

ENCODING OF HINDLIMB KINEMATICS BY SPINOCEREBELLAR CIRCUITRY

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INTRODUCTION

The dorsal spinocerebellar tract (DSCT) represents one of the major projection pathways from the spinal cord to the intermediate part of the cerebellum. The neurons of origin of the DSCT receive converging sensory information from hindlimb muscle, skin and joint receptors and their projection to the cerebellum is considered to be the product of the spinal sensory processing of movement-related information (1, 13, 14).

In fact, earlier studies suggested that DSCT activity might relate to global rather than to local parameters of hindlimb postures and movement (5, 6, 7, 8). Specifically, it was proposed that DSCT neurons might elaborate a representation of the limb endpoint kinematics. The proposal stemmed mainly from the result of a principal component analysis of DSCT responses to step-like trajectories applied passively to the left hindfoot of anesthetized cats (8, 15). The first two principal component (PC) waveforms, which accounted for a large fraction of the ensemble activity of DSCT neurons, were correlated respectively with either the waveform of the limb axis length or orientation trajectories.

This finding was rather suggestive of separate sensory representations of limb axis length and orientation. However, a law of intersegmental covariance that has been found to couple the motion of limb segments (3, 7, 9, 10), because of the passive limb biomechanical properties, might produce a unique correspondence between the limb geometry and the limb axis coordinates. As a consequence, a local joint angle reference frame might become indistinguishable from a global limb axis reference frame, when relating neuronal activity to the limb kinematics. In other words, this segmental interdependence makes it unclear whether such global representations unveiled at the level of the DSCT may result from neural processing or from biomechanical factors alone. Moreover, it raises the question of whether explicit representations of joint angles might also be required to encode local changes in limb geometry.

To address these issues, in the present study we decoupled limb geometry from endpoint position by mechanically constraining the knee joint during passively applied movements patterned after a step cycle. Then, we used principal components

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analysis of DSCT neuronal responses to assess whether the representations of limb axis length and orientation previously found for the first two PC waveforms might be invariant to the local changes in limb geometry imposed by the mechanical constraint, or additional components might be necessary to explain the ensemble activity of DSCT neurons.

METHODS

Four adult cats were anesthetized with pentobarbital (Nembutal, Abbott Pharmaceuticals, Inc.; 35 mg/kg, I.P. supplemented as needed to maintain a surgical anesthesia level throughout the duration of the experiment). They were placed in a stereotaxic apparatus with the hips fixed in position by pins in the iliac crests. The left hindfoot was attached to a small platform connected to a computer controlled robot arm (Microbot AlphaII+, Questech, Inc, Farmington Hills, MI.), which moved the limb through a footpath modeled on a step cycle (Fig 1A) with a velocity profile comparable to that of slow walking (Fig. 1B; see also 16).

The kinematics of the limb movement was recorded by means of a digital video camera (Javelin Model 7242 CCD camera; 60 frames/sec) which acquired the position of reflective markers placed

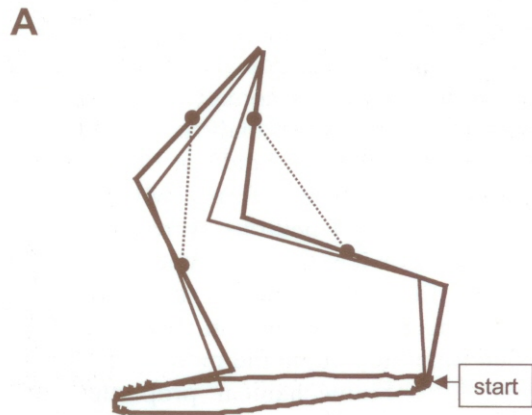
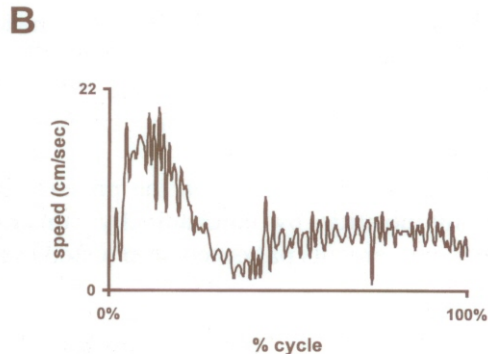


