Vestibular Control of Muscular Tone and Posture
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ABSTRACT: The vestibulospinal system helps to maintain upright posture and head stability. The semicircular canals and their short latency connections to the neck motoneurons, largely via the medial vestibulospinal tract, respond to angular accelerations so as to stabilize the head in space. The paired otolith organs, the utricles placed approximately horizontally, and the saccules vertically, respond to linear acceleration including gravity. Their influence leads, via the lateral vestibulospinal tract, to excitation of ipsilateral extensor motoneurons of the limbs and trunk, and to inhibition of reciprocal flexor motoneurons. Linear displacement of the otoliths leads to bracing of the limbs and body so as to maintain upright posture, and to extend the limbs so as to help in landing after sudden falls.


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merit to the increased extensor tone. Let us now look at the several elements of the vestibulospinal system and see how they modulate tonus and posture.

There are two major types of vestibular end organs, the semicircular canals which respond to angular acceleration of the head, and the utricular and saccular otoliths, which are activated by linear acceleration including gravity. The semicircular canals are embedded in the skull in the temporal bones and the three canals on one side of the head are approximately orthogonal to each other, and very approximately parallel to ones on the other side of the head. In ordinary life, their receptor cells respond to very brief and high angular accelerations which lead to increases or decreases in the tonic firing of the first order vestibular nerves, dependent on the direction of rotation. Because of the mechanics of the end organ, the first order canal afferents relay to the brainstem a signal related to head velocity. All four vestibular nuclei receive this information, with those terminating in the medial and lateral (Deiters') nuclei being of particular importance to the neck, trunk and limbs.

The otolith system consists of two receptors on each side, a saccule and a utricle. Each has a layer of calcareous otoconia embedded in a fibrogelatinous matrix, into which the hairs of the receptor cells protrude. The orientation of the receptors determines whether they are depolarized or hyperpolarized as linear acceleration displaces the immediately overlying otoconia. The utricle is shaped like a shallow bowl and is fixed in the skull in an approximately horizontal plane. The saccule has an upward sweep at its forward end and is fixed in the skull in an approximately horizontal plane. The saccule has an upward sweep at its forward end and is placed approximately vertically.

Figure 1 — Reconstructions of axon collaterals from a single LVST axon at C8. Upper drawings are reconstructions in the transverse plane of B2-B4 axon collaterals shown in the sagittal plane in the lower drawing. The lower border of the central canal (CC) and the lower border of the ventral horn are indicated by the dashed lines. The arrow indicates the injection site. The stem axon could be traced further rostrally (5.9 mm from B1) and caudally (2.7 mm from B7). (From reference 4, with permission).

Whereas each organ has receptors oriented throughout 360°, the utricle has most of its receptors oriented medially or laterally, and the saccule up or down. The primary afferent nerves fire tonically at about 100 spikes/sec and this rate is increased or decreased depending on whether the receptors they innervate are depolarized or hyperpolarized. The firing rate can be modified transiently by brief linear accelerations or can be maintained at a new firing rate by constantly applied linear acceleration, for example, gravity. The first order afferents terminate mostly in Deiters’ nucleus.

Vestibular information destined for the spinal cord is carried by the lateral vestibulospinal tract (LVST), the medial vestibulospinal tract (MVST) and at least in part by the reticulospinal tract (RST). Much of the following is taken from Wilson and Melvill Jones.1

The LVST originates from cell bodies in Deiters’ nucleus and descends entirely ipsilaterally. Its axons travel in the ventral funiculus, quite close to the surface of the cord. Its fibers have a wide range of conduction velocities with the average being quite fast at about 90 meters/sec.2,3 Some axons pass to the sacral cord and some terminate more proximally. Many axons have collaterals leaving the stem axon at right angles4 (see Figure 1). Some stem axons have axon collaterals terminating in both the lumbar and cervical cord, clearly indicating that the same vestibulospinal message is carried to both cord levels. Physiological and anatomical evidence indicate some axons terminate directly on limb extensor motoneurons in Rexed’s lamina IX4,5 while others end on excitatory interneurons which
in turn terminate on extensor motoneurons. There also appear to be terminations on large neurons, probably axial muscle motoneurons, in lamina VIII.\(^4\) Other work suggests termination on inhibitory interneurons innervating ipsilateral flexor motoneurons, as well as on excitatory interneurons reaching contralateral flexor motoneurons. Taken together, there is direct and indirect excitation of ipsilateral limb and axial extensor motoneurons and reciprocal inhibition of ipsilateral flexor motoneurons (see Figure 2). Multiple axon collaterals at different cord levels from single stem axons indicate strong unified postural control.

The MVST originates mostly from neurons in the medial vestibular nucleus but also some from Deiters’ and the descending vestibular nuclei. Axons pass down the ipsi- and contralateral medial longitudinal fasciculi (MLF), and pass in the medial part of the ventral funiculus of the spinal cord. Most terminate in the cervical cord and directly or indirectly innervate neck extensor or lateral neck motoneurons. Many neck motoneurons are influenced by all six semicircular canals, with a highly specific excitatory or inhibitory drive from canal pairs (see Figure 3).

