HOW TO CONSTRUCT AND MOVE A CAT'S NECK

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Abstract — Extensive information has been accumulated over the past several years about the head-neck sensory-motor system, in particular relating to cats. Using still x-ray and cineradiographic analysis, the skeletal geometry of head-neck posture in three dimensions—when an animal is resting, actively orienting, or locomoting—is described. From these descriptions, cervical, vertebral, and craniocervical joint biomechanics for all three rotational dimensions are quantified. These behavioral data on muscle and skeletal movements have been incorporated in a biomechanical, functional anatomical model of the head-neck movement system. Individual as well as groups of neck muscles have been measured in detail and their kinematics determined. The role of a number of these muscles will be described for several reflex and voluntary behavioral contexts, including muscle co-contractions. Having established how each movement is accomplished, the neuronal sensory-motor reflex basis of head-neck system stabilization in space is addressed. The vestibular system is largely responsible for acquisition and maintenance of upright posture. The bilateral semicircular canals (horizontal, anterior, posterior) and otoliths (saccule, utricle) feed information differentially to specific neck muscles: these connections are reviewed with regard to the origin of the reflex arc from each receptor to its destination of specific muscles. Behavioral data from normal animals, and from animals whose vestibular receptor systems are selectively lesioned, will be reviewed to complement the functional interpretation of the sensory-motor transformations. Finally, the requirements for space-time coordinated cat head-neck movements will be synthesized, based on biomechanics, muscle kinematics, canal/otolith connectivity, and selective lesion experiments. © 1997 Elsevier Science Inc.

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Introduction

The head-neck movement system provides an excellent model for studying sensory-motor transformations, because most of the contributing sensory and motor systems are well-researched and described. This review provides a complete description of three areas necessary to describe postural and reflex control of the head-neck movement system: head-neck joint biomechanics, cervical muscle geometry/kinematics, and the vestibular sensory input to neck muscles subserving vestibulocollic reflexes. Skeletal geometry during movement has been measured by x-ray and cineradiography (1-6), and neck muscle kinematics have been determined for several reflex and voluntary behavioral contexts (1,2,5-9). These data have been incorporated in the most thorough head-neck movement model to date.

A detailed description of the vestibular sensory input to neck muscles and behavioral data
from normal and lesioned animals clarify the role of individual labyrinthine receptors for the acquisition and maintenance of the upright resting posture of the head–neck system, and for space–time coordinated head–neck movements, at least for cats.

**Biomechanics**

An essential requirement for a proper functional interpretation of a sensory–motor system is an exact description of the sensory and motor periphery. While extensive information about reflex neuronal operations has been accumulated over the past decades, viable data about the peripheral mechanical apparatus, that is, muscles and bones, in unrestrained behaving animals have become available only recently. The skeletal geometry of head–neck posture in three dimensions, when an animal is resting and during active orienting and locomotion, has been described using still x-ray and cineradiographic analysis (1–4). Cervical vertebrae and head–neck joint biomechanics for all three rotational dimensions have been quantified (1,8,9). These latter data provide the basis for an interpretation of the functional anatomy of the head–neck movement system. Neck muscle kinematics have been measured in detail, and the role of a number of these muscles has been established for several reflex and voluntary behavioral contexts, including muscle co-contractions and the involvement of a given muscle during different head–neck movement tasks (2,6,7). This additional knowledge has also made possible meaningful modelling approaches.

**Structural and Biomechanical Factors Underlying Head–Neck Motor Function**

An understanding of the neural processes responsible for head movement control must begin with a realistic representation of the peripheral system to be controlled. In the past, the head–neck system has often been modelled in a simple fashion, as if the head were a ball mounted on a rigid support by a universal joint permitting three degrees of rotational freedom. However, such a model grossly oversimplifies the structural and mechanical specializations that give the neck its broad repertoire of movement capabilities. As a result, it also oversimplifies the control problem presented to the nervous system by the need to move the head. Thus, it is important to re-evaluate our views regarding structure–function of the periphery, and to incorporate those aspects of structure and biomechanics that appear to have a significant impact on the motor control of the system. Such a re-evaluation must consider at least two major features that have been identified in recent research. The first concerns the multiaxial nature of the cervical column with its more than 20 pairs of architecturally specialized muscles. The second is the obligate linkage between the head–neck complex and the forequarters, bridged by the bones of the shoulder, and more particularly, by the scapula.

Humans and almost all other mammals have seven cervical vertebrae that appear from fluoroscopic studies to be grouped functionally into two independent joint-sets (for example, references (7,9,10)). The rostral joint set above C5 can, by itself, produce movements in three rotational axes. However, the more caudal joints below C5, form a second, independent joint-set with an equivalent range of motion. A movement in one direction at the lower joint-set can be added to a movement in the same direction at the upper joint-set to extend its range, or the two joint-sets can be decoupled and can be made to move in opposite directions (Figure 1). Counterphasic movements at the two joint-sets are essential for many common behaviors. For example, they underlie many visual tracking movements because the head can be translated through extrapersonal space without changing the angle of inclination of the skull, to preserve the line of sight.

