# Cortically Controlled Gait Adjustments in the Cat

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Land-living animals must control the placement of feet precisely in order to avoid numerous obstacles present in natural environments. How does the CPG-generated pattern of locomotion gets adjusted to the features of the environment? It has been shown that an exact positioning of feet on the surface is difficult or impossible after a transection of the corticospinal tract[1] and that the activity of the motor cortex (MC) undergoes dramatic change during transition from locomotion on flat surface to locomotion on irregular terrain.[2–4] These facts, taken together, strongly suggest that the MC plays a decisive role in the control of the precise stepping movements. How is this control incorporated in the CPG generated pattern of locomotion?

The activity of 206 neurons in the MC of the cat was recorded and compared during locomotion on a flat surface and during walking with precise paw placing while overstepping obstacles or walking along a horizontal ladder. Activity of 89% of neurons was modulated in the rhythm of locomotion while walking on the flat floor. The inactivation of MC by the use of tetrodotoxin (10 mol/L, 2 μL) did not have a visible effect on performance of locomotion. That suggests that the modulation of MC activity during locomotion on flat surface had "informational" content. When obstacles along the pathway or the ladder were introduced, the strength of the locomotor modulation of activity changed: it increased in 50% of neurons and decreased in 10% of them. The change in the modulation of the MC activity increased as the requirements for precise paw placing increased. Inactivation of the MC had a totally destructive effect on the ability of subjects to walk with precise paw placing.

These results suggest that the MC conveys very important commands during locomotion with precise stepping, which are needed for the proper adjustments of the gait to the features of the environment. These commands are manifested through the changed strength of the locomotor modulation of activity of MC neurons. The phase of the maximal activity of the neurons in the step cycle, however, was generally kept the same after the transition from locomotion on flat surface to locomotion with the precise paw placing. That ensured the incorporation of the descending cortical commands indestructibly in the CPG-generated pattern of locomotion. It is suggested that the CPG-generated pattern of locomotion gets adjusted to the features of the environment by cortical commands, which correct the amplitude of the muscle contraction but not the phase of the muscle activity in the locomotor cycle.

How are the cortical commands, which are vitally important for the proper adjustment of locomotion to the features of the environment, formed? It was shown that during locomotion the cerebellum secures the frequency modulation of all the tracts descending from the brain stem to the spinal cord in the rhythm of locomotor movements.[5] Our preliminary studies showed that this is likely to be the case with the pyramidal tract as well.[6] Ventrolateral thalamus (VL) is known to transmit signals from the cerebellum to the MC.[7]

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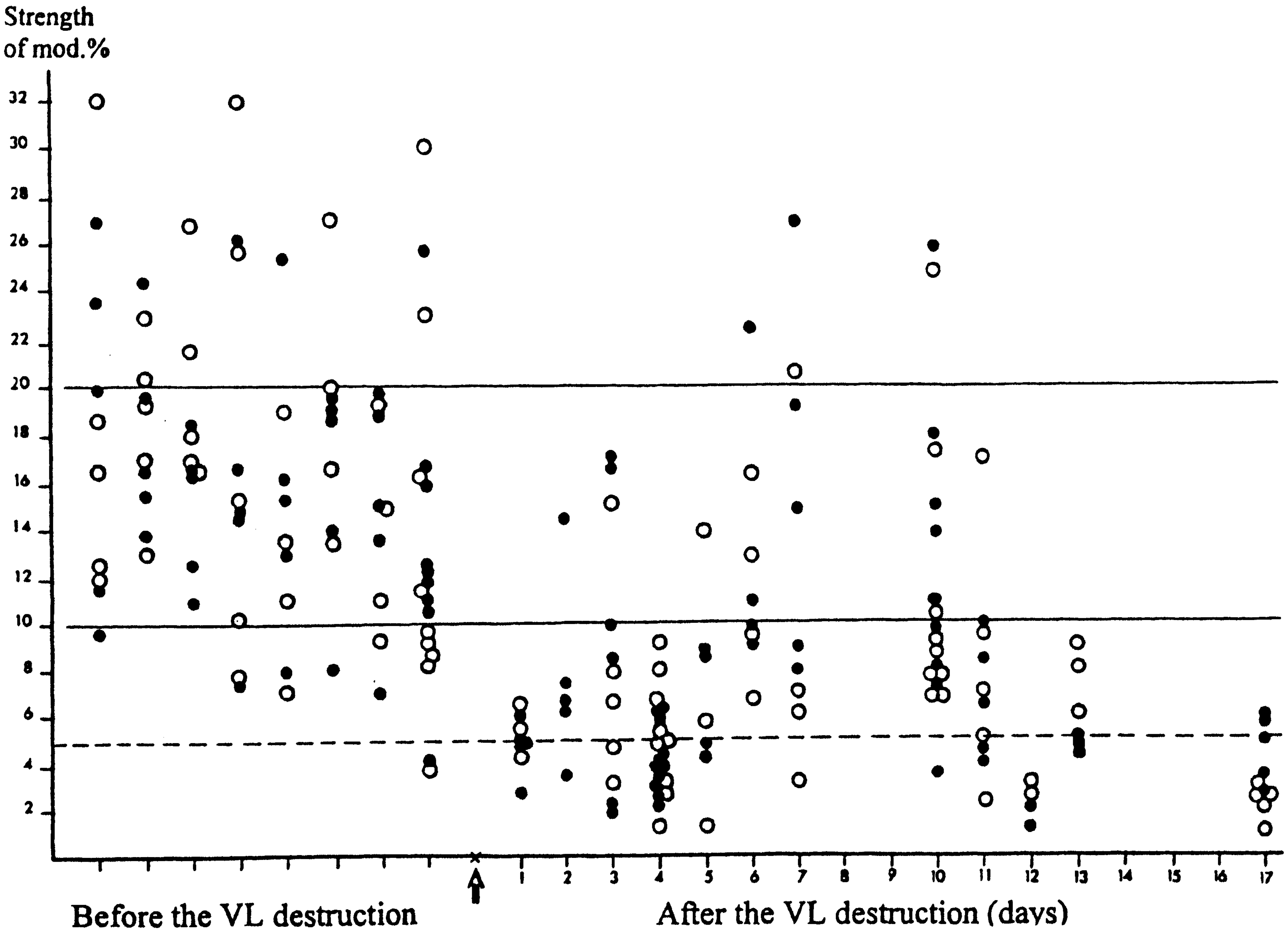

