Task-related changes of transmission in the pathway of heteronymous spinal recurrent inhibition from soleus to quadriceps motor neurones in man

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Summary

An H reflex conditioning technique was used to monitor the transmission of heteronymous recurrent inhibition from soleus to quadriceps motor neurones of the human lower limb. Inhibition declined during quadriceps muscle contraction under all conditions examined, falling to zero at around one-third of the maximum voluntary contraction. Inhibition declined during soleus muscle contraction in sitting, standing and bicycling tasks.

The level of inhibition assessed at a given (weaker than 30%) level of quadriceps contraction was reduced during postural tasks involving quadriceps and soleus co-contraction (standing and late-stance phase of walking) when compared with sitting and performing matched voluntary muscle contractions. The level of inhibition during the mid-power stroke of a bicycling task, which also involved co-contraction of quadriceps and soleus, was greater than during matched voluntary muscle contractions while sitting. It is concluded that the pathway of heteronymous recurrent inhibition from soleus to quadriceps motor neurones is under at least two types of control: one related to the task, which sets the operating range, and a second which couples inhibition to the level of muscle contraction. Multiple control pathways are consistent with the diverse effects on recurrent inhibition reported in subjects with upper motor neurone lesions.

Keywords: recurrent inhibition; spinal cord; motor control; human

Abbreviations: C/T% = conditioned reflex amplitude divided by test reflex amplitude; adjC/T% = ratio of conditioned to test reflex amplitude, adjusted if the conditioning soleus motor discharge differed from 35%M_max; GLM = General Linear Model; %M_max = percentage of the maximum motor discharge; %MVC = percentage of maximum voluntary contraction

Introduction

An influential contribution to discussion on the function of recurrent inhibition of spinal motor neurones was made by Hultborn and colleagues (Hultborn et al., 1979). They proposed that recurrent inhibition acts to regulate gain at the level of motor neurones and that low- and high-gain conditions are appropriate to different motor tasks.

In the original model it was envisaged that recurrent inhibition mediated by Renshaw cells changed the slope (gain) of a linear motor neurone input–output relation. An enhanced level of inhibition would be appropriate to tasks requiring fine control of low levels of motor output (low-gain condition), and a reduced level of inhibition would be appropriate for tasks requiring either high levels of motor output or a large response to input signals (high-gain condition). The model became more complicated when experiments on homonymous recurrent inhibition in man showed that the level of inhibition changed during voluntary contraction of the muscle receiving inhibition. Inhibition increased during weak muscle contraction and then declined during strong contraction (Hultborn and Pierrot-Deseilligny, 1979). Nevertheless, the notion of gain control would still be valid if it were shown that recurrent inhibition, assessed at matched levels of muscle contraction, varies with motor task.
Evidence for such task-dependence has been presented (Katz and Pierrot-Deseilligny, 1999), a particularly clear example being the facilitation of homonymous recurrent inhibition of soleus motor neurones seen during the co-contraction of the soleus with the antagonist tibialis anterior compared with a matched isolated contraction of the soleus (Nielsen and Pierrot-Deseilligny, 1996).

Heteronymous recurrent inhibition is widespread and strong in man (in comparison with the lower limb of the cat). It has been suggested that the heteronymous Ia excitatory pathways evolved to assist the peculiar requirements of bipedal stance and gait in man and that heteronymous recurrent inhibition acts to negate those actions in tasks in which they are not required (Katz and Pierrot-Deseilligny, 1999). In a previous paper we showed that recurrent inhibition from soleus to quadriceps motor neurones can be studied in man using an H reflex method (Iles and Pardoe, 1999). This heteronymous recurrent inhibition was reduced during co-contraction of a test muscle (quadriceps) but not during co-contraction of the test muscle and its antagonist (biceps femoris). This is similar, though not identical to the behaviour of homonymous inhibition. In the present work the investigation was extended to monitor heteronymous inhibition during distinct motor tasks (voluntary contraction, standing, bicycling and walking) at matched levels of activity in the muscles acting about the knee and ankle joints.