The advantages gained by a "two-jointed" neck depend upon the sophisticated orchestration of a variety of muscles crossing different cervical joints. Recent studies in cats (2) have shown that even the simple act of scanning the horizon is accomplished using different kinematics and different patterns of muscle activation when the neck is oriented vertically (and the lower-joint set is extended) than when it is...
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Horizontal, and the lower joint-set is required to perform lateral flexion of the vertebral column. Electromyographic recordings made during turns in vertical and horizontal neck postures revealed that predictable strategies of muscle recruitment are used. One set of muscles, including splenius, obliquus capitis inferior, levator scapulae, and complexus, had a stereotyped pattern of activation regardless of the orientation of the neck. Other muscles, such as obliquus capitis superior, scalenus anterior and longissimus capitis, show large differences in activity according to neck orientation. These observations underline the importance of the kinematics as well as the trajectory in determining the neuromuscular strategies employed by the animal to perform a head movement. They also point to a potentially important role for muscles inserting onto the lower cervical column, such as the levator scapulae and the scalenus muscles, which have often been ignored in models of the head-neck system.

Head movement has long been considered as if its execution depended only upon the neck muscles attaching to the skull and vertebral column. However, many muscles attaching to the neck from the shoulder girdle or ribcage have anatomical relationships consistent with a role in head movement [see reference (11)]. Muscles with scapular attachments appear to have particularly large moment arms coupled with large functional cross-sectional areas (12). These muscular connections suggest that the scapula might be an important bridge between the head-neck complex and the forelimb, which ultimately bears its weight. The importance of this linkage has been emphasized further by biomechanical analyses using stereoscopic x-rays and multi-axis ground-force recordings in sitting cats (13). Inverse static analysis of forces and moments at forelimb joints and the shoulder showed that the scapula is subject to a complex balance of forces. Ground reaction forces are reflected in an especially large parasagittal torque that tends to rotate the dorsal edge of the scapula in a caudoventral direction around the humeral head (Figure 2A). The stability of the scapula is presumably ensured by a counterbalancing torque arising from the tonic contractions of muscles such as occipitospinalis and trapezius minor against gravitational forces tending to flex the head and neck (Figure 2B). Muscles spanning the neck and scapula are often not considered as head extenders and thus have not been subjected to the same level of experimental scrutiny as more deeply placed cervical muscles. Yet the combined observations from the biomechanical and EMG studies reviewed here suggest that they may have a significant role to play in head-neck extension and postural stability.

As head-neck models are developed, it will be important to re-evaluate the boundary conditions that have tended traditionally to restrict head-neck models to representations of upper cervical joints. Results presented in recent studies suggest instead that minimal boundary conditions must include both the scapula and the lower cervical joint set. Further, the models that are developed must consider the problems inherent in bearing the highly mobile head-neck complex on a second multiarticulated pair of weight-bearing columns. Not recognizing the scapula as an intermediary structure important in transmitting forces between the head-neck system and the forelimb-trunk system, would
make it difficult to make sense of muscle activation patterns underlying the balance of forces in the shoulder region.

Coordination of Muscular and Skeletal Components of Voluntary and Reflex Head Movements

An important consideration regarding motor control problems concerns the difference between voluntary movements and reflex behavior. The significance of this fundamental distinction is evident in the eye movement system, where reflex eye movements, such as the vestibulo-ocular reflex (VOR) have three degrees of freedom, whereas voluntary eye movements have only two degrees of freedom. Voluntary eye movements obey Listing’s law, that is, all torsional components are suppressed by an as yet unidentified neuronal mechanism.

In order to determine how variations in the sensory and mechanical demands of the task can alter muscle behavior, the maximal direction of activation of a muscle during reflex and voluntary movements was determined in 24 planes of motion (6). Six neck muscles, biventer cervicis, complexus, splenius capitis, occipitospinalis, rectus capitis posterior major, and obliquus capitis, were recorded intramuscularly (EMG) in three cats during sinusoidal (0.25 Hz) rotations of the head. In the reflex task, the animal’s head was restrained so that it moved with the body as the animal was rotated in the dark. In such case, only the vestibular labyrinth was stimulated, thereby eliciting a vestibulo-collis reflex (VCR). The cervical vertebrae and neck muscles were held in a fixed relationship through-

Figure 2. (A) Torque moments (in Nm) estimated around the glenohumeral joint, using three-dimensional inverse static analysis. Torque moments in inward and outward rotation ($M_{xx}$) and inversion/eversion ($M_{ys}$) are very small, but a sizeable moment in the parasagittal plane ($M_{zs}$) tended to rotate the dorsal margin of the scapula caudoventrally in alert, sitting cats (x: dorsal posterior edge of scapula moves medio-lateral; y: dorsal posterior edge of scapula moves medio-lateral). (B) Presumptive origin for part of the counterbalancing moment to ensure scapular stability. Occipitospinalis is a strap-like muscle linking the skull to the rostral dorsal border of the scapular; it exhibits tonic activity during quiet sitting and standing.
head movements differed from the hypothesized direction by up to 60°. The fact that a unique pattern of activity can be selected by each animal for active tracking responses indicates that the nervous system can generate movements in the same direction using different muscle co-contraction patterns. One explanation for these differences concerns the increased complexity of sensory inputs during voluntary movements. Unlike the VCR, which is elicited by vestibular inputs, voluntary responses could be organized around retinal, somatosensory, and descending, in addition to vestibular inputs.

