directions and those at the corners of the workspace from two directions, also in no fixed order. This design resulted in a total of 62 different movements (see Bosco et al. 1996 for further details).

**Unit activity and data analysis**

Unit firing activity was recorded continuously during each paradigm and, for analysis purposes, the recordings were aligned with respect to the onset of each movement. Subsequent statistical analyses were performed on firing rates estimated from the number of spikes in each 1-s postmovement interval. Note that the first time interval includes the movement time.

We used different analysis models to interpret the data gathered with the two stimulus paradigms. The CO/OC paradigm was designed specifically to assess the broad tuning properties of cells for relatively small deviations of the limb from a standard limb posture. We were interested to know how sensitive the cells were to these deviations and the extent to which their responses were cosine tuned, i.e., broadly tuned for a single best direction (see Bosco and Poppele 1993).

The 20-position paradigm tested each cell’s response to limb displacements throughout the much larger workspace depicted in Fig. 1A. In this case, we were interested to find out how consistent the cell’s behavior was in various parts of the workspace and the extent to which the gradient of activity across the workspace was uniform, as we previously found for the DSCT responses to static limb positions (Bosco et al. 1996).

**COSINE TUNING MODEL.** We used the cosine regression model previously described by Georgopoulos et al. (1982) to quantify the modulation of neuronal activity in the CO and OC paradigms

\[ f(\Theta) = f_0 + f_1 \cos (\Theta - \Theta_p) \]  

where \( f \) represents the neuron’s firing rate for a given postmovement time interval following a movement in the direction \( \Theta \). The movement directions were defined with respect to the horizontal, so that \( \Theta = 0^\circ \) is caudal, and \( \Theta \) increases counterclockwise (see
Fig. 1). $f_0$ represents the mean of the firing rate over the eight movement directions, $f_1$ the amplitude of the cosine modulation, and $\Theta_0$ the neuron’s preferred direction, corresponding to the phase of the best-fitting cosine relative to the reference direction, $\Theta = 0^\circ$. The data were considered to fit this model when the coefficient of determination, $R^2$, was $> 0.7$ ($P < 0.05$).

We analyzed the distribution of preferred directions across units using the Rayleigh test (Batschelet 1981). We tested whether the preferred directions were distributed uniformly or distributed with a bias to a particular direction. We also used a variant of the Rayleigh test that detects multimodal circular distributions (Arendse 1978). This is known as the method of doubling angles and consists of doubling or quadrupling the observed angles to estimate a bimodal distribution along a single axis or a quadraramodal distribution along perpendicular axes.

We compared the observed distributions using the Watson test to determine whether two sample circular distributions differ significantly from one another (Watson $U^2$) (Batschelet 1981).

MULTIVARIATE REGRESSION MODEL. We adopted the following multivariate regression model to quantify the relationship between unit firing rates and foot position and movement for the 20-position workspace

$$f(L, O) = \beta_0 + \beta_1 L + \beta_2 O + \beta_3 dL + \beta_4 dO + \beta_5 d^2L + \beta_6 d^2O$$

(2)

where $f$ is the firing rate in a given postmovement interval, $L$ and $O$ are the length and orientation respectively of the limb axis (Fig. 1A). $L$ is the length of the axis in centimeters (distance between the hip joint and the foot), and $O$ is the orientation of the axis with respect to the horizontal ($O = 0^\circ$ is caudal, and $O$ increases clockwise). Because these terms specify the current position of the limb, we will refer to them as position terms. $dL$ and $dO$ are the change in length and orientation between the current position and the position before the most recent movement. Because the movements were all made at the same speed, these terms specify only the direction and magnitude of the movement to the current position, and we will refer to them as movement terms. $L \times dL$ and $O \times dO$ are terms specifying a multiplicative interaction between position and movement. The terms $\beta_3 - \beta_6$ are the regression coefficients. The rationale for choosing this particular set of predictors was provided by some of the experimental findings and therefore it will be discussed in RESULTS.

For the neurons whose activity was considered to fit the model ($R^2 > 0.4, P < 0.001$), we evaluated the relative contribution of each parameter and its statistical significance for each postmovement interval to determine which kinematic parameters (position, movement, or their interaction) the activity related to most directly. As a measure of this contribution we considered the partial $R^2$ ($r^2$), which represents the fraction of the total variance in the data set that can be explained by a particular predictor given the concurrent correlation of the dependent variable with other predictors in the model. The $F$ ratio and the $P$ value associated with the $r^2$ provided a measure of statistical significance. Because position and movement were each represented by two independent variables (length and orientation), we did not compute the $r^2$ for the variables in Eq. 2 individually, but for each pair that defined a kinematic parameter. For example, the relative contribution of foot position was evaluated by computing $r^2$ and relative $F$ ratio and $P$ value ($P < 0.05$) for the combination of length and orientation of the limb axis ($L$ and $O$ in Eq. 2).