Fig. 1. - *Passive step cycle foot-trajectory.*

A. Stick diagrams show hindlimb geometry for two arbitrary points in the step foot trajectory during unconstrained (gray stick diagrams) and constrained (black stick diagrams) steps. The dashed lines connecting the thigh and the shank segments symbolize the Plexiglas bar that constrained the knee joint motion. A black arrow indicates the point in the foot trajectory (start) corresponding to the beginning of the forward swing and used to align neuronal activity in successive cycles. B. Footpath trajectory velocity is highest in the early portion of the forward swing and lowest at the transition between forward and backward swing.



on the hip, knee, ankle and fifth metatarsal-phalangeal joints. Kinematics data were digitized off-line using a motion analysis system (Motion Analysis, Santa Rosa, CA, model VP110).

Knee constraint.

In order to dissociate limb geometry from foot kinematics we applied a rigid constraint between the thigh and shank that prevented angular motion of the knee joint. A rigid Plexiglas strip (represented by a dashed line in the stick diagrams in Figure 1A) was fixed between surgically implanted pins in the femur (about 5 cm from the femur head) and tibia (about 6 cm from its distal end; see 7 for more details). The knee constraint blocked effectively the motion of the knee joint for three cats where the maximal range of knee motion was within 5° , and reduced the knee motion by about half for the fourth cat. Because of the biomechanical coupling among limb segments, the angular excursion of the other hindlimb joints (hip and ankle) was also affected to some degree.

Neuronal recording.

DSCT unit activity was recorded extraaxonally from the dorsolateral funiculus at the T10-T12 level of the spinal cord using insulated tungsten electrodes (5 M Ω , FHC, Brunswick, ME). Antidromic activation from the white matter of the cerebellum and/or from the restiform body identified units as spinocerebellar. Activity recorded continuously during series of 10-15 passive step-like movement cycles was aligned to the reference starting point at the beginning of the forward swing (black circle in the foot trajectory in Figure 1A). Cycle histograms were computed using binned activity (binwidth: 33.3 ms) from at least 7-10 consecutive cycles.

PC analysis.

From the data-matrix of DSCT response histograms to passive and constrained step cycles we extracted the principal components, that is a small number of linearly independent waveforms accounting for most of the data set variance. The original elements of the data set (i.e. the histograms) are related to the PC waveforms by weighing coefficients, which represent the Pearson product-moment correlations between the elements of the original data set and each of the PCs. PC analysis was performed using SYSTAT (17).

RESULTS

We analyzed the responses of 50 DSCT neurons to step-like movements in both experimental conditions (control and constrained). The knee constraint had variable effects on the DSCT responses, including no discernible effect on the responses of 24 neurons (48%), 3 of which are illustrated in Figure 2 (panels A, C and E; Kolmogorov-Smirnov test $p > 0.05$). The other 26 cells (52%) were all affected to some degree, as illustrated by the 3 examples in the right side of Figure 2 (panels B, D and F). We also noted that most of the changes involved a major difference in responsiveness during the latter part of the forward swing.

In an earlier study, using PC analysis, we found that the variety of DSCT step responses could be explained, for most part, by as few as four PC waveforms. Interestingly, these components were strongly correlated to the waveforms of limb axis length and orientation trajectories (15). Therefore, the finding that local changes in limb geometry imposed by the knee constraint could affect significantly the activity of half of DSCT neurons raises the question of whether these activity changes could be explained by additional response components related to specific local changes in limb kinematics. Alternatively, activity changes might result