Another suggestion is that different muscle synergies have different neural controllers: a species-consistent synergy would be controlled by the reflex pathways, whereas voluntary movements might employ multiple controllers with different spatial properties. Furthermore, the force-length properties of a given muscle were significantly affected by the diversity of vertebral alignments during voluntary movement, thereby producing different patterns of maximal activation for the two tasks, even across animals. In the same context, Banovetz and colleagues (14) also demonstrated that maximal activation directions of muscles performing a VCR were consistent over time and across animals and changed little when the animals were decerebrated, but were affected by head–neck position. Multiple insertions of many of these muscles may produce a change in their action simply as a result of changing the position of an origin or insertion, thereby altering the lever arm and, subsequently, the mechanical advantage of a given muscle (7,15).

To this end, simultaneous video-fluoroscopic and intramuscular neck muscle EMG activity were recorded during sinusoidal (0.25 Hz) voluntary head tracking (4). The focus of these experiments was to examine the relationship between the alignment of the cervical intervertebral joints, body position, and neck muscle activation patterns. Four alert cats were tested, either standing or lying prone while they performed head tracking movements (± 15°) in the pitch plane. Even though the animals were consistently successful in tracking the water spout with their heads, different muscle patterns were used by different individuals. Phase responses...
Figure 3. Schematic of the predominant planes of muscle EMG activation in three alert cats during reflex and voluntary head movements. Each arrow represents the direction and magnitude of a given muscle's activity about two axes of motion (identified by arrows on the bottom of the figure) in accordance with the right-hand rule. The two columns on the left indicate reflex and voluntary activity in pitch (flexion/extension) and yaw (lateral rotation); columns on the right indicate activity in pitch and roll (lateral flexion). (Modified from reference 48, with permission of the Foundation for Physical Therapy).
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of the muscle with respect to the tracking stimuli and amplitude of muscle modulation varied among animals in this study when compared across standing and prone lying cats, but responses varied even from trial to trial within one animal (Figure 4A).

In one of the animals tested in both standing and prone postures, the neck was positioned so that it was vertically (parallel to earth vertical) or horizontally oriented (perpendicular to earth vertical) during head tracking as in reference (2). Temporal relations between the muscles and vertebrae in this animal clearly revealed the influences of cervical versus whole body posture on neck muscle activation patterns. (Figure 4B). Rectus capitis, a deep suboccipital muscle, consistently responded in phase with peak head-up position at all neck and body orientations. Complexus also responded consistently in phase with peak head-up position. Splenius was more influenced by neck orientation and could respond when the head was either peak-up or peak-down. Splenius also exhibited this variability when comparing its activation pattern in the other tested animals, that is, between standing and prone lying cats.

Biventer and occipitocapularis were strongly affected by the position of the body. Biventer commonly responded in phase with peak head-up position when the animal was prone, but shifted to a more variable response around peak extensor velocity when standing. Occipitocapularis had the most variable responses in both body positions, switching between a response related to head flexion (or flexor velocity) when standing, and a response related to head extension (or extensor velocity) when prone. Differences were accentuated in both body postures when the neck was horizontal, possibly as a result of rotation of the scapula onto which occipitocapularis inserts.

Figure 4. Neck muscle activation during tracking tasks. (A) Biventer cervicis activity during two identical trials recorded on the same day from a prone lying cat. Note variability in phase relations between the muscle and the tracking stimulus (bold line). Phases of the muscle with respect to the tracking stimulus are printed to the right of each plot. (B) Phase values of five neck muscles with respect to the tracking stimulus across trials in one cat at different body positions and cervical spine orientations.
Biventer had significantly \( (P < 0.05; \text{Mann-Whitney U-test}) \) greater EMG response gains with a vertical orientation of the neck than with a horizontal one when the animal was prone. Both complexus and splenius exhibited significantly greater gains \( (P < 0.05) \) when standing with a vertical neck than when standing with a horizontal neck, and occipitocervicalis had significantly greater EMG response gains in the standing position regardless of neck orientation \( (P < 0.05) \).

At almost all postures, the vertebrae tended to lag the position of the water spout although the muscles could either phase lead or phase lag the stimulus. The variability in the muscle responses did not appear to affect the vertebral motion which, by comparison, was very consistent. Under all conditions, the complete 30° rotation was not produced by the head or any one of the upper cervical segments. Instead, as shown in Figure 5, the task was accomplished in standing cats by summing the movement of the head with the combined actions of \( C_1 \) and \( C_2 \). Angular excursions at \( C_4-T_1 \) served to maintain the cervical column in a vertical orientation. In prone cats, more angular motion was observed in the lower cervical vertebrae. Spatial patterns of vertebrae in standing cats were observed to travel in a vertical, arcing motion, whereas in prone animals those same vertebrae traveled more diagonally, yet the head was always in line with the water spout.

