

**ASYMMETRIC TONIC LABYRINTH
REFLEXES AND THEIR INTERACTION WITH NECK
REFLEXES IN THE DECEREBRATE CAT**

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SUMMARY

1. Tonic labyrinth and neck reflexes were studied separately and in combination in the decerebrate cat with C1 and C2 spinal roots cut. Reflex effects were observed as changes in length of the isotonicity loaded medial head of triceps.

2. The tonic labyrinth reflexes acted asymmetrically on the medial head of triceps. Side-down rotation of the head produced shortening in medial triceps, whereas side-up rotations of the head resulted in a lengthening.

3. The tonic neck reflexes acted asymmetrically on the medial head of triceps. Side-down rotations of the neck produced a lengthening of medial triceps, whereas side-up rotations of the neck resulted in shortening.

4. Labyrinth and neck reflexes produce opposite effects on the same limb extensor muscle so that, if the neck innervation is intact, head tilting produces no change in muscle length.

5. It is suggested that the interaction between the labyrinth and neck reflexes contributes to the stability of the trunk, allowing the head to move freely on the body without affecting this stability. Labyrinth and neck reflexes need therefore to be considered together as a single system.

INTRODUCTION

Sherrington (1910) and Magnus & de Kleijn (1912) independently discovered that, under certain conditions, rotation of the head of a decerebrate cat about its long axis could alter the extensor tone of the limb musculature. Magnus and his co-workers demonstrated that there were both vestibular and neck proprioceptive contributions to this alteration in

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tone. Their observations formed the basis of extensive work which was summarized in Magnus's classic monograph *Körperstellung* (1924).

The tonic labyrinth reflexes were said by Magnus to act on all four limbs in the same sense, producing maximal extension of all four limbs when the decerebrate cat was in a supine position, with the angle of its mouth at 45° above the horizontal plane, and minimal extensor tone when the animal was prone, with the angle of its mouth 45° below the horizontal plane. Intermediate positions of the animal were said to produce an intermediate degree of extensor tone, again symmetric in all four limbs. In contrast the tonic neck reflexes were described as acting asymmetrically on the limbs, in that the limbs on the side toward which the jaw was rotated became extended and the limbs on the other side flexed (Magnus & de Kleijn, 1912). This description of the tonic labyrinth and neck reflexes acting on the limbs has for many years been generally accepted and still forms an integral part of many textbook presentations of postural reflexes (e.g. Bard, 1968). With the exception of the confirmation of the form of the neck reflexes (McCouch, Deering & Ling, 1951), and in spite of recent advances in the understanding of the mode of action of the utricular receptors (Lowenstein & Roberts, 1949; Trincker, 1962; Fernandez, Goldberg & Abend, 1972; Loe, Tomko & Werner, 1973), Magnus's comprehensive scheme for postural reflexes has not been systematically re-investigated or independently confirmed since its definitive presentation 50 years ago. In all his studies of the independent actions of the tonic labyrinth and neck reflexes on the limbs Magnus (1924) speculated only about the relative contribution that each reflex might make to a given limb posture. He did not suggest any functional significance for the interaction between these reflexes. In all his accounts of the reflexes Magnus emphasized the contrast between the symmetrical influences from the labyrinth and the asymmetric influences from the neck.

The present study develops and extends the use of a preparation introduced by Roberts (1963) in which the labyrinth and neck reflexes can be clearly separated in the same animal, and elicited independently or in combination. This preparation is used to examine the independent and combined action of the labyrinth and neck reflexes on a single extensor muscle in the forelimb of the decerebrate cat. From our results we derive a systematic account of the action of each of these reflexes, as well as a test of Roberts' (1973) hypothesis on the functional significance of the interaction between the tonic labyrinth and tonic neck reflexes. Preliminary reports of this work have been presented elsewhere (Rosenberg & Lindsay, 1973; Lindsay & Rosenberg, 1974; Lindsay & Rosenberg, 1975).

METHODS

The majority of these experiments (twenty-three of thirty-eight) were carried out on cats decerebrated under N_2O/O_2 -Halothane anaesthesia by transecting the brain stem at a precollicular level. In the remainder of the experiments (fifteen of thirty-eight) the section was made at a midcollicular level. The transection was made after tying off the carotid arteries and temporarily occluding the vertebral arteries. The brain anterior to the section was then removed and the anaesthetic discontinued. All the cats breathed spontaneously throughout the course of the experiment.

The dorsal roots of C1 and the dorsal and ventral root of C2 were cut on each side within the vertebral canal under direct vision with the aid of a Zeiss dissecting microscope. The rootlets of C1 were approached through an opening in the atlanto-occipital membrane and were cut immediately adjacent to the spinal cord. To cut the roots of C2, a probe with an offset hook was inserted through the intervertebral foramen and manipulated to gather all the rootlets. The whole root could then be cut through together at a point proximal to the dorsal root ganglion with some assurance that no connexions remained to the ligaments of the intervertebral joints.

The right medial head of triceps (medial triceps) was used throughout. The long and lateral heads of triceps were cut close to their points of insertion on the olecranon process and then retracted. The medial head, along with a small portion of the olecranon process which contained its tendinous insertion, was dissected free. To allow free excursion of medial triceps the surrounding connective tissue was cleared and the fibres of anconeus divided. The right humerus was fixed by bone pins inserted at the lower and midshaft positions so that the forelimb was maintained in an almost vertical position. The muscle was then connected to the puller (Roberts, 1963) with a stout linen thread.

