VESTIBULAR-EVOKED POSTURAL REACTIONS IN MAN AND MODULATION OF TRANSMISSION IN SPINAL REFLEX PATHWAYS

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SUMMARY

1. The effects of galvanic stimulation of the vestibular apparatus (with electrodes on the mastoid processes) have been studied in standing human subjects. With the head turned to one side, subjects swayed towards the anode.

2. Forwards sway was preceded by electromyographic (EMG) activity in quadriceps and tibialis anterior muscles. Backwards sway was preceded by EMG activity in soleus and hamstring muscles.

3. Using the method of H reflex conditioning, forward sway was found to be preceded by inhibition of soleus motoneurones.

4. Interaction between the vestibular-evoked inhibition of soleus motoneurones preceding forwards sway and peripheral reflex inhibition was examined by a spatial facilitation method.

5. Interaction was found between vestibular-evoked inhibition and I a reciprocal, group I non-reciprocal and group I a–I a presynaptic inhibitory pathways. It is concluded that vestibular signals converge on spinal interneurones subserving these inhibitory actions.

6. A 'decoupling' of soleus motoneurones and soleus-coupled Renshaw cells was found in the period of soleus activation preceding backwards sway.

INTRODUCTION

Extensive work on experimental animals, notably the cat, has shown that motor pathways descending from the brain can control most, or possibly all, spinal machinery (Baldissera, Hultborn & Illert 1981). Experiments in man have succeeded in demonstrating some such descending actions during motor behaviour.

Most of the human studies have been restricted to simple voluntary movement (isometric contraction of muscle groups or isotonic tracking tasks) and the question remains whether patterns of descending control differ according to the particular motor task. Furthermore, many experiments have studied the control of spinal machinery during actual movement. Changed activity in spinal machinery is then generally ascribed to descending control, but could arise from altered sensory feedback consequent upon the movement (cf. Rossignol & Gauthier, 1980). We have attempted to extend study to postural reactions, where transmission in spinal machinery can be examined prior to actual movement.

Sway of a standing man, produced by anterior–posterior translation of the support platform, leads to stereotyped patterns of muscle activity in the lower limbs (Nashner, 1981). This would not constitute an ideal situation in which to study descending control of spinal machinery because the motor responses are initiated by movement, and sensory input from the limbs will be altered, alongside activation of the vestibular system. Some components of the sway response can, however, be elicited by activation of the vestibular apparatus alone. This can be achieved most simply by galvanic electrical stimulation (Njiokiktjien & Folkerts, 1971).

Current is passed between electrodes placed on the mastoid processes. If the head is turned to one side, the subject sways forwards or backwards, as the case may be, towards the anode. With the anode anterior this results from contraction of muscles at the front of the thigh and in the anterior crural region. With the head turned to the other side, or electrode polarity reversed, muscles at the back of the thigh and in the posterior crural region are active. This can be conceived of as the response to a false (electrical) sway signal (Lund & Broberg, 1983). We have studied transmission in spinal machinery during the early part of the response to vestibular stimulation, before overt movement occurs, in order to reveal any control from the vestibular system. A preliminary report of some of this work has been published (Iles & Pisini, 1987).

METHODS

Five neurologically normal adult subjects (21–41 years old) of both sexes (three male, two female) were studied with their informed consent. They are identified by initials in the figures.

The basic experimental procedure was to set up a test monosynaptic reflex (H reflex) in the soleus of the right leg of a standing subject. Transmission in various spinal pathways was assessed by comparison of test and conditioned reflexes. This was then repeated during electrical stimulation of the vestibular apparatus to look for evidence of vestibular control of transmission in those spinal pathways.

Electrical stimulation of the vestibular apparatus

Direct current was passed between silver–silver chloride electrodes placed over the mastoid processes. Electrodes were wrapped in gauze soaked in saline and the skin was coated with electrode jelly. The electrodes were conveniently held in place by a pair of audio headphones.

Constant current stimuli were provided by a Neurolog Stimulus Isolator (model NL 800, Digitimer Ltd). Stimulus amplitude ranged from 0·05 to 1 mA and was measured with an ammeter. Stimulus duration ranged from 50 ms to 1 s.

Subjects could usually feel the first three or four such stimuli by a tingling of the skin, but thereafter the stimulus could not be detected (though the resulting sway reactions were sometimes perceptible). The subjects kept their eyes closed and stood on a rigid surface (Hlavacha & Saling, 1986).

The test H reflex

Standard methods for eliciting and recording the soleus H reflex in a sitting subject (Iles & Roberts, 1987) were modified for use in the standing position.

The test stimulus (0·5 or 1 ms duration: Panizza, Nilsson & Hallett, 1989) was applied to the tibial nerve in the popliteal fossa with a ball electrode, held in place by an elastic strap around the knee and a rigid support pivoted from a shaft co-axial with the ankle joint. This permitted anterior–posterior sway to occur with minimal movement of the stimulating cathode. Sway was monitored as the rotation of this support. The stimulating anode was strapped to the lateral surface of the knee.

Recording electrodes were placed far distally to favour soleus responses (cf. Maryniak & Yaworski, 1987).

Activation of spinal inhibitory pathways

Four inhibitory actions on soleus motoneurones were investigated by conditioning of H reflexes.

Ia reciprocal inhibition. This was induced by electrical stimulation of the antagonist, common peroneal, nerve at the caput fibulae (Iles, 1986). Recording electrodes placed over the tibialis anterior muscle were used to monitor direct activation of motor units so that the strength of the peroneal nerve stimulation could be expressed in multiples of the motor threshold ($X\alpha$T). Constant voltage stimuli of $0.7-0.9$ $X\alpha$T were used. Motor threshold was checked regularly to ensure that no movement of the stimulating electrodes had occurred. The interval between conditioning and test stimuli was kept at the optimum for reciprocal inhibition for each subject (2–3 ms), determined by measurement of the inhibitory time curve.