Motion of the cervical spine resulting from the muscular forces was, therefore, relatively invariant for each body position. Consistent joint motion suggests that the variations in the muscle activation patterns were not a result of shifts in the mechanical advantage of the muscle through changing positions of origins and insertions, but instead were organized to prevent such a derangement. Differences in muscle activation patterns could be the result of differences in movement dynamics, muscle velocities, afferent feedback, or of central control (16) where the muscle activation patterns could reflect differing solutions to Bernstein’s (17) problem of redundancy. The signals that the CNS processes when switching between muscle actuators while maintaining vertebral consistency are yet to be determined. We may conclude, however, that postural changes in the form of cervical alignment and body position are two factors that generate some adjustments in the control parameters.

**A Musculoskeletal Model of the Cat’s Head and Neck**

Most of the above parameters were incorporated into a biomechanical model to estimate the isometric moment-generating capacity of the major neck muscles. Few such models exist that accurately describe the multidirectional and multijointed movements available to the head and neck [see, for example, reference (18)]. The
A generic musculotendon model (20) was scaled by each muscle's maximum isometric force, optimal muscle fiber length, pennation angle, and tendon slack length to determine the force-length relation of that specific muscle. Each muscle's maximum isometric force was computed by multiplying the measured physiologic cross-sectional area by a specific tension of 22.5 N/cm² (15). Optimal muscle fiber lengths were measured in three cats. These cats were decerebrated, and the subsequent rigor-fixed fiber and sarcomere lengths were determined while head and neck were held in the vertical resting posture (1). Fascicle lengths were also measured.

Fascicle lengths were determined while head and neck were held in the vertical resting posture (1) in a stereotaxic frame. Sarcomere lengths were measured from biopsies of small bundles of rigorized fibers as described by Selbie and colleagues (10). Fascicle lengths were also measured. These measurements were used to determine the sarcomere length corresponding to the vertical resting posture (Ls) and to determine the optimal muscle fiber lengths. Optimal fiber lengths were calculated by multiplying the measured fascicle lengths by Ls/2.5, where 2.5 μm is the optimal sarcomere length as reported by Heron and colleagues (21). Motion of the neck in the sagittal plane was defined by revolute joints allowing rotation at Skull-C1 and between each of the cervical vertebrae. Rigid body techniques (22) were applied to vertebral position data from three cats making voluntary sagittal plane movements to define each joint.

The head-neck tracking movement for a standing and a prone cat were modeled by matching the position of the model to positions of the cats observed in the cinefluoroscopic recordings (23). The coordinates of markers in T1, C1, C2, C3, C4, and the skull for five positions during the tracking movement from peak head-up to peak head-down were matched. In each case, the model was placed so the position of T1 corresponded to the digitized marker positions of T1 from experimental cinefluoroscopic recordings. The T1-C1 joint was then varied until the position of C1 in the model matched the digitized position of C1 from the experimental data. The procedure was repeated for each joint and vertebra until the position of the model matched the position of the cat. The relative motion of each vertebral joint for the motion could then be determined.

By combining the musculoskeletal geometric data, musculotendon models, and the skeletal kinematics, the musculotendon length, muscle fiber length, moment arm, and force-generating capacity for the range of body positions observed during the tracking movement could be estimated. The model has been used to characterize the intervertebral movement in the cervical spine and to describe the moment arms of the neck muscles at different orientations of head-neck movement for three alert cats performing ± 15° sinusoidal (0.25 Hz) head-tracking movements in the sagittal plane (4).

The relative joint movements, muscle moment arms, and force-producing capacity were examined for five dorsal neck muscles as the animal made the same head-neck tracking movement from two different body postures. The amount of relative motion between the vertebrae to complete the same tracking movement differed in standing and prone animals. A standing cat showed an extension of 25° at Skull/C1 and of 14° at C4/C5, and a flexion of 8° at C4/C5 and 7° at C5/T1 when moving from peak head-down to peak head-up. A prone cat had an extension of 25° at Skull/C1, of 8° at C4/C5, of 6° at C5/C6, and of 5° at C6/C7, and a flexion of 10° at C6/C7 and of 7° at C7/T1; for movement from...
peak head-down to peak head-up (see also references 8 and 9).

Little change was found in the muscle moment arms of any of the muscles in the two postures. Moment arms varied between postural conditions by 2% to 20% and were always less than 0.2 cm. The change in moment arms between postures was less than the variation of moment arms during the course of a cycle from peak head-up to peak head-down.

The capability of each muscle to produce force was examined by determining the operating ranges of the muscle on the force-length curve for the two postures (Figure 6). By looking at the similarity of the operating ranges in the two cases, the effect of altering the position of the body on the ability of the muscle to produce isometric force was determined. Muscles that operate on the plateau region of the force-length curve are capable of generating similar forces throughout the tracking movement. In contrast, the force-generating capacity of muscles declines substantially for postures near peak up position for muscles that operate on the ascending region of the curve.