Methods

Subjects

Six normal subjects (two male, four female), aged 22–53 years, were studied with their informed consent. One further subject was rejected because a quadriceps H reflex was unobtainable. The procedures were approved by the Oxford Sector ethics committee.

Procedures

Essentially the same procedures were used as those described in an earlier paper (Iles and Pardoe, 1999), but because much of the hardware and software has been replaced they are summarized here.

A quadriceps H reflex of ~10% maximum motor discharge was elicited by electrical stimulation of the right femoral nerve and recorded with surface electrodes applied over the vastus lateralis. EMG signals were amplified with a Neurolog NL824 amplifier (Digitim, Welwyn Garden City, UK), filtered below 10 Hz and above 3 kHz, passed through an isolator (Neurolog NL820) and full-wave rectified. Additional higher-gain EMG signals were processed in the same way and then averaged with a time constant of 10 or 500 ms (Garland et al., 1972). The analogue signals were digitized at 5 kHz (CED1401; Cambridge Electronic Design, Cambridge, UK) and processed using Signal software. Baseline EMG levels were measured with the subject fully relaxed and were subtracted from the levels recorded during muscle contraction and from the reflexes.

The quadriceps H reflex was conditioned by activation of soleus motor neurones in the same limb in order to produce heteronymous recurrent inhibition mediated by Renshaw cells. Soleus motor neurones were activated by electrical stimulation of the inferior soleus nerve 22 ms before the femoral nerve stimulus. The soleus motor discharge was monitored as an EMG and expressed as a percentage of the maximum discharge measured from time to time during the session by application of a supramaximal nerve stimulus (%Mmax). The discharges were measured as areas above the baseline. When small changes in the maximum discharge were detected, it was assumed that the change had occurred progressively over time. In most experiments the soleus motor discharge was reflex, but when both direct and reflex discharges were present the areas were summed.

The quadriceps H reflex amplitude was measured as the area above the baseline. The effects of the conditioning stimulus on the quadriceps H reflex were expressed as conditioned reflex amplitude divided by test reflex amplitude, as a percentage (C/T%). Values of <100% indicate recurrent inhibition and values of 100% indicate no inhibition. Typically ~20 conditioned and 20 test reflexes were collected in a pseudorandom sequence and averaged. The averages were repeated at least six times in order to estimate the variance of C/T%.

The experiments were performed during four motor tasks: sitting, standing, walking and bicycling. In those experiments explicitly concerned with the effects of task, the subjects were compared in the standing, walking or bicycling tasks with sitting at matched levels of voluntary muscle contraction.

Standing subjects sat on a high stool with the hip semi-flexed, the knee fully extended and the ankle at 110° and made voluntary contractions of knee and ankle muscles, which were monitored with high-gain EMG recordings averaged with the 500 ms time constant. The processed EMG signals were presented to the subjects visually so that they could produce predetermined levels of muscle contraction, expressed as a percentage of the maximum voluntary contraction (%MVC) that could be maintained for ~3 s. Muscle activity was measured as the mean EMG during a period of 25 ms ending 25 ms before the test stimulus (and so not contaminated with stimulus artefacts).

Standing subjects stood relaxed on a firm surface or, in some cases, were asked to lean forwards or backwards, to wear a rucksack (load 10 kg) or to stand on tiptoe in order to alter the pattern of muscle activity.

Walking subjects performed a very slow walk (1.5 km/h; 30 strides/minute) on a motor-driven treadmill. A microswitch detected the heel-strike and triggered the test stimulus 500 ms later (in late stance). At this time both soleus and quadriceps muscles were weakly active. Since EMG activity varies with time in late stance (Zehr et al., 1998), the high-gain EMG records were averaged with a shorter (10 ms) time constant, and control experiments were performed to relate the
measured EMG to the actual period of time when the test reflex was elicited.