The reticulospinal tracts (RST) originate from reticular formation neurons that also receive input, in part from the labyrinths. Some neck motoneurons receive input from both LVST and RST. Some RST axons reach all levels of the cord, some terminating on motoneurons receiving, and others not receiving LVST input. Others terminate on interneurons. RST influence is largely on flexor motoneurons. In the lumbar cord they tend to be reciprocally distributed to extensor motoneurons receiving LVST inputs.\(^5\) While stimulation of Magoun and Rhine’s inhibitory region in the medial medulla inhibits segmental monosynaptic reflexes, it is not clear how the vestibular system influences this effect.

Let us now consider some of the postural implications of these pathways. The MVST, as noted above, projects largely to the extensor and lateral neck motoneurons. The cells of origin are mostly second order vestibular neurons receiving input from individual semicircular canals. The synaptic patterns of innervation shown in Figure 3 fit with responses to stimulating individual canals.\(^1\) The head rotates in the plane of the canal being electrically stimulated. Functionally, natural canal stimulation results in contraction of neck muscles to counter the applied angular acceleration, and thus results in stabilization of the head. This allows a more stable “platform” on which the otoliths, the main source of LVST influence, rest.

The LVST tends to maintain upright posture by tonic excitatory influence, reaching ipsilateral extensor motoneurons and by inhibition, via inhibiting interneurons, of ipsilateral flexor motoneurons. Ipsilateral labyrinthectomy results in sudden loss of this tone (the effects on eyeball stabilization are not considered here). Lesions to Deiters’ nucleus or to the LVST produce very similar effects on the trunk and extremities. The body curves to the ipsilateral side and the ipsilateral limbs are flexed. There may be rolling to the ipsilateral side. These effects are more dramatic in rabbits than cats, cats more than man. Rabbits often perform many rolls about their long axes until they become wedged against a wall. There is also rotation of the head if the ipsilateral side of the medial nucleus or whole labyrinth is damaged. After a few days, these effects gradually lessen.

The cellular counterparts of compensation in the vestibulospinal system have been little studied but are probably similar to those seen in the semicircular canal system. In the latter, after ipsilateral labyrinthectomy, Type I vestibular nucleus neurons in mono- or pauci-synaptic connection with the horizontal semicircular canal become silent (no longer fire tonically), and are no

**Figure 2** — Diagram of the lateral vestibulospinal track drawn by Tohru Ohgaki (personal communication). Dashed lines are probable connections, solid lines are connections verified either anatomically or physiologically. Roman numerals refer to spinal cord areas after Rexed. Filled cell bodies and terminals are inhibitory, open are excitatory.

**Figure 3** — Schematic drawing of connections between ipsi- and contralateral semicircular canal ampullae and a neck motoneuron. MLF = medial longitudinal fasciculus. LVST = lateral vestibulospinal tract, VN = vestibular nuclei; A, H, P = anterior, horizontal and posterior canal ampullae. (Reproduced with permission from reference 15).
longer sensitive to angular acceleration. As days and weeks go by, they regain spontaneous firing and responsivity to rotation as commissural inhibitory connections from contralateral labyrinth become functionally more powerful.8-9

After months go by, recovery becomes nearly complete, such that the cat may lurch to the ipsilateral side only when performing a vigorous maneuver, or the human falls to the ipsilateral side on doing a Romberg test with the feet placed one foot in front of the other.

If vestibulospinal influences are lost because of bilateral labyrinthectomy or streptomycin damage, an individual cannot stand. After some period of time, the person regains the ability to stand, although never with reliability in the dark. Walking becomes possible only in a halting, lurching fashion, with the head bobbing at each change in vertical acceleration as the heels hit the ground.

Another aspect of vestibulospinal function is brought out during vertical stimulation. Fernandez and Goldberg10 have shown many first order vestibular afferents respond preferentially to linear accelerations in the vertical direction. From this and from their location in the inferior division in the vestibular nerve, they concluded they were of saccular origin. When cats are dropped from a height, their legs extend and toes fan out. Watt showed EMG’s from extensor muscles had a short latency response which was abolished by bilateral labyrinthectomy but not by semicircular canal plugging, the latter blocking canal but not otolith function.11 When human subjects were unexpectedly dropped, there was a short latency EMG response from leg extensors, too rapid to come from a segmental myotatic reflex.12 13 These otolith-determined responses appear to prepare animal or man for landing from a fall.

The vestibulospinal system has both static and dynamic components. The latter are largely under the influence of the semicircular canals and the former under otolih influence. Money and Scott14 demonstrated this in cats placed on a platform which could be tilted. When all the semicircular canals were surgically plugged, thus rendering them inactive, the cats could maintain their balance to slow tilts but would fly off the platform to fast tilts. If the cats then had bilateral labyrinthectomies, thus rendering the otolicts inactive also, the cats would fall from the platform with even slow tilts.

In conclusion, the vestibulospinal system serving the trunk and limbs is under control of the vestibular otolith and canal systems, particularly the former. Both the otolith organs and canals are firmly fixed in the skull. When the otolith system is stimulated by linear acceleration, including gravity, acting on the head, the LVST modifies trunk and limb muscle tonus to maintain posture to respond to sudden falls. Other parts of the vestibular system, the semicircular canals and the MVST, act to stabilize the head of the neck, making a more stable “platform” for the otolith apparatus.

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REFERENCES