Group I non-reciprocal inhibition. This was induced by electrical stimulation of the heteronymous medial gastrocnemius nerve. A second ball electrode mounted on the pivoting arm was placed on the leg 6–10 cm away (distal and medial) from the electrode over the tibial nerve. The anode was placed on the medial side of the knee. Constant voltage stimuli at $0.9-1.0$ $X\alpha$T were used at the optimum conditioning interval determined for each subject (2·0–2·7 ms) by measurement of the inhibitory time curve (Pierrot-Deseilligny, Morin, Bergego & Tankov, 1981).

Group Ia–Ia presynaptic inhibition. Presynaptic inhibition of the Ia afferents responsible for the soleus H reflex was elicited by mechanical activation of Ia afferents from biceps femoris muscle. A physiotherapy vibrator operating at 100 Hz and up to 1 mm peak-to-peak movement was held on the belly of biceps femoris ipsilateral to the test soleus. A pulse of vibration (three cycles) was applied, timed to end 100–200 ms before the test stimulus (cf. Iles & Roberts, 1987; see also Ashby, Stalberg, Winkler & Hunter, 1987).

Recurrent inhibition. We used the protocol described by Hultborn & Pierrot-Deseilligny (1979). A stimulus (S1) was applied to the tibial nerve inducing a reflex H1 which (orthodromically) activates soleus-coupled Renshaw cells and produces recurrent inhibition of soleus motoneurones. On some trials the S1 stimulus was followed (13 ms interval) by a stimulus (SM) supramaximal for motor fibres. Collision of action potentials occurs in the axons of motoneurones discharged in H1. Only these motoneurones are therefore capable of reflex activation by the SM stimulus yielding the H′ reflex. H′ has an amplitude less than or equal to H1. The amplitude of H′ depends upon the strength of recurrent inhibition produced by H1 and all other factors influencing motoneurone excitability. A reference reflex, H_{ref}, matched in size to H′ was used to monitor motoneurone excitability. Any differences in the behaviour of H′ and H_{ref} can be ascribed to changes in the strength of recurrent inhibition (see Hultborn & Pierrot-Deseilligny, 1979 for discussion).

Data analysis

Reflexes were induced at a maximum rate of 0·2 Hz; in some experiments the rate was reduced or varied randomly (between limits of 0·09 and 0·045 Hz). The action of vestibular stimulation, or of any of the spinal pathways was measured by recording test and conditioned reflexes in regular or random sequence. With the exception of the experiment illustrated in Fig. 2 where individual reflexes were measured, groups of sixty-four reflexes were averaged before measurement. These averages were repeated in order to estimate the standard error of the mean (see Iles & Roberts, 1987). Conditioning actions are expressed by dividing conditioned by test reflex amplitude (C/T%).

Interaction between vestibular stimulation and spinal inhibitory pathways was investigated by a method of spatial facilitation. Four groups of reflexes were averaged: test (T), test preceded by vestibular stimulation (T_v), conditioned by a spinal inhibitory pathway (C) and conditioned by both the spinal inhibitory pathway and vestibular stimulation (C_v). Transmission in the spinal inhibitory pathway in the presence and the absence of vestibular stimulation was then compared by calculating $C/T - C_v/T_v$%. Positive values indicate spatial facilitation. Lack of interaction will lead to a zero value.

Subjects could tolerate recording sessions lasting 1–1·5 h in which time some seven to ten data points of the type illustrated in Fig. 5 might be obtained.
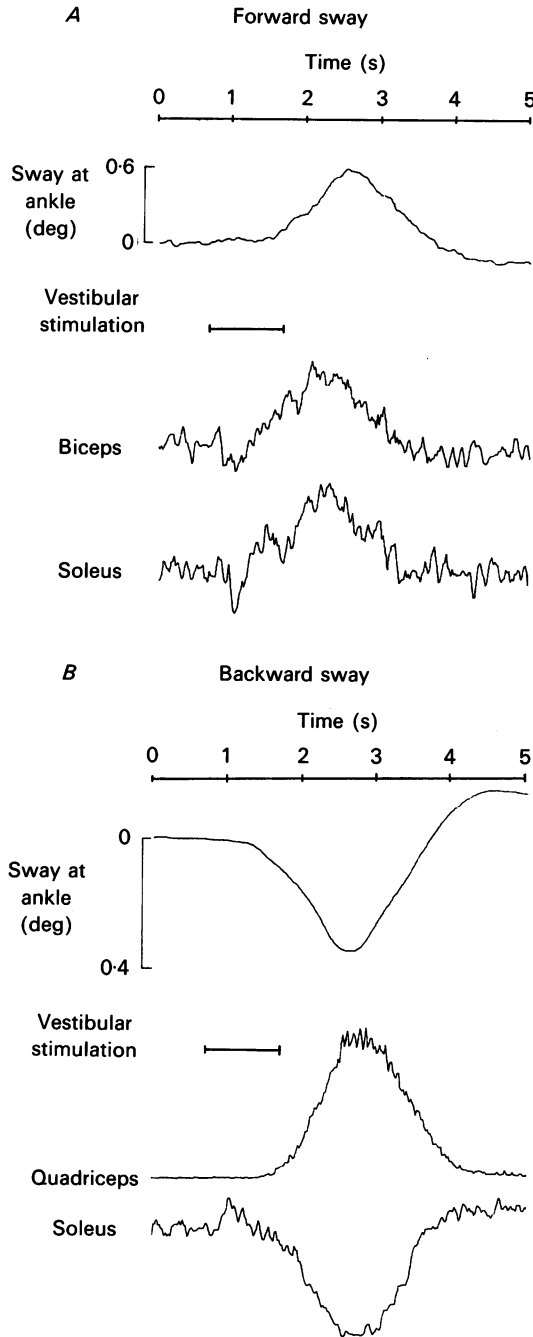
Fig. 1. The effects of galvanic stimulation of the vestibular apparatus on ankle angle and lower limb EMG. Vestibular stimulation commenced 0·7 s after the start of each record and had a duration of 1 s. EMG responses were rectified and integrated (but the records are not calibrated); 256 individual responses were averaged to yield each record. A, subject L. C., forward sway condition. B, subject J. V. P., backward sway condition wearing a loaded rucksack to enhance quadriceps activity. Identical patterns of response were obtained from the other three subjects.