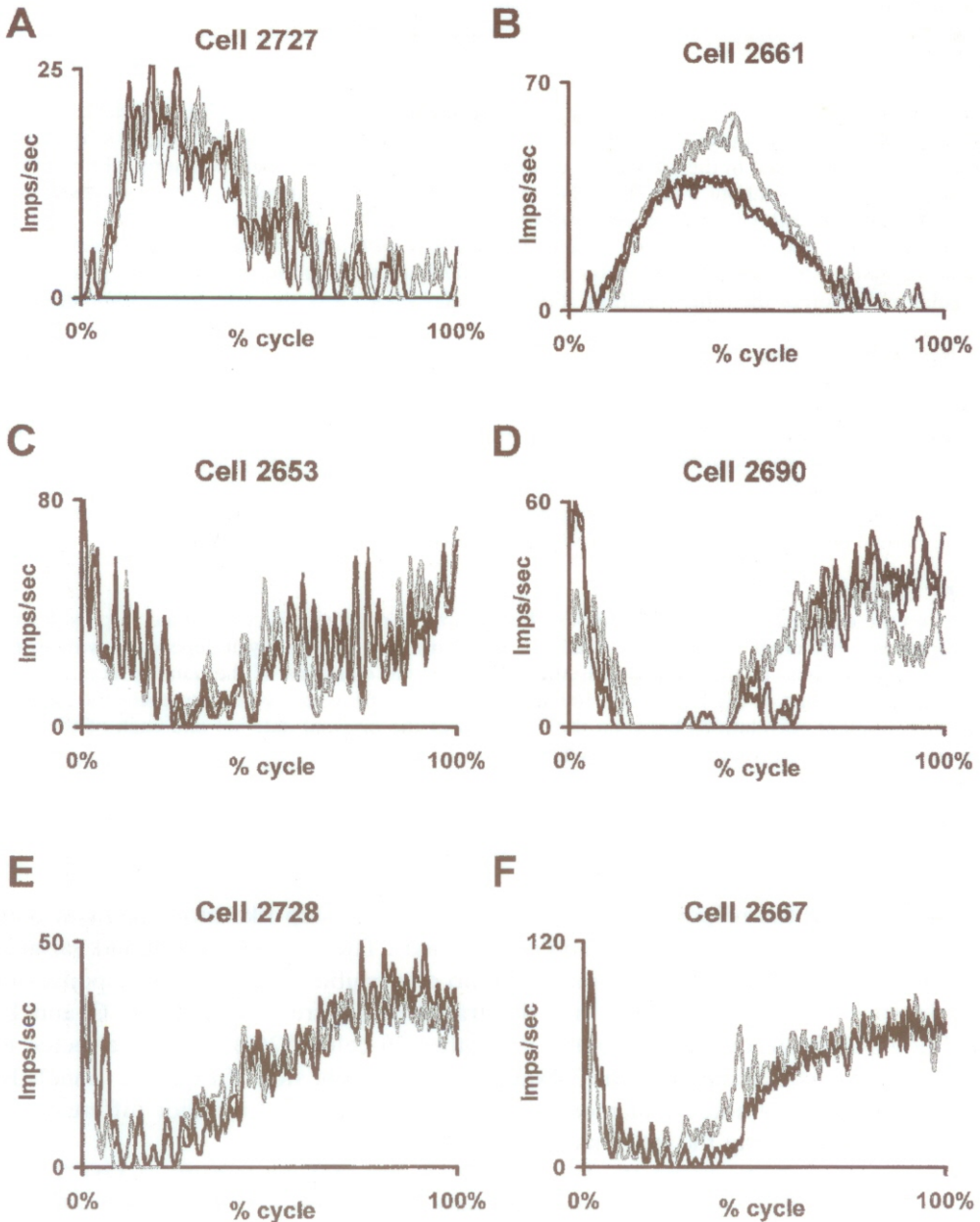


Fig. 2. - Examples of DSCT responses to control and constrained steps.

Cycle histograms of DSCT activity over a movement cycle are aligned with the beginning of the forward swing (Start position in Figure 1A). Two independent trials are plotted for each condition, control (gray curves) and constrained (black curves). A-C-E. Each panel shows responses from individual DSCT cells that were unaltered by the knee constraint. B-D-F. Examples of individual DSCT step responses that showed significant changes with the limb constrained.

