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THE SAGITTAL VESTIBULOCOLLIC REFLEX AND ITS INTERACTION WITH NECK PROPRIOCEPTIVE AFFERENTS IN THE DECEREBRATE CAT

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SUMMARY

1. The sagittal vestibulocollic reflex (v.c.r.) evoked by nose-up, nose-down movements of the head, has been studied in the neck extensor muscle biventer cervicis in the decerebrate cat. Nose-down movements of the head increased, and nose-up movements decreased, electromyographic (e.m.g.) activity in the biventer cervicis muscles of the left and right sides.

2. At low frequencies of sinusoidal head movement (0·1–0·5 Hz), the gain of the sagittal v.c.r. was approximately constant, and e.m.g. modulation showed a phase lead of about 40 deg with respect to head position. At higher frequencies (2–5 Hz), v.c.r. gain increased at a rate close to 40 dB/decade, and phase lead increased to approach 150 deg. The relation between head movement and v.c.r. activity may be described by a transfer function containing two lead terms, with time constants of 0·07 and 0·23 s, and two lag terms, with time constants of 5·3 and 9·9 s.

3. When movements of the head were accompanied by stretching of the biventer cervicis muscles, the gain of the sagittal v.c.r. was increased threefold, at all frequencies between 0·1 and 5 Hz, with no substantial change in phase.

4. Sinusoidal stretching of the biventer cervicis muscles, with the head stationary, evoked a stretch reflex (cervicocollic reflex, c.c.r.) the behaviour of which was similar to that of a second-order system described by a transfer function containing two lead terms with time constants of 0·07 and 0·16 s. This difference in dynamics between the v.c.r. and the c.c.r. indicates that the lag terms in the v.c.r. transfer function reflect the frequency–response properties of the vestibular pathway to the biventer cervicis muscles, as they do not appear when the same muscles participate in the c.c.r.

5. The vectorial differences between the frequency–response of the sagittal v.c.r. with and without concomitant stretching of the biventer cervicis muscles is quantitatively similar to the frequency–response of the c.c.r. evoked by sinusoidal stretching. The inputs from the vestibular and stretch receptors thus appear to sum linearly to produce the increase in v.c.r. gain, at least over the frequency range 0·1–1 Hz.

6. Since most head movements, and all voluntary head movements, involve a rotation of the head in relation to the neck, the potentiation of the gain of the v.c.r. by afferents from stretch receptors (presumably muscle spindles) in the neck muscles is an important factor in the normal reflex stabilization of head position.

INTRODUCTION

Vestibulocollic reflexes (v.c.r.s) originate in the semicircular canal and macular receptors of the inner ear, and act on the extensor muscles of the neck. They play an important role in the reflex stabilization of head position by resisting and counteracting involuntary head movements. There is extensive anatomical and electrophysiological evidence for pathways from the vestibular receptors to the cervical spinal cord, via the vestibular nuclei and reticular formation of the brain stem (for reviews see Wilson & Peterson, 1978; Wilson & Melville Jones, 1979). Recently, Bilotto, Goldberg, Peterson & Wilson (1982) have made quantitative measurements of v.c.r. activity evoked by sinusoidal head movements in the horizontal plane, over a wide range of frequencies (0·05–5 Hz) within the normal physiological range. Other studies of the horizontal v.c.r. using linear systems analysis techniques have employed natural vestibular stimulation over a limited frequency range (Berthoz & Anderson, 1971; Ezure & Sasaki, 1978), or sinusoidal polarization of the ampullary nerves by amplitude-modulated current (Wilson, Peterson, Fukushima, Hirai & Uchino, 1979). These studies have shown that electromyographic (e.m.g.) activity in the neck muscles is modulated in phase with head position at low frequencies of head movement, while at higher frequencies e.m.g. activity is more closely related to the angular acceleration of the head rather than actual head position (Bilotto *et al.* 1982). The afferent input signal from the horizontal semicircular canals is related to the angular velocity of the head over this frequency range (Wilson & Melville Jones, 1979; Tomko, Peterka, Schor & O'Leary, 1981). The horizontal v.c.r. can therefore be described as a first-order lag-lead system, which integrates the afferent input signal at low frequencies to provide a motor output proportional to head position, and differentiates the afferent signal at higher frequencies to give an output related to angular acceleration.

The aim of the experiments described here was to investigate the properties of the sagittal v.c.r. evoked by nose-up, nose-down movements of the head, which have not so far been studied in any detail. Head movements in the sagittal plane stimulate the macular receptors of the utricle and saccule, as well as afferents from the anterior and posterior semicircular canals (Wilson & Melville-Jones, 1979). A further aim of these experiments was to examine the interaction of the sagittal v.c.r. with afferent input from proprioceptors in the neck. Since all voluntary head movements, and most imposed head movements, involve a rotation of the head in relation to the neck, vestibulocollic reflexes are frequently accompanied by cervicocollic reflexes (c.c.r.) arising in cervical proprioceptors. The main source of proprioceptive input for the c.c.r. would appear to be stretch receptors in the neck muscles, as there are few, if any, receptors similar to joint receptors in the upper cervical joints (Richmond & Bakker, 1982). Ezure, Sasaki, Uchino & Wilson (1976, 1978) have shown that deafferentation of the cervical spinal cord reduces the over-all gain of the horizontal v.c.r., and have proposed that muscle spindle afferents from the neck muscles play an important role in the regulation of v.c.r. activity. This proposal has been investigated in the present experiments. A preliminary report of these results has appeared (Dutia, 1984).