The system used for independent support of the head, neck, and trunk is illustrated in Fig. 1. The head was fixed in a head-holder (Roberts, 1951) which was arranged so that the head could be tilted about a horizontal antero-posterior axis. The axis vertebra was clamped and fixed in such a way that it could be rotated about an inclined axis passing in an antero-posterior direction through the vertebral column. The positions of the head-holder and the vertebral clamp were adjusted until the two axes of rotation intersected as nearly as possible at the odontoid process of the axis vertebra, to avoid undue strain on the ligaments when either the head-holder or the neck clamp was moved by itself. The trunk was suspended from a pair of knitting needles, one of which passed through the supraspinous ligament of the upper thoracic vertebrae, and the other passed just ventral to the pelvic girdle at the level of the iliac crests. This method of supporting the animal avoided generating spurious interfering effects from the skin while allowing the labyrinth and the receptors in the intervertebral joints of the neck to be stimulated either independently or together. The head could be rotated while the axis vertebra remained fixed. Under these conditions reflexes arising from the atlanto-occipital or atlanto-axial joints were eliminated by the bilateral section of C1 and C2 (McCouch *et al.* 1951), whereas the remaining intervertebral joints whose movement might elicit neck reflexes remained fixed during the rotation of the head. Thus labyrinth reflexes could be elicited in the absence of neck reflexes. Alternatively, the head could be fixed and the axis vertebra rotated. This procedure produced neck reflexes without labyrinth reflexes because the innervation of the remaining intervertebral joints below the clamp was still intact. The atlanto-occipital and the atlanto-axial joints are the main sources of afferent input for the neck reflexes (Magnus, 1924; McCouch

et al. 1951; K. W. Lindsay, unpublished), but they are not the only source. Cutting C1 and C2 thus reduces the amplitude of the neck reflexes as compared with the intact animal but it does not abolish them. In the comparisons of labyrinth and neck reflexes in this study, the neck torsions applied to the axis vertebra are accordingly larger than those which would normally accompany the head tilts with which they are compared.

The rectal temperature was maintained at approximately 37° C by a thermistor-controlled radiant-heat lamp. The exposed tissues were coated with paraffin to prevent drying.

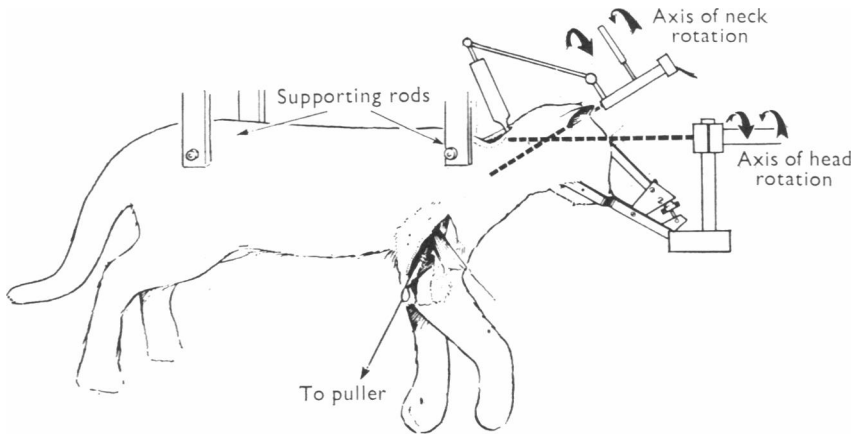


Fig. 1. Diagram of the method used for the independent support of the trunk, neck and head of the cat. The trunk is supported by a pair of knitting needles, one through the supraspinous ligament of the upper thoracic vertebrae and the other just ventral to the pelvis at the level of the iliac crests. The axis vertebra is held in a clamp which can either be rigidly fixed or can be rotated about an inclined axis through the cervical part of the vertebral column. The skull is fixed in a head holder permitting rotation about a horizontal antero-posterior axis. The two rotational axes intersect at the odontoid process of the axis vertebra. Potentiometers are mounted in line with each of the axes.

The effects of labyrinth and neck reflexes on the medial head of triceps were studied as length changes with the muscle under isotonic conditions. In some preliminary experiments the reflexes were examined against a background of a continuous sinusoidally fluctuating force applied to medial triceps. The muscle puller used to deliver controlled constant or sinusoidally fluctuating forces has been described in detail elsewhere (Roberts, 1963). The compliance of the puller is such that the muscle could change length throughout the full range with only negligible change in the applied tension. The length and tension of the muscle were continuously monitored. Changes in muscle length were detected with a Devices photoelectric length transducer (Devices Instruments Ltd, No. 2LD01). The graded filter of the transducer was suspended from the thread used to connect the muscle to the puller. Length changes were calibrated by a micrometer drive. The signal from the length transducer was amplified and then displayed on one channel of a pen recorder (Cambridge, Type 72123). The length measurements were made to the

nearest 0.5 mm on the pen recorder paper which corresponded to 0.1–0.5 mm change in muscle length, depending on the gain of the amplification system in each particular experiment. The reflex response to either labyrinth or neck stimulation varied between 1 and 6 mm change in muscle length. The tension developed by the muscle was measured with an RCA 5734 mechano-electric transducer valve used as a diode in a bridge circuit whose output was amplified and displayed on one channel of the pen recorder. The tension transducer was calibrated by disconnecting the muscle from the puller and applying known weights to the tension transducer along the line of muscle pull. The tension was measured to the nearest 0.5 mm on the pen recorder graph paper, which corresponded to 0.03 N (3 g wt.). The zero of the myograph tended to drift slowly and needed to be re-set from time to time in the course of the experiment. However, the drift in the zero was negligible over the periods of time used to assess particular reflex responses. The resting tension was set at a value between 0.2 N (20 g wt.) and 0.8 N (80 g wt.).

