For maintaining upright posture, there exist postural reflexes such as tonic labyrinthine, neck, and lumbar reflexes, which are induced by movements of the head and body and act on the limb musculature [1, 2]. Lateral vestibular nucleus neurons have been thought to play crucial roles in the postural reflexes, since they receive converging inputs from the vestibular labyrinth as well as neck and limb afferents [3–7] and send outputs to limb extensor motoneurons via the lateral vestibulospinal tract [8]. Thus the lateral vestibulospinal neurons presumably consist of an output path of these postural reflexes. This notion is consistent with the findings that lateral vestibulospinal neurons also receive strong neck input, which is as strong as their vestibular input [9–11]. However, little is known about the relationship between lateral vestibulospinal neurons and the tonic lumbar reflex; there has been no report on lumbar input to vestibulospinal neurons. In this study we investigated the responses of vestibulospinal neurons to lumbar rotation of the caudal body in decerebrate rats.

Experiments were performed in 8 adult male Wistar rats, weighing 280–370 g, which were decerebrated at the intercollicular level under Nembutal anesthesia (50 mg/kg). Extracellular spikes were recorded in the left vestibular nucleus complex with micropipette electrodes filled with 2 M potassium citrate. For antidromic stimulation, bipolar silver ball electrodes were placed on the peridural surface of the left ventrolateral funiculus at the lower thoracic spinal cord (T10–11). The neurons were identified vestibulospinal if they could be excited from the lower thoracic cord with fixed latency and if they could further follow repetitive shocks up to 500/s. The collision test was also performed in some neurons. Their responses to the caudal body rotation were then examined while the head and chest were fixed in space with a stereotaxic frame and a metal clamp. The caudal body attached to a metal plate was alternately rotated around the vertebral axis to the right side-down (contralateral) and to the left side-down (ipsilateral) in a ramp-and-hold manner. The body was then kept in the two inclined positions for 6–12 s, the position between the two being changed with an angular speed of about 25°/s. The magnitude of the rotation was 25° on both sides. During experiments, rectal temperature was maintained with a lamp from 30°C to 36°C. After each experiment, the track of the recording electrode left in situ was recovered in frozen transverse sections of the brain stem to determine the cell location; the sites of recording along the track were then interpolated from accurate depth readings during penetration. To determine the relative locations of recorded cells within the vestibular nucleus.

**Abstract:** In vestibulospinal neurons projecting to the lumbar enlargement, activities were modulated in response to alternate tilts of the caudal body around the vertebral axis. Three types of neurons were found: Type I (37.8%) showed faster firing during the ipsilateral side-down tilt; type II (51.1%) showed the reverse pattern; type III were unaffected. Types I and II may be important in the tonic lumbar reflex. [The Japanese Journal of Physiology 54: 495–498, 2004]
complex, we stained the sections with neutral red. The cell distribution map was then graphically transformed from the transverse plane to the horizontal plane.