METHODS

Experiments were carried out on sixteen adult male cats weighing 1·6–2·5 kg. Under halothane–nitrous oxide anaesthesia, the left femoral artery and vein and the trachea were cannulated, and the carotid arteries ligated. The animals were decerebrated by a section through the superior colliculi, and the brain rostral to the section was removed by suction. Arterial blood pressure was continuously monitored, and maintained above 100 mmHg, if necessary, by slow I.V. infusion of metaraminol tartrate (Aramine, Merck, Sharp and Dohme Ltd., 100 μg/ml in 5 % dextrose saline). Body temperature was maintained at 37–38 °C with the aid of a homoeothermic blanket. The animals developed symmetrical decerebrate rigidity after withdrawal of the halothane mixture, and breathed without assistance. Recording of vestibulocollic reflexes did not begin for at least 2 h after decerebration.

The head of the animal was fixed in a head-holder which was attached to a d.c. printed-circuit motor (G16M4, Printed Motors Ltd., Bordon, Hants) via a steel–PTFE bearing. The body was fixed in a prone position in a rigid metal frame by spinal clamps at L7 and T1. The motor was positioned so as to produce nose-up, nose-down movements of the head in the sagittal plane, with the axis of rotation passing transversely through the atlanto-occipital joint. The mean head position was adjusted to be 12 deg nose down with respect to earth horizontal. Sinusoidal wave forms at frequencies between 0·1 and 5 Hz were provided to the motor position–servo controller by a function generator. The fidelity of the performance of the motor and head-holder assembly was measured using an accelerometer fixed to the head-holder. Harmonic distortion of the actual head movement was less than 3 % at 0·7 Hz, and less than 14 % at 5 Hz, for the range of amplitudes used in these experiments.

The dorsal and lateral muscles of the neck were exposed as far as the T1 vertebra, and their rostral ends were detached from the skull. The biventer cervicis muscles of the left and right sides were exposed by reflecting the splenius muscles, and the nerves to splenius and the greater auricular nerves were cut bilaterally. The biventer cervicis muscles were carefully separated down the mid line, freed of connective tissue and attached to a rigid bar by means of stout threads (2/0) stitched into their rostral terminations. The length of the muscles was adjusted to be the same as that before detachment from the skull with the head in its mean position (12 deg nose down). The soft tissues around the atlanto-occipital joint and on the dorsal surface of the C1 vertebra were scraped away, so as to remove possible sources of proprioceptive input from this joint which might be stimulated during movements of the head. Once all of the dorsal and lateral muscles of the neck were disconnected from the skull, and the axis of rotation correctly positioned through the atlanto-occipital joint, sagittal head movements of 10–12 deg amplitude did not produce detectable movements of the vertebrae below C1. Thus, movements of the head only stimulated the vestibular receptors of the inner ear, without stimulation of neck proprioceptors. This experimental arrangement is similar to that described in detail by Lindsay, Roberts & Rosenberg (1976), modified so as to allow sagittal head movements while preserving intact the innervation of the biventer cervicis muscles. In two experiments, the dorsal roots of the C1 spinal nerves were exposed bilaterally and crushed (cf. Lindsay *et al.* 1976). Since the results from these experiments did not differ from those in which the C1 nerves were intact, this procedure was not carried out routinely. In bilaterally labyrinthectomized animals, movements of the head did not evoke reflex responses in the neck muscles, confirming that these responses arose in the vestibular receptors and were not due to stimulation of cervical proprioceptors (Dutia & Myles, 1984).

The exposed tissues were coated with a mixture of Vaseline and paraffin to prevent dessication. The surface temperature of the exposed muscles of the neck was monitored intermittently and maintained at 37–39 °C by radiant heat. Bipolar silver ball electrodes (diameter *ca.* 1 mm) were stitched onto the surface of the biventer cervicis muscles of the left and right sides, using fine (6/0) thread. The electrode pair on each muscle was separated by 7–10 mm, usually with one electrode on either side of the second tendinous inscription. The compound e.m.g. thus recorded was differentially amplified, filtered (80–1000 Hz), full-wave rectified and then digitized by a Cromemco System Three microcomputer. The e.m.g. activity in the biventer cervicis muscles was averaged during 3–120 cycles of sinusoidal head movement at different frequencies between 0·1 and 5 Hz. For each frequency, the cycle period was divided into either 256, or the largest possible integer less than 256, bins. The minimum number of bins per cycle was 100. The rectified e.m.g. activity in the left and right biventer cervicis muscles was sampled at 4 kHz via two 8-bit analog-to-digital channels, and numerically integrated over the duration of each bin in the cycle. A third 8-bit analog input channel recorded actual head position.

