The Postural Effect of Lesions of the Vestibular Nuclei:
A Note on Species Differences Among Primates

Edward Tarlov, M.D.*

Surgical Neurology Branch, National Institute of Neurological Diseases and Stroke,
National Institutes of Health, Public Health Service, Department of Health, Education
and Welfare, Bethesda, Maryland

The pathology of human spasmodic torticollis has not been convincingly demonstrated and therefore the recent papers on abnormalities of head posture resulting from experimental lesions in the brain stem have evoked considerable interest. Lately I have had an opportunity during the course of a study of the primate central vestibular connections to observe 10 Macaques, a baboon, and a chimpanzee with experimental lesions of the vestibular nuclei. Lesions of similar extent produced strikingly different postural effects in the species examined. The data indicate that lesions in the central nervous system that are responsible for abnormalities of posture in monkeys may have quite different effects on the posture of the higher primates.

Materials and Methods

Ten immature and adult Rhesus Macaques (Macaca mulatta), a large male baboon (Theropithecus gelada), and an immature female chimpanzee (Pan troglodytes E. P. Walker) were studied. None of the animals had been previously used in any other studies or operations.

Lesions in the right lateral floor of the fourth ventricle were placed with a fine curved glass suction pipet under direct vision, after elevation of the cerebellar vermis through a suboccipital craniectomy. The animals were deeply anesthetized and sacrificed by perfusion following postoperative survival times of between 6 and 16 days. Longer survivals interfered with optimal selective silver staining of degenerated axons.

After fixation, frozen sections were cut at 25 to 30 μ in frontal, sagittal, or horizontal planes. Serial sections every 450 to 500 μ were stained with cresyl violet or luxol fast blue and cresyl violet. The Nauta-Gygax and, in some cases, the Fink-Heimer silver stains for degenerated axons were used on adjacent series. The sections stained for cells were projected onto Kodak photomechanical T paper and photographed. Nuclear boundaries and destruction of tissue by the lesion were drawn directly onto these photographs, and reconstructions of the brain stem and the extent of the lesion were made from tracings of these photographs. A detailed description of each of these lesions, the extent of damage, however slight, to surrounding regions, and the rostral projections of degenerated fibers is given elsewhere.

The terminology used to describe the vestibular nuclei is that of Brodal and Pompeiano. In addition to the four classical vestibular nuclei (the superior vestibular nucleus of von Bechterew, the medial vestibular nucleus of Schwabale, the lateral vestibular nucleus of Deiters, and the spinal vestibular nucleus), two other regions are indicated in Figs. 1 to 4. These are the interstitial nucleus of the vestibular nerve, whose cells lie interspersed among the fibers of the vestibular nerve, and the area x, a small group of cells lying between the caudal tip of the spinal vestibular nucleus and the lateral cuneate nucleus. The abbreviations for the terminology are given below.

A.pt. area postrema
Am. nucleus ambiguus
B.cj. brachium conjunctivum
C.r. restiform body
Cu.L. lateral cuneate nucleus
Cu.m. medial cuneate nucleus
D.mo.X dorsal motor nucleus of the vagus
F.L.m. medial longitudinal fasciculus
G. gracile nucleus
G.L. lateral geniculate body
N.po. pontine nuclei
N.t.s. nucleus of the tractus solitarius
N.V me. mesencephalic nucleus of the trigeminal nerve
N.V mo. motor nucleus of the trigeminal nerve

Received for publication July 26, 1968.