The present report is based on 45 vestibulospinal tract neurons in 8 decerebrate rats. The latencies of antidromic spikes from the lower thoracic spinal cord ranged from 0.9–2.5 ms; the mean (±standard deviations, SD) was 1.72 ± 0.41 ms. These neurons were tentatively divided into three groups on the basis of response pattern to lumbar rotation, one having faster firing during the caudal body tilt toward the side ipsilateral to the recording site (ipsilateral side-down), the second one having faster firing in the opposite tilt (contralateral side-down), and the third no modulation in firing. Examples of the three groups of neurons are illustrated in Fig. 1. The neuron shown in Fig. 1A discharged rhythmic bursts in the resting condition where the caudal body was kept steady in a midposition (without tilt). The resting discharges had a mean firing frequency of 13.5 Hz. During lumbar rotation, the firing activity increased (20.5 Hz) when the body was rotated toward the ipsilateral side-down position and held there, but it decreased (7 Hz) in the opposite position. Faster spiking in the ipsilateral side-down tilt, compared with that in the contralateral side-down tilt, was observed in 17 neurons, which were called type I neurons. The firing frequency in the ipsilateral side-down phase was 39.4 ± 30.3 Hz (mean and SD for the 17 neurons); but that of the opposite phase was 23.0 ± 22.1 Hz. Thus the modulation depth (the ratio of the frequency difference of the ipsilateral and contralateral side-down tilts to the mean of the two frequencies of both side-down tilts) was obtained as 0.74 ± 0.40 (mean and SD for the 17 neurons). Concerning the relationship between resting discharges and those in the two side-down tilts, three cases were observed. First, the resting firing was higher than or similar to that during the ipsilateral side-down tilt (10 of 16 cells tested). Second, the resting firing positioned between the ipsilateral and contralateral side-down tilts (5/16). Third, it was lower than or similar to that during the contralateral side-down (1/16). In the first case, a rhythmic modulation of firing frequency by the body tilt might be due to net inhibitory influence of the lumbar afferents. In the third, net excitatory modulation could occur, and in the second, both excitatory and inhibitory modulations took place. Among these three modulation modes, no difference was noticed in modulation depth. The type I vestibulospinal tract neurons were in the caudolateral region of the lateral vestibular nucleus (red dots in Fig. 2).

Figure 1B shows a neuron of the second group.
This neuron rather tonically discharged in the resting state with a frequency of about 17 Hz. When the body was alternately tilted, the cell exhibited faster firing during the contralateral side-down tilt than during the ipsilateral tilt. The firing frequency in the contralateral tilt, which was 18 Hz, was similar to that of resting. The frequency in the opposite tilt was 8 Hz; thus the neuron received net inhibitory influence from the lumbar afferent during ipsilateral side-down tilt. Faster firing in the contralateral side-down tilt, compared with that in the ipsilateral tilt, was found in 23 vestibulospinal neurons, called type II neurons. The ground averages for the 23 neurons (mean and SD) of the firing frequencies of contralateral and ipsilateral side-down tilts were $33.3 \pm 25.0$ Hz and $21.7 \pm 19.4$ Hz, respectively. The mean modulation depth was $0.66 \pm 0.55$, similar to that of the type I neurons (see above). In the second group the most dominant modulation mode was again a net inhibitory one. The neurons with resting discharges having higher than or similar to maximal peak firing in the contralateral side-down tilt were observed in 11 of 21 cells tested. Nevertheless, net excitatory modulation mode was more often observed in the second group than in the first, since 4 of the remaining 10 cells had resting discharges lower than or similar to the minimal peak frequency of firing in the ipsilateral side-down tilt, and the remaining 6 cells had resting levels between the two side-down tilts. There was no clear difference of the modulation depth among the three modulation modes. The locations of individual cells of this group are represented in blue dots in Fig. 2. They were found again in the caudolateral region of the lateral vestibular nucleus. Note that type II neurons appeared to be distributed more anteriorly and laterally than type I neurons.

There were 5 vestibulospinal neurons of which firing was not modulated by the caudal body tilt (type III neurons, Fig. 1C). Their firing rates were in a range of 12–90 Hz, the mean and SD was $58.2 \pm 32.2$ Hz. The locations of the cells are represented with green dots in Fig. 2. They were found in the same region as the neurons of the two groups previously mentioned.

The present study indicates that some vestibulospinal tract neurons projecting to the lumbar enlargement receive input from lumbar afferents that are excited by the lumbar rotation on the vertebral axis. These neurons presumably give excitatory influence to the hind-limb extensor motoneurons [12]. Therefore the lumbar rotation such as caudal body tilt can modify the activity of the hind-limb musculature via these vestibulospinal neurons. This may correspond to the tonic lumbar reflex, which has been considered a counterpart of the tonic neck reflex [2]. Thus the present study suggests that the vestibulospinal neurons...
lospinal tract neurons consist of an output path of the tonic lumbar reflex. There were type I and II neurons, type I showing faster firing in the ipsilateral side-down tilt and type II firing faster in the opposite phase. If both types contribute to the tonic lumbar reflex, the reflex could be more complex and multiplicative than previously thought [13].

REFERENCES