**FIGURE 1.** Changes in the strength of frequency modulation of MC neurons after the bilateral VL lesions during locomotion in one cat. Each column presents strength of modulation of the activity of neurons encountered during one-day recording session. Strength of modulation (%) was calculated as the difference between the maximum and the minimum number of spikes in the averaged post-event time histogram bins divided by the total number of spikes. *Filled circles* present the strength of modulation during walking on the flat surface; *open circles* present the strength of modulation during walking along the ladder. *Solid lines* indicate the range of the strength of locomotor modulation in which 75% of MC neurons fall in normal subjects. *Dotted line* indicates the level when there is no statistically reliable modulation of activity. *Arrow* shows the day when the bilateral VL lesion was made. After the bilateral VL lesion, the cat could not make any correct steps on the crosspieces of the ladder for three days, for those days the "most successful" steps (attempts) were taken for the analysis although the cat had missed a crosspiece. On the fourth day the cat was able to make few correct steps on the ladder. The ability to walk along the ladder improved considerably over the next couple of days, and by the seventh day the cat performed with a 100% success rate on the ladder. However, the activity of the MC remained altered for the period of observation (17 days).

Bilateral lesions in the VL resulted in a significant drop in the strength of the locomotor modulation in the MC during locomotion on flat surface (FIG.1). A well-expressed decrease also occurred in the strength of modulation of activity of MC neurons during walking with precise paw placing along the ladder (FIG.1). After the lesion there were few descending commands going out from the MC to the spinal locomotor mechanism for the adjustment of the gait to the terrain. Cats were totally unable to walk on the ladder during the first days after the lesion.

Recordings made from the cerebellum showed that the step-related activity is widely spread through different regions of the cerebellar cortex and in the deep cerebellar nuclei.[5,8] Our pilot data show that the activity of nucleus dentatus (ND) and nucleus interpositus (NI) of cerebellum experiences a significant change during transition from locomotion on flat surface to locomotion with the precise paw placing. These changes were different in