DIRECTONAL MODEL. The results of the cosine tuning model may be interpreted directly in terms of a best direction with respect to some reference position. However, this model does not explicitly separate the contributions of position and movement. The multivariate regression model does make this separation by attributing separate coefficients to position and movement effects, but the results of this analysis may not be interpreted directly in terms of directions. Instead, the responses are characterized by gradients of activity with respect to the workspace geometry or with respect to local preferred movement directions. For the position modulation alone, we found previously that the gradients of activity tended to be linear throughout the workspace, corresponding to a plane in $L$, $O$ space (Bosco et al. 1996).

The results of these two types of analysis cannot be compared directly because they are expressed in fundamentally different coordinate systems. The coordinate framework for the cosine model (equivalent to a Cartesian space with linear coordinates centered at the reference foot position) is homogeneous, whereas the framework for the multivariate regression model (a polar coordinate space centered at the hip) is nonhomogeneous because one coordinate has a linear dimension and the other an angular dimension. Furthermore, regression coefficients are highly dependent on the unit of measure used, and therefore cannot distinguish the relative contribution of independent variables having different dimensions. Nevertheless, we were able to compare the positional tuning determined with the two movement paradigms by transforming the foot positions in the larger workspace (Fig. 1A) into coordinates com-
parable to those used for the cosine tuning model. We then applied the cosine model to the foot positions in the larger workspace to determine a preferred direction.

For this purpose we adopted the positional gradient function described by Kettner et al. (1988), which is equivalent to the cosine model in Eq. 1, and may be expressed as

\[ F(S) = f_0 + h|S|^\alpha \cos(\arg S - G) \]  

(3)

where \( F \) represents the firing rate in a given postmovement interval estimated from Eq. 2 for a foot position \((L, O)\). Each position then is reexpressed in the coordinates of a vector \( S \) having its origin at the reference foot position illustrated in Fig. 1, and pointing to the foot position. The distance from the reference position to the foot position is \(|S|\), and the direction is \( \arg S \) (directions defined as for \( \Theta \) in Eq. 1). This reference frame for foot position is therefore the same as that used for the cosine tuning model. \( f_0 \) is the mean firing rate over the entire workspace, and \( h \) is the rate of change of discharge rate with distance from the origin in the direction angle of the maximal activity gradient \( G \). We used the estimated position-related firing rates, \( F(S) \), in a regression analysis (Eq. 3) to determine \( G \) for the full workspace (20 positions in Fig. 1A), and a smaller workspace of 12 positions (the 6 center positions in Fig. 1A plus the 3 positions directly above and the 3 directly below) for each tuned cell.

We used the SYSTAT programs to evaluate each of the above regression models (Wilkinson 1990).

**RESULTS**

The time course of unit activity after limb movement provides a basis for distinguishing between two alternative ways the DSCT might signal both limb movement and position, namely whether the signals occur concurrently or primarily in separate postmovement time intervals. Our previous investigations were focused on either the early postmovement activity to demonstrate directional tuning (Bosco and Popple 1993, 1996) or the later postmovement activity as it related to passive postures (Bosco et al. 1996). In the experiments reported here, we examined the full temporal course of activity resulting from limb movements.

**Behavior in a small workspace**

**BROAD TUNING.** We first examined the behavior of 125 DSCT neurons in response to movements centered on a limb position approximating a normal standing position (Lacqua-niti et al. 1990) using the CO and OC movements described in METHODS and Fig. 1. These were 2 cm movements of the foot occurring in <400 ms, followed by a hold period of 8 s. OC movements all converged at the same final foot position, whereas the CO movements each had a different final foot position located on a circle with a 2 cm radius. In principle it should be possible to separate the effects due to limb movement and position by comparing responses with these two types of movement. Modulation of a cell’s firing rate after OC movements should reflect only movement related responses, whereas the activity after CO movements should reflect responses related to both limb position and movement.

Within this sample of neurons, we found that 103/125 (82.4%) were significantly modulated by CO movements (\( P < 0.05 \); cosine tuning model, Eq. 1 METHODS). The activity of two units is illustrated in Fig. 2. In each set of records, the top rasters represent the activity after CO movements and the bottom rasters the activity after OC movements in the same direction. The responses show an increase or decrease in firing depending on the movement direction, followed by a gradual return toward a more constant activity level in the later postmovement intervals.