For analysis, the number of bins in the cycle was normalized to 256 by scaling. The integrated e.m.g. activity was divided by the number of cycles of sinusoidal head movement presented, to give a cycle-average of e.m.g. modulation (see Fig. 1, for examples). The amplitude and phase of e.m.g. modulation at the same frequency as the frequency of head movement were obtained by Fourier analysis of the averaged e.m.g. data. Phase angle was measured with respect to the maximum nose-down position of the head. The gain of the vestibulocollic reflex was calculated as the percentage modulation of the mean e.m.g. activity per degree of head movement (Bilotto *et al.* 1982), and expressed in dB (0 dB = 1 % modulation/deg). The d.c. term in the Fourier transform was used as the mean e.m.g. level. We chose to calculate gain with respect to head position rather than acceleration as for the horizontal v.c.r. (Ezure & Sasaki, 1978; Bilotto *et al.* 1982), since vestibular stimulation in the sagittal v.c.r. is not limited to the semicircular canals alone (cf. Schor & Miller, 1981). The ratio of the amplitude of e.m.g. modulation to the second harmonic in the e.m.g. signal was taken to be a measure of harmonic distortion, and was greater than 2:1 in acceptable data. The signal-to-noise ratio was measured as the ratio of the amplitude of e.m.g. modulation to the r.m.s. amplitude of the remaining frequency components above the second harmonic, and was typically greater than 1·5 in acceptable data.

In some experiments, reflex modulation of e.m.g. activity was studied with the biventer cervicis muscles still attached to the skull, to compare the reflex response to combined vestibular and cervical afferent input. In these experiments, the splenius muscles were detached from the skull and denervated in the normal way, but the remaining muscles of the neck, and the innervation of the C1 joint, were intact. In two experiments, the biventer cervicis muscles were attached to a small torque motor and stretched sinusoidally while the head remained stationary. Data from these experiments were analysed in the same way, except that the gain was calculated as the percentage modulation of background activity per millimetre stretch of the muscle, and phase was measured with respect to the maximum extended position of the muscle.

RESULTS

The sagittal v.c.r.

Nose-down movements of the head increased, and nose-up movements decreased, e.m.g. activity in the biventer cervicis muscles of the left and right sides. Typical records, obtained by averaging the rectified e.m.g. over 3–100 cycles of sinusoidal head movement, are illustrated in Fig. 1. An example of simultaneously averaged activity in the left and right muscles during head movement at a frequency of 1 Hz is shown in Fig. 1*A*. Fig. 1*B* shows the response of the left biventer cervicis muscle in the same experiment to vestibular stimulation at various frequencies. In order to show the gain of the reflex response at each frequency, the averaged records have been normalized with respect to the actual amplitude of head movement employed. The sinusoids superimposed on the averaged records were obtained by Fourier analysis of the data, and represent the amplitude and phase of e.m.g. modulation at the same frequency as the movement of the head.

At all frequencies of head movement the muscles of the left and right sides were activated in phase with each other, and were thus used synergistically (Fig. 1*A*). This is in contrast to the reciprocal, antagonistic pattern of activation of the same muscles studied by others in the horizontal v.c.r. (Ezure & Sasaki, 1978; Wilson *et al.* 1979; Bilotto *et al.* 1982) and in the v.c.r. evoked by roll tilt (Schor & Miller, 1981).

In five preliminary experiments, we established that in the sagittal v.c.r., as in the horizontal v.c.r. (Ezure & Sasaki, 1978), the amplitude of e.m.g. modulation evoked by a given head movement was dependent on the mean ('background') level of e.m.g. activity, by comparing the reflex response to head movement with the biventer cervicis muscles held at several different lengths. In order to allow comparison between muscles and to compensate for variation in the mean level of e.m.g. activity in the same muscle, modulation amplitude was normalized by expressing it as a percentage of the mean activity, as done by others (see Methods; Bilotto *et al.* 1982). In these preliminary experiments, we also established that the amplitude of reflex response was related linearly to the amplitude of head movement, by measuring the gain of the v.c.r. during head movements of varying amplitudes at a given frequency. The amplitudes used were 3–10 deg peak-to-peak at frequencies between 0·1 and 1 Hz, and 1–5 deg peak-to-peak at 2 and 3 Hz. The values of v.c.r. gain obtained for each frequency were not dependent on the amplitude of head movement, except for amplitudes larger than 3 deg at 2 and 3 Hz when the averaged e.m.g. modulation became non-sinusoidal and gain decreased. Subsequent experiments were therefore carried out in the linear range of the sagittal v.c.r., using head movements of between 1 and 2·5 deg at frequencies above 2 Hz, and rejecting averaged data which appeared non-sinusoidal on visual examination or showed harmonic distortion greater than 50 %.

