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Responses of interposed and dentate neurons to perturbations of the locomotor cycle

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Summary. This study examined the relationship of antidromically identified neurons in the dentate and interposed nuclei to perturbed and unperturbed locomotion in the pre-collicular, mid-mamillary, decerebrate cat. During treadmill locomotion two methods were used to perturb the step cycle. In the first, the treadmill was braked in different phases of the step cycle, the "treadmill" perturbation. In the second, the motion of the ipsilateral forelimb was interrupted by a rod placed transiently in the limb's path, the "single limb" perturbation. Most interposed cells were modulated during locomotion, their discharge being highly correlated with the EMG of the ipsilateral biceps or triceps. When the locomotion was perturbed, the modulation ceased for the duration of the perturbation. A few interposed cells displayed activity patterns unrelated to the EMG but were responsive to perturbations of a single limb. These responses may be explained by the putative activation of peripheral afferents produced by the perturbation. Most dentate cells were not modulated during unperturbed locomotion but did respond to features of the treadmill perturbation. Usually the response was coupled to the resumption of treadmill motion. A minority of dentate neurons was modulated slightly during unperturbed locomotion. Their modulation was less dramatic than that of interposed cells and was only weakly related to limb movement or EMG activity. Like the interposed neurons, these dentate cells responded to the treadmill perturbation with a cessation of modulation. All dentate cells were unresponsive to single limb perturbations. In a preparation lacking cerebral cortical input, the findings show that neurons of the interposed and dentate nuclei are modulated differently during perturbed and unperturbed treadmill walking in the decerebrate cat. The activity of interposed neurons is related to specific features of EMG activity recorded from muscles in the ipsilateral forelimb. Although some dentate cells were weakly modulated during unperturbed locomotion, the majority of these neurons responded most dramatically to the occurrence of a perturbation which completely stopped the walking behavior.

Key words: Cerebellum – Dentate nucleus – Interposed nuclei – Locomotion – Single-unit activity

Introduction

Hypotheses on the cerebellum's role in motor control suggest this structure contributes to many different aspects of a movement including its initiation and termination, timing, trajectory control, and postural stability (Soechting et al. 1976; Meyer-Lohmann et al. 1977; Brooks 1985; Thach et al. 1985). Some authors have argued that different parts of the cerebellum contribute uniquely to the control of a movement (Thach 1978; Strick 1983). This view was supported by the early ablation studies of the cerebellar nuclei (Sprague and Chambers 1959). Sprague and Chambers' studies provided evidence that each sagittal zone contributed differently to postural control. Cooling studies by Brooks and colleagues indicated a segregation of motor function among the cerebellar nuclei. Dentate cooling produced hypermetric movements with an increase in velocity and acceleration (Conrad and Brooks 1974). In contrast, interposed cooling resulted in slower hypometric movements. Recent anatomical and electrophysiological studies demonstrate that the cerebellum

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can be further subdivided based on the organization of its afferent and efferent projections. Division of the cerebellar cortex and nuclei in up to nine sagittal zones in some parts of the cerebellum raises the issue of differentiation of function among these very restricted cerebellar regions (Voogd and Bigare 1980; Yu et al. 1985).

The purpose of this experiment was to examine and compare the responses of neurons in the dentate and interposed nuclei during normal and perturbed locomotion in the decerebrate cat. We asked the question: How does input from the spinal cord modulate neurons in the cerebellar nuclei? Locomotion is generated by interneurons of the spinal cord and regulated by brainstem centers (Grillner 1975). Because decerebration removes cortical input via the pontocerebellar projection, it is possible to determine how neurons in the interposed and dentate nuclei respond to motor patterns generated by noncerebral structures. Findings in this "reduced" preparation may help define the basic response properties of the cerebellar nuclei to this class of spinal input in the normal animal. Many previous studies focused on relating the behavior of these cells to learned voluntary limb movements in intact primates (Conrad and Brooks 1974; Thach 1978; Strick 1983; Wetts et al. 1985; Chapman et al. 1986). Locomotion represents a class of movement behavior which may potentially reveal differences or similarities in the roles of the dentate and interposed nuclei. Although the cerebellum is not essential for generating the normal step cycle (Grillner 1975), many of its afferent and efferent systems are modulated during walking and related motor behaviors (Arshavsky et al. 1972a; Arshavsky et al. 1972b; Arshavsky et al. 1980; Udo et al. 1981; Arshavsky et al. 1983; Arshavsky et al. 1984). We have studied the responses of cerebellar nuclear cells to perturbations of the locomotor cycle, given the considerable literature supporting the role of the cerebellum in corrective movements (Gilman et al. 1981).

Several studies imply that the intermediate region of the cerebellar cortex and the associated interposed nuclei are closely linked to movement kinematics or the underlying musculature (Soechting et al. 1978; Mackay and Murphy 1979; Giuffrida et al. 1980). The intermediate region of the cerebellum receives direct afferents from the spinal cord and projects predominantly to the cells of origin of the rubrospinal and reticulospinal tracts (Bloedel and Courville 1981). Cerebellar afferents, Purkinje cells in the pars intermedia and neurons in the interposed nuclei are all highly modulated during scratching and locomotion (Orlovsky 1972; Arshavsky et al. 1972a; Arshavsky et al. 1972b; Arshavsky et al. 1980; Ohno and Kanazawa 1982; Arshavsky et al. 1983; Armstrong and Edgley 1984a, b; Arshavsky et al. 1984). In addition interposed neurons are tightly correlated with the EMG activity of individual muscles involved in limb movements (Soechting et al. 1978; Thach 1978). The responses of interposed neurons to perturbations of the wrist are not dependent on movement instructions, but instead are related to the characteristics of the task (Strick 1983). Thus the intermediate region of the cerebellum and interposed nuclei have been implicated in the ongoing control of both automatic and voluntary movements (Mackay and Murphy 1979). This study will examine whether this view can be extended to the responses of interposed neurons to perturbation of the step cycle.

Perhaps because of the interconnections between the dentate nucleus, thalamus and motor cortex (Evarts and Thach 1969; Gilman et al. 1981) the role of the lateral cerebellar nucleus in locomotion has not been widely addressed. However, there is some evidence the dentate nucleus receives spinal inputs mediated via infratentorial structures (Bantli and Bloedel 1977). Some studies suggest this nucleus is not concerned with locomotor activity (Ohno and Kanazawa 1982; Arshavsky et al. 1983) but rather with the early stages of a voluntary movement including its formulation and initiation (Meyer-Lohmann et al. 1977; Thach 1978). This view is based on the finding that the discharge of neurons in this nucleus is often related to motor "set" rather than the characteristics of the task itself (Strick 1983; Hore and Vilis 1984; Chapman et al. 1986). These observations suggest the output of the dentate nucleus is involved in the synthesis of the movement and possibly the early phases of movement execution rather than the control and/or regulation of precise patterns of muscle activity (Brooks 1985; Thach et al. 1985).

The present experiments will demonstrate that dentate and interposed neurons are both responsive during locomotion but with very different characteristics. Interposed neurons were generally highly modulated and tightly coupled to forelimb EMG activity suggesting continuous involvement with the ongoing movement and its kinematics. A smaller population of interposed cells was less coupled to the forelimb step cycle and better related to the perturbation. In contrast, dentate cells were poorly modulated during unperturbed locomotion and not coupled to the forelimb step cycle. Dentate cells were most responsive at the resumption of the locomotor cycle following treadmill braking. Preliminary observations from these experiments have been published previously (Schwartz et al. 1983; Schwartz et al. 1984).

Material and methods

Animal preparation

Fifty cats weighing 2–3.5 kg were anesthetized with halothane (2–4%) following a subcutaneous injection of atropine (0.04 mg/kg). After a tracheostomy the animal was respired artificially, and anesthesia was continued with halothane administration. Expired pCO_2 was monitored and maintained at 3–4%. Rectal temperature was maintained at 38.5° C by an infrared lamp and heating pad. Teflon coated, stainless steel EMG wires were inserted percutaneously into the biceps brachii and lateral triceps muscles of the right forelimb. The cat's head was mounted stereotaxically and the animal suspended over a treadmill by supporting its hindquarters with an elastic band. The skull was exposed and a small drain placed at the cisterna magna to help prevent accumulation of CSF.

Following a suitable craniotomy, the cat was decerebrated with multiple lesions from a single radiofrequency electrocoagulating electrode. This resulted in a planar lesion, 2 mm thick extending 9 mm laterally in both directions from the midline. This pre-collicular mid-mamillary lesion extended from the border of the brainstem at A 3.7 to the ventral margin at P 7.3 (Hoarsely-Clark, 23°). With a properly placed lesion the animal would walk spontaneously when the treadmill was turned on and remain quiescent when the belt was stationary. The completeness of this lesion was histologically verified with sagittal sections of the brainstem.

After the decerebration approximately 1/2 cm^3 of cerebral cortex was removed bilaterally to minimize swelling due to accumulation of intraventricular CSF. The cerebellar cortex was exposed and covered with agar. Antidromic stimulating electrodes were stereotaxically placed across the decussation of the brachium conjunctivum. Anesthesia was discontinued and the respirator removed.