Actions of vestibular stimulation on motoneurones of the lower limb

Electromyogram (EMG) recordings

A preliminary analysis of the response to vestibular stimulation was made by recording the EMG from flexor and extensor muscles operating at both the knee and ankle joints. The EMG were full-wave rectified and integrated before averaging. A randomly varied cycle duration for vestibular stimulation (11–22 s) was used to avoid any coincidence with the resonant frequency of the body behaving as an inverted pendulum.

Forward sway. With the head and trunk turned to face over the right shoulder and the stimulating anode placed over the left mastoid process, the subjects swayed forward in response to vestibular stimulation. The earliest clear EMG response to the stimulus consisted of a reduction of on-going activity in both soleus and biceps femoris muscles (Fig. 1A). In subjects wearing a rucksack containing 20 kg of load, resting activity in soleus was reduced, the reduction was smaller, and an excitation of tibialis anterior and quadriceps was observed. These changes in muscle activity commenced before any movement about the ankle joint was detected. The changes are presumably responsible in part for the forward sway beginning 600–800 ms after the start of the stimulus.

The actual sway was accompanied by the converse pattern of muscle activity: increases in soleus and biceps, reduction of any pre-existing activity in tibialis anterior and quadriceps. Identical responses were obtained with the head turned to face over the left shoulder and an anode over the right mastoid process. We will describe either situation as the 'forward sway' condition of stimulation and pattern of response.

Backward sway. With the direction of current flow between the mastoid processes reversed (or head rotated to the opposite side) subjects swayed backwards. The earliest muscle response to the stimulus consisted of an increased activity in soleus and biceps femoris. Sway commenced with a latency of 600–800 ms and was accompanied by a reduction in soleus (Fig. 1B) and biceps activities, and an increase in tibialis anterior and quadriceps activities. Strong bursts of EMG were seen in tibialis anterior and quadriceps on those trials in which the subjects came close to overbalancing backwards (cf. Allum & Pfaltz, 1985). The pattern of response was identical with both combinations of head rotation and current direction leading to posterior location of the anode. We will describe either situation as the 'backward sway' condition of stimulation and pattern of response.

Soleus H reflex testing

In order to obtain better temporal detail and more reliable information for inhibitory actions on soleus, an analysis was made by conditioning H reflexes.

Variability in the reflex. The reliability of the experimental method was investigated in one subject. The amplitudes of 256 successive H reflexes induced while standing are illustrated in Fig. 2. During the second and fourth quarters of the recording period the reflexes were conditioned by vestibular stimulation (forwards sway condition).

There is considerable variability in test reflex amplitude during standing. The variability is about three times greater than in the same subject sitting and performing a small voluntary contraction (compare with Fig. 1*A* in Iles & Roberts, 1987; the coefficient of variation of reflex amplitude was 0·28 for standing, 0·1 for
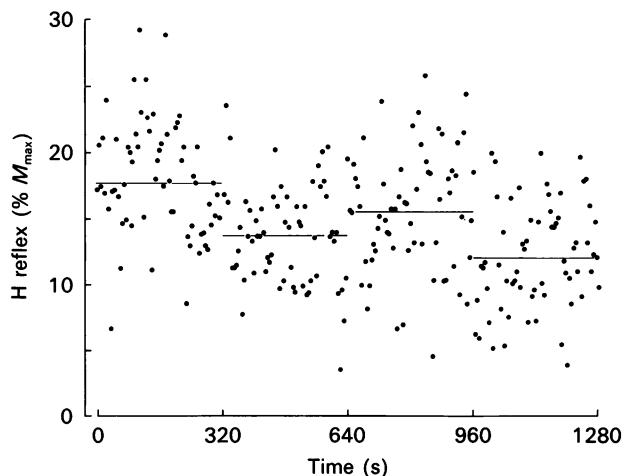

Fig. 2. The effect of galvanic stimulation of the vestibular apparatus on the soleus H reflex (subject J. F. I., forward sway condition). The peak amplitude of 256 successive reflexes induced at 0·2 Hz are plotted as a percentage of the maximal direct motor response (M_{max}) that could be recorded from the muscle. In the second and fourth quarters of the recording period vestibular stimulation was applied (220 ms conditioning interval). The horizontal lines give the mean amplitude in each quarter.

sitting). In consequence of this variability large numbers of reflexes had to be averaged to detect statistically significant conditioning actions. In all other experiments groups of sixty-four reflexes were averaged before measurement. Despite the variability it can be seen from Fig. 2 that vestibular stimulation inhibited the reflex (as would be anticipated from the results of EMG recording – Fig. 1*A*). The inhibition is superimposed on a slow drift in reflex amplitude (no adjustments were made to the test stimulus or electrodes in this experiment). In subsequent experiments the effects of drift were minimized by interpolating conditioned reflexes between test reflexes (in regular or random order) and by readjustment of stimulus parameters after each group of reflexes was averaged.

Conditioning during forward sway. The conditioning action of vestibular stimu-lation was expressed as the ratio of conditioned to test reflex amplitude using intervals between the start of the vestibular stimulus and the test stimulus from 30 to 1600 ms (Fig. 3*A*). An inhibitory action was present for intervals between 150 and 500 ms (in different subjects), corresponding to the period of reduced EMG activity from around 200–600 ms (Fig. 1*A*). At longer conditioning intervals excitation was found; but whereas in the EMG recording a single period of excitation was evident, the H reflex method suggests that there may be an early period maximal at about 700 ms, and a later period around 1200 ms in the two shorter subjects and beyond 1500 ms in the taller ones. In all subjects there was evidence of a very small facilitation of soleus at 80–100 ms.