Head and neck positions were monitored by potentiometers giving voltage changes linearly related to spindle rotation and mounted with their spindles in line with the appropriate axis (Fig. 1). The head and neck positions were changed manually and the signal from the appropriate potentiometer was amplified and displayed on one channel of the pen recorder. Head and neck rotations were confined to 30° rotations on either side of the vertical. Head and neck positions were measured to within 2° by protractors aligned perpendicularly to the axis of rotation. In some cases head or neck rotations were carried out in 10° increments. The direction of rotation was designated as 'side-down' when the vertex of the skull or the neural spine of the axis vertebra was rotated toward the limb being studied, and 'side-up' for rotations in the opposite sense. 'Nose-up' and 'nose-down' was used to indicate upward or downward movements of the head alone in the sagittal plane. Although the velocity of rotation could not be accurately controlled, it was estimated to lie between 15 and 120 deg/sec. After each movement the new position was maintained for several seconds, in some cases up to 40 sec. A sustained response in these conditions is referred to as 'tonic'. In these experiments the deflexion of the cupula may be expected to follow the time course of the velocity of the head movement (e.g. Melville-Jones & Spells, 1963; Goldberg & Fernandez, 1971). The observations on the tonic component of the labyrinth reflex are therefore considered to be uncontaminated by canal effects.

The latency between the beginning of a head or neck rotation and the onset of a reflex response was measured by triggering the sweep on a storage oscilloscope manually just before starting the movement of the head or neck. Head or neck position and muscle length signals were displayed together and the delay was read directly from the face of the oscilloscope as the interval between the onset of head or neck rotation and the onset of the reflex response in the muscle under test, using a calibrated sweep speed.

RESULTS

Tonic labyrinth reflex

In thirty animals, fifteen decerebrated at a precollicular level, and fifteen at an intercollicular level, the reflex response of the medial head of triceps (medial triceps) to head rotation was tested 764 times, the axis vertebra remaining throughout clamped in the normal position in each case. In 598 of these tests (78.4%) the muscle showed clear responses to either direction of head rotation and the response persisted as long as the head

remained tilted. In thirty-five tests (4.5%), only a phasic response was seen in the muscle, although the side-up or side-down position of the head was maintained. In the other 131 tests (17.1%) there was no response to either side-up or to side-down head rotation. It is the sustained or 'tonic' responses that will be dealt with in what follows.

A typical example of the reflex response of medial triceps to two complete cycles of side-up and side-down rotations is illustrated in Fig. 2. The tension in the muscle was first adjusted to approximately 60 g wt. (0.57 N)

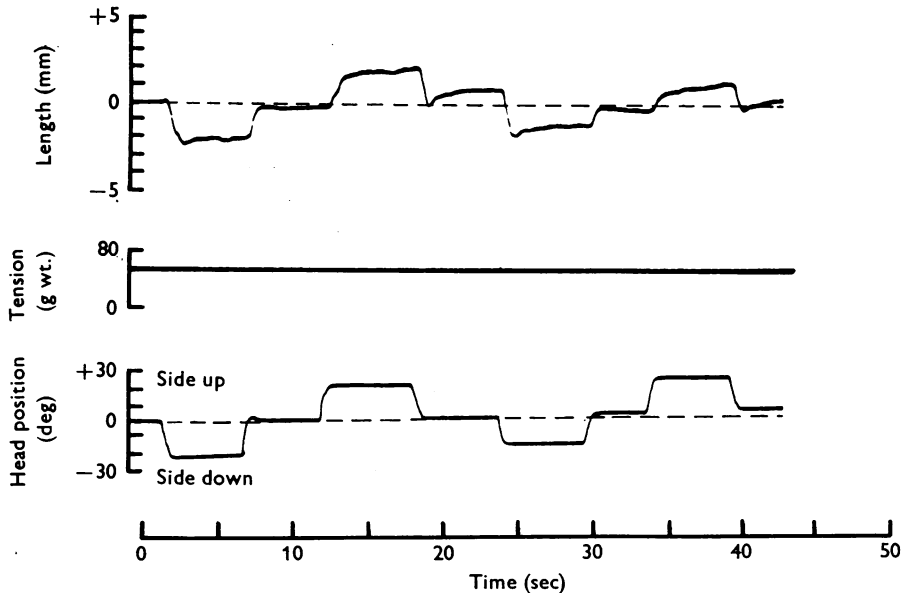


Fig. 2. Records of muscle length, muscle tension and head position. Medial head of triceps: decerebrate cat: C1 and C2 cut: axis vertebra clamped.

and it was maintained at this value while the labyrinth reflexes were being tested. The head was first tilted 20° side-down and held for a time at this position. The muscle shortened rapidly and then relaxed slightly to leave the tonic component of the reflex. In the example illustrated in Fig. 2, the peak shortening was 2.5 mm, the muscle then relaxed 0.5 mm, and stayed at this length so long as the head was held in the side-down position. An initial transient change in muscle length occurred in 33% of the tests. Once the tonic component of the reflex appeared to have become firmly established, the head was rotated back to the normal position. The muscle relaxed back to a length close to that observed initially at that head position. After an interval of 5 sec the head was tilted 20° side-up and fixed at this position. The muscle lengthened 2 mm and remained at this

length during the time the head was held in the side-up position. When the head was returned to the normal position, the muscle rapidly shortened to its original length and then relaxed slightly. The latency from head movement to change in muscle length was usually about 100–150 msec. A

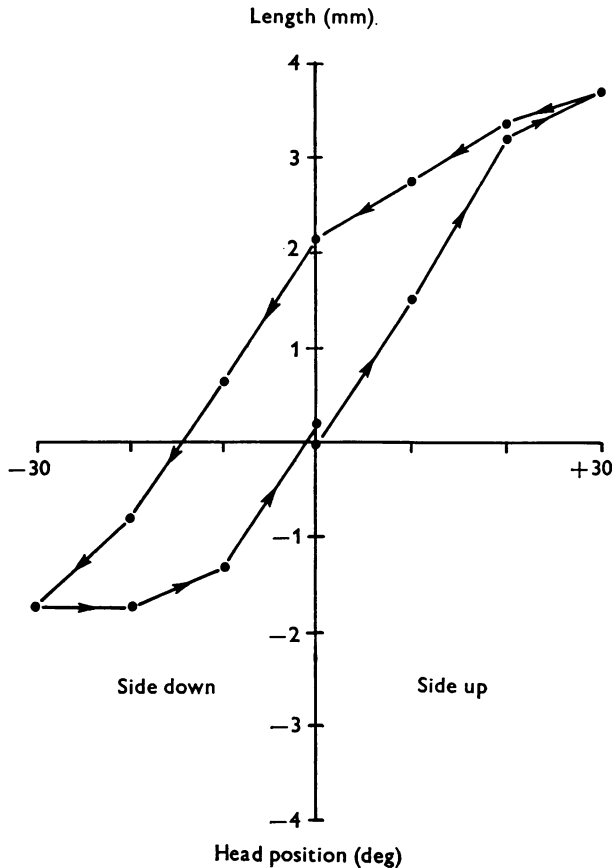


Fig. 3. Isotonic length change in medial triceps plotted against head position. Decerebrate cat: C1 and C2 cut; axis vertebra clamped. The head was tilted in 10° steps in the sequence indicated by the arrows with pauses at each new position. The values plotted are the muscle lengths 5 sec after each new position had been reached.