Locomotion and perturbation methods

The right front leg was attached with a stiff wire to a lever arm on a potentiometer to produce a signal proportional to the displacement of the leg (Shik et al. 1968). The axis of the potentiometer was placed just lateral and in a coaxial position relative to the shoulder joint. The end of the lever arm was attached via the wire to the leg just proximal to the radiocarpal joint. During the step cycle the displacement signal reflected the forelimb angle relative to the fixed position of the suspended animal. This signal had a positive slope during forward progression of the leg. In this phase of locomotion the elbow flexes, followed by flexion of the radiocarpal joint and shoulder (Arshavsky et al. 1965). Elbow flexion coincides with foot lift-off at the speeds used in this study (less than 3 km/h). Lift-off defines the beginning of swing phase, and elbow flexion corresponds to the beginning of leg protraction. Therefore, the minimum point in the displacement signal corresponds closely to the beginning of swing phase. Similarly it can be argued the maximum point in the record reflects the beginning of the leg retraction and foot touch-down, that is, stance onset. Although the predominant component of the displacement signal with a positive slope corresponds to the swing phase and that with a negative slope to the stance phase, we did not measure lift-off and touch-down directly. Therefore, we will refer to these two periods of the step cycle as leg protraction and retraction. This signal was fed through a threshold detector which produced a pulse as a critical limb position was approached from either the anterior or posterior direction. This trigger was used to time on-line computer data acquisition as well as time the perturbation devices.

Controlled locomotion was achieved by using a motorized treadmill with variable speed (0.2–0.5 m/s). Two perturbation systems were used. The first, which will be referred to as "treadmill perturbation", consisted of stopping the treadmill for a brief period. A dynamic braking system permitted the belt to be smoothly decelerated and stopped from a speed of 0.2–0.5 m/s in 90 ms and reaccelerated in a similar fashion after a variable delay. During the treadmill perturbation all four legs were simultaneously stopped. Perturbations of a single leg were achieved with an air cylinder controlled by a transistor and a Skinner valve. When activated, a bar projected from the cylinder across the path of the moving limb. This perturbation will be referred to as the "single leg perturbation".

The phase of the step cycle in which the perturbation occurred was determined by a delay circuit triggered by the right forelimb displacement. Selection of the individual step cycle to be perturbed was controlled by randomly gating the trigger pulse to the delay circuit. The treadmill perturbation could be timed to occur at any time throughout the step cycle. Single limb perturbations were applied during forward or backward limb motion. When timed to occur during the forward motion of the limb, the dorsum of the right foot would strike the extended bar, the foot would flex and the animal would step over the bar with a minimal interruption in the limb's forward progress. When the limb struck the bar as it moved posteriorly, it would be arrested for the duration of the perturbation. The control signal to trigger the transistor of the air cylinder is presented in the relevant figures. This is not a precise representation of the bar displacement which was somewhat slower. However, the time at which the limb struck the bar can be determined from the limb displacement record.

Recording and cell identification

Nuclear cells were stereotaxically located in either the right dentate (P 9.5, L 7.3–6.8) or interposed (P 9.5, L 3.8–4.3) nuclei and isolated with glass micropipettes (1–4 MΩ) filled with pontamine sky blue (Hellon 1979). Several criteria were required for identification of a nuclear cell. The latency of antidromic activation from the brachium conjunctivum was within a 1–3 ms window and was invariant at different stimulus intensities and frequencies. Collision of the antidromically activated spike and spontaneously occurring orthodromic spikes was also required. At the end of a penetration, pontamine sky blue was iontophoretically injected to mark the last cell's location. Since this dye is water soluble, the position of the dye spots were noted as the tissue was sectioned. The dye spots were often lost during the counterstaining procedure (cresyl violet). Although all electrode tracks were checked histologically, only those dots which were visible after counterstaining were included in Fig. 15.

Once a cell was properly identified, on-line histograms were constructed while the animal was walking. Fifty to 100 sweeps over a period of 1,700 ms (2–3 step cycles) were averaged. Phase triggered histograms (PTHs) of discriminated nuclear neuronal activity, right forelimb biceps and triceps EMG activity, and forelimb displacement traces were generated during perturbed and unperturbed locomotion.

Data analysis

In addition to the on-line PTHs the data were analyzed off-line. Some of the phase triggered histograms were analyzed with a cumulative sum (cusum) technique to delineate the response associated with a perturbation and the degree to which the responses were modulated. The cusum was constructed by summing the series of previous PTH bin counts from which a mean activity level obtained from a segment of background activity was subtracted. Background activity was taken from an unperturbed

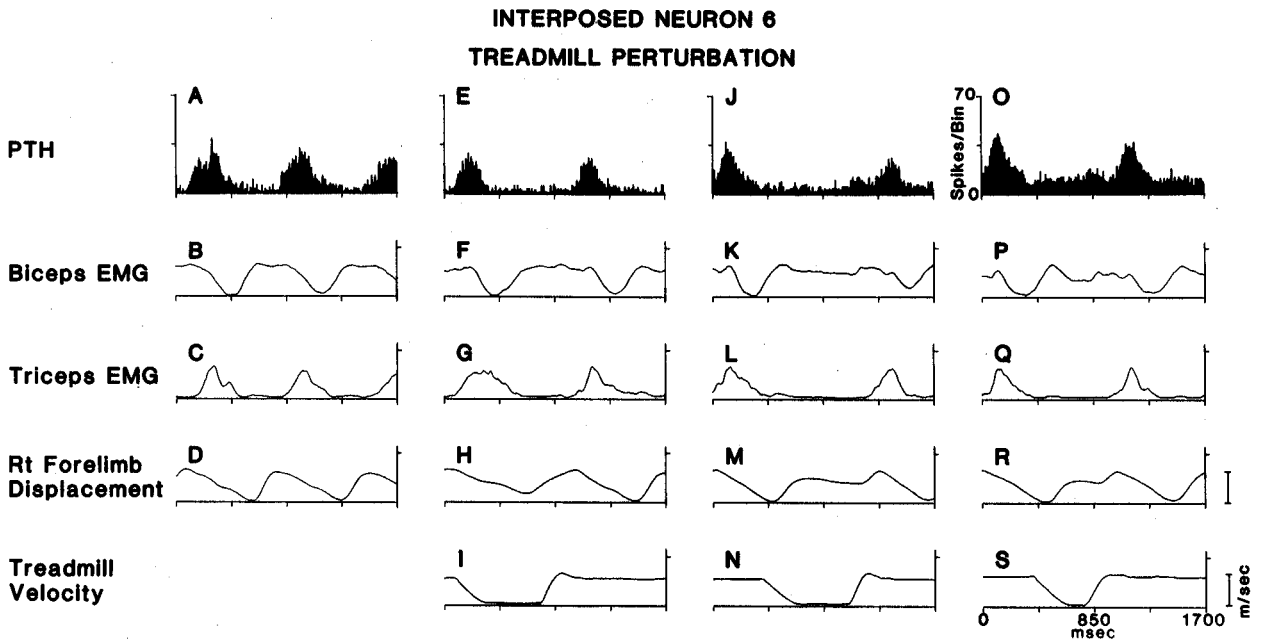

Fig. 1A–S. Relationship of the activity of an interposed neuron to triceps and biceps EMG during treadmill perturbation. Top row: Phase triggered histograms (PTH) of unitary discharge. Second row: Rectified, integrated (τ = 20 ms) biceps EMG. Third row: Triceps EMG. Fourth row: Displacement of the right forelimb (forward direction is up; vertical bar = 10.7 cm). Bottom row: Treadmill speed (vertical bar = 0.38 m/s). **A–D** Unperturbed trials. **E–I** Treadmill perturbation beginning 100 ms after the trigger and lasting 800 ms. **J–N** Perturbation beginning 400 ms after the trigger and lasting 800 ms. **O–S**: Perturbation 400 ms after the trigger lasting 500 ms. In both the unperturbed and perturbed trials the increase in interposed discharge was well related to the increase in triceps EMG activity. Unless otherwise specified in this and all subsequent figures, all PTHs were constructed from 50 consecutive sweeps and bin widths = 5 ms

step cycle. The significance of a cell's response was determined by comparing the slope of the cusum calculated for perturbed step cycles to the standard deviation of the cusum slope calculated from the background activity (unperturbed step cycles). If the value of the cusum slope calculated from the data of interest was greater than three times the SD of the cusum slope of the background segment, the signal was considered to differ from the noise (ie., a response was present). This corresponds to a P value of less than 0.05 for a normal distribution. The slope of the cusum calculated in this manner is non zero only if the neuronal discharge is different from background.

Cusums are shown only for cells which were weakly modulated during unperturbed locomotion. This technique was especially useful in detecting the responses of dentate cells to the treadmill perturbation. Responses were indicated by a constant non-zero slope in the cusum. These responses were often superimposed on a baseline activity which was slightly modulated throughout the step cycle. The cusum technique allowed a statistical decision as to the time course and intensity of the perturbation related response. For the more highly modulated interposed and dentate cells, the cusum analysis did not provide any additional response details as compared to the phase triggered histograms and was omitted from the presentation.

Spike triggered averaging (STA) was used to examine the correlation between nuclear neuronal activity and the EMG of the biceps and triceps of the right forelimb. Emphasis was placed on determining whether the shape of the STA was modified in perturbed trials relative to unperturbed trials. STAs were calculated by accumulating the 800 ms of integrated rectified EMG activity that occurred after any spike falling within the 1700 ms period of the PTH. Each 800 ms of EMG activity was normalized to an amplitude of $\pm$ 1 and added to the other EMG segments. The final STA was normalized by dividing by the number of spikes, producing an average bounded by $\pm$ 1. The amplitude of the response is directly related to the degree of correlation between the neuron and the EMG. An amplitude of 2 would represent perfect correlation.

Results

Interposed neurons

We recorded 52 cells in the interposed nuclei during locomotion. Forty-six of these cells were modulated, varying their discharge rhythmically during the step cycle. Six were not modulated as judged from the histograms and lacked significant responses in the cumulative sum analysis.