Conditioning during backward sway. The time course of H reflex conditioning during backward sway (Fig. 3*B*) was the reverse of that for forward sway. An excitation of soleus was present between 150 and 500 ms corresponding to the increased EMG activity from around 200–600 ms (Fig. 1*B*). At longer conditioning
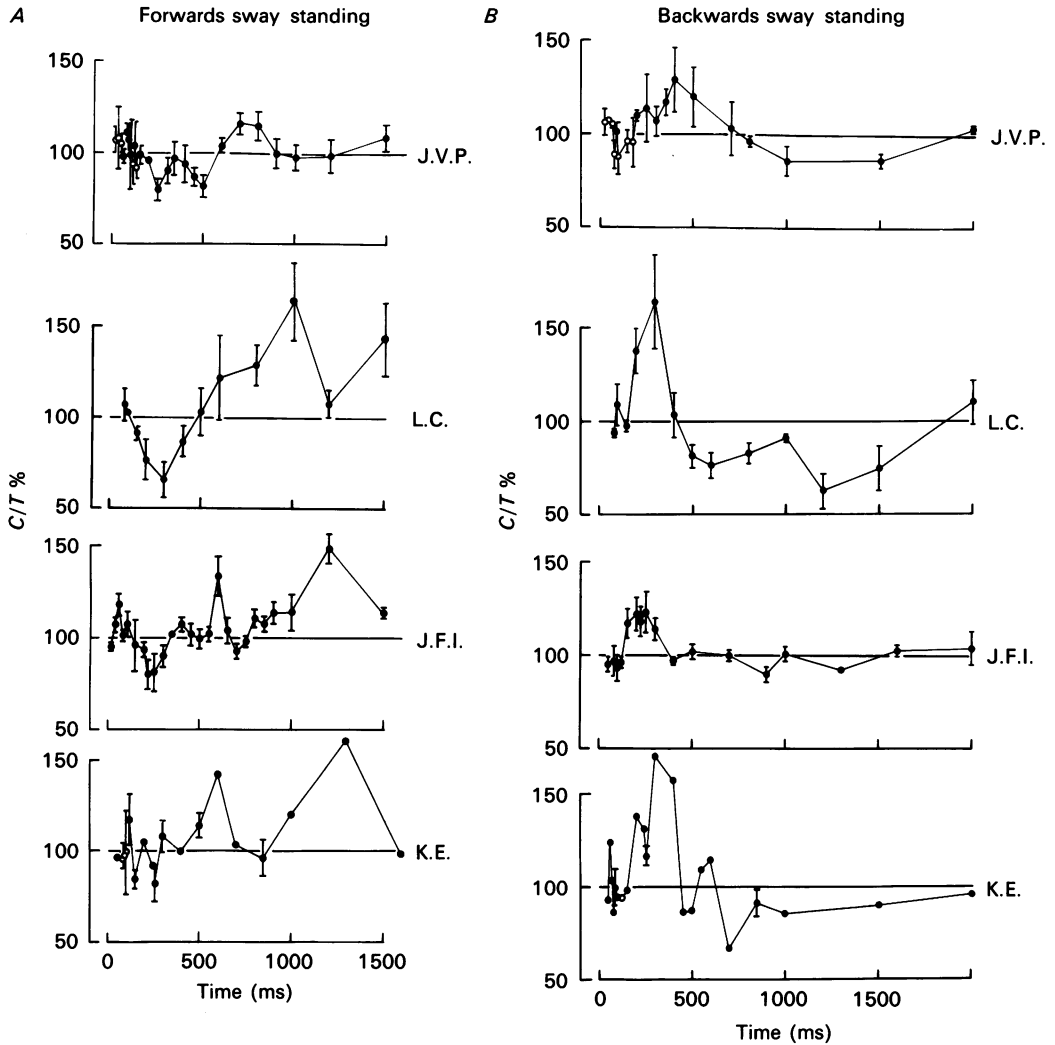

Fig. 3. Time course of soleus H reflex conditioning by galvanic stimulation of the vestibular apparatus in four subjects. Data from the subjects are arranged in size order (J.V.P. tallest, K.E. shortest). Vestibular stimulation commenced at zero time and had a duration of 1 s. Conditioning action is expressed in the form conditioned reflex as a percentage of test reflex amplitude (*C/T*%, ordinate, 100% is no effect). Each point represents the mean with standard error bars obtained from three to twelve separate averages at each conditioning interval (with the exception of a few intervals for subject K.E. where only single averages were performed). *A*, forwards sway condition. *B*, backwards sway condition.

intervals inhibition was found. At short intervals of 80–100 ms a very small inhibition was evident.

Subjects sitting or supine. The H reflex conditioning technique was used on two subjects (the authors) in sitting and supine positions, but with the experimental
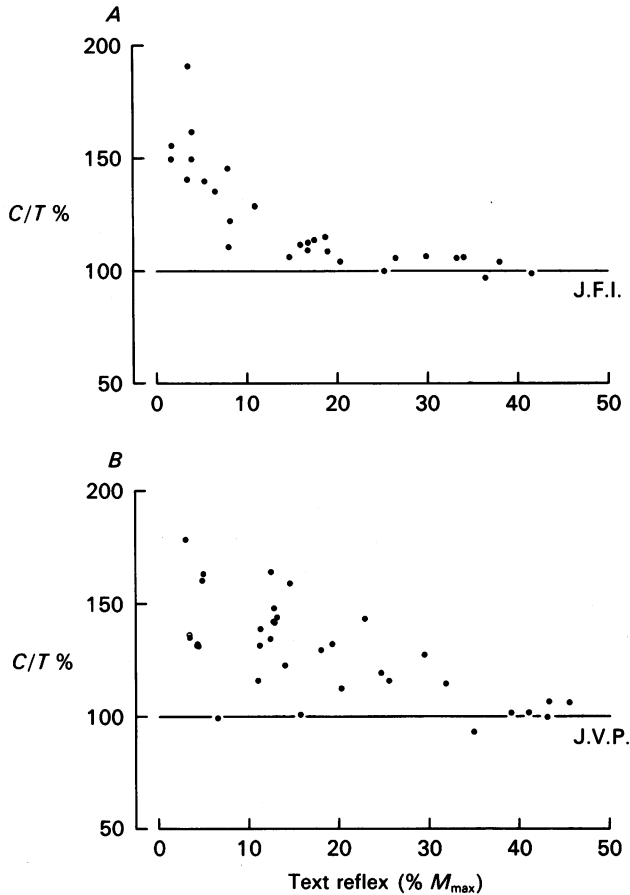