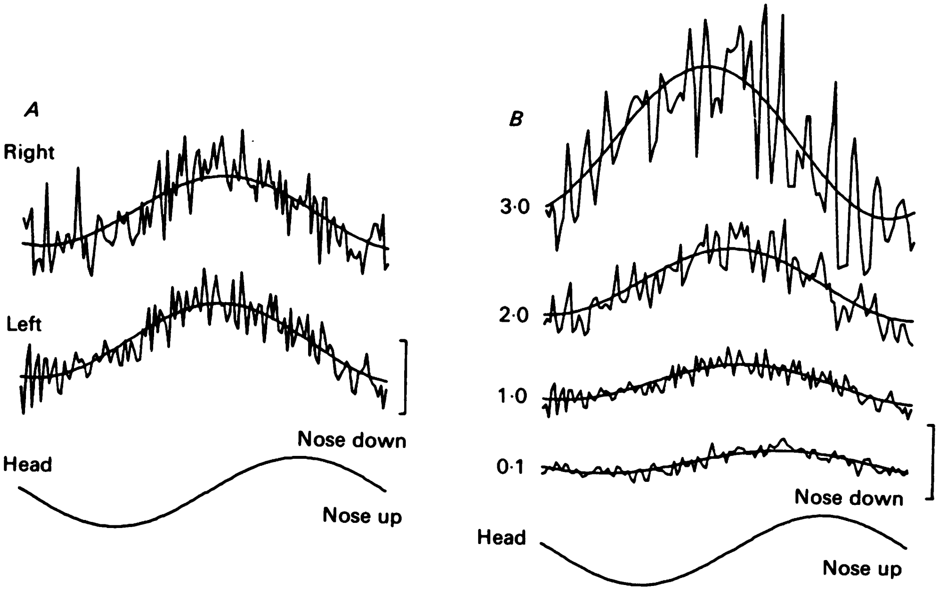

Fig. 1. Averaged rectified e.m.g. activity in biventer cervicis during sinusoidal head movements in the sagittal plane. *A*, simultaneously averaged e.m.g. records from the muscles of the left and right sides, over 25 cycles of head movement at 1 Hz. Amplitude calibration: 5 μV/cycle.deg of head movement. *B*, averaged records from the left muscle in the same experiment as *A*, during head movement at 0·1, 1·0, 2·0 and 3·0 Hz. Amplitude calibration: 10 μV/cycle.deg.

The gain and phase of the reflex response varied with the frequency of head movement, as illustrated in Fig. 1*B*. At low frequencies (0·1 Hz, Fig. 1*B*) the reflex gain was relatively small, and the point of maximum e.m.g. activity was close to the maximum nose-down position of the head. However, even at this frequency of head movement the reflex modulation of e.m.g. activity showed a significant phase lead with respect to head position, of around 40 deg. At higher frequencies (1, 2 and 3 Hz, Fig. 1*B*) the gain of the v.c.r. increased, and the point of maximum e.m.g. activity occurred progressively earlier in the cycle. In the example shown in Fig. 1*B*, reflex gain increased from 3·6 %/deg (11·1 dB) at 0·1 Hz to 38·8 %/deg (31·8 dB) at 3 Hz, while phase lead increased from 43 deg at 0·1 Hz to 122 deg at 3 Hz. At higher frequencies gain increased further to reach 118·5 %/deg (41·5 dB) at 5 Hz, and phase lead also increased reaching 148 deg at 5 Hz.

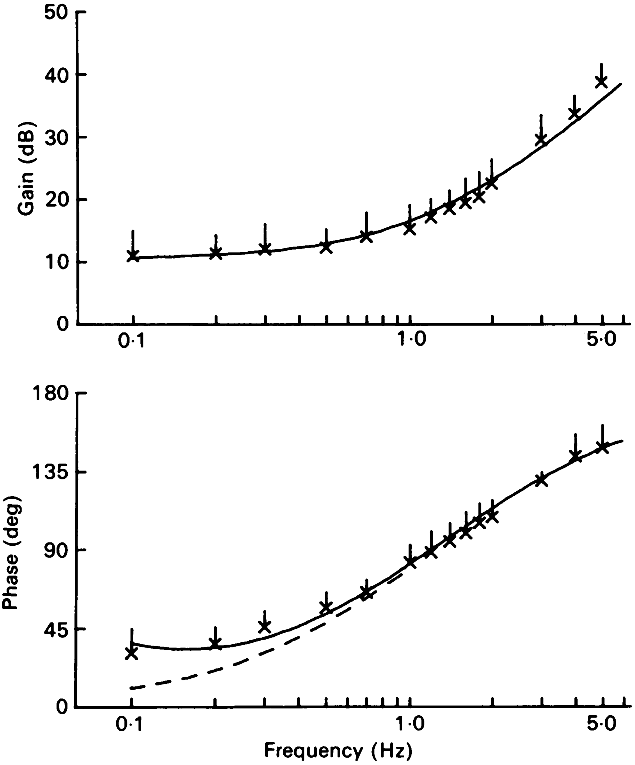

Fig. 2. Bode plot of gain and phase of the sagittal vestibulocollic reflex plotted against frequency of head movement. In this and following Figures, data shown are mean values (+1 S.D.). Continuous curve represents the transfer function shown in eqn. (1). Dashed line in phase plot represents the predicted behaviour of a pure second-order system (see text).