Thirty-three of the 46 modulated interposed neurons had responses which closely resembled the EMG activity in the two representative forelimb muscles. These neurons were evenly divided between those correlated to the flexor (17 were in phase with the biceps) and those to the extensor (16 were in phase with the triceps). Figures 1–4 illustrate the response of one interposed neuron which had a pattern of discharge resembling the EMG of the triceps. During normal locomotion the animal generated approximately three step cycles during each 1700 ms sweep (Fig. 1A–D). The histograms began as the leg started backward, at which point the biceps

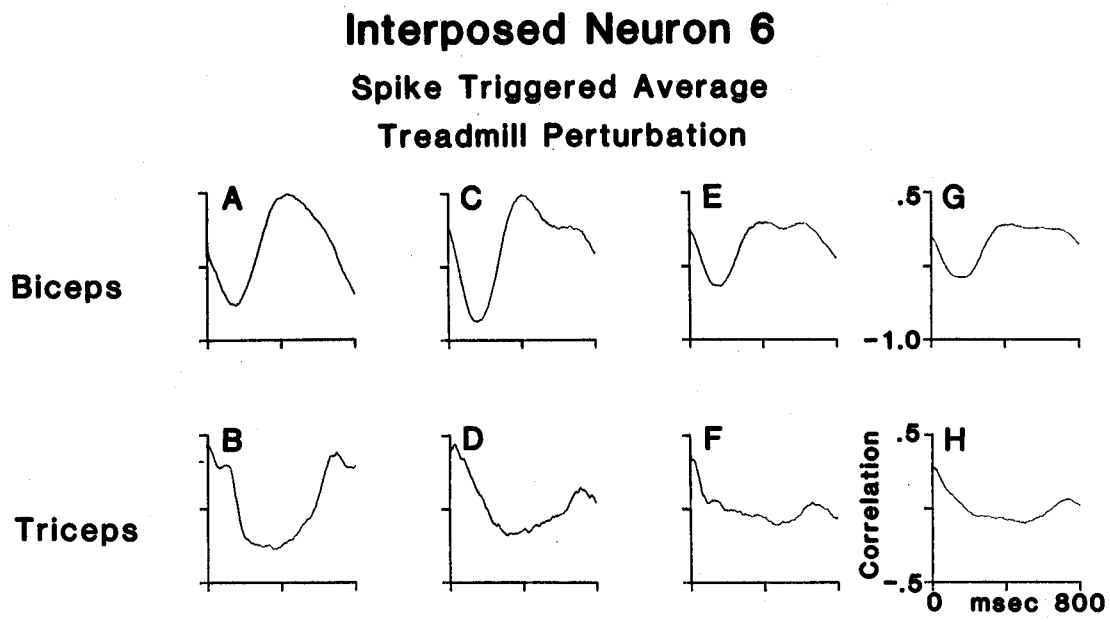

Fig. 2A–H. Spike triggered average (STA) between the activity of the same interposed neuron studied in Fig. 1 and the triceps and biceps EMG. Top row: Spike triggered averages of the biceps EMG. Bottom row: Spike triggered averages of the triceps EMG. **A, B** STAs calculated from unperturbed trials in Fig. 1A–D (983 spikes). **C, D** STAs from trials in Fig. 1E–I (795 spikes). **E, F** STAs from trials in Fig. 1J–N (1008 spikes). **G, H** STAs from trials in Fig. 1O–S (2018 spikes). The phase of the EMG of both muscles relative to the occurrence of a spike was unaltered by these different perturbations. All STAs in this and the following figures have 2 ms bin widths

activity was maximum. All references to the step cycle are relative to the right forelimb, the extremity ipsilateral to the recorded neuron. Peak triceps activity occurred during the first third of retraction and was reciprocal to the biceps. The interposed cell discharged in phase with the triceps activity and with approximately the same time course. When the treadmill was halted at the beginning of retraction (E–I) the right forelimb did not completely stop, but its progression was slowed (H). This was associated with a prolonged triceps burst (G) and an increase in the duration of the subsequent biceps activity (F).

In the next series of trials the treadmill arrest occurred during protraction of the right forelimb (Fig. 1 J–N). The limb was stationary during this perturbation (M). When the treadmill accelerated, the limb again flexed. Biceps activity resumed its normal pattern, and the triceps activity continued to be reciprocal after the delay imposed by the perturbation. This interval between triceps bursts was equal to the perturbation duration. Notice for both perturbations (E–I and J–N) the phase relationship between the triceps EMG and the interposed neuronal activity remained constant. In another set of trials the step cycle was again interrupted during protraction, but for a short duration (Fig. 1 O–S). Although the duration of the perturbation was shorter, the relation between triceps activity and the nuclear cell discharge was preserved. Again the change in the interval between the peaks of interposed activity was equal to the duration of the perturbation.

To examine the correlation between neuronal discharge and individual muscle activity and to define changes in this relationship, spike triggered averages (STA) of the integrated rectified EMG were constructed. The STAs in Fig. 2 were obtained from the same data shown in Fig. 1. Figure 2A, B are the STAs of the unperturbed runs and correspond to the first column of Fig. 1. The STA represents the temporal profile of the EMG response after the occurrence of the spike at t = 0. Figure 2B shows that the averaged triceps activity was greatest when a spike occurred and then decreased to a minimum 400 ms later. Since the peak correlation occurs at t = 0, the triceps activity is in phase with the neuronal activity.

Similar arguments can be made for the biceps STA (Fig. 2A). During locomotion the large extensors and flexors of the limb are inversely correlated, and the high correlation of the spike train with the triceps is related to a comparable level of correlation with the biceps. Comparison of Figs. 1A–B and 2A show that the interposed cell fired most often at the point of the step cycle when the biceps activity was decreasing to half its maximal value. The shape of the biceps STA (Fig. 2A) resembles that of a corresponding phase triggered average for this muscle (Fig. 1B) except it is more rounded.

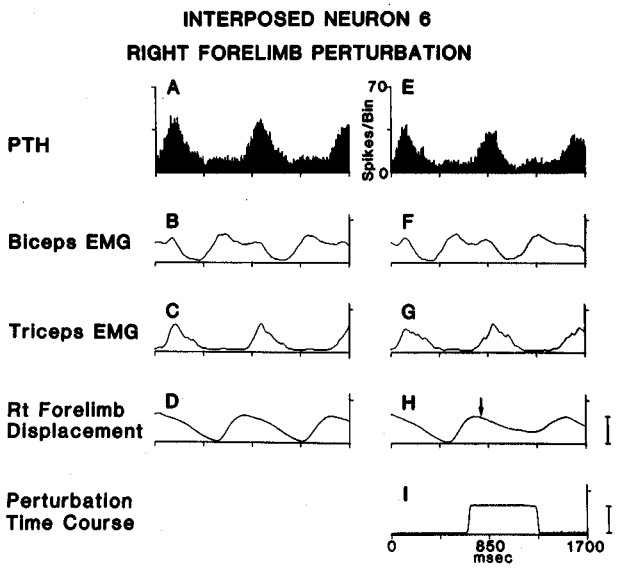

Fig. 3A–I. Effect of a single limb perturbation on the same interposed neuron examined in Figs. 1 and 2. **A–D** Unperturbed trials. **E–I** Trials in which the ipsilateral forelimb struck an obstacle during stance phase (the calibration bar = 10.7 cm in **H** and 7.6 cm in **I**). The occurrence of the perturbation did not change the cell's discharge nor its relation to the triceps EMG

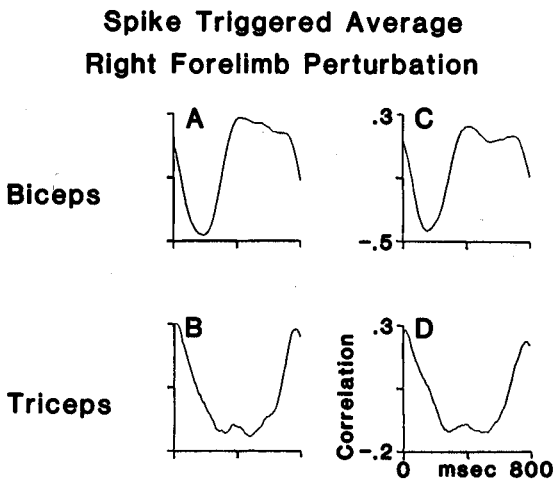

Fig. 4A–D. Spike triggered averages calculated from the trials in Fig. 3. **A, B** Unperturbed trials in Fig. 3A–D (2692 spikes). **C, D** Perturbed trials in Fig. 3E–I (2579 spikes). The spike triggered averages of both muscles were unaltered by the perturbation

The STAs (C–H) in Fig. 2 were constructed from the same data used in the PTHs (E–S) of Fig. 1. In Fig. 2D, F, H the shape of the triceps STA in the first 400 ms remained relatively similar to the nonperturbed runs (B). Slight changes in the duration and shape of the peak correlation partially reflect the difference between the step cycle durations in the perturbed and unperturbed conditions. Also, the interaction of the trigger spike with the EMG pattern of the next step cycle will occur at long latencies. Therefore, the first 400 ms of the STAs is the most useful interval in comparing different experimental runs. As for the triceps, the first 400 ms of each biceps STA is relatively consistent and independent of the perturbation (Fig. 2A, C, E, G). The plateau in the STA of the perturbed runs (C, E and G) is likely the result of the maintained biceps activity during the perturbation (Fig. 1F, K, P). Both the phase triggered histograms (Fig. 1) and STAs (Fig. 2) demonstrate the tight coupling between the discharge of this interposed neuron and the associated EMG activity of the biceps and triceps. This relationship was not disrupted by the different treadmill perturbations.

Figure 3E–I shows the results from the same cell when a single limb perturbation was applied to the right forelimb. The bar was extended into the trajectory of the limb approximately 600 ms after the sweep began. Approximately 100 ms later the limb struck the bar (arrow), and was partially arrested for the next 200 ms (H). Despite the modification of the limb's trajectory (H), there was very little change in the biceps activity (F) compared with the control run (B). Nor was there a unitary response evoked as a consequence of the limb striking the bar (E). The STAs determined for these same runs (Fig. 4) indicate that the single limb perturbation did not alter the relationship between the cell's discharge and either the biceps (A and C) or the triceps (B and D) activity.