Fig. 4. Effects of test reflex amplitude on the soleus H reflex facilitation (backwards sway condition). Conditioning action ($C/T\%$ ordinate) is plotted against test reflex amplitude (abscissa) expressed as a percentage of the maximal direct motor response recorded from soleus. *A*, subject J.F.I., 220 ms conditioning interval. *B*, subject J.V.P., 400 ms conditioning interval. Each point is an average obtained from sixty-four reflexes (thirty-two conditioned, thirty-two test).

conditions otherwise entirely unchanged. No clear conditioning action of vestibular stimulation was found for either the forward or backward sway conditions. This was still the case when the experiment was repeated (sitting position) during a small voluntary contraction of soleus (2 N m plantar flexion torque measured at the ankle).

Stimulus parameters. The vestibular stimulation strengths used in these experiments (0·35–0·5 mA) were chosen to be just below perceptual threshold when repeated at the chosen rate in each subject. The effects of changes in stimulus current

were studied in a separate series of experiments. All components of the conditioning action in both forward and backward sway conditions scaled approximately linearly with stimulus current (range 0·1–1·0 mA). There was no indication that a threshold current was required for any action.

The stimulus duration was set at 1 s in the experiments illustrated in Figs 1–3. In a separate series of experiments it was found that a stimulus of 100 ms duration produced as much conditioning action as longer stimuli (up to 1 s). Stimuli briefer than 100 ms had smaller effects, stimuli of 40 ms duration were almost ineffective (at a strength of 0·6 mA).

Reflex parameters. The effects of test reflex amplitude on the conditioning actions of vestibular stimulation were examined in a separate series of experiments. The inhibitory action on soleus preceding forward sway was not dependent on test reflex amplitude (the range of amplitudes that could be studied in the present experiments was 4–45 % of the maximal direct motor response recorded in soleus). The facilitatory action preceding backwards sway was, however, very sensitive to changes in test reflex size (Fig. 4).

Spatial interaction between vestibular and spinal inhibitory actions on soleus H reflexes

The experimental approach used was to measure the strength of a spinal inhibitory action by conditioning soleus H reflexes, and then to repeat the measure during concurrent stimulation of the vestibular apparatus. Vestibular stimulation was timed to correspond to the period of inhibition preceding forward sway previously documented for each subject (data of Fig. 3A). Thus four groups of (sixteen) reflexes were recorded: test reflexes (T), test reflexes with concurrent vestibular stimulation (T_v), reflexes conditioned from a spinal inhibitory pathway (C) and reflexes conditioned from both the spinal pathway and vestibular stimulation (C_v). Spinal inhibitory action was calculated without and with vestibular stimulation. The results are expressed as the difference between the two conditioning actions ($C/T - C_v/T_v$ %); positive values indicate spatial facilitation, a zero value indicates no interaction.

Inhibitory conditioning actions could vary with test reflex amplitude (although no clear effect was found – see above). For this reason, the reflexes in the presence of vestibular stimulation (C_v, T_v), which would otherwise be smaller as a result of the vestibular inhibitory action, were increased in amplitude (until $T_v = T$) by a small increase in the stimulus applied to the tibial nerve.

In order to avoid errors resulting from a drift in reflex amplitude the four kinds of reflex were induced in either a regular sequence (C, T, C_v, T_v, C...) or a pseudo-random sequence. Because of the variability of reflexes in the standing subjects many estimates of vestibular interaction, each based on sixty-four (four × sixteen) reflexes, were made for each type of spinal inhibitory pathway.

Interaction with Ia reciprocal inhibition

Reciprocal inhibition was induced by stimulation of the antagonist muscle nerve. The depth of the inhibition was deliberately varied by using a range of stimulus strengths. Spatial interaction between vestibular and Ia reciprocal inhibition is

illustrated in Fig. 5*A*. In this and subsequent figures the estimates of spatial interaction ($C/T - C_v/T_v\%$) have been plotted against the value of the spinal inhibitory action alone ($C/T\%$). Spatial facilitation is present where reciprocal inhibition is weak (for the region $C/T > 70\%$, Wilcoxon two-tailed matched pairs test: $P < 0.00001$).
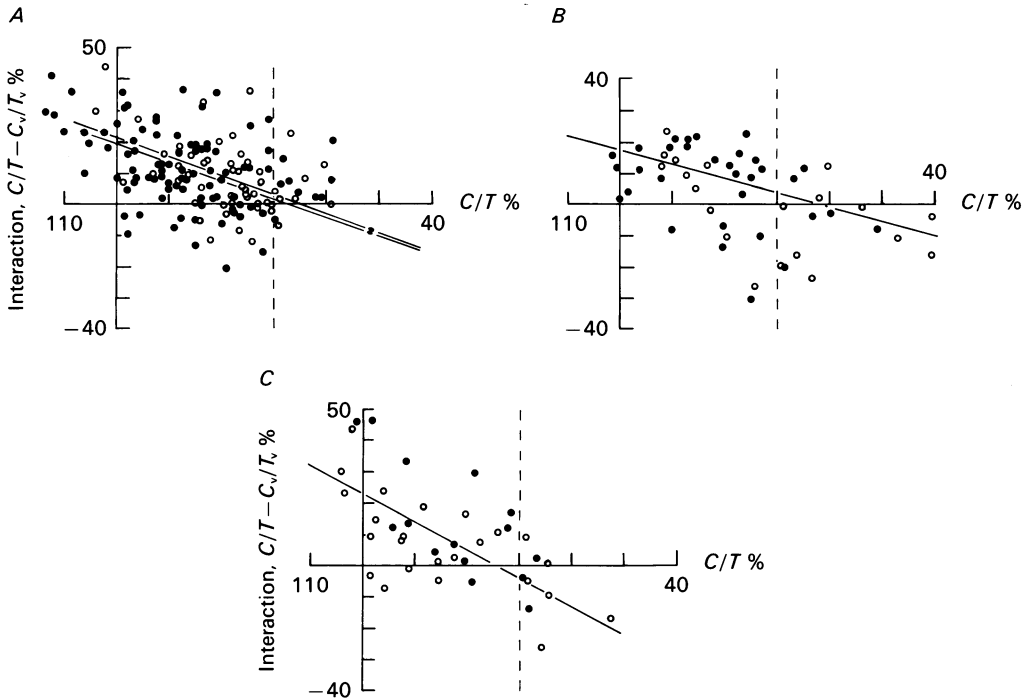