second sequence of head tilts produced a similar set of asymmetric responses with some hysteresis (see below). The usual pattern of labyrinth reflexes for lateral rotations of the head was that side-down head rotations produced shortenings in medial triceps on that side, whereas side-up rotations produced relaxations. According to Magnus's scheme (Magnus

& de Kleijn, 1912; Magnus, 1924) a rotation in either direction would be expected to produce a shortening.

In many cases after returning the head to a previously held position the muscle did not return to the length originally observed at this position (Fig. 2). The hysteresis could best be observed when the head position was changed stepwise in increments of 10° from normal to 30° side-up to 30° side-down and then back to normal (Fig. 3).

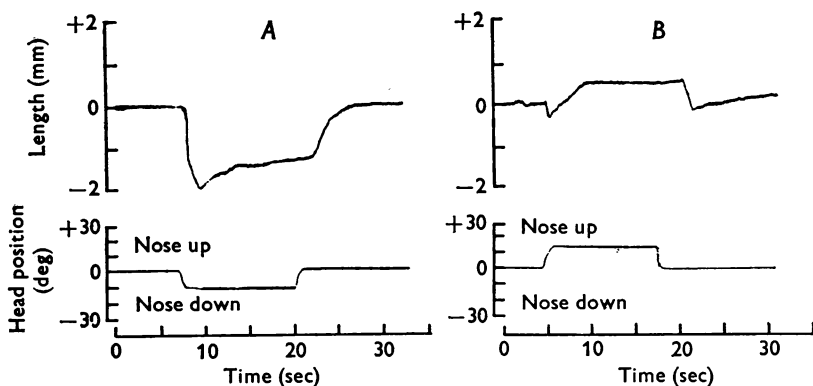


Fig. 4. *A*, isotonic length changes in medial triceps during a nose-down tilt and *B*, a nose-up tilt. Decerebrate cat: C1 and C2 cut: axis vertebra clamped.

The muscle length at each of the thirteen maintained positions was measured 5 sec after the position was reached. Muscle length was then plotted against head position and the points connected by straight lines in the order in which the different positions were reached. Successive 10° side-up rotations produced incremental lengthenings. When the direction of rotation was reversed, the muscle shortened but at each position its length was greater than that previously observed at that head position. At 30° side-down the direction of rotation was again reversed and the head was returned to the normal in 10° steps. In this case the muscle always adopted a shorter length than that previously observed at each of the side-down positions. The hysteresis loops always occurred in an anticlockwise direction.

In three preparations the reflex response of medial triceps to nose-up and nose-down head rotations in a sagittal plane were examined. Clear results were observed in only one preparation. A typical result from this preparation is illustrated in Fig. 4. The axis vertebra was clamped and the head rotated in a sagittal plane about an axis passing through the atlanto-occipital joint. Lowering the head and fixing it at 12° nose-down produced

a sustained shortening of medial triceps, whereas fixing the head at 15° nose up resulted in a sustained relaxation. In Magnus's scheme (Magnus & de Kleijn, 1912; Magnus, 1924) raising the head should produce a shortening of medial triceps, whereas we observed a clear relaxation in all those instances in which raising the head elicited a clear reflex response.

Reproducibility of the responses. The reproducibility of the labyrinth reflex for each direction of head rotation was assessed by repeated trials. The results of 371 side-down head rotations and 393 side-up head rotations showed that 73.6% of the side-down head rotations produced sustained shortenings in medial triceps, with sustained lengthenings occurring in only 4.0% of the trials. In the 393 side-up head rotations, relaxations of medial triceps occurred in 76.1% of the trials and sustained contractions in only 2.8% of the trials. By far the most common pattern for the tonic labyrinth reflex on medial triceps was that side-down head rotations produced shortening, whereas side-up head rotations produced lengthening.

Effect of level of decerebration. The relation between the reproducibility of the labyrinth reflex and the level of decerebration can be shown by comparing the reflex responses to side-down head rotation in the precollicular cats with those in the intercollicular cats. The variability of the reflex was less in the intercollicular cats than in the precollicular cats. In 216 side-down head rotations in intercollicular cats shortenings occurred 91.6% of the time and lengthenings only 0.1% of the time. On the other hand, for 145 side-down head rotations in the precollicular cat shortenings occurred only 53.1% of the time and lengthenings in 15.9% of the trials. In addition the eight preparations which did not show any responses at all to head rotations were decerebrated at a precollicular level. The number of times that no response occurred decreased from 31.0% in the precollicular cat to 8.3% in the intercollicular cat.

Tonic neck reflex

The reflex responses of medial triceps to side-up and side-down rotations of the axis vertebra were examined in twenty-two cats. Eleven were decerebrated at a precollicular level, and eleven at an intercollicular level. The reflex response to rotation of the axis vertebra was tested 318 times. In 226 tests (71.1%) there were sustained length changes to both directions of neck rotation. In fourteen (4.4%) cases there were only phasic changes in muscle length and in the remaining seventy-eight (24.5%) tests there were no responses to either direction of neck rotation.