Of the 46 interposed cells which were modulated during locomotion, 33 (72%) exhibited the tight correlation (as judged by the PTHs and the amplitude and consistency of the STAs) of the cells' discharge with forelimb EMG. Of these 33, 27 were studied during the treadmill perturbation. Twenty-two of these cells exhibited cessation in their modulation with the treadmill perturbation. Five cells had a complex response to the perturbation. The strong correlation with either the biceps (12/22) or the triceps (10/22) in this group of cells was not modified by the treadmill braking or the single limb perturbation. These data can be interpreted as showing that the cell's activity is highly related to the locomotor cycle. It should be emphasized that high correlations would exist between these neurons and any muscle rhythmically modulated in the step cycle.

Seven of the 46 modulated interposed cells were not consistently coupled to the activity of either ipsilateral forelimb muscle. The activity pattern for

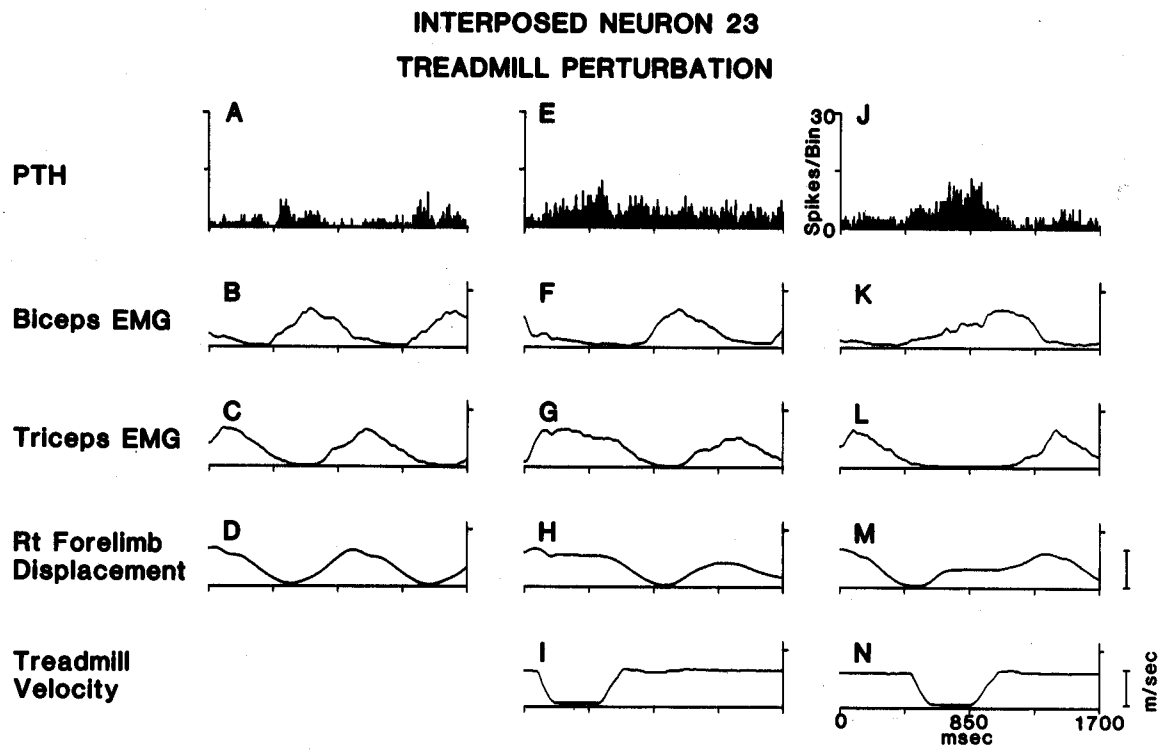

Fig. 5A–N. Response of a different interposed neuron to treadmill perturbation. **A–D** Unperturbed trials. **E–I** Treadmill perturbation 550 ms in duration applied 100 ms after t = 0. **J–N** Same perturbation applied 500 ms after t = 0. In **M** the calibration bar = 9 cm, in **N** the bar = 0.28 m/s

one of these cells is displayed in Figs. 5–8. During unperturbed locomotion, this slowly discharging (8/s) neuron increased its rate at the transition between stance and swing phase (Fig. 5A). Examining only the normal locomotion data might suggest that this cell's discharge was related functionally to the biceps EMG activity. When the treadmill was arrested at the initiation of limb retraction (E–I), the cell's activity increased during the interval in which the limbs were stationary. In contrast to unperturbed locomotion (A–D), the increased discharge was better correlated to the increased triceps EMG activity. A large increase in discharge was observed when the perturbation arrested the ipsilateral forelimb in mid-flexion during protraction (J–N). In this run the activity of the interposed unit appeared better related to the biceps EMG.

The STAs generated from the same trials are shown in Fig. 6 and confirm the changing relationship between the cell's discharge and the EMG activity. During unperturbed locomotion the biceps STA reached a maximum at a latency of 150 ms (A), and the triceps reached a minimum at the same latency. When the step cycle was perturbed during stance (C and D) the form of STA changed dramatically. The peak biceps activity (C) shifted to a later latency of 550 ms and the minimum in the triceps activity shifted to 300–400 ms. Perturbation during forelimb retraction (E and F) also altered the STAs. Peak biceps activity occurred at 250 ms (E). The triceps STA was flat for the first 250 ms (F) due to the absence of triceps activity during the perturbation.

This interposed cell responded to the perturbation of a single limb as shown in Fig. 7. In the first run (E–I) the leg struck the bar during retraction 100 ms after the bar was protruded (arrow, H). The perturbation produced an increase in unitary activity clearly related to the stimulus. In addition, the unitary activity associated with the second step of the cycle was reduced. When the perturbation duration was reduced to 200 ms but was activated at the same time in the step cycle (J–N), a somewhat larger and longer response was evoked. The response again had two components, an initial increase in activity shortly after the limb hit the bar followed by a longer duration increase as the leg was pressed against the bar. As seen in E and J, the duration of the response was not related to the duration of the perturbation. This may have resulted from the failure of the two perturbations to affect differentially the timing of the step cycle (compare H and M). Alternatively this cell's response may have been evoked by the activation of either cutaneous, muscle or joint receptors. This interpretation is consistent with the change in

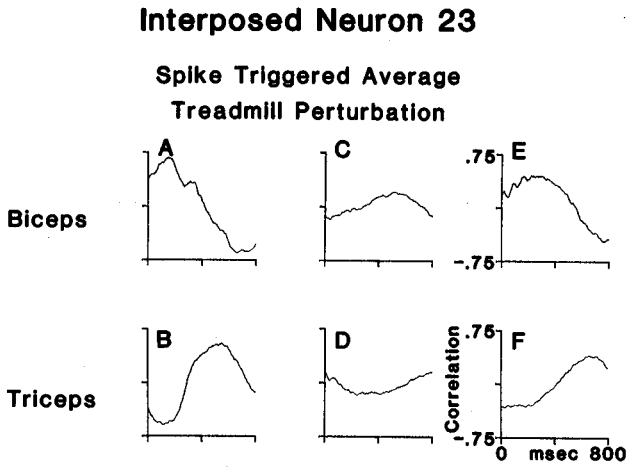

Fig. 6A–F. Spike triggered averages calculated from trials in Fig. 5. **A, B** STAs from unperturbed step cycles in Fig. 5A–D. **C, D** STAs from trials in Fig. 5E–I (757 spikes). **E, F** STAs from trials in Fig. 5J–N (633 spikes). There was a dramatic shift in the STA of the biceps EMG (compare **A** to **C**) and a change in the shape of the early part of the triceps STA, indicating that the perturbation dissociated the unitary activity from both the biceps and triceps EMG

the neuron's activity when the limb struck the bar during protraction and then stepped over the obstacle (O–S). The limb struck the bar 700 ms after the trigger, as indicated by the arrow in the displacement record (R). This was followed by an increase in the activity of the interposed cell.

Spike triggered averages demonstrated that the discharge rate was not tightly coupled to the forelimb EMG activity (Fig. 8). For example in C when the movement of the forelimb was arrested during retraction (see Fig. 7E–H) the peak in the biceps STA occurred at a 400 ms latency, 300 ms later than in the unperturbed trials (A). Consistent with the PTH data in Fig. 7J–N, the STAs from the trials in which a short duration treadmill perturbation was used (E, F) were similar to those in C, D. However, when the limb struck the obstacle during protraction the opposite relationship was found (G, H). The peak of the biceps and triceps STA was shifted toward the origin, as compared to the unperturbed run (A, B). For this interposed neuron the relationship between its discharge and the forelimb EMG was altered by the perturbation. The neuron's activity was more highly correlated with the perturbation than with the activation of either muscle.