Fig. 5. Spatial interaction between inhibition evoked by galvanic stimulation of the vestibular apparatus (forwards sway condition) and spinal inhibitory actions. The interaction is plotted (ordinate) as the difference in spinal inhibitory action on the H reflex in the absence and presence of vestibular stimulation ($C/T - C_v/T_v\%$). Vestibular stimulation produced a *ca* 15% reduction in reflex amplitude which was compensated by boosting the test reflex stimulus. The abscissa expresses the strength of the spinal inhibitory action alone ($C/T\%$). Data from subjects J.F.I., J.V.P. and K.E. have been combined. Each point is obtained from sixty-four reflexes. Filled circles refer to a regular sequence of reflexes, open circles refer to pseudo-random sequence. Regression lines have been fitted to the data (in *A* the upper line is for the pseudo-random sequence). Points falling above the abscissa indicate spatial facilitation, points falling below the abscissa indicate occlusion. The vertical dashed line (at $C/T = 70\%$) indicates the approximate cross-over from facilitation to occlusion. *A*, spatial interaction with I a reciprocal inhibition. *B*, spatial interaction with group I non-reciprocal inhibition. *C*, spatial interaction with group I a–I a presynaptic inhibition.

Interaction with group I non-reciprocal inhibition

Non-reciprocal inhibition was induced by stimulation of the medial gastrocnemius nerve. The depth of inhibition was varied by adjustments to the stimulus. Spatial interaction with vestibular inhibition is illustrated in Fig. 5*B*. Spatial facilitation is

present when the non-reciprocal inhibition is weak (for the region $C/T > 70\%$: Wilcoxon test, $P = 0.002$), but occlusion is favoured when inhibition is stronger (for the region $C/T < 70\%$: $P = 0.032$).

Interaction with group Ia–Ia presynaptic inhibition

Soleus Ia afferents were presynaptically inhibited by biceps femoris Ia afferents activated by pulsed vibration. The strength of inhibition was systematically varied by alteration of the interval between the vibration and the test stimulus and by adjustment of vibration amplitude. Spatial interaction with vestibular-evoked inhibition is illustrated in Fig. 5C. Spatial facilitation is present when the inhibition is weak (for the region $C/T > 70\%$: Wilcoxon test, $P < 0.005$).

Interaction with recurrent inhibition

The protocol of Hultborn & Pierrot-Deseilligny (1979) was used on subject J.F.I. with a 13 ms interval between SM and S1 stimuli.

In the backwards sway condition the H′ reflex was unchanged ($-0.28 \pm 4.25\%$), whereas H_{ref} reflexes were increased by 20% (H1 reflexes were kept at the same amplitude). Put another way changes in recurrent inhibition of the H′ reflex almost exactly cancelled out the increase in motoneurone excitability produced by vestibular stimulation and revealed by the H_{ref} reflex. The forwards sway condition could not be studied because no H′ reflex was obtainable during vestibular inhibition of soleus.

DISCUSSION

Effects of vestibular stimulation on motoneurones

The consensus view from experiments using perturbations of natural stance in man is that the vestibular system has an important role in compensation for small, low-frequency sway, particularly about the ankle joints (see Allum, Keshner, Honneger & Pfaltz, 1988; Hayashi, Miyake & Watanabe, 1988; Moore, Rushmer, Windus & Nashner 1988; Dichgans & Diener, 1989; Kleiber, Horstmann & Dietz, 1990). The shorter latency EMG responses to galvanic stimulation of the vestibular apparatus observed in the present experiments (Fig. 1), are therefore to be predicted. The strictly reciprocal actions on ankle flexor and extensor muscles are consistent with the fact that reciprocal relations are conserved under conditions of natural sway despite variations in response strategy (Horak & Nashner, 1986). Responses to vestibular stimulation were only observed in standing subjects – this may be a reflection of strategy selection (cf. Nashner, 1985; Horak, Diener & Nashner, 1989; Nardone, Giordano, Corra & Schieppati, 1990). Dieterich, Brandt & Fries (1989) have reported otolith actions on lower limb muscles in standing, but not sitting or supine subjects. The EMG responses observed at longer latency, after sway had been initiated, presumably result from activation of a combination of vestibular, muscle, trunk and plantar receptors (Horstmann & Dietz, 1990; Magnusson, Enborñ, Johansson & Pykko, 1990).

Responses to galvanic vestibular stimulation depended on head position relative to the lower limbs. This is consistent with earlier reports that sway direction varies with head rotation (Nashner & Wolfson, 1974; Lund & Broberg, 1983; Hlavacka &

Njiokiktjien, 1985; Tokita, Ito & Takagi, 1989). Integration of vestibular and head position signals is essential in species where the head can be turned relative to the supporting limbs. In the cat integration has been observed in the vestibular nuclei and reticular formation of the brainstem and on propriospinal neurones and spinal interneurones (see Manzoni, 1988; Wilson, 1988; Manzoni, Pompeiano, Barnes, Stampacchia & D'Ascanio, 1989; Wilson, 1991). Neck rotation has been observed to alter soleus motoneurone excitability in man (Hayes & Sullivan, 1976; Traccis, Rosati, Patrashaksis, Bissahou, San & Aiello, 1987 and see Rossi, Mazzocchio & Scarpini, 1987).