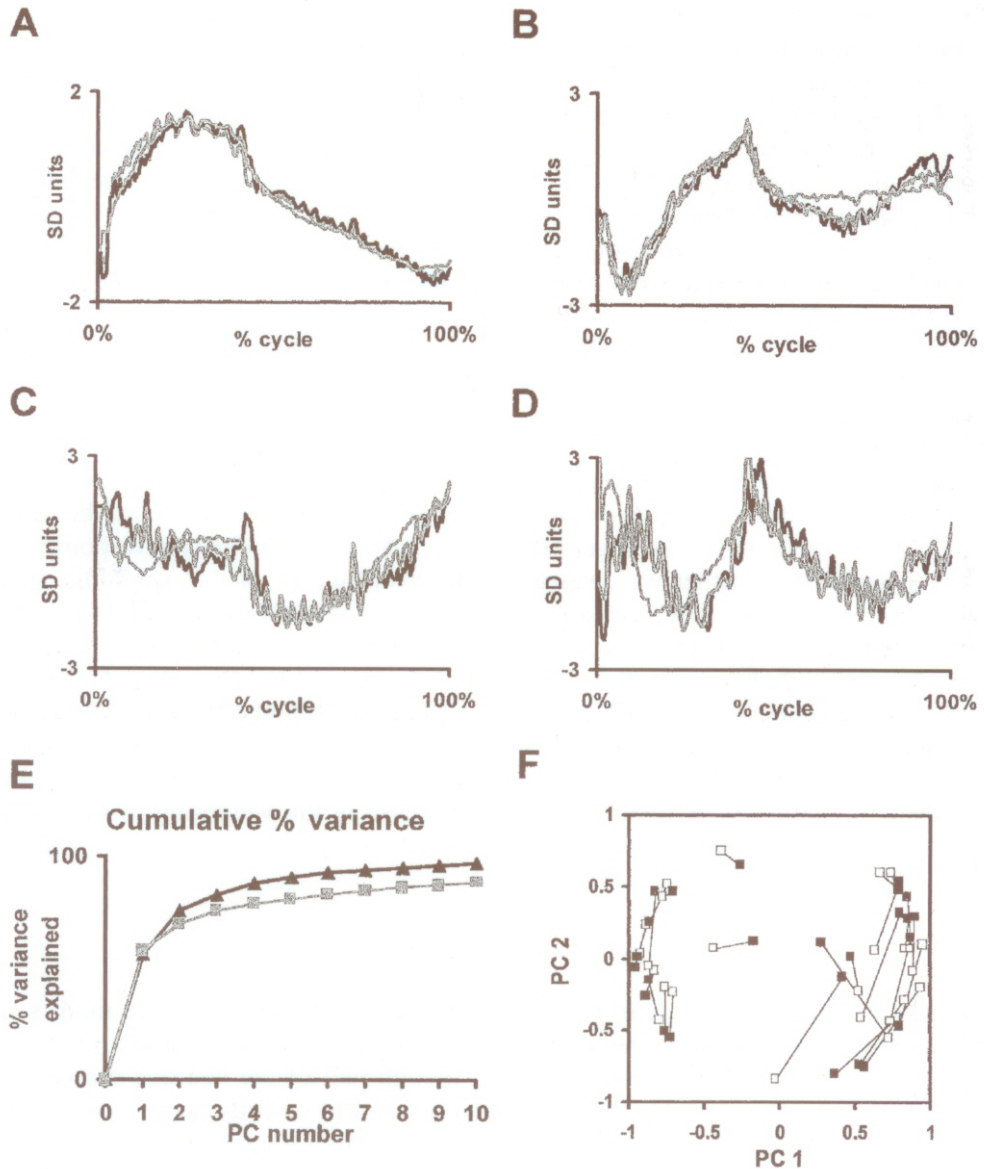


Fig. 3. - *Principal component analysis of response histograms.*

A-D. The first four principal components (PCs) extracted from 50 control responses (thick gray curves) and from the 26 responses that were changed by the knee constraint (black curves). The PCs are compared with a set of PCs extracted from an independent sample of 160 DSCT neurons (thin gray curves). E. Cumulative percentage of the variance in response waveforms in each data set explained by the first ten PCs. F. Scatterplot of weighting coefficients for the first two PCs. Open symbols represent the control responses and filled symbols represent knee-constrained responses for the 26 neurons that were affected by the knee constraint. A line joins the response representations for each individual cell.