Biventer cervicis, complexus, occipitoscapularis, rectus capitis, and splenius had very similar operating ranges for both body postures. The ranges differed by less than 4% between the postures. The endpoints of the operating ranges differed by less than 5%. Thus, the isometric force-generating capacity of a particular muscle for a given body position during the tracking movement was similar whether the cat was in a standing or prone posture. Biventer cervicis, occipitoscapularis, rectus capitis, and splenius operated primarily on the plateau region of their force-length curves. Thus, the isometric force-generating capacity of these muscles varied little during the tracking movement. By contrast, complexus operated primarily along the ascending limb of the force-length curve. As muscle lengths decreased for postures near peak up position, the ability of complexus to produce force declined.

A three-dimensional biomechanical model was developed to estimate the relative joint movements, muscle moment arms, and range of muscle fiber lengths that occur during the head tracking movement. The kinematics of the track-

![Figure 6. Operating ranges of 5 neck muscles on the isometric force-length curve. The thin solid line represents the entire active force-length relation of the muscle. The thin dashed line represents the entire passive force-length relation of the muscle. Vertical ticks indicate the point on the force-length curve corresponding to "normal" resting posture (1). Model results (thickened part of the solid line) are drawn for tracking movement from standing and prone postures. Biventer cervicis, occipitoscapularis, rectus capitis posterior major, and splenius capitis operated primarily around the plateau region. Complexus operated primarily along the ascending limb.](image)
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... movement differed when cats made the movement from standing or prone body postures. Analysis of the model suggested that the force-generating capacity of five of the major neck extensors was similar during the head and neck tracking movement whether animals were in prone or in standing body position. While the relative joint movements in the cervical spine were dependent upon body posture, the isometric force-generating capacity of the examined neck extensors is not dependent on the body posture from which the head tracking movement is made.

Vestibular Reference Frames

The functional interpretation of the resting head-neck posture and of reflex head-neck movements requires detailed information about the spatial organization of vestibular inputs, one of the major postural control regulators. The projection patterns of the labyrinthine receptors, the semicircular canals, and the ooliths are explained below in light of the available detailed description of the biomechanics of the head-neck ensemble, that is, passive range of motion of head-neck joints and neck muscle kinematics [see above and references (5,6,9)].

**Projection Patterns from the Semicircular Canals to the Neck Muscle Motoneurons**

Stimulation of a particular semicircular canal nerve produces a head movement in the plane of the canal it innervates (24), indicating that a spatially congruent and meaningful set of neck muscles is being activated by this particular canal nerve. To understand the neural mechanisms underlying the generation of co-contractions of functional sets of neck muscles, information on neural connections from individual canal nerves to motoneurons of every neck muscle is required. Wilson and Maeda (25) first analyzed the input pattern of individual canal nerves to some neck extensor motoneurons. However, equivalent input patterns to many other neck muscles have not as yet been determined. Thus, the functional context between the six semicircular canal nerves and different neck muscles was further determined by recording intracellular postsynaptic potentials (PSPs) from cervical motoneurons following electrical stimulation of individual canal nerves in anesthetized cats.

Motoneurons that supply single muscles have a homogeneous pattern of canal input. Four such input patterns could be identified (26,27) (Table 1). All of them had identical inputs from the horizontal canal nerves in common, receiving disynaptic excitation (EPSPs) from the contralateral and disynaptic inhibition (IPSPs) from the ipsilateral horizontal canal. Inputs from the four vertical canals were different. These four input patterns were as follows: The first input pattern was observed in rectus capitis posterior motoneurons at C1. These motoneurons received disynaptic excitation from the bilateral anterior canals and disynaptic inhibition from the bilateral posterior canals (28) (Figure 7A). This particular input pattern is identical to that reported

| Table 1. Canal–Neck Muscle Innervation Patterns for the Production of Compensatory Head–Neck Movements. |
|--------------------------------------------|--------------------------------------------|--------------------------------------------|--------------------------------------------|
| Pattern 1: Biventer and rectus capitis posterior (extension) | Pattern 2: Sternocleidomastoid (side tilt, ipsi) | Pattern 3: Obliquus capitis inferior (side tilt, contra) | Pattern 4: Longus capitis (flexion) |
| Ipsi | Contra | Ipsi | Contra | Ipsi | Contra | Ipsi | Contra |
| AC | EPSP | EPSP | IPSP | EPSP | EPSP | IPSP | IPSP |
| HC | EPSP | IPSP | IPSP | EPSP | IPSP | IPSP | IPSP |
| PC | EPSP | EPSP | EPSP | EPSP | EPSP | EPSP | EPSP |

Four distinct innervation patterns have been identified in the indicated muscles that were studied. Note that horizontal canal input is identical in all cases. The four patterns correspond to the head movement kinematics of each muscle (extension, flexion, or side tilt). AC, anterior semicircular canal; HC, horizontal semicircular canal; PC, posterior semicircular canal (data from references (26,28)).
for complexus and biventer motoneurons (25). The second input pattern was found in sternocleidomastoideus motoneurons, which received disynaptic excitatory input from the contralateral anterior and posterior canals, and disynaptic inhibition from the ipsilateral anterior and posterior canals. The third pattern was observed in motoneurons innervating the obliquus capitis inferior muscle. Motoneurons of this muscle received excitatory input from the ipsilateral anterior and posterior canals, and disynaptic inhibition from the contralateral anterior and posterior canals. The fourth pattern was found in longus capitis motoneurons. These neurons received disynaptic excitation from the bilateral posterior canals and inhibition from the bilateral anterior canals.