The recordings from cell 1892 (Fig. 2A) show the difference between movement-related activity following the OC movements and the additional position-related activity for CO movements. After a 3–4 s transient change in activity in each record, the later activity levels after each of the OC movements are comparable, whereas the later levels are clearly modulated after CO movements. This pattern was not seen in all cells, however. The more commonly observed pattern (57% of modulated cells) is illustrated in Fig. 2B (cell 1967). It is evident in this case that the cell was modulated during the entire 8-s period by both CO and OC movements.

A quantitative analysis of these data are shown in Fig. 3, A and B. The three parameters of the directional cosine model are plotted as a function of postmovement time from directly above and the 3 directly below for each tuned cell. For this purpose we adopted the positional gradient function [crease in firing depending on the movement direction, followed by a gradual return toward a more constant activity level in the later postmovement intervals.

Figure 3C summarizes the normalized behavior of the entire ensemble (\( n = 103 \)) of tuned cells recorded.

The activity after movement was generally well represented by the cosine tuning model as shown by the high \( R^2 \) values. After both the CO and OC movements, the amplitude of the cosine modulation decayed rapidly during the first 1–3 s and then more slowly thereafter. The modulation was always greater for the CO movements, but the preferred directions tended to be the same for both types of movement. The modulation levels in the later postmovement intervals were somewhat variable across cells as illustrated by the two examples in Figs. 2 and 3. A number of cells (43%) exhibited movement related activity for only a few seconds after OC movements. The responses of cell 1892 (Figs. 2A and 3A) illustrate an example in which the modulation after OC movements fell below significance after ~4 s after the movements.

The activity of the majority of cells (57%) was well modulated by OC movements for the entire 8-s period, however (illustrated by cell 1967; Figs. 2B and 3B). Moreover, the movement related activity did not appear to decay further after ~5–6 s. In fact, we observed the activity of one cell for 30 s after each movement and found a persistent level of activity related to movement direction for the entire postmovement period. Such long periods of modulated activity after OC movements were not expected because the movement occurred entirely within the first 1-s interval, and the foot was stationary in the same position after each movement for the remainder of the 8-s hold period.

We will examine this issue further below, in the context of a more comprehensive statistical model. Note, however, that the average population behavior illustrated in Fig. 3C shows a persistent modulation for OC movements lasting ~8 s, and the average modulation amplitude after 8 s was still nearly half of the modulation amplitude observed in the first second. The average \( R^2 \) for tuning in the population does fall below significance after the third or fourth second,
However, due to the behavior of cells like 1892, which had very low $R^2$s in the later postmovement intervals.

The persistence of movement-related modulation suggests that the process responsible for the movement modulation may have long time constants of decay. Alternatively, some mechanical hysteresis may exist in the limb kinematics during these movements such that the limb does not actually return to the same posture after each OC movement.

The latter explanation can be ruled out if we assume that the joint positions represent the relevant kinematic variables. As shown in Fig. 1B, the position of the ankle joint, which underwent the largest movement in this paradigm, differed by <2 mm, or <10% of its total excursion, for each placement of the foot to the center position. This cannot account for the magnitude of the average modulation by OC movements in the latter postmovement intervals, because that was nearly half the magnitude of the modulation induced by the 2-cm CO movements.

In addition to the persistence of modulation after a movement, the cosine analysis also shows two other properties of the cells’ behavior. One is the difference in modulation amplitude for the two types of movement that was evident even during the first postmovement interval (including the movement time). This difference remained constant throughout the postmovement period (in the amplitude plots of Fig. 3), suggesting that it reflects the cells’ responses to limb position. If so, it may be taken as evidence for a concurrent modulation by limb position and movement.

The analysis also suggests that the preferred direction for movement tends to coincide with the preferred position direction. It is implied by the similarity of preferred directions obtained with CO and OC movements for each cell. A significant difference in preferred directions for movement and position would have biased the CO results away from the OC results and also may have caused an apparent change in the preferred direction for position in the later postmovement intervals, as the movement modulation decayed relative to the position modulation. Instead, the two sets tended to coincide and remain constant over the entire 8-s period as illustrated in Fig. 3. In fact, the average difference in the CO and OC preferred directions (Fig. 3C) was nearly zero for the entire 8-s postmovement period. The slight divergence evident in the later intervals can be accounted for by cells which showed no significant modulation (and therefore non-significant direction values) in these intervals for OC movements. We also will examine this point further below.