from different weighting among invariant response components that are related to the limb axis.

In order to address this issue, we applied a principal component analysis (PCA) separately to each dataset (control and constrained) of DSCT step responses. For the 50 step responses in the unconstrained condition, we found that the PC waveforms were essentially the same as those derived from a larger (and separate) data set in the previous study (Fig. 3A-D, thick vs thin gray traces). About 75% of the variance was explained by the first three PCs with less than 4% of the variance accounted for by any of the higher order components. In addition, the PC waveforms extracted from the 26 responses that were changed by the knee constraint were basically identical (Fig. 3A-D, black traces).

Therefore, the changes in DSCT step responses observed when the limb was constrained cannot be accounted for by new or missing response components. This might imply that the same basic components are activated under both experimental conditions but they occur in different combinations for some cells when the knee is constrained. In fact, we noted that the overall cumulative variance explained by the PCs was somewhat different for the changed responses (Fig. 3E). In particular, the contribution of the second PC was larger (19.7% vs 11.5%) for the changed responses.

To examine this further we determined the distributions of the weighing coefficients for the first 2 PCs (which explain most of the data set variance) and found that the changes in waveform that occurred when the knee was constrained were accompanied largely by changes in the weighting of the second PC (Fig. 3F). This is evident in the 2-dimensional distribution in Fig. 3F, where a line connecting the control (open symbols) and constrained (solid symbols) response coefficients tracks the behavior of each affected cell. The generally vertical orientation of the lines indicates that the changes involved mostly an increase in the weighting of the second PC, with relatively smaller changes in the first PC weighting.

DISCUSSION

In the present study we constrained the motion of the knee joint to modify the relationship between limb geometry and limb endpoint and found that DSCT response components were invariant, even though half of the neurons showed significant activity changes. These activity changes could be fully accounted for by a modified weighting of existing response components rather than by any new or missing components.

The finding that the response components were unchanged by the knee constraint further supports our earlier proposal, based on the strong correlations between the PC waveforms and the limb axis trajectories, that the first PC waveform is a representation of the limb axis orientation trajectory and the second PC a representation of the length trajectory (8, 15). In addition, the lack of any changes in the PC waveforms corresponding to the changes in joint angle trajectories suggests that the DSCT population activity has no direct relationship with specific joint angles.

From these considerations, a general coding scheme might emerge which accounts for DSCT behavior during passive hindlimb movements. In essence, the neural circuitry parses a global representation of hindlimb kinematics into two independent representations. Previous studies suggest that these are separate neural representations of the limb axis orientation and length, including their position and movement components (7, 8, 15). The various components of this kinematics representation are then distributed with different weightings among the output elements of DSCT circuitry generating the variety of DSCT responses observed experimentally. Thus we propose that, within this framework, local information, such as changes in single joint stiffness, might be encoded without requiring specific and explicit local representations. In this way such specific information is encoded in the context of the whole limb status.

In conclusion, it is relevant to note that this type of coding scheme found at the lowest levels of sensory processing might be congruent with the variables, namely the limb axis kinematics that have been proposed for the control of motor behaviors such as gait and stance (1, 3, 9, 10, 11, 12).