The described canal–neck muscle innervation patterns are consistent with head movements expected in response to natural head rotation (5) and with that induced by electrical stimulation of individual canal nerves (24). When rotating the head to one side in the horizontal plane (yaw movement), all neck muscles on the contralateral side may be activated, those on the ipsilateral side may be inhibited to aid a compensatory head movement to the contralateral side. When the head is rotated downward about the bitemporal axis (pitch-down movement), both anterior canals will be excited, while both posterior canals will be inhibited. In such case, neck muscles receiving the first-described input pattern will contract, while muscles receiving the fourth input pattern may contract, whereas those receiving the first input pattern may be inhibited. When the head is tilted to one side about the naso-occipital axis (roll movement), the ipsilateral vertical canals will be excited while the contralateral ones will be inhibited. The obliquus capitis inferior on the ipsilateral side and neck muscles on the contralateral side receiving the second input pattern may thus be activated to bring back the head to an upright position.

The different input patterns thus allow a classification of the respective neck muscles into four functional groups. Neck muscles receiving the first input pattern can be regarded as neck extensors (dorsiflexors), those of the fourth input pattern as neck flexors (ventroflexors); muscles of the second and third input patterns can be regarded as ipsiversive and contraversive tilt muscles, respectively. All neck muscles are considered to be more or less lateral rotators.

Figure 7. Synaptic potentials in 2 neck muscles following stimulation of the 6 ampullary nerves. (A) In rectus capitis posterior motoneurons, EPSPs are evoked from the bilateral anterior canals (Ant) and IPSPs from the bilateral posterior canals (Post) (Pattern 1, see also Table 1 and Figure 11). (B) In obliquus capitis inferior motoneurons, ipsilateral vertical canal stimulation elicits EPSPs, contralateral stimulation IPSPs (Pattern 3, see also Table 1). Note that PSPs following horizontal canal stimulation (Lat) are identical in both cases. [From reference (28)]
since they receive a similar input pattern from the horizontal canals. Further quantitative analysis is required to confirm the qualitative nature of the input patterns from the six semicircular canals to the discussed neck muscles’ motoneurons, and to understand their respective functional roles during compensatory head movements.

**Differential Activation of Neck Muscles by Saccular and Utricular Afferents**

While the semicircular canal output subserves dynamic rotational postural reflexes, the otoliths, utriculus, and sacculus induce linear acceleration and static postural responses. The spatial reference frame for the latter is still a matter of debate (for example references 29–31). Otolith reflexes could, on one hand, be coded in an otolith-specific reference frame or, alternatively, follow the geometry of the semicircular canal organization. At present, data exist that support either one of the two viewpoints. The adequate stimulus to activate optimally the receptor cells in the utriculus from resting position is static tilt out of the horizontal plane, or horizontal linear acceleration. The sacculus receptors will be maximally stimulated by linear vertical acceleration. These assumptions are based on electrophysiological data (31,33), and on anatomical and geometrical considerations (see, for example, reference 34): the sacculus maculae are orientated vertically; those of the utriculus system horizontally (see reference 35). The orientation of otolith sensitivity vectors, for example, for the utriculus and the sacculus, shows a distinct spatial organization differential (32,33). The utriculus receptor cells detect static displacements and linear accelerations predominantly in horizontal directions (from fore–aft to left–right). The sensitivity vectors spread out in a fanlike fashion in a horizontal plane that outwardly (lateral) is slightly tilted upward. The sacculus is sensitive largely to vertical linear accelerations. Its sensitivity vectors spread out in a vertical plane that upwardly (dorsally) is slightly tilted inward. In monkeys, the two planes are close to orthogonal (about 90°).

The differential role of these two otolith receptor systems in vestibulocollic reflex behavior was demonstrated by their characteristic projections to neck motoneuron pools (36–39). Electrical stimulation of the utricular nerve evokes EPSPs with disynaptic latency in almost all ipsilateral extensor motoneurons (36), and disynaptic EPSPs in all ipsilateral flexor motoneurons (37) (Figure 8). In contralateral extensor and flexor motoneurons, the initial responses to

**Utricular Nerve Stimulation**

![Figure 8. Synaptic potentials following utricular nerve stimulation in neck extensor and flexor motoneurons. EPSPs are elicited in ipsilateral extensor and ipsilateral flexor motoneurons (1,2), whereas IPSPs are recorded in contralateral extensor and contralateral flexor motoneurons (3,4). Stimulus intensity is indicated in µA and as multiples of the \( N_1 \) threshold (x\( N_1 \)). Arrows indicate the onset of the IPSPs (3,4).](image-url)
utricular stimulation usually are IPSPs of trisynaptic linkage (36,37) (Figure 8). Thus, the utriculoneck innervation pattern essentially differentiates between left and right sides.