**Behavior in a large workspace**

**REFERENCE FRAME FOR DIRECTIONAL TUNING.** The results reported above were obtained in a small workspace with the limb axis aligned approximately with the vertical. However, the responses of 53 cells to CO movements also were examined from three different postures to determine how the cells’ preferred directions related to the orientation of the limb axis. Our previous perturbation experiments showed that the population directional responses or directional biases were better related to the limb axis than to the extrinsic vertical (Bosco and Poppele 1996). In that case, the evidence for a limb-centered coordinate system was based on consistent shifts of the mean directional biases of DSCT population.
responses when perturbations were applied in different limb postures. However, the perturbations evoked transient peaks of activity that were each tuned to a different direction and individual cells showed various behaviors in the different postures.

In the current experiments, we used three postures in which the length of the limb axis was identical but its orientation was either vertical or tilted forward or backward by 13°. We compared differences in preferred directions between the forward inclination and vertical (Fig. 4A), between backward inclination and vertical (Fig. 4B) and between forward and backward inclinations (Fig. 4C). Although there was considerable variability across cells, the median difference for each comparison (-----) was close to the differences in limb orientation (---); shifts of 16, -14, and 39°, corresponded to axis rotations of 13, -13, and 26°, respectively.

**DIRECTIONAL BIAS ACROSS NEURONS.** In addition to the tendency for preferred directions to be referred to the limb axis, we also found a tendency for preferred directions to cluster in certain directions. This may be seen in the distributions of directional preferences (Fig. 5), which show that the distribution was neither uniform nor unimodal. The distribution of preferred directions for position modulation (Fig. 5A) was estimated from the modulation in the eighth second after CO movements in 54 cells that showed no significant modulation in the eighth second after OC movements. The distribution suggests at least two and possibly four modes about which the preferred directions clustered. According to the Rayleigh test (see METHODS), there was a significant bias (P < 0.001) toward a bimodal distribution having oppositely directed modes along an axis directed 6° behind the limb axis. A trend toward a quadramodal distribution with a primary axis 19° forward of the limb axis and a second axis perpendicular to the first, was also highly significant (P < 0.001). The distribution of preferred directions for all tuned movements determined for 2 different limb orientation angles, ---, difference between limb orientation angles; ----, median of the preferred direction distributions (n = 53 cells). A: limb vertical vs. limb rotated backward (13°). B: limb vertical vs. limb rotated forward (13°). C: limb forward vs. limb backward (26°).
cells in the eighth second, i.e., including cells that were significantly modulated in the eighth second after OC movements (Fig. 5B; n = 92), was not statistically distinguishable from the distribution in Fig. 5A (Watson test; \( \alpha > 0.1 \)), although it was less likely (\( P < 0.05 \)) to conform to a quadramodal distribution. The axes of the best-fit quadramodal distribution for each case are indicated by dashed lines in Fig. 5, A–C.

The distribution of preferred directions for movement was estimated from the modulation during the first second after OC movements when the modulation due to movement was strongest (Fig. 5C). Again the Rayleigh test indicated a highly significant bidirectional bias (\( P < 0.001 \)) along an axis directed 11° forward of the limb axis, and a less significant quadramodal bias (\( P < 0.05 \)) with a primary axis directed 27° forward. This distribution was again not statistically distinguishable from those in Fig. 5, A or B (Watson test; \( \alpha > 0.1 \)). These results may be compared with the population directional biases reported previously in response to limb perturbations (Bosco and Poppele 1996) (replotted in Fig. 5D).

The multidirectional tuning induced by perturbations was biased in directions along the limb axis and in the backward direction that were similar to those found with the cosine tuning model. However, the perturbation also induced a forward bias, not evident in the distributions plotted in Fig. 5, A–C, that was associated with peaks of activity occurring ~100 ms after perturbation onset. This discrepancy could reflect the difference in time resolution of the measurements in the two paradigms. In the perturbation paradigm, we averaged unit activity over several hundred trials and analyzed each 8-ms postmovement interval, whereas the responses to OC movements were estimated from a single trial with a temporal resolution of 1 s. Thus an activity peak occurring in a specific postmovement interval may have been lost in the average activity level over 1 s.

**interaction between movement and position responses.** The above analysis of cell activity suggests that movement and position signals are processed simultaneously, which raises the question of whether position and movement signals are simply additive, as suggested by the results presented in Fig. 3, or involve some nonlinear interactions.