The typical pattern of the tonic neck reflex acting on medial triceps is illustrated in Fig. 5. The head remained fixed while the axis vertebra was rotated toward side-down and side-up positions in turn. These positions were maintained for a minimum of 5 sec. The axis vertebra was first

rotated 15° side-down. After a short delay medial triceps lengthened and remained extended as long as the neck clamp was held in the side-down position. When the neck was returned near to the normal, the muscle shortened. After a further 6 sec, the neck was rotated 25° side-up and fixed at this position. Medial triceps contracted and remained shortened as long as the neck was held in the side-up position. Delays of approximately

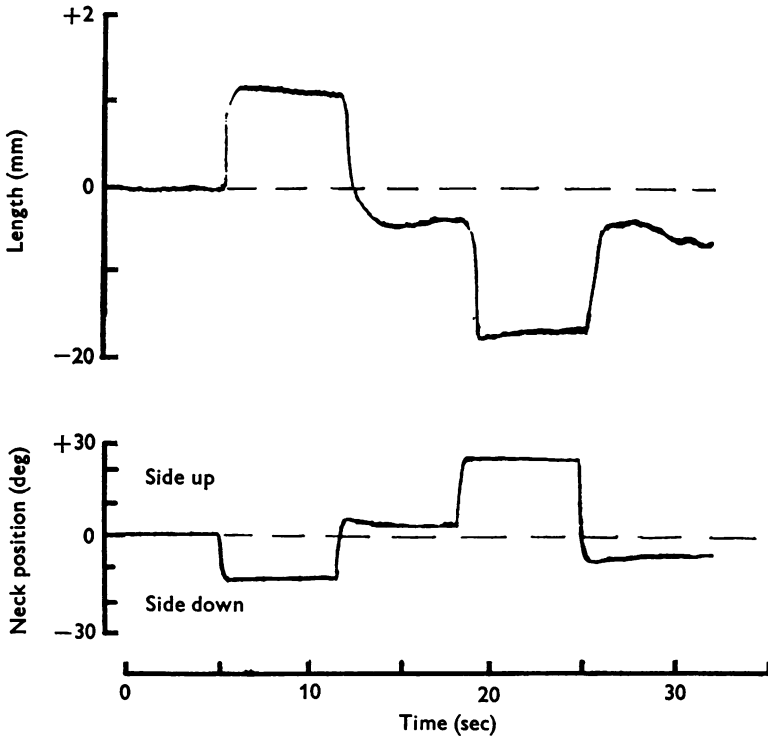


Fig. 5. Isotonic length changes in medial triceps elicited by neck torsion. Decerebrate cat; C1 and C2 cut; head fixed.

100–150 msec occurred in each case between neck movement and muscle response. The tonic neck reflexes acting on medial triceps were found to be asymmetric and thus in agreement with earlier reports of these reflexes on intact limbs (Magnus & de Kleijn, 1912; McCouch *et al.* 1951). The common pattern of the neck reflexes was that side-down rotations of the neck produced lengthening of medial triceps, whereas side-up rotations of the neck produced shortening.

The tonic nature of the neck reflexes acting on medial triceps was clearly demonstrated in experiments in which a side-up or side-down neck position was maintained for several seconds. Fig. 6 illustrates a case where the neck

was rotated 20° side-up and fixed in this position for approximately 40 sec. The shortening of medial triceps produced by the side-up rotation of the neck persisted so long as the neck remained in the side-up position. Con-

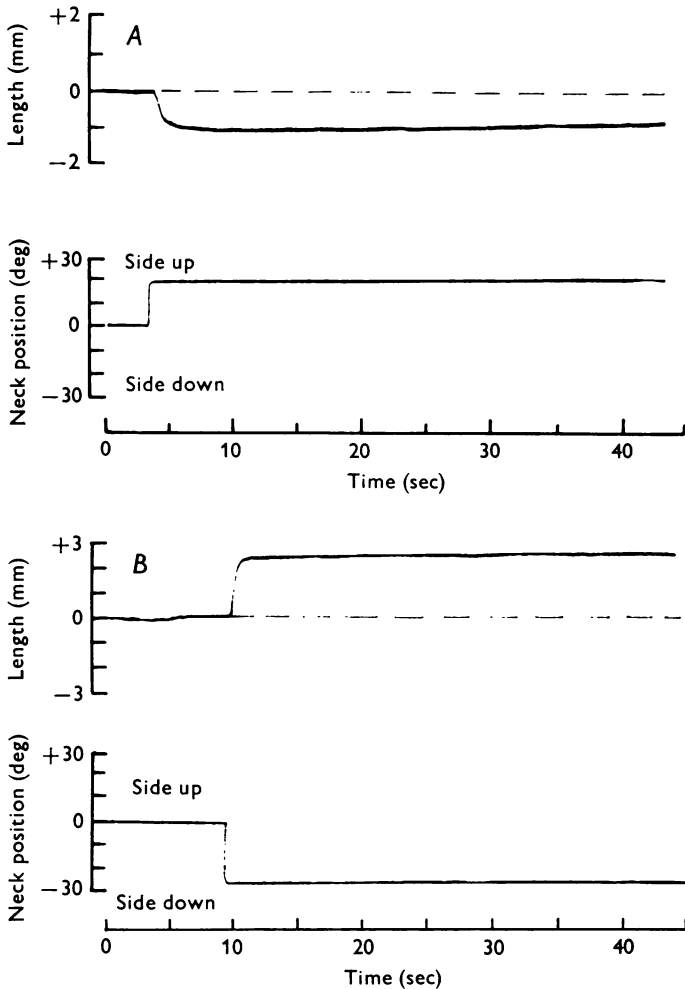


Fig. 6. Isotonic length changes in medial triceps during sustained neck torsion: *A* toward side-up; *B*, toward side-down. Decerebrate cat: C1 and C2 cut; head fixed.

versely, when the neck was rotated 30° side-down (Fig. 6), the muscle lengthened. This lengthening of medial triceps was sustained so long as the neck remained fixed in the side-down position.