* Present address: Neurosurgical Service, Massachusetts General Hospital, Boston, Massachusetts.
Fig. 1. Sections showing extent of lesions involving vestibular complex. Comparable lesions that produced severe postural abnormality in Macaques were associated with only slight postural disturbance in the baboon and even less in the chimpanzee. A. Macaque V-2. Frontal sections progressing from caudal to rostral. Lesion involved right spinal, medial, lateral, and superior vestibular nuclei and injured superior cerebellar peduncle and posterior column nuclei. Animal had severe cephalic and trunk torsion (see Fig. 5 left). B. Macaque V-3. Sagittal section; left side is rostral. Lesion involved medial and spinal vestibular nuclei. The animal’s marked postural abnormality was similar to that of Macaque V-2. C. Baboon V-1-67. Sagittal section; left side is rostral. Lesion involved right superior, medial, lateral, and spinal vestibular nuclei. Animal had only slight postural disturbance, with ipsilateral inclination of its head. D. Chimpanzee C-1-67. Sagittal section; right side is rostral. Lesion of superior, medial, lateral, and spinal vestibular nuclei, also damaged superior cerebellar peduncle. The animal demonstrated only very slight and transient postural disorder which lasted 3 days (see Fig. 5 right).

N.V.s. principal sensory nucleus of the trigeminal nerve
Ne.IV trochlear nerve
Ne.VII facial nerve
O.i. inferior olive
Ru. red nucleus
S.n. substantia nigra
T.O. optic tract

Ve.L. lateral vestibular nucleus (Deiters)
Ve.m. medial vestibular nucleus (Schwalbe)
Ve.s. superior vestibular nucleus (Bechterew)
Ve.sp. spinal vestibular nucleus
Ve.in. interstitial nucleus of the vestibular nerve
Fig. 2. Horizontal sections showing extent of lesions that do not produce marked postural disturbances in Macaques; the rostral direction is toward the top of the illustration.  A. Macaque V-9. Animal with normal posture. Lesion involved only caudal tip of right spinal and medial vestibular nuclei, rostral tip of gracile nucleus and restiform body with slight extension into reticular formation beneath caudal tip of spinal vestibular nucleus (section V-9-14, ventral to section V-9-15). This lesion in the vestibular complex and reticular formation was caudal to those which produced cephalic deviation. Note that this injury to the posterior column nuclei, restiform body, and this caudal portion of the reticular formation was not associated with postural abnormality. Compare to Fig. 4 A and B which show lesions extending into more rostral portions of the reticular formation beneath the lateral vestibular nucleus and produced severe postural abnormalities. B and C. Macaques V-7 and V-8. Very slight cephalic deviation. Small lesions in both animals involved portions of right medial vestibular nucleus.

Observations
The striking species differences in the postural effects of similar lesions involving all portions of the vestibular complex are illustrated by the following three cases.

Macaque V-2. Extensive lesion ablating entire vestibular complex on right side. Marked tonic torsion of the neck (Fig. 5
Fig. 3. Lesions that produced postural disturbances described in Macaques; the rostral direction is toward the top of the drawing.  
A. Macaque V-4. Lesion involved all four of the main vestibular nuclei and the area x. Section V-4–23 shows involvement of superior, medial and lateral vestibular nuclei. Section V-4–25 depicts involvement of medial and spinal vestibular nuclei and area x. This animal exhibited marked degree of cephalic deviation. B. Macaque V-5. Large lesion of medial vestibular nucleus and caudal tip of spinal vestibular nucleus. C. Macaque V-10. Lesion of medial, lateral, and spinal vestibular nuclei. Both Macaques V-5 and V-10 exhibited less severe postural abnormality than Macaque V-4.

*left*). On awakening from anesthesia, the animal exhibited a marked torsion of its neck and trunk. The head was markedly tilted to the right with the occiput drawn toward the right shoulder. The torsion of the trunk resulted in a forward displacement of the right shoulder. This posture was not static; the animal would attempt to bring its head to a normal position but with a quick movement would then return the head to its rotated position. When it could be coaxed away from the side of its cage, the animal exhibited rolling movements, falling to the right side. Nystagmus at rest with its quick component to the left was observed. At rest the animal tended to hold its right extremities in flexion and its left extremities in extension. When disturbed in its cage, it would repeatedly turn to the right around an axis perpendicular to the ground. As it leaped through the
Fig. 4. Lesions involving reticular formation beneath lateral vestibular nucleus, the rostral direction is toward the top. Postural abnormality was more pronounced than that associated with lesion of this extent in vestibular complex alone. A. Macaque V-6. Lesion of medial, spinal and lateral vestibular nuclei, extending into the reticular formation beneath the lateral vestibular nucleus. B. Macaque V-11. Lesion involves medial, spinal and lateral vestibular nuclei and the reticular formation beneath the lateral vestibular nucleus. In both of these cases, the postural disturbance was more pronounced than in the cases illustrated in Fig. 3, apparently due to involvement of the reticular formation beneath the lateral vestibular nucleus. Damage to the reticular formation further caudally (see Macaque V-9, Fig. 2 A) was not associated with a postural disturbance.