A graphic examination of the relationship between position and movement sensitivity is provided for two cells in Fig. 6. The preferred tuning directions and modulation amplitudes were determined from the cosine regression for activity recorded during the first postmovement time interval for movements toward each of six foot positions (● in Fig. 1A). They are represented graphically as vectors pointing in the corresponding preferred direction. The lengths of the vectors are proportional to the amplitude of the movement modulation. The activity related to each foot position is represented by the size of the circle and this corresponds to the d.c. coefficient of the cosine regression model (\( f_0 \), Eq. 1, METHODS). The location of each circle corresponds to a foot position.

The amplitude of the movement modulation scales with foot position in a roughly planar manner for both neurons presented in Fig. 6, and the gradients of the position and movement modulation appear to be collinear for both neurons. In other words, the data suggest that the position and movement signals may interact in a multiplicative way forming gain fields of activity.

**multiple regression model.** To have a more quantitative estimate of the gradient of DSCT activity throughout the entire sagittal workspace of the limb, we employed a regression model to quantify the extent to which the modulation of each cell’s firing rate reflected foot position or movement or their combination as a linear sum or multiplicative interaction.

The rationale for selecting the particular set of variables to predict the neural discharge was provided by experimental findings described in earlier reports and also by some of the results reported above. In one earlier study, we found that the best predictors of DSCT discharge related to limb position were the length and the orientation of the limb axis (Bosco et al. 1996). From both the perturbation experiments (Bosco and Poppele 1996) and the data presented above, it appeared that the movement modulation could be represented similarly in a limb-based reference frame. Thus we found it convenient for this study to express both movement and position variables in the polar coordinate system of the limb axis, defined by its length, \( L \), and orientation, \( O \) (Fig. 1A). Finally, we took into account the nonlinear interaction between position and movement described in the previous section by including the corresponding products (\( O^*dO \) and \( L^*dL \)) in the regression model.

The multivariate model based on this choice of variables (\( Eq. 2 \), METHODS) thus included position, movement, and gain terms, and it explained a statistically significant frac-
Using this approach, we found that the majority of the DSCT neurons whose activity was significantly explained by the model (51/79; 64%) were modulated by both position and movement (\( P < 0.05 \)). Most of these cells (46/51; 90%) were modulated by movement and position simultaneously, in agreement with our interpretation of the cosine analysis above. Interestingly the multiplicative interaction terms were significant in almost every case (45/46; 98%). We found only 5/51 (10%) cells in which movement and position modulation occurred serially. Most of the other modulated cells (25/79; 31.6%) were modulated exclusively by foot position, whereas only very few (3/79; 3.8%) were sensitive to movement only (see Fig. 7). These results confirm an earlier report based on a separate population of 78 cells which found that 64% of the modulated cells were tuned to both position and movement direction, while the others were tuned only for position (Bosco and Popple 1993). Table 1 contains a summary of the statistical results obtained with each of the regression models.

The relative contribution of the model terms for position and movement for those cells modulated by both depended on the time course of the neuronal activity. This is illustrated in Fig. 8 for the same two cells depicted in Fig. 6. One (cell 2058; Fig. 8A) was primarily sensitive to changes in orientation and the other (cell 2104; Fig. 8B) was primarily sensitive to changes in length. The time course of the average regression coefficients for all the modulated cells is plotted in Fig. 8C. The coefficients of the position terms (\( L, O \)) were nearly constant throughout the entire 8-s recording time, whereas those of the movement (\( dL, dO \)) and interaction (\( L*dL, O*dO \)) terms decayed progressively during the first 4 s to a level that remained nearly constant for the remainder of the hold period. The time course of the initial decay had an exponential time constant of \( \sim 2.8 \) s, which was quite similar to the time course of the initial decay of the amplitude of modulation after OC movements (time constant \( \sim 2.6 \) s; Fig. 3C). It is not clear to what extent these average trends reflect changes occurring in individual cells or changes across cells, as some cells were no longer modulated by movement in the later postmovement intervals.

![FIG. 6. Effect of position modulation on movement response. For each of the 6 foot positions illustrated (○) in Fig. 1A, the modulation of cell activity is represented by a circle and →. Size of the circle is proportional to the cell’s firing rate at each position. The direction of the arrow indicates the preferred direction for movement from that position, and the length of the arrow the amplitude of the movement modulation. A: cell 2058, modulated by changes in limb orientation, increasing for backward rotations and decreasing forward. The direction of preferred tuning depends on limb orientation, as shown in Fig. 4, and the amplitude depends on the position response. B: cell 2104, modulated primarily by changes in limb length, increasing downward.](image)