Although the cells described in Figures 1–8 represent the majority (40 of the 46) of the modulated interposed cells studied, additional patterns of activity were observed. Four cells were broadly modulated, and the modulation of the two cells

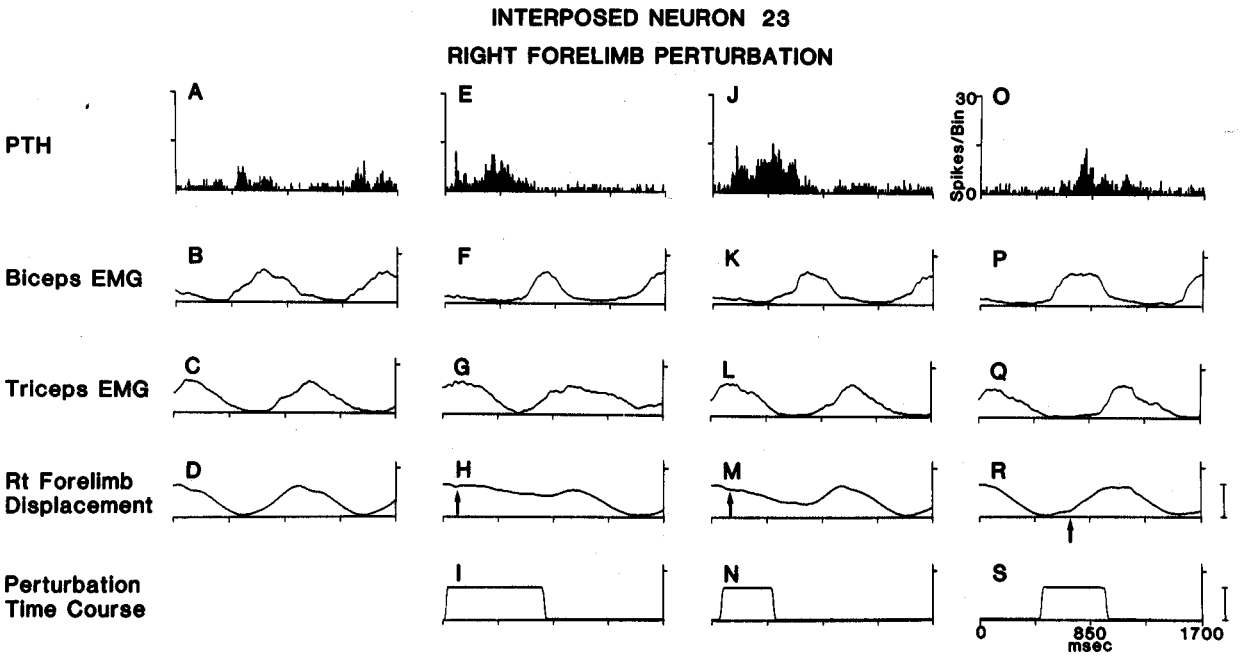

Fig. 7A–S. Activity of the same interposed neuron during unperturbed locomotion and single limb perturbation. **A–D** Unperturbed step cycles. **E–I** Step cycles perturbed with a prolonged perturbation (800 ms duration) at the beginning of stance phase. **J–N** Perturbation applied slightly later in retraction for 400 ms. **O–S** Perturbation applied during protraction. Each time the limb struck the bar, regardless of direction or phase of the step cycle, the cell responded with an increase in discharge rate. In **R** the calibration bar = 9 cm, in **S** the bar = 7.6 cm

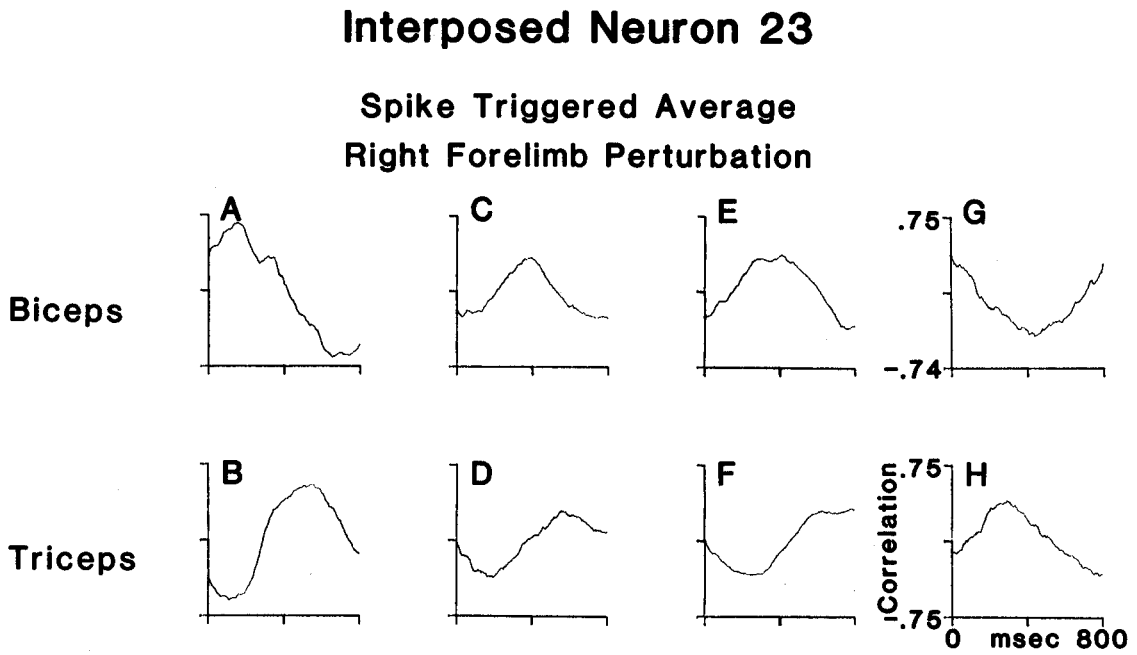

Fig. 8A–H. Spike triggered averages corresponding to the trials in Fig. 7. **A, B** Unperturbed trials in Fig. 7A–D (308 spikes). **C, D** STAs of trials in Fig. 7E–I (447 spikes). **E, F** STAs from trials in Fig. 7J–N (661 spikes). **G, H** STAs from trials in Fig. 7O–S (381 spikes). The single limb perturbation changed the phase of the EMG activity in the STAs of both muscles (compare **C** to **G** and **D** to **H**)

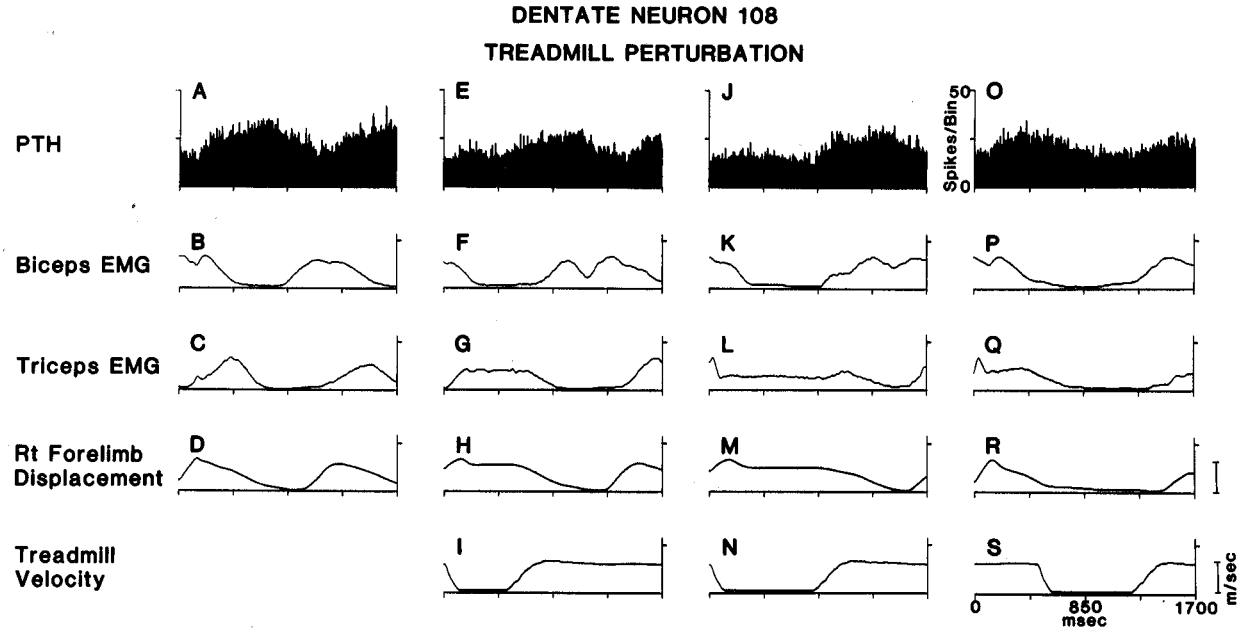

Fig. 9A–S. Activity of a dentate neuron that was modulated during locomotion. **A–D** Unperturbed step cycle. **E–I** A treadmill perturbation applied at the beginning of the sweep for 700 ms. **J–N** A longer lasting treadmill perturbation applied at the beginning of the sweep. **O–S** Same perturbation as in **H** applied at the end of stance phase. The modulation of the cell was arrested when locomotion ceased during the perturbation. The calibration bar in **R** = 6.4 cm, in **S** the bar = 0.38 m/s

tested with perturbations was arrested. The discharge of two interposed neurons was apparently related to the back legs. Only six interposed units were unmodulated during locomotion. Two of these were tested with perturbations and both had complex responses with the treadmill perturbation.