Bicycling subjects used a bicycle ergometer (crank length 17.5 cm) working against frictional torques of up to 30 N m at around 40–50 r.p.m. The seat was set at the maximum comfortable height, and in some experiments it was then reduced by 10 cm. The test stimulus was triggered 50 ms after the mid-power stroke (90°) position. This time was chosen because the quadriceps and soleus muscles were both active (Jorge and Hull, 1986; Neptune et al., 1997). Control experiments were performed to adjust the measured EMG to correspond to the time of the test reflex, as for walking.

In the experiments comparing sitting with other tasks, the reflex repetition rate and test reflex amplitude were matched between tasks.

## Results

### Conditioning action from soleus to quadriceps assessed with quadriceps H reflexes

In all six subjects, inhibition of the quadriceps reflex was produced when the soleus nerve conditioning stimuli were applied at an interval of 22 ms before the test stimulus to the femoral nerve. These data conform to those presented for eight subjects in a previous paper (Iles and Pardoe, 1999); two subjects (J.F.I. and J.P.) are common to both investigations. For the reasons presented in the previous paper, it is assumed here that the observed inhibition is predominantly a heteronymous recurrent inhibition.

### Scaling of recurrent inhibition with conditioning motor discharge

In the previous paper it was shown that the recurrent inhibition measured in supine subjects scaled with the conditioning soleus motor discharge. Data for one subject studied sitting, standing, bicycling and walking are illustrated in Fig. 1. The slopes of the regressions were negative and significantly different from zero in all four tasks. The thresholds for inhibition were investigated by projecting the regression lines to the ordinate at zero soleus motor discharge. In no task was the estimate of C/T% at zero motor discharge significantly different from 100% (99, 99, 100 and 99% in Figs 1A–D, respectively). It would be expected that recurrent inhibition is only produced when motor neurones are activated and that it would scale with motor discharge.

In the remaining experiments described in this paper, the effect of the amplitude of the conditioning motor discharge on recurrent inhibition was removed by adjusting the conditioning stimulus to the soleus nerve with the aim of producing a constant soleus motor discharge of 35 %M_max (this value was chosen because a discharge of this amplitude could usually be evoked reflexly). In practice, the desired value could never be obtained exactly. In order to avoid rejecting excessive amounts of data, the values of C/T% measured with a soleus motor discharge different from 35 %M_max (but falling within 15% of that figure) were adjusted on the basis of the linear relationships between C/T% and soleus motor discharge illustrated in Fig. 1:

\[
\text{adjC/T\%} = 100 + 35 (C/T\% - 100)/(%M_{\text{max}} \text{ of soleus})
\]

The relationships illustrated in Fig. 1 and the earlier publication are slightly convex upwards. However, adjusting the C/T% values with the following optimum power law relation did not make any practical difference (the values of adjC/T% differed by less than 1%):

\[
\text{adjC/T\%} = \{100^{1.6} + 35 (C/T\%^{1.6} - 100^{1.6})/(%M_{\text{max}} \text{ of soleus})\}^{0.625}
\]

Therefore, in the results presented here the linear relation is employed.

### Effects of muscle contraction on recurrent inhibition

#### During voluntary muscle contraction in sitting subjects

The effects of a voluntary isolated contraction of the quadriceps on recurrent inhibition in one sitting subject are illustrated in Fig. 2A. Inhibition declined with quadriceps contraction and disappeared with a contraction of ~30% of the maximum voluntary contraction measured with the high-gain, rectified and integrated EMG (30% MVC). The relationship was convex upwards, as previously reported for supine subjects (Iles and Pardoe, 1999), and has been made more linear in the figure by plotting adjC/T% against the square root of quadriceps contraction. The slope of the regression is significantly greater than zero (P < 0.0001).

The effects of a voluntary isolated contraction of the soleus on recurrent inhibition in a sitting subject are illustrated in Fig. 2B. Inhibition declined with soleus contraction. The slope of the regression is significantly greater than zero (P < 0.0005). This observation was confirmed in two other subjects.