In some cases the tonic response to a rotation of the neck was preceded

by a short phasic component (Fig. 7). In this case following a side-down rotation of the neck, the muscle lengthened rapidly and then slowly shortened to a final tonically maintained length. A phasic component of the neck reflex occurred in twenty-seven of the tests (12.0%) where sustained responses were obtained.

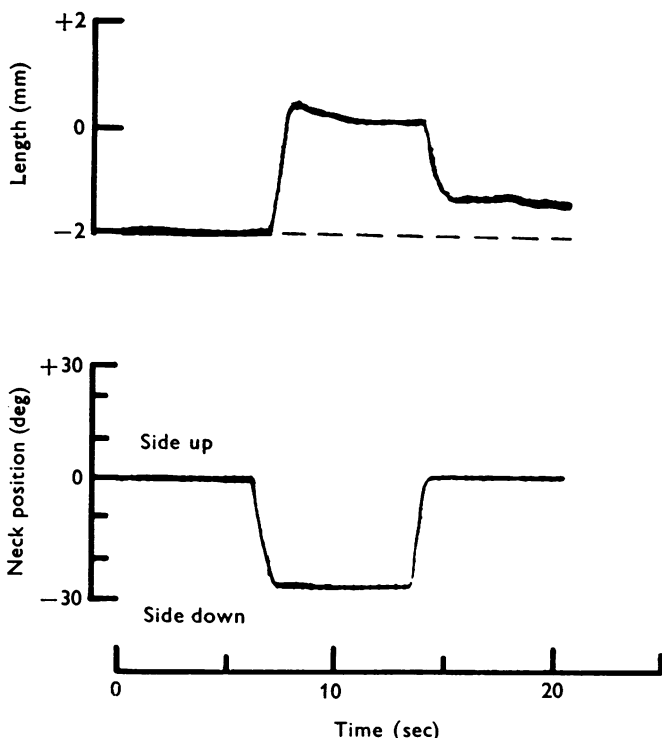


Fig. 7. Isotonic length changes in medial triceps elicited by neck torsion. Note phasic component and marked hysteresis. Decerebrate cat: C1 and C2 cut; head fixed.

Fig. 7 also clearly illustrates the hysteresis that was observed in neck reflexes as well as in labyrinth reflexes (Fig. 3). When the neck was rotated back to the normal from 25° side-down the muscle did not return to the length previously observed at this position. A hysteresis in the neck reflex response is also seen in Fig. 5 where, in order to return to the muscle length previously seen at 3° side-up (before the rotation to 25° side-up), the neck had to be rotated to 6° side-down.

Reproducibility of response. The reproducibility of the reflex response of medial triceps to both directions of neck rotation was assessed on the

basis of 318 trials. The results of 160 side-down neck rotations and 158 side-up neck rotations showed that 76.3% of the side-down neck rotations produced sustained lengthenings, with a phasic shortening occurring in only one test; whereas side-up neck rotations produced sustained shortenings in 63.9% of the trials, with a phasic lengthening occurring in only 1.9% of the trials. Thus the common pattern for the tonic neck reflexes acting on medial triceps was that side-down neck rotations produced lengthenings of medial triceps, whereas side-up neck rotations produced relaxations.

Effect of level of decerebration. The level of decerebration had a small effect on the reproducibility of the response but apparently had a strong effect on the ability to elicit a sustained neck reflex. The variability of the reflex response did not differ in the two preparations. However, in fifty-five side-down neck rotations in the precollicular cats, no responses were seen in 29.1% of the trials, whereas in ninety-nine side-down neck rotations in the intercollicular cats, responses failed to appear in only 15.2% of the trials. A similar set of figures holds for side-up neck rotations.

Interaction between tonic labyrinth and tonic neck reflexes

The above results (e.g. Figs. 2 and 5) show that, when acting independently, the tonic labyrinth and tonic neck reflexes produced opposite effects on medial triceps when the head or neck was rotated in a particular direction. Side-up rotations of the head produced relaxations of medial triceps, whereas side-up rotations of the neck produced shortening. Conversely, side-down rotations of the head produced shortening and side down rotations of the neck produced lengthenings. However, under normal conditions head and neck movements usually occur together. Accordingly, the action of labyrinth and neck reflexes were examined in combination, and the results are presented in this section. Fig. 8A illustrates the effect of superimposing a tonic neck reflex on a pre-existing tonic labyrinth reflex. The head was first rotated 20° side-up and fixed at this position. The medial head of triceps lengthened, and after the tonic labyrinth reflex had been established for 6 sec, the axis vertebra was also rotated 20° side-up. This produced a shortening in the muscle, which returned close to its original length. Thus the net effect of a simultaneous side-up rotation of both head and neck was to leave the muscle length almost unchanged. When the axis vertebra was then returned to normal the medial head of triceps returned to the length determined by the 20° side-up position of the head. When the head was also returned to its normal position, the muscle returned close to the length originally observed at this position. The direction and sequence of the head and neck rotations were then both reversed and a labyrinth reflex was superimposed on a tonic neck reflex

(Fig. 8*B*). The axis vertebra was first rotated 20° side-down and fixed at this position to elicit a sustained lengthening of medial triceps. Once the tonic neck reflex had become firmly established, the head was rotated 20° side-down. This produced a shortening in medial triceps which returned the muscle close to its initial length. The combined effect of a simultaneous side-down neck and head rotation thus resulted in almost no net reflex change in the length of medial triceps. Once the head was returned to the normal medial triceps returned to the length determined by the existing side-down neck rotation. Finally, when the axis vertebra was returned to normal, medial triceps returned to its initial length.