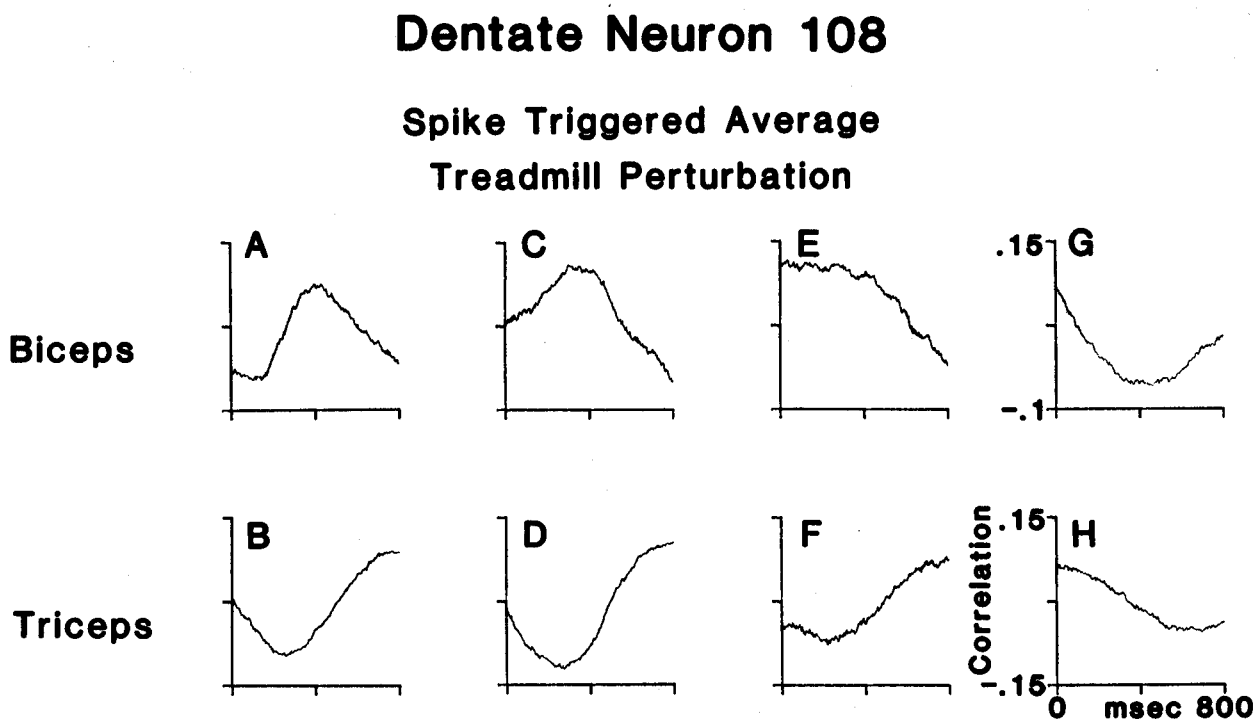

Fig. 10A–H. Spike triggered averages corresponding to the trials in Fig. 9. **A, B** STAs of unperturbed trials in Fig. 9A–D (3483 spikes). **C, D** STAs from trials in Fig. 9E–I (3508 spikes). **E, F** STAs from trials in Fig. 9J–N (3436 spikes). **G, H** STAs from trials in Fig. 9O–S (3653 spikes). The phase shifted in the STAs of both muscles in the perturbation trials

Dentate cells

In contrast to interposed cells, only a minority of dentate neurons (33 of 243 cells) were modulated with normal locomotion. Of the 210 cells not cyclically modulated during unperturbed locomotion, 83 were examined during perturbations. Of these, 51 showed changes in their discharge rate with the perturbations.

A representative of one of the 33 modulated dentate neurons is illustrated in Figs. 9 and 10. This neuron was broadly modulated during normal locomotion (A–D). The depth of modulation as judged by its STA was characteristically less than modulated interposed neurons. In fact this cell had a greater depth of modulation than most dentate neurons. Additionally its activity was not tightly correlated with the time course of either muscle's EMG. When locomotion was briefly interrupted by a treadmill perturbation in early retraction (E–I), the modulation was reduced. With a longer perturbation (J–N), the cell's modulation was suppressed until the treadmill was reaccelerated. Timing the longer duration perturbation to occur at the end of retraction (O–S) also arrested the modulation until the step cycle resumed.

The STAs in Fig. 10 show that during unperturbed locomotion, peak unitary activity occurred when the biceps EMG was near its minimum and when the triceps activity was about half maximal. Note that the peak to peak amplitude in the STA is about an order of magnitude smaller than for the interposed neuron in Fig. 2. The relationship between the biceps EMG and neuronal activity was altered when the step cycle was interrupted with the longer duration perturbation. When perturbations were applied at the beginning (E, F) or at the end (G, H) of retraction, the peak unitary activity was associated with maximal biceps activity. Not only do these STAs differ from those obtained from unperturbed locomotion trials (A, B), but the relationship between the dentate cell's activity and the EMG responses was dependent on the phase of the step cycle in which the perturbation was applied. When the perturbation occurred at the beginning of retraction, the peak unitary discharge was associated with minimal triceps activity (F). In contrast when the perturbation occurred late in retraction, the peak unitary discharge occurred with the maximal triceps activity (H).

Most of the dentate cells examined in this experiment were not well modulated during unperturbed

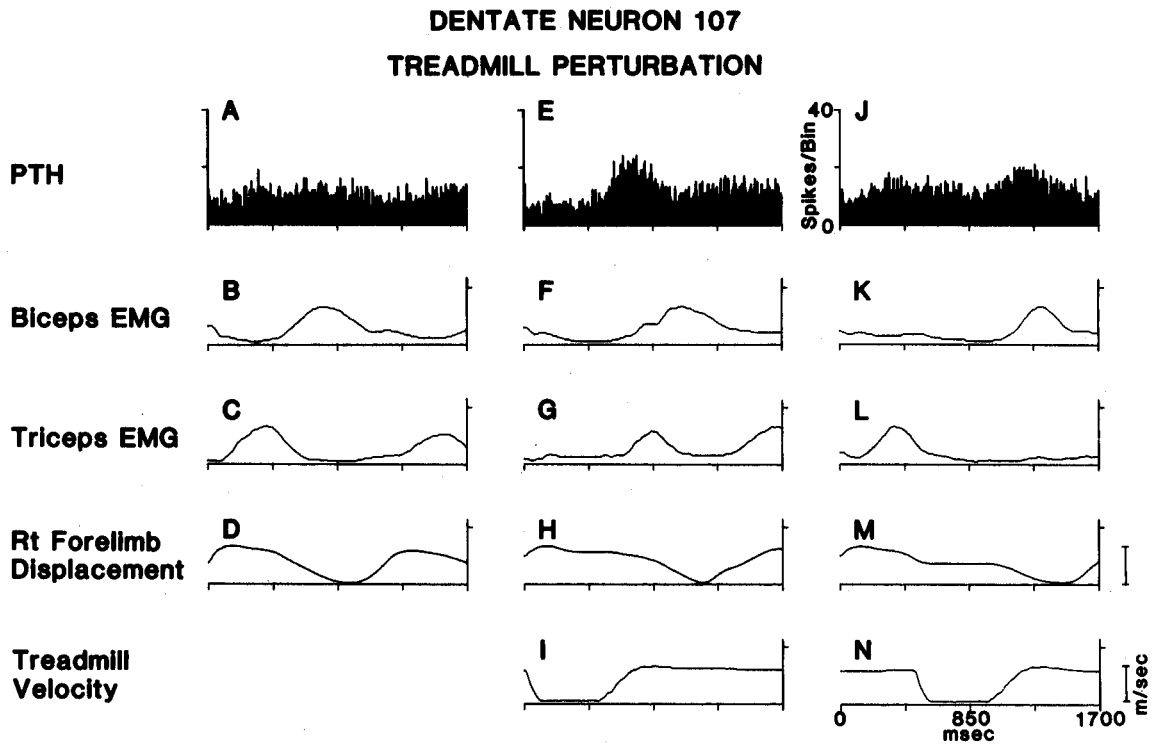

Fig. 11A–N. Response of a weakly modulated dentate neuron to treadmill perturbation. **A–D** Unperturbed trials. **E–I** The step cycle was arrested at the beginning of the sweep during early stance phase for approximately 600 ms. **J–N** The step cycle was perturbed later during retraction. This cell was poorly modulated during unperturbed locomotion, but responded with an increased discharge rate upon resumption of locomotion after the perturbation. The histograms and averages in this figure were constructed from 100 sweeps. In **M** the calibration bar = 9 cm, in **N** the bar = 0.3 m/s

walking as shown in Fig. 11. In the unperturbed trials only a small amount of modulation was present (A). During perturbations early in retraction (E–I) the small modulation ceased. Upon resumption of locomotion there was a large increase in discharge rate. A similar perturbation placed later in the cycle (J–N) elicited a comparable response. Notice that the relationship of the unitary response to the triceps EMG was dependent upon the phase at which the perturbation was applied. A cusum analysis was used to evaluate the significance of the response (Fig. 12). This analysis compared subsequent 50 ms "windows" of the cusum slope of the unperturbed run to successive slopes from the perturbed run. Bins which deviated by more than three standard deviations from control are denoted by a bar under the abscissa of the PTH. The incremental height of the bar indicates an additional standard deviation above this threshold. Because of the very weak modulation during unperturbed locomotion, only a few bins surpassed the three standard deviation threshold in the unperturbed trials (bars under the abscissa in A). However, the increase in activity produced by arresting the step cycle in early stance phase (C–E) was significant.

The increase in discharge occurred when the treadmill was accelerating and locomotion was reinitiated. This response had a fixed relation to the perturbation. Clearly, the relationship of the neuronal response relative to the EMG activity was quite different following perturbations applied at different phases of the step cycle. This feature was very characteristic of most dentate neurons' response to the perturbation and was a striking contrast to the responses of most interposed neurons.

For most dentate neurons, perturbation of a single limb did not modify the cell's discharge (Fig. 13). In E–I the limb was arrested during retraction, and in J–W the limb trajectory was altered when the limb moved forward. Neither perturbation elicited a response from the cell, as confirmed by cusum analysis in Fig. 14.