#### During other motor tasks

The relationship between recurrent inhibition and quadriceps muscle contraction during standing, bicycling and walking in a single subject is illustrated in Fig. 3B–D (the same subject as illustrated in Fig. 2). The quadriceps activity was varied during standing by asking the subject to lean forwards or backwards. During bicycling, quadriceps activity increased in response to the addition of frictional load. During walking a very small increase in quadriceps activity was achieved by asking the subject to lean backwards while wearing a loaded rucksack. The slopes of the regressions are significantly greater than zero for standing and bicycling (P = 0.027 and P < 0.0001, respectively) but not for walking.
Recurrence inhibition

Fig. 1 Relation between recurrent inhibition of quadriceps motor neurones and conditioning soleus motor discharge for one subject. Recurrent inhibition estimates from single averages (C/T%: values of less than 100% indicate inhibition) are plotted (ordinate) against soleus motor discharge, expressed as %M\text{max} (abscissa). (A) Data from a recording session with the subject sitting. (B) Data collected during standing. (C) Data collected during the power stroke of bicycling. Torque 2.3 N m. (D) Data collected in late stance during walking. Quadriceps contraction was 1, 5, 2 and 9% MVC; soleus contraction was 0, 6, 3 and 7% MVC in A–D, respectively.

Although the data are presented as regressions of inhibition on quadriceps activity, during these tasks the activity of the soleus muscle also changed. During the standing task, a backward lean increased quadriceps activity and decreased soleus activity. During bicycling and walking quadriceps and soleus activity were positively correlated. These relations are summarized in Fig. 3A, in which regressions of soleus activity on quadriceps activity are plotted for the experiments illustrated in Fig. 3B–D.

During standing it was possible to modulate soleus activity somewhat independently of quadriceps activity by asking the subject to contract the soleus and lift the heels off the floor. When this was done a significant reduction in inhibition was observed, but only in those experiments in which quadriceps activity was kept at a low level (<8% MVC) by a small forward lean. The same relationships were documented in two other subjects.

During bicycling it was possible to adjust quadriceps and soleus activity independently by taking advantage of the fact that activity in both muscles was increased by adding frictional load, whereas a selective increase in quadriceps activity (and a slight decrease in soleus activity) was caused by reducing the seat height by 10 cm (Jorge and Hull, 1986). Using this manoeuvre, it was shown in the subject of Fig. 3 that recurrent inhibition was diminished during elevated voluntary activity of either the quadriceps or the soleus muscle when activity in the other muscle was kept constant. This corresponds to the result obtained during isolated muscle contraction while sitting.
The analyses were performed with Minitab release 11 (Minitab Data Analysis Software, MINITAB Inc., State College, Pa., USA). There was a significant interaction of task and quadriceps activity for the three subjects studied, i.e. both task and quadriceps activity affect recurrent inhibition and each modulates the effect of the other. This analysis was not feasible for the other subjects, in whom time constraints only permitted comparison of the sitting task with one other task. Furthermore, even in the three subjects with large data sets, the data were accumulated over several experimental sessions that might not be completely comparable, and for this reason single comparisons (sitting versus one other task) made in the same experimental session were analysed for these subjects as well.

Comparison of sitting with one other task
In these experiments, recurrent inhibition and muscle activity were measured from four to six averages during the motor task (standing, bicycling or walking). The levels of muscle activity were then matched by the subject, who performed voluntary contractions in the sitting position. Thereafter, tasks were interleaved. The effect of task on recurrent inhibition was assessed with the $t$-test.

The matching of muscle activity by voluntary contraction when sitting was never exact. In order to compensate for this, the values of inhibition (adjC/T%) in the sitting task were further adjusted for any inaccurate match of quadriceps or soleus contraction (whichever was the larger) using coefficients from the data illustrated in Fig. 2, and the significance of the $t$-test was evaluated again. A similar approach has been used in a comparison of reciprocal inhibition during sitting and walking tasks (Petersen et al., 1999). This compensation was approximate because the details of interaction of the effects of quadriceps and soleus contraction were not evaluated, although qualitatively the contraction of one muscle diminished the effect of contraction of the other. However, a conservative view was taken: if a previously significant difference in recurrent inhibition was made insignificant by the adjustment, it was counted as insignificant. If a previously insignificant difference was made significant then it was counted as marginally significant.