air, its body rolled to its right. The rolling movements and nystagmus were transient and cleared by the fourth day, but the severity of the postural abnormality persisted and had not lessened by the time the animal was sacrificed on the eleventh day. In spite of a mild right-sided hypotonia to passive movement, more pronounced in the arm than in the leg, the animal was quite agile and difficult to catch. Nembutal anesthesia, given at the time the animal was sacrificed, abolished the abnormal posture.

The lesion involved the right vestibular complex, completely destroying the superior and spinal vestibular nuclei, the area x, the interstitial nucleus of the vestibular nerve, and, but for a thin rim ventrally, all of the medial and lateral vestibular nuclei. It also damaged the most ventral fibers of the superior cerebellar peduncle, the right nucleus of
the tractus solitarius, the restiform body, and the dorsal column nuclei. The medial longitudinal fasciculus and the motor nuclei of the extraocular muscles were intact (Fig. 1 A).

Baboon B-1–67. Extensive lesion involving all portions of the right vestibular complex. Slight tonic inclination of the head to the right. When fully awake after operation the animal was seen to have a slight but definite cephalic tilt to the right of about 15° from its normal vertical axis and a tendency to hold its face to the left. This deviation was strikingly less pronounced than the abnormality of posture resulting from a similar lesion in Macaque V-2, and there was no torsion of the trunk. The postural abnormality was, however, more pronounced than that of chimpanzee C-1–67. During the first day a transient nystagmus at rest with its quick component to the left was observed. The animal's unpleasant disposition made an examination of muscle tone unfeasible, and it was sacrificed after 9 days. Its cephalic deviation had persisted in a mild form to this time.

Histologically, the lesion had ablated the medial vestibular nucleus, the interstitial nucleus of the vestibular nerve, the area x, and nearly the entire superior, spinal, and lateral vestibular nuclei. The superior cerebellar peduncle was not damaged by the lesion (Fig. 1 C).

Chimpanzee C-1–67. Extensive lesion involving the entire right vestibular complex. Very slight and transient tonic inclination of the head to the right (Fig. 5 right). On the first postoperative day, a moderate inclination of the head and trunk to the right side was apparent. The animal tended to hold its face to the left. By the third day, at the time the photograph in Fig. 5 was taken, a moderate deviation of the head was still present, and the animal preferred to use its right extremities in the flexed position. The head tilt, however, diminished progressively during the postoperative course, and when it was sacrificed at 14 days no deviation of the head was apparent. The only abnormality noted was that the animal did not seem quite as nimble as normal.

Histological examination demonstrated that the lesion had destroyed nearly the entire vestibular complex on the right side, involving the caudal part of the superior vestibular nucleus, the medial vestibular nucleus, the rostral half of the spinal vestibular nucleus, the lateral vestibular nucleus, and
the interstitial nucleus of the vestibular nerve. In addition, the inferior portion of the right superior cerebellar peduncle, the nucleus of the tractus solitarius, the restiform body, and the posterior column nuclei had been slightly damaged. Although the lesion was nearly identical in its anatomical extent to the lesion in Macaque V-2, the postural effect was strikingly different (Fig. 5).