The sagittal v.c.r. was studied in detail over the frequency range 0·1–5 Hz in eighteen biventer cervicis muscles in nine cats. The frequency dependence of e.m.g. gain and phase lead was in each case similar to that shown in Fig. 1*B*. The reflex response of the muscles to various frequencies of head movement was reproducible for at least 7 h after the start of recording, and the values of phase lead and gain were quantitatively similar between animals. Mean values of gain and phase for the eighteen muscles were calculated for each frequency of head movement, and are plotted against frequency as a Bode diagram in Fig. 2. At frequencies below 0·5 Hz, the gain of the sagittal v.c.r. is approximately constant, and there is a phase lead of 30–50 deg with respect to head position. E.m.g. modulation at these frequencies is therefore nearly in phase with, and proportional to, the actual head displacement (e.g. 0·1 Hz, Fig. 1*B*). At frequencies of head movement between 2 and 5 Hz, however, v.c.r. gain increases rapidly, at approximately 40 dB/decade, and phase lead increases to reach nearly 150 deg. At these frequencies the maximum e.m.g. activity in each cycle becomes more nearly in phase with the maximum nose-down acceleration (e.g. 3 Hz, Fig. 1*B*), and is no longer proportional to the head displacement itself but instead to its second derivative, angular acceleration.

The dynamic properties of the sagittal v.c.r. over this frequency range are therefore similar to those of the horizontal v.c.r. (Bilotto *et al.* 1982), in that the reflex response progressively changes from being related to actual head position at low frequencies, to being related to angular acceleration at higher frequencies. Sagittal movements of the head stimulate not only semicircular canal afferents as in the horizontal v.c.r., but also afferents from the macular receptors. It is clear nevertheless from the similarity in dynamics between the two reflexes, that the sagittal v.c.r. may be described by a transfer function similar to that proposed for the horizontal v.c.r. by Ezure & Sasaki (1978) and Bilotto *et al.* (1982). Their transfer functions relating v.c.r. output to head movement contain two poles (lag terms, which integrate above their respective corner frequencies) with time constants of 5·0 and 6·7 s, and two zeros (lead terms, which differentiate above their respective corner frequencies) with time constants of 0·07 and 0·13 s (median values from Bilotto *et al.* 1982). The continuous lines in Fig. 2 represent the transfer function,

$$H(s) = G(1+t_1 s)(1+t_2 s)\frac{t_3 s}{(1+t_3 s)}\frac{t_4 s}{(1+t_4 s)}, \tag{1}$$

where the gain constant, $G = 11{\cdot}0$ dB, and the time constants, $t_1 = 0{\cdot}07$ s, $t_2 = 0{\cdot}23$ s, $t_3 = 5{\cdot}3$ s and $t_4 = 9{\cdot}9$ s.

This function differs from that proposed by Bilotto *et al.* (1982) only in the choice of angular displacement, rather than acceleration, as the input variable in our analysis. The values for the time constants in the above equation were obtained using an interactive curve-fitting program, and provide the best fit as judged by eye to the gain and phase data in Fig. 2. The terms containing t_1 and t_2, with time constants corresponding to corner frequencies of 2·2 and 0·7 Hz respectively, are the two zeros (or lead terms), which between them account for the second-order increase in v.c.r. gain and phase lead at frequencies above 1 Hz. The separation between the two zeros is required in order to fit the slope of the phase curve in the middle frequencies. The terms containing t_3 and t_4 are the two poles (or lag terms), with time constants corresponding to corner frequencies of 0·03 and 0·016 Hz respectively. These terms are required to account for the phase behaviour at frequencies below 0·3 Hz, which deviates from that of a pure second-order system modelled by the two lead terms alone (Fig. 2, dashed line).

Interaction between the v.c.r. and cervical afferents

The interaction of the sagittal v.c.r. with the c.c.r. was examined in twelve muscles from six animals (of the eighteen muscles from nine animals whose results are shown in Fig. 2). The gain and phase of the reflex response were first determined with the biventer cervicis muscles still attached to the skull so that they were stretched as the head moved downwards (v.c.r. + c.c.r.), and then redetermined when the muscles were detached from the skull and held fixed at their resting lengths (v.c.r. alone, the results of these latter determinations being included in Fig. 2). In the absence of head movements, e.m.g. activity in the biventer cervicis muscles after detachment from the skull was within 20 % of that while they were still attached.