![FIG. 7. Different types of modulation found. Results of partial regression analysis to determine which parameter, position or movement, best accounted for a cell’s modulation. 93.7% of the cells were either modulated solely by position (31.6%), solely by movement (3.8%) or simultaneously by both (58.2%). The postmovement activity of the few remaining was sequentially modulated by movement and position.](image)
TABLE 1. Summary of results of cosine tuning and multivariate analysis

<table>
<thead>
<tr>
<th>Cosine tuning model</th>
<th>No. of Cells</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>125</td>
<td>100.0</td>
</tr>
<tr>
<td>Total tuned</td>
<td>103</td>
<td>82.4</td>
</tr>
<tr>
<td>Tuned center-out</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First s</td>
<td>103</td>
<td>100.0</td>
</tr>
<tr>
<td>Up to 8 s</td>
<td>92</td>
<td>89.3</td>
</tr>
<tr>
<td>Tuned out-center</td>
<td></td>
<td></td>
</tr>
<tr>
<td>First s</td>
<td>87</td>
<td>84.5</td>
</tr>
<tr>
<td>Up to 8 s</td>
<td>47</td>
<td>45.6</td>
</tr>
<tr>
<td>Tuned center-out, not out-center for 8 s</td>
<td>54</td>
<td>52.4</td>
</tr>
<tr>
<td>Multivariate model</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>97</td>
<td>100.0</td>
</tr>
<tr>
<td>Total modulated</td>
<td>79</td>
<td>81.3</td>
</tr>
<tr>
<td>Partial regression analysis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>79</td>
<td>100.0</td>
</tr>
<tr>
<td>Position only</td>
<td>25</td>
<td>31.6</td>
</tr>
<tr>
<td>Movement only</td>
<td>3</td>
<td>3.8</td>
</tr>
<tr>
<td>Both</td>
<td>46</td>
<td>58.2</td>
</tr>
<tr>
<td>Sequential both</td>
<td>5</td>
<td>6.3</td>
</tr>
<tr>
<td>Duration of movement modulation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>54 (46 + 8)</td>
<td>100.0</td>
</tr>
<tr>
<td>At least 2 s</td>
<td>47</td>
<td>87.0</td>
</tr>
<tr>
<td>At least 4 s</td>
<td>37</td>
<td>68.5</td>
</tr>
<tr>
<td>At least 6 s</td>
<td>34</td>
<td>63.0</td>
</tr>
<tr>
<td>At least 8 s</td>
<td>34</td>
<td>63.0</td>
</tr>
<tr>
<td>Cells common to both analyses</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td>Cosine</td>
<td>46/125</td>
<td>36.8</td>
</tr>
<tr>
<td>Multivariate</td>
<td>46/97</td>
<td>47.4</td>
</tr>
</tbody>
</table>

However, both cells illustrated in Fig. 8 show similar decay in the movement coefficient values.

The changes occurring across cells in the population are illustrated in Fig. 8D. As we noted above, the duration of movement modulation in the postmovement period was quite variable among cells. Although the movement terms in the regression model were significant throughout the entire postmovement period for most of the cells (34/54; 63%), the movement coefficients became insignificant within the first 6 s for the others. Figure 8D shows the number of cells that continued to be modulated significantly by movement for each of the later postmovement intervals.

DIRECTIONAL SENSITIVITY The cosine tuning model suggested that preferred directions for movement and position tended to be aligned with the limb axis. Preferred directions in the multivariate regression model correspond to gradients of activity, which tend to be linear for both position and movement throughout the workspace in the L, O plane. However, as explained in METHODS, regression coefficients are highly dependent on the unit of measure used and therefore cannot distinguish the relative contribution of independent variables having different dimensions such as L and O.

To compare the positional tuning estimated from the two types of analysis, we used a another version of the cosine tuning model (Eq. 3; METHODS) to estimate tuning directions from responses in the whole workspace. We used the positional coefficients from the multivariate analysis (β1 and β2 in Eq. 2) to estimate the position-related activity at each foot position. These values of activity provided the input to a cosine model based on the distance and direction of each position from a reference position (the foot position in Fig. 1A) to determine the direction of the activity gradient in this homogeneous coordinate system. We performed this analysis for two workspace sizes, one including only the 12 center-most positions (the 6 center positions in Fig. 1A plus 3 directly above and 3 directly below) and the other including the entire workspace of 20 limb positions. The rationale for examining the center of the workspace separately relates to the previous finding (Bosco et al. 1996) that there was a tight planar covariation of limb joint angles within this re-