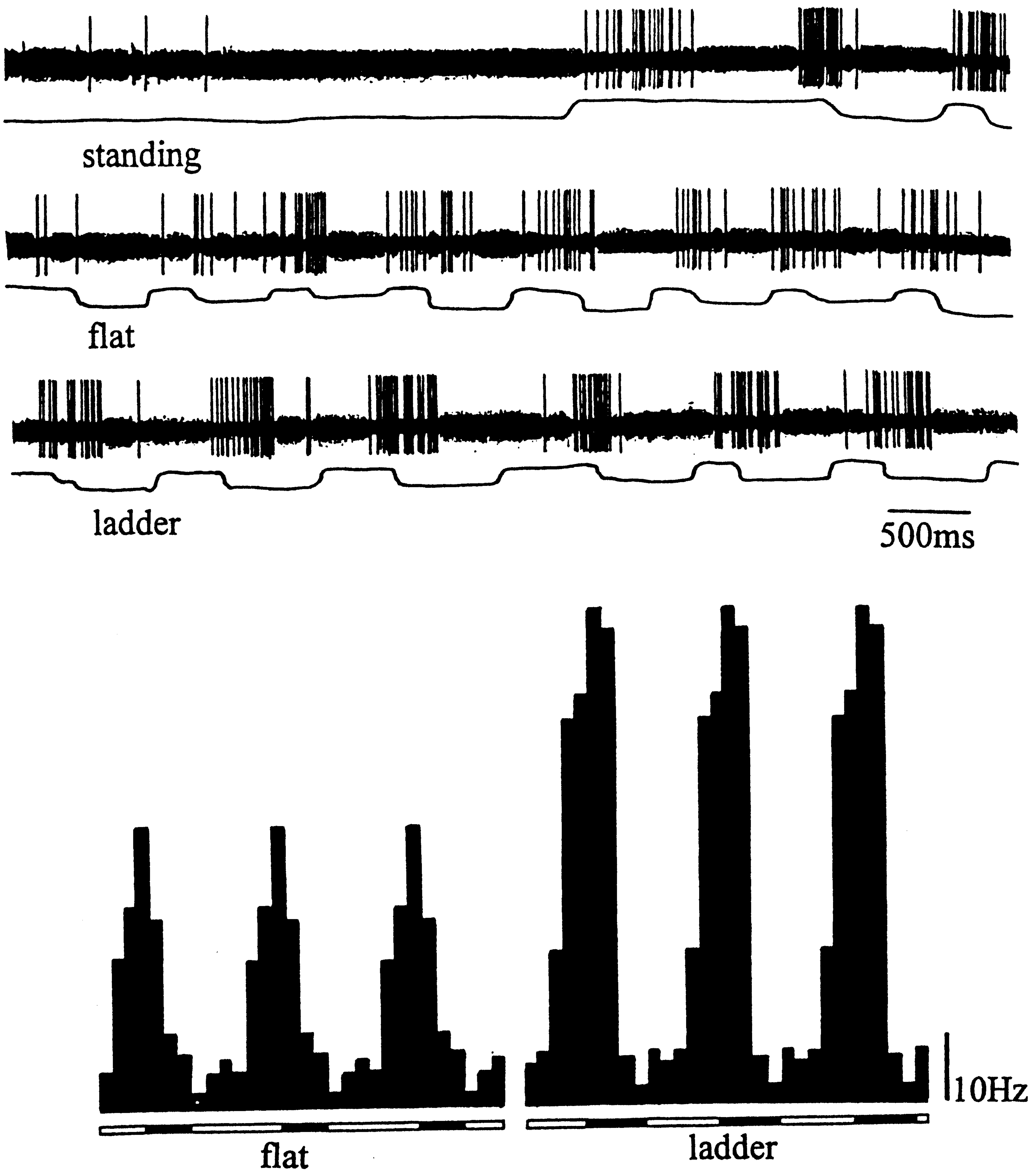

**FIGURE 2.** An example of activity of a neuron from nucleus dentatus of cerebellum while standing, and during locomotion on the flat surface and along a ladder. *Bottom lines* indicate the stance and swing phases of the forelimb ipsilateral to the neuron (deflections down and up, respectively). The corresponding phase distributions of the neuron's activity are presented in the *lower panel* of the figure. The *filled bar* at the bottom shows the swing phase and the *open bar* shows the stance phase of the cycle for the forelimb ipsilateral to the site of recording.

the neuronal populations of ND and NI. While the activity of neurons in the NI changed primarily in the mean rate, the activity of neurons in the ND experienced also a change in the strength of the locomotor modulation (FIG. 2). That change in activity of ND neurons resembled that of the neurons in the MC: it was predominantly an increase in the strength of the locomotor modulation of neuronal activity with the phase being kept the same. This suggests that the cerebellum possesses information which, if reached in the MC, could influence it in such a way that the described changes in the cortical activity will appear during locomotion on flat surface and upon the transfer to precise stepping movements.

It is suggested that the commands, which are essential for the proper adjustment of locomotion to the features of the environment, are mainly formed in the cerebellum. After being formed these commands are conveyed to the MC via the VL thalamus for the output to the spinal cord and possibly also for an additional tuning in accordance with other inputs to the MC. Further analysis is needed to determine specific contributions of the cerebellar and the other inputs to the MC to the cortically controlled gait adjustments, which are used in complex natural environments.

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