Records of H reflexes conditioned at various intervals by vestibular stimulation confirm the pattern of vestibular action on soleus motoneurones observed in EMG records (compare Figs 3 and 1). In the 'forward sway' condition soleus motoneurones are inhibited for a period lasting from 100 to 500 ms after the start of vestibular stimulation. In the 'backward sway' condition the motoneurones are excited during the same time interval. No significant movement (at the ankle joint), was observed until the end of this period and so it can be concluded that these actions on soleus motoneurones result directly from the vestibular stimulation.

Effects of vestibular stimulation on spinal machinery

We have directed most attention towards the inhibition of soleus motoneurones induced at short latency by vestibular stimulation in the 'forward sway' condition. Since this inhibition precedes any movement it must result from vestibular activation of pathways descending to the spinal cord. The issue to be resolved is whether these pathways influence soleus motoneurones through 'private' spinal machinery or through machinery that can be recognized by other criteria, such as activation by a peripheral (reflex) input. This was examined using the spatial facilitation method.

Spatial facilitation using the H reflex

If descending and peripheral inhibitory actions share spinal interneurones then the inhibition induced by combined stimulation should exceed the sum of that produced by each pathway separately. This spatial facilitation should be strongest when the separate actions are each very small, representing individually subthreshold excitation of the shared interneurones. If either inhibitory action is very large, then it should monopolize many of the shared interneurones leading to occlusion: the situation where the inhibition resulting from combined stimulation is less than the sum of the individual actions. The same situation will hold if one of the excitatory actions on the interneurones consists of the removal of an inhibitory input.

Accordingly in the present experiments the inhibition produced by a peripheral stimulus alone was evaluated by conditioning the H reflex and expressed as conditioned reflex amplitude as a percentage of the test reflex amplitude ($C/T\%$). The same inhibitory action was then evaluated during conjoint stimulation of the vestibular apparatus in the 'forward sway' condition ($C_v/T_v\%$). A positive value for the difference between these two values ($C/T - C_v/T_v\%$) was taken as evidence for spatial facilitation and a negative value as evidence for occlusion.

One difficulty with this experimental approach is that the reflexes conditioned by

conjoint stimulation (C_v), are compared with a test reflex (T_v), already diminished in amplitude as a result of vestibular stimulation. If estimates of inhibition were to vary (inversely) with reflex size then a spurious spatial facilitation would result. In fact very little effect of reflex size was observed. Nevertheless, experiments were performed with the amplitude of T_v increased to that of T by boosting the test stimulus. Provided that inputs to the soleus motoneurone pool are not differentially distributed this will produce equivalent test reflexes.

Interaction with inhibitory pathways

The data illustrated in Fig. 5 indicate spatial facilitation between the inhibition induced by vestibular stimulation in the forward sway condition and weak inhibition in the Ia reciprocal, group I non-reciprocal, and group Ia–Ia presynaptic inhibitory pathways. The facilitation was weaker when the peripheral inhibitory action was strong and tended to become an occlusion when the peripheral inhibition exceeded 30% ($C/T < 70\%$). We did not extensively study interaction in the backward sway condition (except with recurrent inhibition) because of the potential confusion between reduced spatial facilitation and occlusion. The variability observed in Fig. 5 results in large measure from the variability in H reflex amplitude found in standing subjects (Fig. 2).

Spatial facilitation indicates that the descending pathways activated by vestibular stimulation act on interneurones that mediate all three peripheral inhibitory actions. The observation of occlusion during strong peripheral action lends further support to this suggestion. Rossi & Mazzochio (1988), have recently reported that the facilitation of reciprocal inhibition from cutaneous afferents (Iles, 1983), can be converted into occlusion in a similar manner.

The spatial facilitation observed in these experiments even under the most favourable conditions of very weak peripheral inhibition was small ($C/T - C_v/T_v = 20\%$), compared to the effects observed in the cat (see Baldissera *et al.* 1981). Moreover, equally small effects have been reported for cutaneous facilitation of non-reciprocal inhibition (Bergego, Pierrot-Deseilligny & Mazières, 1981), joint afferent facilitation of non-reciprocal inhibition (Iles, Stokes & Young, 1990), contralateral primary afferent facilitation of reciprocal inhibition (Delwaide & Pepin, 1991) and cutaneous facilitation of reciprocal inhibition (Rossi & Mazzochio, 1988). Two explanations for the smallness of all these effects could be advanced. The first is that the relative timing of the two inputs to an interneurone is critical for achieving spatial facilitation. In man, being much larger than the cat, temporal dispersion of the inputs when they reach the lumbar spinal cord may ensure that the critical timing is only present for a small proportion of the interneurones. This explanation is unlikely to apply in the case of prolonged vestibular stimulation as used in the present experiments. The second explanation is that most work showing substantial spatial facilitation has been performed on anaesthetized animals. In these cases the membrane potential of spinal interneurones is likely to be substantially below firing threshold with consequently a large capacity for summation of individual excitatory inputs. In conscious humans, interneurones may already be close to firing with less opportunity for summation. On the other hand, occlusion may require less critical timing of inputs and will certainly be favoured if interneurones are close to firing.

Ia reciprocal inhibition. Rossi, Mazzochio & Scarpini (1988) have reported that backward tilt of a sitting subject increases reciprocal inhibition of soleus motoneurones ($C/T - C_v/T_v = 13\%$). Although the relationship between the vestibular stimulation induced by static tilt of sitting subjects, and galvanic stimulation of those standing in the present experiments is not clear, the direction and extent of spatial facilitation of reciprocal inhibition are very similar (Fig. 5A).