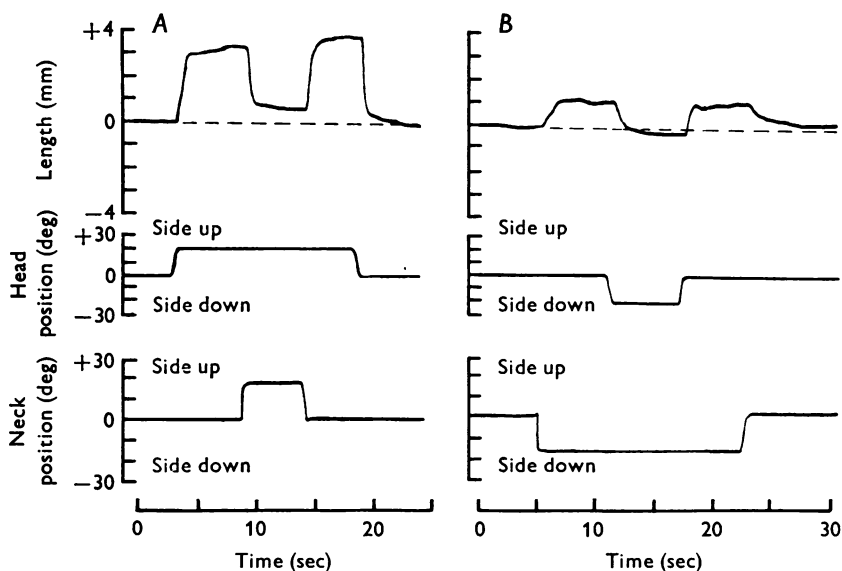


Fig. 8. Isotonic length changes in medial triceps elicited by combinations of head tilt and neck torsion in the same direction. Decerebrate cat: C1 and C2 cut. *A*, neck reflex superposed on labyrinth reflex; *B*, labyrinth reflex superposed on neck reflex.

Interaction between labyrinth and neck reflexes could also be observed when the head and neck were rotated in opposite directions. The axis vertebra was first rotated to 15° side-up and fixed at this position to elicit a sustained shortening in medial triceps. Once the tonic neck reflex response had become established, the head was rotated 20° side-down and fixed at this position. This rotation of the head resulted in a further contraction of medial triceps. When the head was returned to normal, medial triceps relaxed to the length determined by the existing side-up position

of the neck. Finally, when the axis vertebra was returned to the normal, the muscle relaxed back to its original length.

These interactions between labyrinth and neck reflexes depended on receptors located in the lower cervical joints, where as under normal

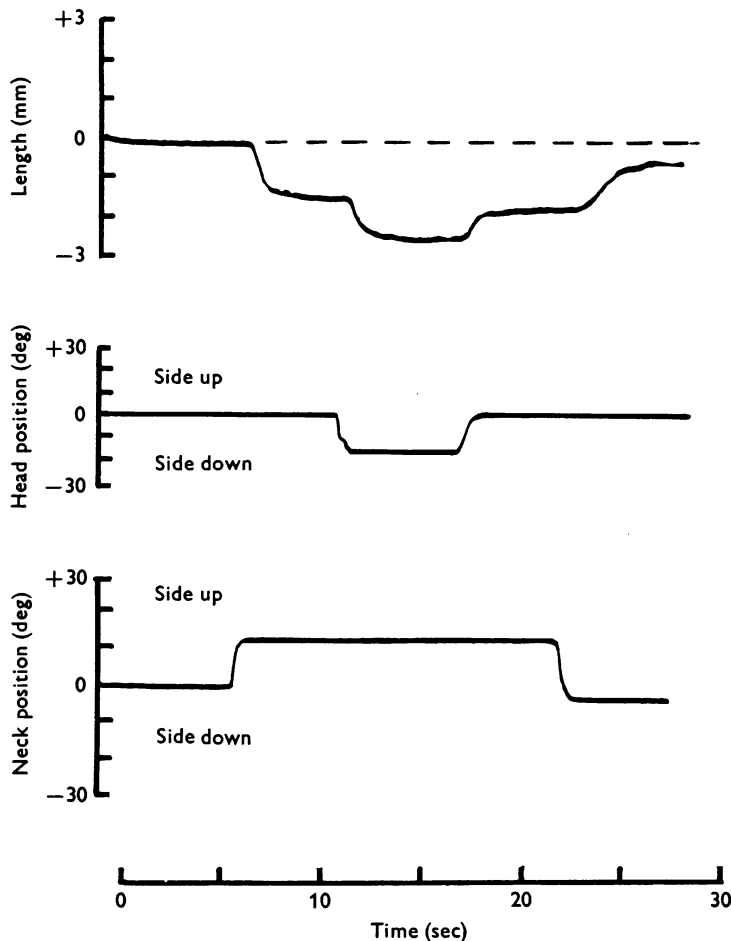


Fig. 9. Isotonic length changes in medial triceps elicited by the combination of head tilt and neck torsion in opposite directions. Decerebrate cat: C1 and C2 cut.

conditions the majority of the afferent input for the neck reflexes comes from C1 and C2 (Magnus, 1924; McCouch *et al.* 1951; K. W. Lindsay, unpublished) which had been cut in our preparation. The next step was to study the interaction between labyrinth and neck reflexes when C1 and C2 were initially left intact and then cut later. With C1 and C2 intact, a

rotation of the head alone should elicit both labyrinth and neck reflexes. Fig. 10*A* illustrates the consequences of a head rotation on medial triceps when C1 and C2 were left intact, the rest of the procedure for setting up the preparation being exactly as before. Rotation of the head from 30° side-up to 30° side-down did not produce any detectable change in muscle length. However, if C1 and C2 were now cut (Fig. 10*B*), it was found that when the head was rotated from 30° side-up to 30° side-down, labyrinth reflexes of the type already described were revealed. The interaction between labyrinth and neck reflexes described in Fig. 10 is representative of the results from twelve cats.