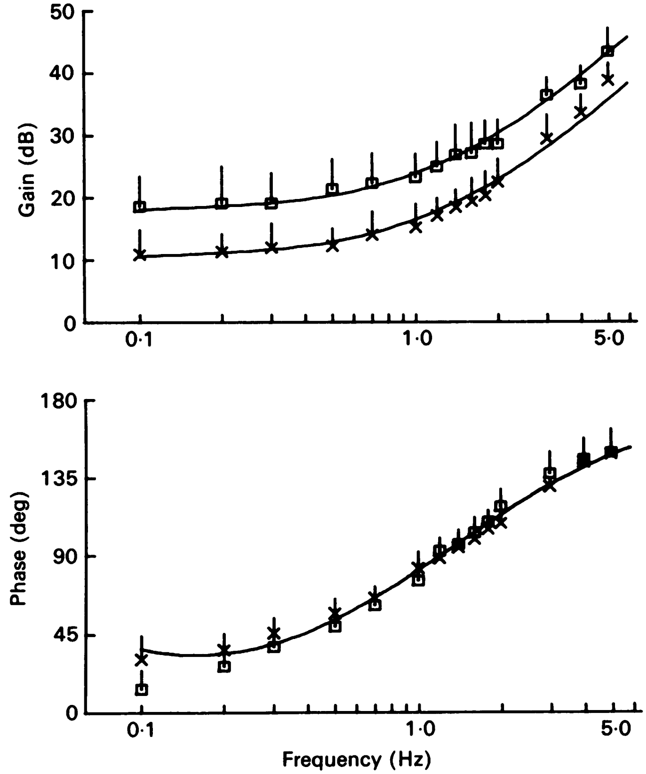

Fig. 3. Gain and phase of the sagittal v.c.r. with (☐) and without (×) concomitant stretching of the biventer cervicis muscles. Continuous lines represent the transfer function in eqn. (1), with $G = 19$ dB (☐), and $G = 11$ dB (×).

Fig. 3 shows the mean values of gain and phase of the reflex response with the biventer cervicis muscles still attached to the skull (☐, v.c.r. + c.c.r.) and with the muscles at a fixed length (× , v.c.r. alone, same data as in Fig. 2). It is clear from Fig. 3 that when head movements are accompanied by stretching of the muscles, the gain of the combined reflex response is higher than that of the v.c.r. alone, by about 10 dB at all frequencies between 0·1 and 5 Hz. This 10 dB gain increase represents a threefold increase in amplitude of the reflex response to head movement, when the vestibular input is accompanied by input from stretch receptors in the biventer cervicis muscles. The phase behaviour of the combined v.c.r. + c.c.r. reflex is very similar to that of the v.c.r. at all frequencies, except at frequencies below 0·2 Hz where the combined reflex response appears to show a smaller phase lead than the v.c.r. (Fig. 3). Interaction between the v.c.r. and the c.c.r. evoked by muscle stretching therefore causes an increase in the gain of the reflex response at all frequencies of head movement, with no substantial change in phase over a wide frequency range.

The cervical afferents most likely to be stimulated during movements of the head are those from muscle spindles present in large numbers in the muscles of the neck (Richmond & Bakker, 1982). In four muscles from two further animals, the frequency–response characteristics of the stretch reflex evoked by sinusoidal stretching of the biventer cervicis muscles were determined, using a small torque motor to apply 2–3 mm amplitude stretches to the muscles at frequencies between 0·1 and 5 Hz while the head remained stationary (see Methods). The mean values of gain (% modulation/mm stretch) and phase of the stretch-evoked c.c.r. from these experiments are plotted against frequency of head movement in Fig. 4 (◇). The stretch-evoked c.c.r. like the v.c.r. shows a progressive phase advance and gain increase at frequencies above 1 Hz. However, the c.c.r. differs from the v.c.r. in its behaviour at low frequencies (below 0·5 Hz), in that the phase advance shown at these frequencies by the v.c.r., and modelled by the two lag terms in its transfer function, is not shown by the c.c.r. The phase behaviour of the c.c.r. is therefore much closer to the predicted behaviour of a pure second-order system, with a transfer function containing only the two lead terms,

$$H(s) = G(1+t_1 s)(1+t_2 s). \tag{2}$$

The continuous curve plotted through the c.c.r. data in Fig. 4 represents the above function with $G = 21$ dB, $t_1 = 0{\cdot}16$ s and $t_2 = 0{\cdot}07$ s. This difference between the v.c.r. and the c.c.r. is significant, in that it implies that the process which causes the phase advance at low frequencies in the v.c.r. lies within the vestibular pathway to the biventer cervicis muscles, and is not seen when the same muscles participate in the c.c.r.

A quantitative estimate of the contribution from the c.c.r. to the combined reflex response (v.c.r. + c.c.r. in Fig. 3) was obtained by performing a vectorial subtraction of the v.c.r.-alone frequency response from that of the combined reflex, on the assumption that the interaction between the vestibular and cervical afferent inputs is linear. The estimated gain and phase of the input from cervical afferents at each frequency calculated in this way are also plotted in Fig. 4 (+), and may be compared with the actual frequency–response characteristics of the c.c.r. evoked by muscle stretching (◇).