Recording locations

The positions of the recording sites in the interposed and dentate nuclei are shown in Fig. 15. Consistent with the above inferences, the neuronal responses in the interposed nuclei differed from those in the

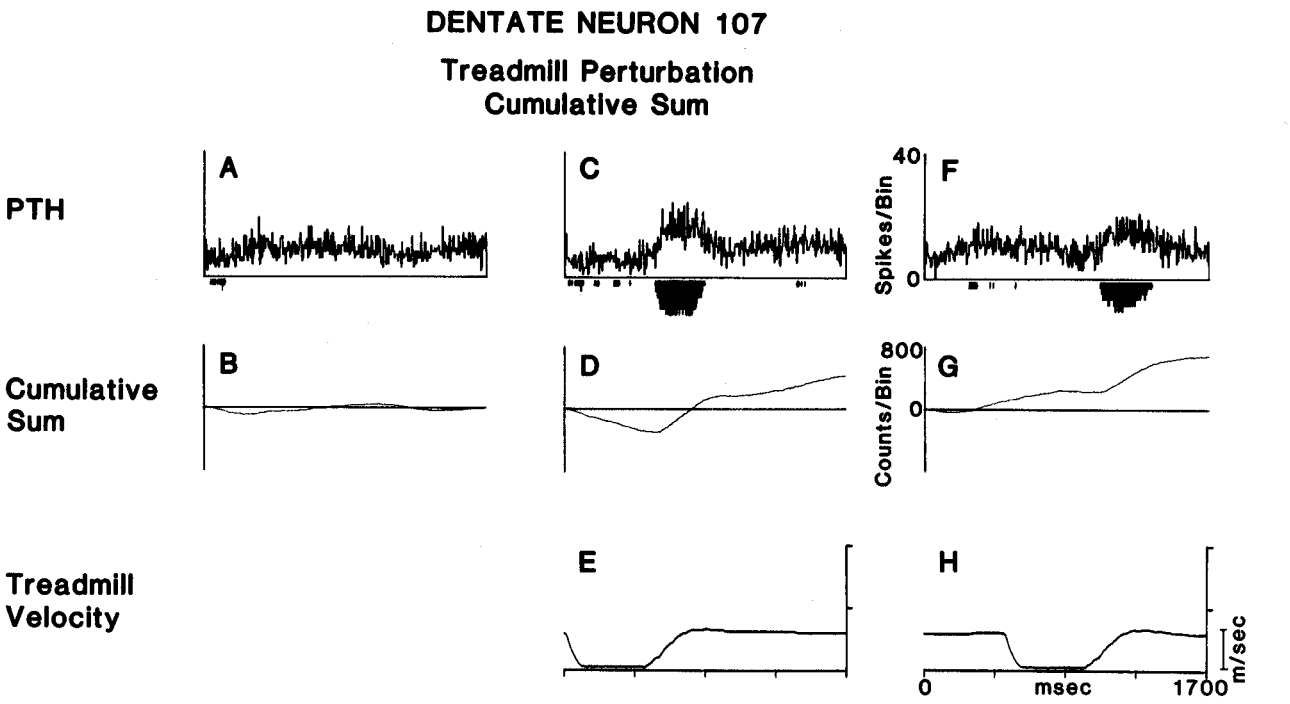

Fig. 12A–H. Cumulative sum analysis of the responses shown in Fig. 11. The cusum of the unperturbed trials (**B**) shows that the activity of this cell is only weakly modulated with only a few bins of the PTH showing statistical significance (**A**). When the step cycle was perturbed in early retraction the large increase in activity at the end of the perturbation was clearly significant (8 SD). A comparable increase in neuronal discharge at the end of the perturbation also occurred when the step cycle was arrested in the middle of retraction (**F–H**). The calibration bar = 0.38 m/s

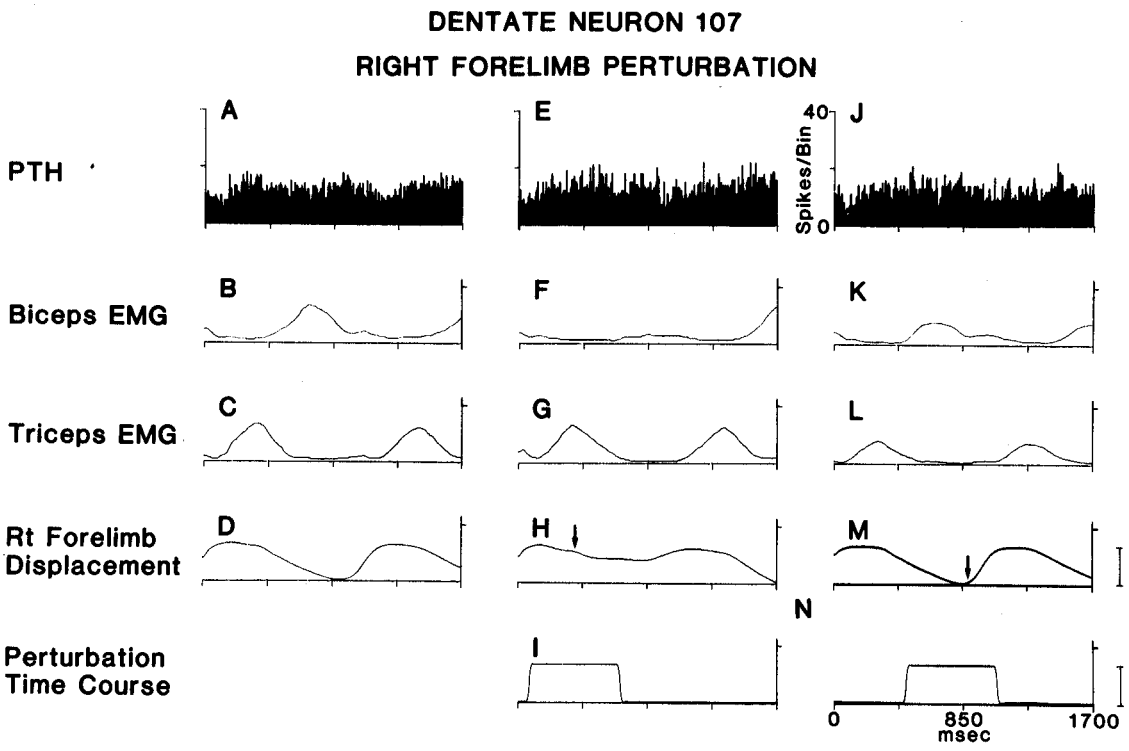

Fig. 13A–N. Response of same dentate neuron analyzed in Fig. 11 and 12 to single leg perturbation. These PTHs and averages were constructed from 100 sweeps. **A–D** Unperturbed trials. **E–I** 500 ms single limb perturbation. **J–N** Same perturbation applied during protraction. Perturbations of the ipsilateral forelimb did not elicit a response from this cell. In **M** the calibration bar = 9 cm; in **N** the bar = 7.6 cm

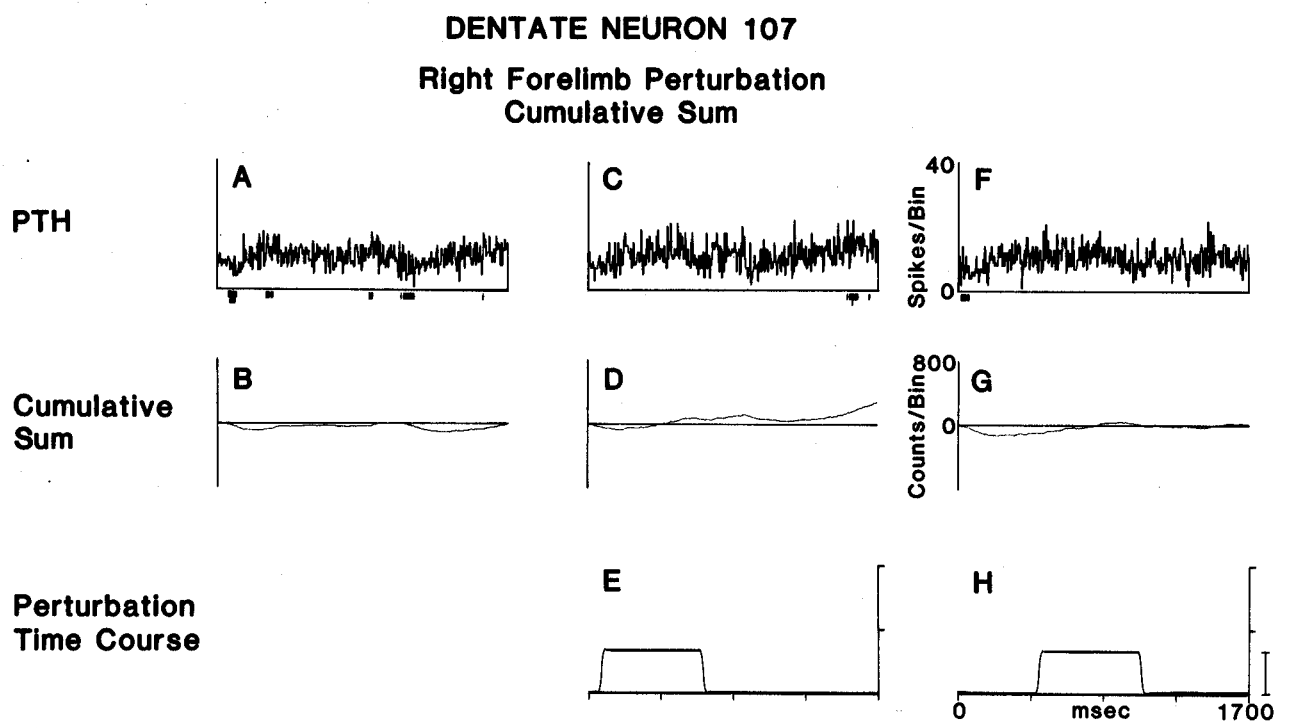

Fig. 14A–H. Cumulative sum analysis of responses in Fig. 13. In **B** the cusum indicates that the PTH of unperturbed trials (**A**) is only weakly modulated. When the limb was arrested during retraction (**C–E**) there was no response to the perturbation. There was also no response of the dentate neuron when the step cycle of this limb was interrupted during protraction (**F–H**). The calibration bar = 7.6 cm

dentate nucleus. Interposed cells with discharge rates modulated with the step cycle were correlated with the activity of the biceps and/or triceps muscles. The perturbation experiments required neurons responsive to forelimb movements which may account for the observation that all of the recorded interposed neurons were in the posterior interposed nucleus. This nucleus has been shown to project via the dorsomedial magnocellular red nucleus to forelimb motor nuclei (Giuffrida et al. 1980; Asanuma et al. 1983b). This may reflect a selection bias making it difficult to comment on the apparent lack of responsive or modulated neurons in the anterior interposed nucleus. Neurons with unmodulated activity which nonetheless responded to the perturbation were primarily restricted to the dentate nucleus. Lastly the neurons with specific response characteristics do not appear confined to any region in either nucleus, although a larger cell population is required before this conclusion can be stated with certainty.