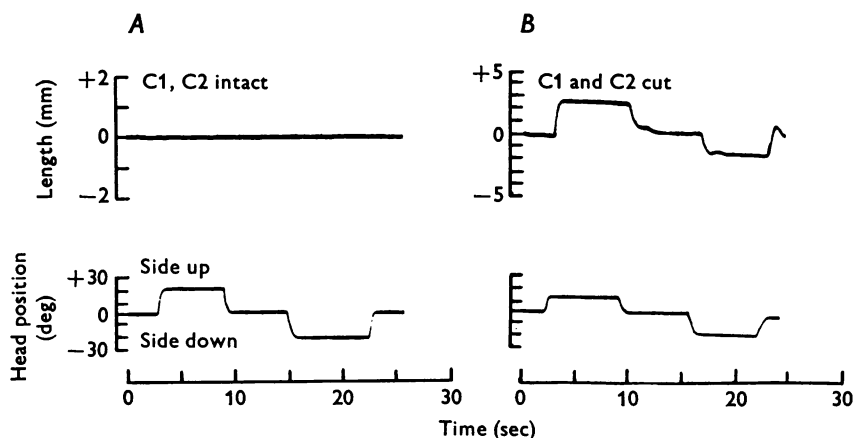


Fig. 10. Isotonic length changes in medial triceps elicited by head tilting with the axis vertebra clamped. *A*, before and *B*, after section of C1 and C2 (same cat). Note that when both labyrinth and neck afferent input are intact, interaction of these reflexes leaves the muscle length unchanged.

Control experiments were carried out on two acutely labyrinthectomized cats. In these preparations head rotations generated neck reflexes acting on the limbs. However, if C1 and C2 were bilaterally sectioned and the axis vertebra clamped, then head rotations did not produce reflex effects on the limbs. Conversely, if the head remained fixed while the axis vertebra was rotated, the usual neck reflexes were observed acting on the limbs.

DISCUSSION

It is clear that our results on the tonic labyrinth reflexes differ from those reported by Magnus (Magnus & de Kleijn, 1912), while his scheme of neck reflexes is confirmed.

We find that the tonic labyrinth reflexes act on the medial head of

triceps in an asymmetric fashion. The medial triceps shortened when the head was rotated either toward side-down (Fig. 2) or toward nose-down (Fig. 4). Conversely, medial triceps lengthened when the head was rotated either toward side-up (Fig. 2) or toward nose-up (Fig. 4). These asymmetric tonic labyrinth reflexes were observed on repeated trials.

Descriptions of Magnus & de Kleijn's (1912) experimental procedure for examining the tonic labyrinth reflexes suggest that they investigated rotations only about a bitemporal axis. However, they clearly intended their conclusions to be applicable to any direction of rotation. According to their account maximal extension occurs in all four limbs when the animal is brought into a supine position, implying that any direction of rotation of the head from a prone to a supine position should produce a contraction in the medial head of triceps. Our results show clearly that this is not what happens. Side-up (Fig. 2) and nose-up (Fig. 4) rotations of the head produced relaxations of medial triceps.

There are differences of technique that might be relevant to this discrepancy. Magnus immobilized the neck in plaster and rotated the whole animal. We have tilted the head or neck while the trunk was held stationary on a separate support (Fig. 1) and have been careful to minimize changes in skin stimulation during the tilting.

The receptors initiating the reflex responses to head tilting are presumably the neuromasts of the otolith organs of the labyrinth. The semi-circular canals can be excluded from contributing to the tonic reflexes on the grounds that, once the skull has been brought to rest after a change in position, the residual effect of the sequence of angular accelerations and decelerations is negligible (Roberts, 1967; Melville Jones & Milsum, 1970). While there are a few recorded instances of otolith receptors giving similar response patterns when the skull is tilted in either direction, the great majority of reports demonstrate different response patterns for different directions of rotation (Lowenstein & Roberts, 1949; Trincker, 1962; Fujita, Rosenberg & Segundo, 1968; Peterson, 1970; Vidal, Jeanerod, Lifchitz, Levitan, Rosenberg & Segundo, 1971; Fernandez *et al.* 1972; Loe *et al.* 1973). It is therefore reasonable to expect that the reflex responses initiated from the otolith organs in the labyrinth will be different for different directions of tilting.

We agree with Magnus & de Kleijn (1912) in finding that the pattern of the tonic neck reflexes is asymmetrical (Fig. 5). However the response in the neck reflexes is in the opposite sense to that in the tonic labyrinth reflexes for the same direction of head and neck rotation. Side-down rotations of the neck resulted in a lengthening of medial triceps (Fig. 5), whereas side-up rotations of the neck produced a shortening in medial triceps (Fig. 5). This pattern of the tonic neck reflexes corresponds to that

described for intact limbs by earlier workers (Magnus & de Kleijn, 1912; McCouch *et al.* 1951).

Roberts (1973) suggested that, in the intact animal, normal movements of the head, in which both labyrinth and neck proprioceptors would be stimulated, should result in no net reflex change in the posture of the limbs. This suggestion has received some indirect support. Ajala & Poppele (1967) showed that rotation of the head of the decerebrate cat leaves the position of the forelimbs unchanged. Poppele (1967) observed reflex changes in gastrocnemius and soleus muscles following head rotation, only after a unilateral labyrinthectomy. Ehrhardt & Wagner (1970) noted that there was no sustained change in the discharge frequency of lumbar motoneurons after lateral rotation of the head with neck innervation intact.

The experiments in which the neck denervation was postponed (Fig. 10) establish that the neck reflexes and labyrinth reflexes act precisely in opposition, both sets of reflexes being asymmetric in the distribution of their effects.

Roberts (1973) in summarizing his earlier work on labyrinth and neck reflexes (Roberts, 1967) suggested that the function of the opposed action of the labyrinth and neck reflexes was to provide an effective stabilizing action of the limbs on the trunk, while permitting movements of the head with respect to the body. Changes in the position of the head leave the position of the limbs unchanged because the effect of a change in head tilt is offset by a change in the effect from the neck. The present results support this suggestion.

It follows that neck reflexes are as important as labyrinth reflexes in the maintenance of postural equilibrium and that both should be considered together as a single system.

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