Despite the different musculoskeletal organization, comparisons of neural organization with the cat may be valid (Dunbar, Horak, Macpherson & Rushmer, 1986). Experiments on the cat (summarized in Baldissera *et al.* 1981) have shown vestibulospinal facilitation of interneurones mediating Ia reciprocal inhibition of flexors. These interneurones in turn inhibit the 'opposite' interneurones responsible for inhibition of extensors such as soleus (cf. Baldissera, Cavallari, Fournier, Pierrot-Deseilligny & Shindo, 1987 for the upper limb in man). A simple explanation for the enhanced reciprocal inhibition of soleus during backward tilt and in the forward sway condition would then be a withdrawal of vestibulospinal facilitation of extensor coupled interneurones and thus disinhibition of the interneurones mediating reciprocal inhibition of soleus. However, other routes involving propriospinal or reticulospinal facilitation of flexor coupled interneurones, or Renshaw cells (see below) remain possibilities.

Group I non-reciprocal inhibition. Descending control of interneurones mediating non-reciprocal inhibition in the cat has been described. However, it is not yet known whether all such actions are mediated by the dorsal reticulospinal system and if the interneurones would be modulated by vestibular activation (see Iles, Jack, Kullmann & Roberts, 1989). Thus the pathways responsible for the modulation of transmission of non-reciprocal inhibition illustrated in Fig. 5B are unclear.

Group Ia–Ia presynaptic inhibition. In the cat presynaptic inhibition of Ia afferents by group I afferents is controlled by the ventral reticulospinal system. Neurones of the medullary inhibitory area which give rise to the ventral reticulospinal system are known to receive convergent vestibular and neck afferent signals (Manzoni, 1988). This pathway may be responsible for the modulation of presynaptic inhibition illustrated in Fig. 5C.

Interaction with recurrent inhibition. A weak voluntary contraction of soleus causes the H' reflex to fall by about 40% and the reference H reflex to increase by about 100%. This indicates a facilitation of recurrent inhibition (see Pierrot-Deseilligny, Katz & Hultborn, 1983). A strong contraction causes the H' reflex to increase more than H_{ref}, indicating a reduction of recurrent inhibition ('decoupling'). Results obtained on subject J.F.I. (J. F. Iles & J. V. Pisini, unpublished observations) during voluntary contractions are identical to those reported by Pierrot-Deseilligny and colleagues.

In the present experiments an intermediate situation was found – H' was almost unchanged during vestibular stimulation. Since the activation of soleus motoneurones during backwards sway is smaller than in the weak voluntary contraction (10% maximal voluntary contraction as used by Hultborn & Pierrot-Deseilligny, 1979, see below) the most likely explanation is that vestibular stimulation leads to some decoupling of soleus motoneurones and soleus-coupled Renshaw cells. This conclusion would be entirely consistent with the strong decoupling shown by Rossi

et al. (1987) during static backward tilt. As these authors observe, such decoupling could contribute to changes in reciprocal inhibition of soleus motoneurones. Vestibular modulation of Renshaw cells has been studied extensively in the cat (see Pompeiano, Manzoni, Barnes, Stampacchia & D'Ascanio, 1990).

Comparison of vestibular actions on spinal machinery with those observed during voluntary muscle contraction

Vestibular stimulation in the forward sway condition facilitated reciprocal, non-reciprocal and presynaptic inhibition. These inhibitory pathways are also modulated during voluntary isometric contraction of soleus (see Iles, 1986; Iles & Roberts, 1987; Pisini, 1987). During strong soleus contraction inhibitory transmission operates at a low level, weaker soleus contraction (analogous to the forward sway response) is associated with a higher level of inhibitory transmission. Although there is qualitative agreement between the controls of inhibitory transmission during vestibular-evoked postural reactions and voluntary contraction, there are quantitative differences.

In order to make comparisons with voluntary contraction the change in torque generated by soleus in the forward sway condition needs to be estimated. This can be done in three ways. First, the very weak vestibular stimulation we have used produces approximately 60% reduction in the average tonic EMG activity recorded from soleus in standing subjects. This should correspond to a 60% reduction in the average active torque generated by each soleus (i.e. 60% of 0·165 N m: Smith, 1957). Second, Nashner & Wolfson (1974) illustrate a torque pulse of 0·2 N m in force plate records during vestibular stimulation (resulting from action in both limbs during a backward sway response). Third, measurement of the angular acceleration at the ankle joint in the earliest phase of forward sway, combined with estimates of the body's moment of inertia (by approximation as a rigid cylinder pivoted about one end), also gives a value of around 0·1 N m for the change in torque generated by each soleus muscle.

Vestibular stimulation in the forward sway condition changes the level of inhibitory transmission $(C/T - C_\mathrm{v}/T_\mathrm{v}\%)$ by about 10% when the spinal inhibitory action alone is around 20% $(C/T = 80\%$, see Fig. 5). Changes in transmission of this extent during voluntary contraction require a reduction in soleus-generated torque of about 2 N m. Thus a transient vestibular action producing a soleus relaxation of 0·1 N m increases spinal inhibitory transmission to about the same extent as a reduction in voluntary contraction twenty times greater. Although these calculations are subject to considerable error, the twentyfold difference in calculated values does indicate some real quantitive difference in behaviour. Put another way, the vestibular action on spinal inhibitory transmission is large relative to its effect on soleus motoneurones. The fact that some indication of decoupling of soleus Renshaw cells was obtained is consistent with this view because decoupling is only evident in strong voluntary contractions. The quantitative differences between vestibular and voluntary control might, however, be smaller if comparison was made with dynamic voluntary contraction (e.g. Crone, Hultborn, Jespersen & Nielsen, 1987; Meunier & Morin, 1989; Meunier & Pierrot-Deseilligny, 1989).

The qualitative similarities between the control of transmission in the spinal cord

induced by vestibular action and that found in voluntary contraction lends support to the notion of modules of spinal cord machinery that can be utilized in a variety of tasks (Georgopoulos & Grillner, 1989).

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