Discussion

Characteristics of interposed neuron responses

Our results demonstrate that the discharge of the majority of interposed neurons is tightly correlated to the EMG patterns associated with *a specific phase of the step cycle.* This finding is in basic agreement with the work of Orlovsky (1972). He described many neurons in the interposed nuclei which were modulated during hindlimb locomotion. Although the step cycle phases in which the firing rate peaked were widely distributed, more neurons increased their discharge rate during retraction than protraction. Similar results were found by Armstrong and Edgley (1984b). They also observed a wide dispersion in the phase relationship, but the "average" neuron increased its firing rate during protraction. We did not quantitate the peak firing rate to step cycle phase relationship in our study. Rather we looked at the correlation between EMG patterns and neuronal discharge rate. We found no preferential step cycle phase; half the modulated neurons were in phase with the triceps, the other half with biceps. Perturbations of the step cycle did not alter this phase relationship. Even when the step cycle was perturbed the correlation was preserved. For many cells the modulation was often highly correlated with the EMG activity of either the triceps or biceps. It should be emphasized these results only demonstrate that the modulation of interposed neurons is highly coupled to a muscular activity related to a specific phase of the step cycle. An argument that these interposed

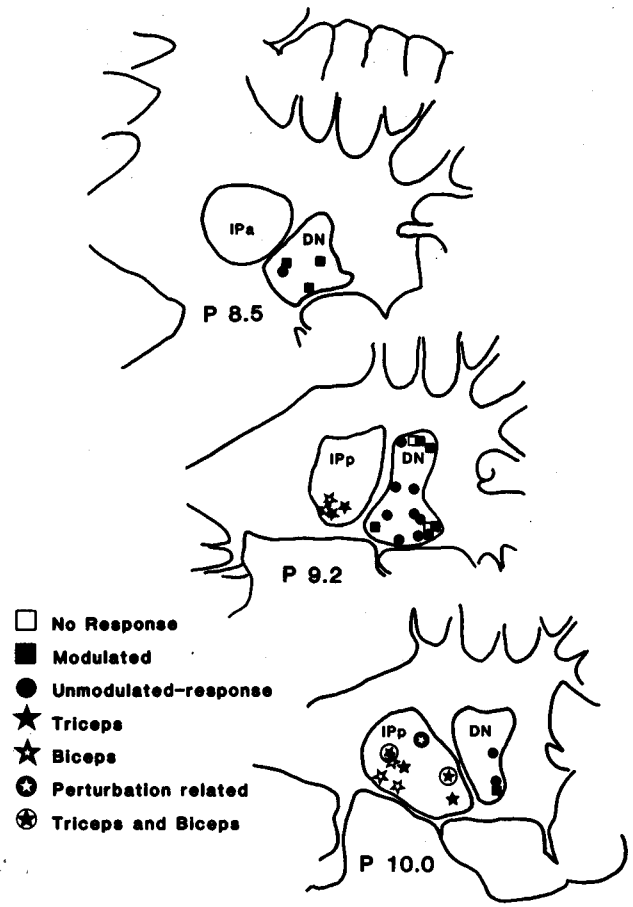

Fig. 15. Three representative frontal hemisections of the interposed and dentate nuclei. These symbols show the type of neuronal response found at the indicated electrode position. Dentate neurons which responded during the experiment had activity that was either modulated (filled squares) or unmodulated during normal walking. Some unmodulated dentate neurons did not respond during the perturbation (empty squares), but many of these cells (filled circles) responded to the perturbation. Modulation of interposed neurons was generally related to either biceps (white stars) or triceps activity (filled stars). Locations where both types of interposed cells were found are marked with an encircled, filled star. Interposed neurons whose activity was modulated by the single limb perturbation are shown by encircled, white stars

neurons are only related to the biceps and triceps cannot be made, since many other muscles would be active with comparable phase relationships during the step cycle (Grillner 1975; Wetzel and Stuart 1977). In a task involving forelimb reaching in the cat (Soechting et al. 1978) it was found that the EMG of the forelimb biceps and triceps was correlated to the activity of ipsilateral interposed cells, but not in a causal manner. One possibility is that the interposed and EMG activity share a common input possibly derived from a spinal pattern generator.

A smaller population of interposed neurons did not exhibit the same degree of coupling with a specific phase of the step cycle. As shown in the STAs in Figs. 7 and 8, the correlation of the neuronal activity with forelimb EMG was dependent upon the perturbation. The neuronal response may result from the activation of limb peripheral receptors by the rod during the perturbation. Since receptive field analysis was not performed on each neuron, this argument cannot be substantiated without additional experimentation.

A number of authors have proposed that the intermediate sagittal zone of the cerebellar cortex and the interposed nuclei are involved in the regulation of ongoing motor activity (Giuffrida et al. 1980; Strick 1983). Ventral spinocerebellar tract (VSCT) cells appear to receive an input from the central pattern generator responsible for spinal locomotion (Arshavsky et al. 1983), since they are modulated during hindlimb locomotion even with the dorsal roots cut (Arshavsky et al. 1972a; Arshavsky et al. 1972b). VSCT cells are also modulated during fictitious scratching and in spinalized animals (Arshavsky et al. 1984). Both the intermediate region of the cerebellar cortex and the interposed nuclei receive inputs from the VSCT and its forelimb equivalent, the rostral spinocerebellar tract (Bloedel and Courville 1981). Based on these data and the organization of inputs to the VSCT proposed in the comparator hypothesis of Lundberg (Lundberg 1971), activity in the VSCT likely reflects the combined action of descending projections and spinal generator outputs.

Interestingly a subset of interposed neurons receives a different class of information, possibly reflecting the activation of peripheral cutaneous muscle or joint receptors during the perturbed and unperturbed step cycles. These responses could be mediated by a number of direct and indirect spinocerebellar pathways that respond to the activation of exteroceptive and proprioceptive receptors (Bloedel and Courville 1981). In addition to signalling activity in these pathways, some data suggest that the interposed output is partly responsible for the modulation of descending pathways. For example, cerebellectomy abolishes the normal cyclic modulation of neurons in descending spinal tracts during locomotion (Arshavsky et al. 1983). Consequently the integration of several classes of information in the interposed nuclei could provide a mechanism by which the action of descending pathways and peripheral inputs contribute to the descending control of spinal reflexes and the regulation of the locomotor generator.

Characteristics of dentate neuron responses

During perturbed and unperturbed locomotion the activity of dentate neurons differed greatly from that

of interposed cells. The majority of dentate neurons were not modulated during unperturbed locomotion. However, this group of cells was responsive to perturbations involving the arrest and resumption of the locomotion. In contrast with the results of Arshavsky et al. (Arshavsky et al. 1980), a few dentate neurons were modulated during unperturbed locomotion. Unlike interposed cells, this subpopulation's discharge could be easily uncoupled from forelimb EMG activity by perturbation of the step cycle.

These observations address several pertinent issues of dentate function. First, the data illustrate dentate nuclear neurons can be modulated with motor behavior in the absence of the thalamus and cortex, even without input from the cortico-pontine system. Previous studies illustrated that dentate neurons respond to peripheral inputs via indirect spinocerebellar pathways (Bantli and Bloedel 1977), but don't receive direct spinal input as do interposed neurons. Also, the output of the dentate nucleus modifies the excitability of neurons in reticulospinal and rubrospinal projections (Bantli and Bloedel 1976; Tolbert et al. 1978; Hames et al. 1981; Vitek 1984). In high decerebrate preparations, microstimulation of the dentate nucleus can alter the excitability of gamma motoneurons (Vitek 1984), alpha motoneurons (Bantli and Bloedel 1976; Vitek 1984) and cutaneous and proprioceptive reflex pathways (Bantli and Bloedel 1975; Bantli and Bloedel 1976). These observations suggest the possibility that the dentate nucleus monitors alterations in locomotion and then modifies brainstem-spinal pathways involved in regulating the spinal pattern generator independent of the thalamus and cortex. These dentato-spinal projections may provide an additional system for modifying the gain of spinal reflexes throughout the step cycle (Forssberg et al. 1976; Wand et al. 1980).

Our findings in the decerebrate cat are not unlike those found in intact animals. Dentate neuronal activity in primates performing single joint arm movements is modulated at or before the start of the movement (Thach 1970; Thach 1978; Strick 1983; Wetts et al. 1985; Chapman et al. 1986). A major target of dentate output is the parvocellular red nucleus which in turn projects to the inferior olive (Strominger et al. 1979; Asanuma et al. 1983a; Asanuma et al. 1983b). This nucleus contains cells which respond prior to corrective movements in monkeys performing a wrist pronation – supination task (Shinoda et al. 1980). These responses were unrelated to EMG activity. Similarly, many of the dentate neurons in our study of the walking cat increased their discharge rate when locomotion was resuming at the end of the perturbation. This response was clearly unrelated to EMG patterns of the forelimb muscles. Another cerebellar system also responds to sudden alterations of movement. Using the same paradigm as this study, complex spikes were evoked at the resumption of locomotion after a treadmill perturbation (Wang et al. 1985). Climbing fiber responses were also evoked when monkeys encountered an unexpected perturbation when using a handle to make wrist movements (Gilbert and Thach 1977). These findings emphasize the importance of the cerebellum as a structure involved in compensating for unexpected changes in movement.

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