Thirteen experiments were performed on six subjects to compare standing with the sitting task. In 12 experiments, recurrent inhibition was weaker (i.e. adjC/T% was larger) in the standing task compared with sitting. In six experiments the difference was significant and in one it was marginally significant. Six experiments were performed on two subjects comparing the power stroke of bicycling with the sitting task. Recurrent inhibition was stronger in the power phase of bicycling compared with sitting. Five experiments were significant and one marginally so.

**Effects of task on recurrent inhibition**
**Subjects studied during three tasks or all four tasks**
In two subjects, a complete set of data covering all four tasks, such as the data illustrated in Figs 2A and 3B–D, was available, and another subject was studied during three tasks (sitting, standing and walking). These data sets were analysed by the General Linear Model (GLM) with inhibition as the response, task as a categorical predictor (a factor with four or three levels) and quadriceps activity (transformed by taking the square root) as a covariate. The model formula was

$$\text{adjC/T\%} = \text{task} \times (\%\text{MVC for quadriceps contraction})^{0.5}$$
The nature of the inhibitory action on quadriceps motor neurones

Various arguments were presented in an earlier paper leading to the conclusion that the inhibition observed with the method used in the present experiments is a heterosynaptic recurrent inhibition from soleus to quadriceps motor neurones (Iles and Pardoe, 1999). One of the arguments was based on the almost linear relationship observed between inhibition and the conditioning soleus motor discharge for supine subjects and the threshold at zero soleus motor discharge, both of which would be predicted for recurrent inhibition. These observations have now been extended to sitting subjects and to the more complex motor tasks of standing, bicycling and walking. It is therefore concluded that the method can monitor heteronymous recurrent inhibition during the range of motor tasks explored in the present paper, provided either that the conditioning soleus motor discharge is kept constant or the effects of any changes are allowed for during analysis. Because of the strong relationships observed between inhibition and soleus motor discharge, the present experiments used both a narrow (30%) range of soleus motor discharge and also adjusted for any changes within that range.

It was possible to produce adequate soleus H reflexes for the conditioning volley in all the tasks except standing and standing leaning backwards, in which the reflex was depressed (Katz et al., 1988). In standing, the maximum soleus H reflex was typically 20 %M_max rather than the 40 %M_max observed in sitting subjects, and the stimulus to the soleus nerve was increased until the combined M and H responses were on average close to 35 %M_max.
This required a stimulus of 1–1.2 times the motor threshold. A stimulus that is above the motor threshold may activate gastrocnemius motor axons, producing an additional excitation of Renshaw cells that is not monitored, or excite Ib afferents, producing non-reciprocal inhibition (Iles and Pardoe, 1999). This would lead to overestimation of recurrent inhibition. Since recurrent inhibition was weaker in standing than in sitting, these effects cannot be responsible for that result. On the other hand, stimuli that exceed the motor threshold may activate cutaneous and group II afferents, which are known to depress recurrent inhibition in the cat (Wilson et al., 1964; Fromm et al., 1977). Analysis of the data from standing subjects did not reveal any significant depression of recurrent inhibition when stimuli exceeded the motor threshold, which is therefore unlikely to be an explanation for the differences observed between standing and sitting subjects.