SUMMARY

Earlier work from our laboratory showed that principal component waveforms (PCs) from an ensemble of DSCT movement responses correlated with either the waveform of the limb axis length or orientation trajectories, suggesting that DSCT circuitry might elaborate an explicit representation of limb endpoint kinematics independent from limb geometry. In this study, we tested this idea by decoupling limb geometry from endpoint position with mechanical constraints that blocked the motion of the knee joint during step-like movements applied passively to the hindlimb of anesthetized cats. Only about half of the 50 cells studied showed statistically different response patterns when the limb was constrained compared to the unconstrained condition (control). However, the PC waveforms extracted from responses that showed significant changes with the knee constrained were found to be identical to those extracted from control responses. Instead, the differences between constrained and control responses could be accounted for by changes in the weighting of PCs suggesting a modulation of global response components rather than an explicit representation of local parameters.

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REFERENCES

1. BIANCHI, L., ANGELINI, D., ORANI, G.P. AND LACQUANITI, F. Kinematic coordination in human gait: relation to mechanical energy cost. *J. Neurophysiol.*, **79**: 2155-2170, 1998.
2. BLOEDEL, J.R. AND COURVILLE, J. Cerebellar afferent systems In: *Handbook of Physiology. Sect. 1. The Nervous system. Motor control*. Edited by V.B. Brooks. Bethesda, MD, Amer Physiol Soc. Vol 2: 2, 1981.
3. BORGHESE, N.A., BIANCHI, L. AND LACQUANITI, F. Kinematic determinants of human locomotion. *J. Physiol., Lond.*, **494**: 863-879 1996.
4. BOSCO, G., RANKIN, A. AND POPPELE, R. (1996) Representation of passive hindlimb postures in cat spinocerebellar activity. *J. Neurophysiol.*, **76**:715-726.
5. BOSCO, G. AND POPPELE, R.E. Representation of multiple kinematic parameters of the cat hindlimb in spinocerebellar activity. *J. Neurophysiol.*, **78**: 1421-1432, 1997.
6. BOSCO, G., POPPELE, R.E. Low sensitivity of dorsal spinocerebellar neurons to limb movement speed. *Exp. Brain Res.*, **125**: 313-322, 1999.
7. BOSCO, G., POPPELE, R. AND EIAN, J. Reference frames for spinal proprioception: Limb endpoint based or joint-level based? *J. Neurophysiol.*, **83**: 2946-2955, 2000.
8. BOSCO, G., RANKIN, A. AND POPPELE, R.E. Does the spinocerebellar circuitry provide an explicit and independent representation of limb axis length and orientation? *Neural Control of Movement, Abst.*, **5**: 4, 2000.
9. GRASSO, R., BIANCHI, L. AND LACQUANITI, F. Motor patterns for human gait: backward versus forward locomotion. *J. Neurophysiol.*, **80**: 1868-1885, 1998.
10. LACQUANITI, F. AND MAIOLI, C. Independent control of limb position and contact forces in cat posture. *J. Neurophysiol.*, **72**: 1476-1495, 1994.
11. LACQUANITI, F. AND MAIOLI, C. Coordinate transformations in the control of cat posture. *J. Neurophysiol.*, **72**: 1496-1515, 1994.
12. MAIOLI, C. AND POPPELE, R.E. Parallel processing of multisensory information concerning self-motion. *Exp. Brain Res.*, **87**:119-125, 1991.
13. OSBORN C.E. AND POPPELE R.E. Parallel distributed network characteristics of the DSCT. *J. Neurophysiol.*, **68**: 1100-1112, 1992.
14. OSBORN C.E. AND POPPELE R.E. Sensory integration by the dorsal spinocerebellar tract circuitry. *Neuroscience*, **54**: 945-956, 1993.
15. POPPELE R.E., BOSCO G. AND RANKIN A. Independent representations of limb axis length and orientation in spinocerebellar response components. *J. Neurophysiol.*, **87**:409-422, 2002.
16. SHEN, L. AND POPPELE, R.E. Kinematic analysis of cat hindlimb stepping. *J. Neurophysiol.*, **74**: 2266-2280, 1995.
17. WILKINSON, L. *The System for Statistics*. Evanston, IL, SYSTAT, Inc 1990.