Further Examples in Macaques. In the Macaque, pronounced abnormalities of posture as described above were produced by lesions involving the entire vestibular complex (Macaque V-4, Fig. 3 A), the medial and spinal vestibular nuclei (Macaque V-5, Fig. 3 B), or the medial, lateral, and spinal vestibular nuclei (Macaque V-10, Fig. 3 C). When lesions extended into the reticular formation beneath the lateral vestibular nucleus, these abnormalities of posture were even more pronounced (Macaques V-6 and V-11, Figs. 4 A and B). On the other hand, lesions confined to portions of the medial vestibular nucleus produced only slight deviation of the head (Macaques V-7 and V-8, Fig. 2 B and C).

Controls. That areas outside the vestibular complex, underlying reticular substance and the eighth nerve are not responsible for the effects observed may be seen from our own cases in Table 1. For example, Macaque V-9 exhibited no abnormal posture following placement of a lesion in the restiform body, the area x, the posterior column nuclei, and the caudalmost tips of the medial and spinal vestibular nuclei. Ipsilateral cephalic deviation has not been observed in primates following lesions confined to the posterior column nuclei, the restiform body, or the superior cerebellar peduncle.20

Discussion
This study demonstrates that the severity of the striking postural disorder resulting from unilateral destruction of the vestibular nuclei in the monkey9,10,19,22 diminishes as one ascends the phylogenetic scale to the anthropoids. In the monkey a marked tonic deviation of the head and rotation of the occiput toward the side of the lesion occurs. In the chimpanzee the effect upon posture of an extensive lesion in the vestibular complex anatomically equivalent to a lesion that produces marked cephalic and trunk torsion in the monkey is both slight and transient. The effect in the baboon appears to be intermediate between the Macaque and chimpanzee. In the monkey, an identical syndrome is seen following labyrinthectomy2,17,21 and eighth nerve section.30,21 In the baboon and chimpanzee, a postural abnormality, which as described seems similar to that described here, follows labyrinthectomy.8 The effect of unilateral ablation of the vestibular nuclei seems to parallel in primate phylogeny the effects of ablation of more peripheral portions of the vestibular system.

In man, the effect of unilateral eighth nerve section on posture is minimal. A very slight and transient cephalic deviation following eighth nerve section for Ménière's disease has been mentioned,3 but it is slight enough to have escaped the notice of most authors.4,5,18 This marked difference in the response of man and the lower animals to eighth nerve section led Dandy and Kunkel to remark: "Indeed, had the devastating effects of dividing the auditory nerve in dogs and cats antedated the operation on human beings, the cure of Ménière's disease by this operative attack might well have been delayed."

One would expect from the comparative data presented here that unilateral destruction of the vestibular nuclei in man would produce a much less striking postural abnormality than that seen in the monkey. This marked species difference in the effect of brain stem lesions upon posture in primates indicates that findings such as those from the careful work of Foltz, et al.,24 in experimental monkeys may not be applicable to man.

Summary
In monkeys a severe disorder of posture results from unilateral lesions of the vestibular complex. The effect of similar lesions is less pronounced in the baboon and even less severe in the chimpanzee. In the monkey the disorder consists in a tonic ipsilateral deviation of the head and ipsilateral rotation of the occiput and trunk. The ipsilateral limbs are held preferentially in flexion and the contralateral limbs in extension. There is a mild hypotonia to passive movement of the ipsilateral limbs. The abnormality of head posture is the most striking and persistent feature of the disorder in monkeys. In the ba-
boon a moderate deviation of the head appears. In the chimpanzee, a similar deviation of the head appears but does not persist.

This study demonstrates that the severe postural abnormalities resulting from lesions of the vestibular nuclei in Macaques do not occur in the higher primates.

Acknowledgments

It is a pleasure to thank Dr. John M. Van Buren, in whose laboratory this work was carried out, for his assistance, encouragement, and inspiring example. Special thanks are due Miss Rosemary Borke and Mr. Vernon Mastin for their painstaking histological preparation of many of the specimens.

References

Primate Posture after Vestibular Nuclei Lesions