The curve drawn through the estimated values of gain represents the same function as for the measured c.c.r. (eqn. (2)) except that the gain constant (G) used is lower (15 dB). The phase of the estimated cervical contribution closely follows that of the actual c.c.r. at frequencies up to 1 Hz, above which it deviates somewhat from the measured behaviour of the c.c.r. There is a difference in absolute gain between the estimated and measured c.c.r., as gain is calculated with respect to head movement in one case and with respect to muscle stretch in the other: rotation of the head about the atlanto-occipital joint stretched the biventer cervicis muscles unevenly, with the rostral ends being more extended than the middle and caudal regions, while the stretch applied by the torque motor was more nearly along the longitudinal axis of the muscle and was transmitted with less attenuation to all regions of the muscle. The values of gain measured for the stretch-evoked c.c.r. (Fig. 4, ◇) are therefore likely to be over-estimates. It is clear nevertheless from Fig. 4, that the measured properties of the c.c.r. are similar to the estimated properties of the cervical input in the combined v.c.r. + c.c.r. response (Fig. 3). The potentiation of the gain of the sagittal v.c.r. by its interaction with the c.c.r. is therefore likely to be due to the afferent input from muscle stretch receptors, presumably muscle spindles, in the muscles of the neck.

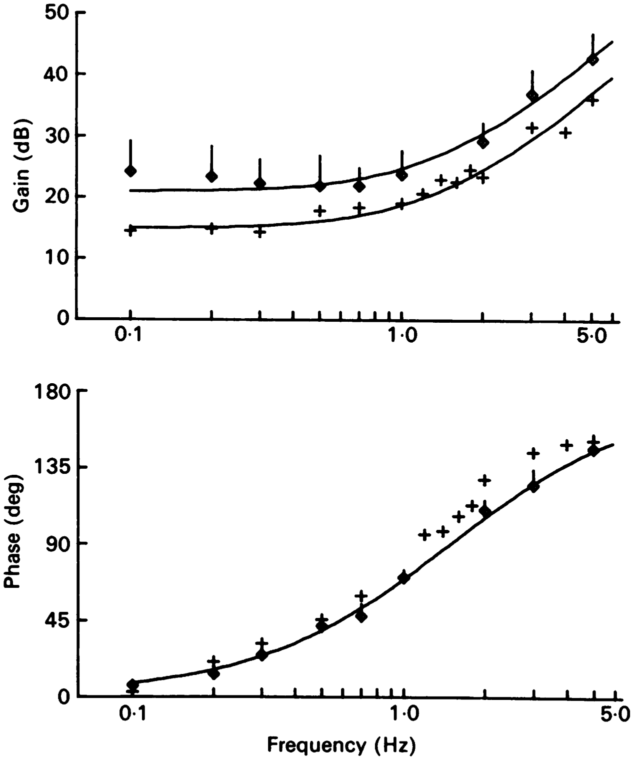

Fig. 4. Gain and phase of the cervicocollic reflex response to sinusoidal stretching of the biventer cervicis muscles with the head stationary (◇), compared with the vectorial difference between the v.c.r. + c.c.r. and v.c.r.-alone data shown in Fig. 3 (+).

DISCUSSION

Our results extend the previous description of vestibular reflexes acting on the muscles of the neck (Berthoz & Anderson, 1971; Ezure & Sasaki, 1978; Schor & Miller, 1981; Bilotto *et al.* 1982), to include the vestibulocollic reflex evoked by head movements in the sagittal plane (the sagittal v.c.r.). Like the horizontal v.c.r. (Bilotto *et al.* 1982) and the v.c.r. evoked by roll tilt (Schor & Miller, 1981), the sagittal v.c.r. is a compensatory mechanism which contributes to the maintenance of head stability, by counteracting displacements of the head in the sagittal plane. Unlike the v.c.r. in the horizontal and roll planes, in which the muscles of the left and right sides are activated out of phase with each other, the sagittal v.c.r. evokes synergistic, bilaterally symmetric activity in the neck extensors. This is consistent with v.c.r. action in the other planes of head movement, as in each case the reflex acts to maintain head stability by activating those neck muscles most appropriate to resist the imposed head displacement. This synergistic action is consistent with the known short-latency projections from the anterior and posterior semicircular canal nerves to neck motoneurones (Wilson & Maeda, 1974), and the pattern of head movements evoked by electrical stimulation of canal afferents by implanted electrodes in the awake cat (Suzuki & Cohen, 1964).

In addition to afferents from these canals, sagittal movements of the head also stimulate the utricular and saccular receptors, which are sensitive to the orientation of the head with respect to gravity. Our results show that the frequency–response characteristics of the sagittal v.c.r., the inputs of which arise both in canal and macular receptors, do not differ greatly from those of the horizontal v.c.r. (Bilotto *et al.* 1982), the input of which arises only in the horizontal semicircular canals. This similarity in dynamics of the two reflexes presumably reflects their similarity in function, in the maintenance of head stability: both reflexes show increasing gain and phase advance at high frequencies, as may be expected in control systems operating on a load with significant inertia. It is interesting, however, that the actions of the two reflexes at low frequencies are also broadly similar. This implies that the tonic position-related afferent input from the macular receptors does not have a major part to play in the sagittal v.c.r., at least over the range of frequencies and amplitudes of head movement used in these experiments.