**Effects of contraction of muscles acting at the knee and ankle joints**

The aim of the present investigation was to discover whether heteronymous recurrent inhibition from soleus to quadriceps motor neurones varies with the motor task. The previous paper had shown that inhibition varies with test muscle contraction, and it was necessary to discount this effect when investigating the influence of task. The present experiments confirmed that inhibition declines with both the test muscle contraction (quadriceps) and source muscle (soleus) contraction in sitting subjects. These effects tended to occlude each other and may therefore operate through the same machinery, although an alternative explanation is mutual inhibition of Renshaw cells activated from each of the two muscles (Ryall, 1970). The situation in the other tasks is difficult to determine because of our rather limited ability to dissociate changes in soleus contraction from changes in quadriceps contraction. Nevertheless, significant reductions in inhibition with quadriceps contraction were observed in both standing and bicycling subjects, despite the fact that soleus and quadriceps activities are negatively correlated during standing and positively correlated during bicycling. This may indicate that the effect of quadriceps contraction is the most powerful. In bicycling it was possible to confirm that contraction of the quadriceps and of the soleus independently lead to a reduction in recurrent inhibition. This was done by inducing changes in muscle activity, by altering seat height and frictional load.

Because of the strong relationship observed between inhibition and muscle contraction, we retained that relationship in one method of data analysis (GLM). In the other analysis (pairwise comparisons of sitting and other tasks), we discounted the effects of muscle contraction by asking subjects to perform matched contractions and by applying an approximate compensation for any residual mismatch.

**Effects of task on heteronymous recurrent inhibition**

GLM analysis in three subjects for whom data were available in three or four tasks showed significant interaction of the effects of task and quadriceps muscle activity on recurrent inhibition. This can be seen in the different slopes and intercepts of the regressions illustrated in Figs 2A and 3B–D. Further analysis was performed on these and additional subjects comparing sitting and one other task in single experimental sessions with matched contraction of knee and ankle muscles.

In all the experiments bar one comparing sitting and standing tasks, there was less inhibition when standing (Fig. 4). In six experiments the difference was not significant. A retrospective analysis of these experiments showed that the level of quadriceps activity was higher in the non-significant experiments (mean 15.3% MVC) compared with the significant experiments (mean 4.4% MVC). It is possible that the reduction of recurrent inhibition which accompanies quadriceps muscle contraction makes it more difficult to detect a further reduction due to task, although another explanation in terms of the degree of quadriceps and soleus co-contraction is offered below. In all six experiments in which sitting and walking were compared, there was significantly less inhibition during the late stance phase of walking. All experiments comparing sitting and bicycling showed more inhibition during the mid-power stroke of bicycling.

![Fig. 4 The effects of task on recurrent inhibition of quadriceps motor neurones. The change in the estimate of recurrent inhibition (adjC/T%) when transferring from sitting to the other tasks is plotted (ordinate; more inhibition is plotted as negative) for every experiment (24 experiments on six subjects). Significant changes (after any adjustment for inadequately matched muscle contraction) are indicated by solid bars and marginally significant changes by the cross-hatched bars. The significant and insignificant experiments during the standing task have been separated. The histogram bars are arranged in date order of experiments (left to right).](image-url)
**Postural co-contraction and heteronymous recurrent inhibition**

Heteronymous recurrent inhibition from quadriceps to ankle muscle motor neurones (i.e. in the reverse direction to the one described in the present paper) has been studied recently during sitting and standing tasks (Barbeau et al., 2000). Inhibition from the quadriceps to ankle muscles was reduced during postural co-contraction compared with matched voluntary contractions in sitting subjects. This is completely analogous to the present results, in which postural co-contraction of the soleus and quadriceps in the standing subjects was accompanied by reduced recurrent inhibition from soleus to quadriceps motor neurones. Recurrent inhibition from quadriceps to soleus was not reduced (compared with sitting) in an isolated soleus postural contraction (Barbeau et al., 2000). The analogous situation could not be examined in the present experiments because recurrent inhibition is weaker in the soleus to quadriceps direction and almost vanished during a strong isolated quadriceps contraction in both the postural (backward lean) and sitting tasks. However, it may be relevant that in those standing experiments that were significantly different from sitting (Fig. 4) there was more co-contraction (mean soleus 6.0% MVC) than in the insignificant experiments (mean soleus 2.9% MVC).