FIG. 8. Multivariate analysis of postmovement activity in a large workspace. Normalized coefficients for position (●, ▲) and movement (∙, ▼) modulation by limb length (×, ▼) and orientation (●, ▲). A and B: same cells illustrated in Fig. 6, A and B, respectively. Regression coefficients (Eq. 2, METHODS) normalized to maximum values. Cell 2058 maxima: β1 = −0.96 ips/cm, β2 = −0.94 ips/deg, β3 = −22.4 ips/cm, β4 = −2.8 ips/deg. Cell 2104 maxima: β1 = 1.000 ips/cm, β2 = −0.20 ips/deg, β3 = −5.27 ips/cm, β4 = −0.89 ips/deg. C: average normalized coefficients for entire cell sample (n = 51). The normalized coefficients for the nonlinear interaction terms (not plotted) were essentially the same as the movement terms. D: number of cells with significant movement modulation in each postmovement time period indicated.
gion of the workspace that was less pronounced when the more extreme limb positions were taken into account. Nevertheless, the distribution of gradient directions from the reference position to the 12 positions in the center of the workspace (Fig. 9A) was statistically indistinguishable from the distribution of directions for the entire workspace (Fig. 9B; Watson test $\alpha > 0.1$). Both distributions had significant quadrangular components with the primary axis inclined 11 and 12° forward of the limb axis, respectively (Rayleigh test $P < 0.05$). The distributions were also indistinguishable from the distribution of preferred directions for position shown in Fig. 5A (Watson test, $\alpha > 0.1$).

**Discussion**

The results presented here show that most DSCT cells are simultaneously modulated by both the position and movements of the hindfoot. The movement related activity can persist for many seconds after a movement and therefore represents a memory trace of recent movements. Both types of modulation are broadly tuned with respect to position or movement direction throughout the sagittal workspace and the tuning tends to be aligned with limb axis. The two forms of modulation summate to control the cells’ firing rates, and they also interact nonlinearly. In effect, the amplitude of the modulation evoked by a given movement depends on the position of the foot.

The basic findings that lead to these conclusions, namely the persistent responses to movement, simultaneous coding of position and movement direction, and the alignment of unit activity gradients and preferred directions with the limb axis, were quite consistent for two sample populations studied with two different stimulus paradigms covering different extents of the limb workspace and with the use of two different methods of analysis.

**Position and Movement Modulation.** Perhaps the most unexpected finding was the persistent responses to movement observed in a majority of the cells. The role of some sort of kinematic hysteresis in this behavior seems unlikely because we found that the ankle joint, which underwent the largest movement of the free joints, showed no appreciable hysteresis in returning to the center position in the series of CO, OC movements (Fig. 1B). Because the center position always was achieved with an accuracy of $<10\%$ of the center-radial distance, it implies that the joint angles and total limb position were nearly identical for each occurrence of the center position. Furthermore, a purely mechanical explanation cannot account for $\sim30\%$ of the movement-sensitive cells, which showed no persistent modulation beyond 4 s after movement onset. Furthermore, this latter behavior cannot be attributed simply to a lower sensitivity to movement because the same cells often had large amplitude responses to movement (Fig. 2A).

The persistent modulation lasting $\geq 8$ s in $\sim60\%$ of movement-modulated cells is more likely to reflect the properties of sensory receptors or presynaptic circuitry impinging on these neurons. For example, muscle spindles have been shown to exhibit long after-effects that could possibly account for some of the postmovement modulation (Proske et al. 1992). It is also possible that cutaneous and joint receptors might be activated differently by movements to the same position from different directions. In fact, both Pacinian corpuscles (Alvarez Buylla and Ramerez de Arellano 1953) and joint receptors (Grigg and Greenspan 1977) have been shown to exhibit hysteresis. Moreover, we cannot exclude that central modulatory processes may play a major role in this behavior. For example, studies in the locust have pointed out that presynaptic inhibition can play a role in modifying or compensating for receptor hysteresis (Hatsopoulos et al. 1995). Whatever the mechanism though, the net result is that the DSCT activity stores a record of the direction of movement leading to the current limb position for many seconds after the movement. The issue of just how persistent this signal might be when the limb is in more-or-less continuous motion cannot be resolved with our data. However, because an arbitrary sequence of movements (as in the 20-position paradigm) did not seem to bias the results, it suggests the movement modulation might be reset in some way by each movement.

A similar persistence of directional tuning was also reported by Prud'Homme and Kalaska (1994) for neurons in the primate primary somatosensory cortex in response to multidirectional arm movements. Together, their results and ours allow some further interpretation. For one, they imply that directional response persistence does not depend on the experimental preparation or anesthetic state. We found the effect with passive movements in the anesthetized cat, whereas Prud’Homme and Kalaska found it with both passive and active movements in the alert monkey. The two results also imply that this property could represent a common feature of limb proprioception that is present in the early stages of sensory processing at the spinal cord as well as in relatively advanced stages of processing at the cerebral cortex.