In response to stimulation of the saccular nerve (38,39), the initial responses in bilateral extensor motoneurons were EPSPs (Figure 9) of disynaptic and trisynaptic latencies. Ipsilateral projections were always disynaptic, contralateral ones could be di- or trisynaptic. IPSPs were evoked in almost all bilateral flexor motoneurons with disynaptic or trisynaptic latencies (Figure 9). The sacculoneck motoneuron relationship thus has a qualitatively bilaterally symmetric organization regarding flexors and extensors.

These findings indicate quite a different projection pattern between utricular and saccular information to neck extensors and flexors regarding their function in spatial orientation (Figure 10): One utriculus projects to neck extensors and flexors in a unilateral fashion, that is, the ipsilateral extensors and flexors receive excitatory input (EPSPs), whereas the contralateral extensors and flexors receive inhibitory input (IPSPs). This innervation pattern is comparable to the horizontal canal system, where ipsilateral flexors and extensors are inhibited and the contralateral ones are excited [28]; Table 1: Patterns 1 and 4]. The innervation pattern of the sacculus is quite different and similar to that of the vertical semicircular canals, where the input to neck flexors and extensors also shows a bilaterally symmetric organization (Table 1: Patterns 1 and 4). For example, extensor motoneurons on both sides receive disynaptic EPSPs from an anterior canal, and disynaptic IPSPs from a posterior canal [see reference (28); Table 1: Pattern 1]. This differential organization of otolith output accounts for the picture of lesion symptoms following ablation of individual statoreceptors (see below).

Collectively, these findings suggest that different symmetry planes apply to the two systems, in a fashion similar to the semicircular canal system. Clearly, the major sensory-to-motor output channel of the utricular system concerns movement in the horizontal plane (Figure 10A), for example, in left-right and anterior–posterior directions, as suggested by the respective directional sensitivity vector distributions (32,40). The utriculus thus detects and compensates for side tilts and flexion–extension displacements of head and/or body. In the former case, the utriculi of both sides would operate as a left-right differentiating system, and in the latter case, the two utriculi would provide the same sensory output, working as a fore–aft movement detector.

**Saccular Nerve Stimulation**

![Figure 9. Synaptic potentials following saccular nerve stimulation in neck extensor and flexor motoneurons. EPSPs were recorded in ipsilateral and contralateral neck extensor motoneurons (1,2), and IPSPs in ipsilateral and contralateral flexor motoneurons. Stimulus intensity shown in µA and as multiples of the N1 threshold (xN1T). Arrows indicate the onset of EPSPs (1,3) and IPSPs (2,4).](image-url)
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The sacculus system, by contrast, seems to be principally controlling postural movements occurring in an up-down (and to some degree, also anterior-posterior) direction (32,33), being mainly concerned with vertical linear accelerations.

**Utriculus**

**Horizontal Acceleration**

**Contralateral Extensor & Flexor**

**Ipsilateral Extensor & Flexor**

**Sacculus**

**Vertical Acceleration**

**Bilateral Extensor**

**Bilateral Flexor**

Figure 10. Schematic of spatial organization of utriculoneck and sacculoneck reflexes. Muscles shown by an open symbol are excited, those marked by hatching are inhibited during horizontal (utriculus) and vertical (sacculus) accelerations. The utriculoneck system operates along a left-right, the saculoneck along a fore-aft symmetry plane, indicating their differential involvement in postural control mechanisms in physical space. In the illustrated case, the utriculus would work in left-right differentiating mode, that is, during a leftward horizontal linear movement, the left utriculus would supply excitatory output, the right one inhibitory output. By contrast, both sacculi would provide excitatory output during a downward vertical movement, and presumably inhibit their respective postural control circuits during upward movement. Thus, the sacculi of both sides would function in an identical fashion during vertical linear accelerations (indicated by the double arrow).

Postural Effects Following Otolith Lesions

Unilateral lesion of the utricular system produces a pronounced side tilt of the head-neck ensemble (41) that is identical to that observed after hemilabyrinthectomy (42). The symptom is largely due to the described synaptic qualities in the vestibulocollic system, that is, utricular inputs elicit EPSPs in ipsilateral neck extensor and flexor motoneurons, and IPSPs in contralateral extensor and flexor motoneurons (36,37). Thus, the lesion symptoms, in essence, reflect this bilaterally asymmetric projection pattern of the utriculo-motor system.

The postural symptom following unilateral saccular lesion is a slight side tilt of head and neck away from the side of the lesion (43); see also reference (44). This lateral deviation of the head-neck ensemble is much less pronounced than that following a complete hemilabyrinthectomy, or even an isolated unilateral otolith extirpation (41). It can now be explained on the basis of the above-described results: saccular inputs elicit EPSPs in bilateral neck extensor motoneurons and IPSPs in bilateral flexor motoneurons, however with a more powerful projection to the ipsilateral side. Thus, a unilateral saccular lesion would only cause a slight differential in tonic resting activity between the both sides.

The above synaptic connectivities, however, do not entirely explain the classical lesion symptoms per se, which are also perceptual consequences of a sensory lesion and their resulting acute compensatory righting reflex manifestations. In essence, a lesioned animal attempts...
to regain its equilibrium zero set-point by rotating in the opposite direction, thus trying to eliminate or reduce an apparent postural disturbance.