The hypothesis of reduced heteronymous recurrent inhibition in postural co-contraction is supported by the present results on the stance phase of walking. During late stance there was co-contraction (mean quadriceps 10.4% MVC; mean soleus 6.8% MVC). Standing and the stance phase of walking share some common features in that both have a postural weight support role and generate reactive balance adjustments (Tang et al., 1998; Grasso et al., 2000; Sinkjaer et al., 2000). The fact that heterosynaptic recurrent inhibition from soleus to quadriceps motor neurones was reduced in stance suggests some common organization of the spinal cord in these two postural tasks.

During the mid-power stroke of bicycling there was co-contraction (mean quadriceps 7.5% MVC, mean soleus 9.9% MVC for the experiments of Fig. 4). Bicycling and walking are similar tasks in that they consist of rhythmic flexion–extension movements of the limbs but differ in that there is no postural balance component in bicycling on a fixed ergometer. The fact that recurrent inhibition increased during bicycling supports the hypothesis that a reduction in inhibition relative to sitting is characteristic of postural co-contraction, and not of co-contraction in non-postural tasks.

These observations all support the previously articulated view that recurrent inhibition may be concerned principally with posture and the organizational processes underlying adaptation of postural responses to voluntary movements (Rossi et al., 1992; Mazzocchio et al., 1994), but in the negative sense in that postural tasks are accompanied by a reduction in heteronymous recurrent inhibition. Recurrent inhibition is absent in the intrinsic muscles of the digits (Illert and Kummel, 1999; Katz and Pierrot-Deseilligny, 1999) which have very little postural function. It is possible that the ability to switch from a low- to a high-gain condition for motor neurones is a prerequisite for an adequate response to disequilibrium during the maintenance of posture. However, the differences between the sitting and bicycling tasks suggest that changes in recurrent inhibition are not completely restricted to postural tasks.

**The origin of task-dependence of heteronymous recurrent inhibition**

There are various explanations that could be put forward for task dependence of recurrent inhibition. It is possible that different quadriceps motor units with different projections from Renshaw cells are employed in the various tasks. There is no indication of this, and such an explanation could be tested by performing experiments on single motor units. Single units have been studied for inhibition directed from quadriceps to ankle muscles (Barbeau et al., 2000), although it would be technically very difficult to study single units in the walking and bicycling tasks used here.

The present experiments matched activity only in the quadriceps, the soleus and the strict antagonist muscles in the different tasks. In the walking and bicycling tasks, many more muscles were active, particularly the hip extensor muscles. Activity in the motor neurones of these muscles might influence the Renshaw cells responsible for recurrent inhibition from the soleus to the quadriceps. It is unlikely that these potential sources of excitation of Renshaw cells are a complete explanation for our observations because the walking and bicycling tasks were both accompanied by hip extensor activity but showed opposite changes in recurrent inhibition compared with sitting. Nevertheless, the activity of other muscles is likely to have some effect.

Similarly, Renshaw cells are known to be influenced by sensory inputs, and the sensory background, such as joint angle and movement, was not perfectly matched in the different tasks. This could contribute to the observed task differences in recurrent inhibition. However, a major influence on Renshaw cells is likely to be from supraspinal centres via descending motor pathways. There is evidence for vestibular actions on recurrent inhibition, and vestibulospinal actions in general are modulated according to postural task (Rossi et al., 1987; Iles and Pisini, 1992; Day, 1999). This suggests that motor pathways originating in the brainstem may be responsible for the dependence of heterosynaptic recurrent inhibition on postural task. Recurrent inhibition is also under inhibitory control from the motor cortex in man (Mazzocchio et al., 1994; Iles, 1996). This (or some other) pathway may be responsible for the changes in recurrent inhibition which accompany contraction of the test muscle.
The suggestion that there may be two pathways for the control of recurrent inhibition, one related to task and the other coupled to test muscle contraction, is consistent with observations on patients with upper motor neurone lesions (Mazzocchio and Rossi, 1997). Spastic patients show various levels of recurrent inhibition at rest, depending on the nature of the lesion (reduced inhibition in spastic paraparesis, normal or increased inhibition in paraplegia). However, in all patient groups the modulation of inhibition during movement is impaired.

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**References**


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