Another finding of interest is the nonlinear interaction between position and movement modulation. The multiplicative interaction of a simultaneous modulation by two different parameters is similar to the behavior seen in posterior parietal cortex (Andersen et al. 1985; Brotchie et al. 1995). In that case, responses to visual stimuli are modulated by eye position and by visual stimuli, and the eye position modulation determines the gain of the visual response. In the DSCT neurons, we found that the amplitude of the move-
ment modulation depended on the limb position, and this was accounted for by a multiplicative interaction between position and movement in the regression analysis. The analogy can be taken even further. The parietal cells have a visual response characterized by a retinocentric receptive field having a direction and distance from the fovea. The gaze, or eye position, is relative to the body or head. Analogously, the DSCT responses to movement have a preferred direction relative to the limb axis, and the foot position, which modulates the response, is defined by the length and orientation of the limb axis relative to the hip. Drawing on the hypothesis of Andersen et al. (1993), we suggest the possibility that DSCT activity represents an intermediate step in a transformation of kinematic information from a limb-centered reference frame to a body-centered reference.

The dual modulation of DSCT cells also suggests a dual organization of the circuitry responsible for the modulation. For example, the finding that about a third of the modulated cells were sensitive only to limb position suggests that the position modulation may be elaborated separately from the movement modulation. In fact, the properties of the position modulation (magnitude, gradient) were similar for cells that were modulated by movement and those that were not. Both movement and position modulation were associated with directional gradients that tended to be congruent. However, when we examined movement responses with high temporal resolution, each cell exhibited a sequential tuning to different directions (Bosco and Poppele 1996). Such differences in directional coding for movement and position also suggest that the two kinds of modulation may be elaborated separately. Even so, the magnitude of the movement modulation was nearly always dependent on the position modulation.

The schema suggested by these findings is of two pathways conveying sensory information to the DSCT: one is specifically sensitive to limb position, and perhaps analogous to the Group II inputs described by Edgley and Jankowska (1988); the other elaborates movement information that interacts with the position modulation, either at the level of the DSCT neurons or in some presynaptic circuit. Because the interaction is multiplicative, it suggests some sort of gain control as might occur within an interneuronal pool modulated by position and/or at DSCT synapses that are modulated by position. The movement pathway seems more complex than the proposed position pathway because it seems to include elements of the gain modulation. It also may contain elements responsible for the long persistence of movement modulation, given the current lack of an explanation based on some more peripheral mechanism.

COORDINATE FRAMEWORK. From the results of our previous analyses of DSCT behavior, we proposed the possibility that DSCT activity represents kinematic information in a polar coordinate framework centered at the hip and defined by the limb axis. The results presented here remain consistent with that proposal. The motivation for the proposal came primarily from behavioral results that showed that cats regulate limb orientation and length to control their posture (Lacquaniti and Maioli 1994; Lacquaniti et al. 1990). The finding that the preferred directions of broadly tuned DSCT cells depended on limb orientation and were not uniformly distributed across cells also supported this proposal. What is added by the current study is that each cell may be characterized by a single preferred direction or gradient in the workspace, and this also tends to be aligned with the direction of the limb axis.

The directional gradients across cells are not uniformly distributed, but they tend to cluster in directions that are nearly aligned with the limb axis or an axis perpendicular to it. Although this could be interpreted as resulting from an intrinsic reference frame associated with the limb axis (Soechting and Flanders 1992), we also must be cautious not to overinterpret results based only on passive movements in anesthetized animals. For example, DSCT neurons are at least as sensitive to muscle forces as they are to limb kinematics (Osborn and Poppele 1989). Although we have not examined the relationship between DSCT activity and limb forces, it is likely that in a more normal state, the DSCT activity will be found to relate to both kinematics and forces.

Limb kinematics also may covary with some other limb parameter, such as compliance, for example. In fact, it has been shown that limb posture is associated closely with passive limb compliance in the human arm (Mussa-Ivaldi et al. 1985). Consequently, we suggest that the DSCT coding of limb kinematics we described might be due to a similar relationship between kinematics and compliance in the passive hindlimb. Thus the observed correlations may hold true primarily to the extent that limb kinematics correlate with limb compliance. If so, it could suggest a functional role for the DSCT to encode limb compliance in some manner. Any conclusions about this, however, must await further experimental evidence obtained in more appropriate behavioral states.

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