**Spatial Coordination of Vestibulocollic Reflexes**

The slight but distinctly different projection patterns of the vestibulospinal connectivity now allow an interpretation of the spatial coordination of vestibulocollic reflexes in a fashion similar to that for the vestibuloocular reflexes (45). The input patterns shown in Table 1 (for biventer, complexus, rectus capitis posterior, sternocleidomastoideus, obliquus capitis inferior, and longus capitis) now provide the physiological basis for such an interpretation.

Let us consider the biventer cervicis muscle in this example (Figures 11A, 11B, and 11C). Biventer has an ipsilateral roll and an upward pitch component [6]; see also above), and in context of vestibular reflexes, both sides always have to be taken into consideration (Figure 11A). During a left-ear-down head tilt, exciting the ipsilateral anterior and posterior canal receptors and inhibiting the contralateral ones (Figure 11B), we would expect a rightward compensatory head movement. The right-side biventer would receive excitatory input from the left (contralateral) and the right (ipsilateral) posterior canal (via disinhibition of the inhibitory vestibulocollic connectivity because the left-side head tilt inhibits the right-side vertical canals). At the same time, it receives inhibition from the left (contralateral) posterior canal, and also from the ipsilateral anterior canal (inhibition of the excitatory connectivity). In such case, the excitatory and inhibitory components arriving at this muscle may as well cancel, and no involvement of biventer results for roll movements (Figure 11B). Since the neuronal connectivity is bilaterally symmetric, the mirror image of this activation pattern will arrive at the

![Figure 11. Spatial coordination of vestibulocollic reflexes about the transverse (pitch) axis (panels A, B, and C) and the longitudinal (roll) axis (panels D, E, and F) using the examples of biventer and sternocleidomastoideus muscles. (A) Canal–muscle matrix of biventer (see also Table 1); (B) Canal–muscle input pattern during left-ear-down head tilt; (C) Canal–muscle activation pattern during pitch-down head movement; (D) Canal–muscle matrix of sternocleidomastoideus (see also Table 1); (E) Canal–muscle input pattern during pitch-down head movement; (F) Canal–muscle activation pattern during left-ear-down head tilt. In the scenario shown in B and E, the net excitatory/inhibitory input (+ + + +) will inactivate the muscles; in C and F, the collective excitatory input (+ + + +) will cause the respective muscles to contract. IAC: left anterior canal; IPC: left posterior canal; AC: right anterior canal; PC: right posterior canal; +: activation; -: inhibition.]
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left-side muscle. During a pitch-down movement, a different scenario can be envisioned: in such case, both anterior canal receptors are excited, and those from the posterior canals are inhibited (Figure 11C). Now the anterior canal connectivities as well as the posterior canal connectivities transmit excitatory input (from the posterior canals again via disinhibition of inhibitory circuits) and, given the bilateral symmetric organization of the reflex, both muscles will contract. The kinematic components for roll will likely cancel, while those for pitch-up will add to each other, and the required compensatory head movement will ensue (Figure 11C).

The same thought experiment can also be carried out for a different input pattern (Figures 11D, 11E, and 11F). Sternocleidomastoidaeus has a predominantly lateral tilt function for the head. Given the vestibular input pattern, the bilateral muscles would receive excitatory and inhibitory inputs during pitch-down movements, and likely, no activation would occur: excitatory input would arrive from the contralateral anterior and the ipsilateral posterior canal (from the latter via disinhibition of the inhibitory connectivity) and inhibitory input from the ipsilateral anterior and the contralateral posterior canal) (Figure 11E). During left-ear-down tilt of the head, all four vertical canals will transmit excitatory input to the right sternocleidomastoidaeus (excitatory connections from the contralateral canals, and disinhibition of inhibitory connections from the ipsilateral canals). Since the connectivities are mirror symmetric, the antagonistic left-side muscle will be silenced at the same time (Figure 11C).

The demonstrated scenario clearly spells out that the vestibulocollic connectivity also can be treated in a straightforward fashion within the three-dimensional reference frame of the semicircular canals, just like the vestibulo-oculomotor system [see also references (31,46)]. While the geometry of the extrocular muscles undoubtedly reflects the canal orientation, the same is not immediately obvious for the head—neck muscles. The now available detailed biomechanical and electrophysiological studies allow this direct comparison with the VOR system and the implementation of its operational principle for the spatial coordination of head—neck movements.

In theory, there should have been no question about the organization of vestibuloneck reflexes in vestibular coordinates based on even the early selective semicircular canal lesion experiments by Flourens (47) and the selective canal stimulation experiments by Suzuki and Cohen (24) in which head movements were elicited in the plane of a particular receptor system. Furthermore, many second-order vestibular neurons arborize into oculomotor as well as neck—motor motoneuron pools. Thus, a common signal encoding the same spatial coordinates is distributed to eye muscles as well as neck muscles (29).

The collective results clearly spell out the need for a multidisciplinary approach when dealing with a complex sensory—motor system such as the head—neck movement system. Future investigations will have to address evolutionary and functional questions, in particular, whether the results obtained in quadrupedal specimens can be extrapolated to postural control mechanisms in bipedal mammals such as monkeys and humans [see for example references (3,9)].

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