The frequency dependence of the sagittal v.c.r. may therefore be interpreted in a similar way to that of the horizontal v.c.r. (Bilotto *et al.* 1982), mainly in terms of the afferent inputs from the anterior and posterior semicircular canals and their central integration. It has been proposed (Bilotto *et al.* 1982) that one of the zeros and one of the poles (containing t_1 and t_3 respectively) in the transfer function of the horizontal v.c.r. are determined by the frequency–response characteristics of the afferent input from the horizontal semicircular canals (Tomko *et al.* 1981), while the remaining terms (containing t_2 and t_4) are determined by the properties of the central pathways mediating the v.c.r. Our values for the time constants t_1 and t_3 in the sagittal v.c.r. (0·07 and 5·3 s respectively) are very close to the values obtained by Bilotto *et al.* (1982) for the horizontal v.c.r. (0·07 and 5·0 s). This is compatible with the proposal that these time constants reflect the properties of the afferent input from the semicircular canals, the horizontal canals in the one case and the anterior and posterior canals in the other. The remaining time constants (t_2 and t_4) are, however, somewhat longer in the sagittal v.c.r. (0·23 and 9·9 s respectively) than in the horizontal v.c.r. (0·13 and 6·7 s). This implies that the frequency–response characteristics of the central pathways are different in the two reflexes, with the sagittal v.c.r. pathway having slightly lower corner frequencies (0·7 and 0·016 Hz) than the horizontal v.c.r. (1·2 and 0·023 Hz).

The longer time constants of the central pathways in the sagittal v.c.r. may be the result of an interaction between the inputs from the semicircular canals and the macular receptors, even though the macular afferent input is not sufficient to modify the phase behaviour of the v.c.r. at low frequencies. Stimulation of the saccular nerve evokes short-latency potentials in neck motoneurones (Wilson, Gacek, Maeda & Uchino, 1977), and utricular afferents do play an important role in the v.c.r. evoked by roll tilts, as shown by the reflex response to slow tilts (Berthoz & Anderson, 1971) and by experiments in 'canal-plugged' cats (Schor & Miller, 1981). Further experiments are required to extend the sagittal v.c.r. data to frequencies below 0·1 Hz, and establish the nature and extent of the contribution of macular afferents to the sagittal v.c.r.

Our results show that the phase behaviour of the c.c.r. evoked by sinusoidal stretching of the biventer cervicis muscles is similar to that of a simple second-order system, and unlike that of the v.c.r. which deviates from the predicted behaviour of a second-order system at low frequencies (Fig. 3). This indicates that the two lag terms in the transfer function of the v.c.r., which model this phase deviation, are indeed introduced by the vestibular pathway to the biventer cervicis muscles, and are not present when the same muscles participate in the c.c.r. Thus, our results provide experimental evidence in support of the proposal (Bilotto *et al.* 1982) that these lag terms are determined by the properties of the afferent input from the vestibular receptors and its central integration. The fact that the transfer function of the c.c.r. contains two lead terms similar to those in the v.c.r. suggests that, while one of the terms is determined by properties of the peripheral input (from semicircular canals in the v.c.r. and muscle stretch receptors in the c.c.r.), the other lead term may represent either a C.N.S. component which is shared by the two reflexes, or two separate C.N.S. elements with similar frequency–response characteristics.

The potentiation of the gain of the sagittal v.c.r. by input from cervical proprioceptors, as demonstrated in our experiments, is consistent with the finding of Ezure *et al.* (1976, 1978) that deafferentation of the cervical spinal cord reduces the over-all gain of the horizontal v.c.r. Our results show that the interaction between the vestibular and cervical proprioceptor inputs increases the reflex gain at all frequencies over the range 0·1–5 Hz. The fact that the properties of the stretch reflex correspond quite closely with the estimated properties of the cervical component of the combined v.c.r. + c.c.r. reflex (Fig. 4), indicates that the vestibular and stretch receptor inputs sum linearly to produce the combined reflex output, at least over the frequency range 0·1–1 Hz. Since most movements of the head are accompanied by changes in length of the muscles of the neck, the proprioceptive input from stretch receptors (presumably muscle spindles) in these muscles is an important factor regulating the head-stabilizing function of the vestibulocollic reflexes. Thus, inputs from cervical proprioceptors, which interact with vestibular reflexes in the control of limb posture (Lindsay *et al.* 1976), also have a significant role to play in the vestibular control of head position. However, while the vestibular and neck reflexes in the forelimb tend to cancel each other so as to allow the head to move freely on the trunk (Lindsay *et al.* 1976), their effects on the muscles of the neck are synergistic and additive, in a manner appropriate for the stabilization of the head on the neck.

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