Distribution of Heterogenic Reflexes Among the Quadriceps and Triceps Surae Muscles of the Cat Hind Limb

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ABSTRACT

Neural signals from proprioceptors in muscles provide length and force related linkages among muscles of the limbs. The functions of this network of heterogenic reflexes remain unclear. New data are reported here on the distribution and magnitudes of neural feedback among quadriceps and triceps surae muscles in the decerebrate cat. The purpose of this paper was to distinguish whether inhibitory force feedback is directed against muscles by virtue of the motor unit composition or articulation of the muscle. These studies were carried out using controlled stretches and measurements of the resulting force responses of individual quadriceps and triceps surae muscles. Responses were evoked over a wide range of background force levels. In agreement with earlier electrophysiological studies, excitatory length feedback strongly linked the vastus muscles, but excitatory reflexes between each vastus and rectus femoris muscles were weak. We also observed a substantial excitatory linkage from the vastus muscles to the soleus muscle. In contrast, force-related inhibition was absent in the heterogenic reflexes among the vastus muscles, but strong and bi-directional between each vastus muscle and the rectus femoris muscle, and between triceps surae and quadriceps muscles. We conclude that short-latency feedback in the hindlimb is organized according to muscle articulation. Length feedback within muscle groups regulates joint stiffness while interjoint length feedback may compensate for the effects of non-uniform inertial properties of the limb. Force feedback is organized to regulate coupling between joints and, along with length feedback, determine the mechanical properties of the endpoint.
INTRODUCTION

Neural feedback from receptors in skeletal muscle projects back to the muscle of origin as well as to other muscles in both humans and cats (Brooke and McIlroy, 1985; Eccles, et al., 1957; Edgley, et al., 1986; Koceja, 1995; Meunier, et al., 1990; Misiaszek and Pearson, 1997; Roby-Brami and Bussel, 1990). Knowledge of the intermuscular distribution of this feedback is essential to an understanding of the functions of proprioceptive pathways in motor coordination. Recent work (Nichols, 1989) based on mechanographic analysis in decerebrate animals (Liddell and Sherrington, 1924) has shown the existence of two classes of rapid feedback. Heterogenic length feedback acts with approximately the same time course as the stretch reflex and leads to excitation of muscles with synergistic actions and inhibition of antagonistic muscles (Nichols, 1999; Nichols and Koffler-Smulevitz, 1991). The magnitudes of these reflexes are essentially independent of background force and, in the triceps surae and pretibial flexor muscles of the cat, correspond to the distribution of group Ia afferents from muscles spindles (Eccles, et al., 1957; Scott and Mendell, 1976). Since the distribution of group Ia effects appears as a dominant factor in the distribution of this feedback, these pathways are likely to regulate joint stiffness in a directional manner as predicted by an extension of the myotatic unit concept (Nichols, et al., 1999).

The other class of heterogenic feedback is inhibitory and increases with active background force in the muscle of origin (Bonasera and Nichols, 1994; Nichols, et al., 1999). This feedback is widely distributed among antigravity muscles in the hindlimb and appears to arise at least in part from Golgi tendon organs. The principles that govern the distribution of this feedback remain unclear. It has been argued that excitatory force feedback, which is apparently expressed during locomotion (Pearson, 1995; Pearson and Collins, 1993; Prochazka, 1996), is
widely distributed among extensor muscles to provide a loading reflex (Dietz and Duysens, 2000). Widespread group I excitation has also been observed in the fictive locomotion preparation (Angel, et al., 1996; Guertin, et al., 1995), although group I excitation may be weak from the quadriceps to the triceps surae muscles. Force-related inhibition, however, is not uniformly distributed across antigravity muscles. Among the triceps surae muscles, inhibitory feedback extends from either gastrocnemius lateralis or medialis (LG or MG) muscles to soleus (SOL), but not between LG and MG (Nichols, 1994; Nichols, 1999). These data suggest that either motor unit type or articulation govern the distribution of this feedback. Inhibitory force feedback has also been observed to link the triceps surae muscles with the muscles of ankle stabilization (Nichols, 1994), suggesting that the distribution of inhibitory force feedback links muscles that cross different axes of rotation. Single motor unit studies have shown that type I motor units in MG are not inhibited by the stretch of MG (Dacko, et al., 1996), supporting by exclusion the hypothesis that inhibitory force feedback links muscles that cross different joints or axes of rotation.

The systems of quadriceps and triceps surae muscles provide a means of further validating our proposed rules governing the distribution of the above classes of heterogenic feedback. The quadriceps muscles consist of single joint vastus (VL, VM, VI) and two joint rectus femoris (RF) muscles. The activation patterns of RF are more divergent from those of V than are the patterns of MG and LG from those of SOL (Engberg and Lundberg, 1969). It can be predicted from this behavioral data that length feedback between RF and the vastus muscles is weaker than length feedback among the vastus muscles. This prediction is supported by studies of the distribution of monosynaptic Ia feedback in anesthetized preparations (Eccles, et al., 1957), but this distribution of feedback has not been described in the unanesthetized state as has
the reflex organization for the triceps surae muscles. Under the proposed rules, feedback between quadriceps and triceps surae muscles should be predominantly inhibitory and force related. Electrophysiological evidence showed that the only excitatory linkage between the two muscle groups is monosynaptic excitation from the vastus intermedius to the soleus muscle (Eccles, et al., 1957).

The quadriceps muscles also provide a means of testing the hypothesis that inhibitory force feedback is distributed according to articulation, because articulation and motor unit type can be dissociated in this muscle group. The vastus muscles contain both homogeneous and heterogeneous fiber types (Ariano, et al., 1973). In particular, VI is composed essentially entirely of type I muscle fibers, while VM and VL are heterogeneous. Our hypothesis predicts that short-latency force feedback should link RF with each vastus muscle, but not link muscles within the vastus group.

In this paper, we describe the relative distributions of excitatory, presumably length feedback and inhibitory force feedback among the quadriceps and triceps surae muscles. We found the distributions of the two kinds of feedback to be complementary and in line with our predictions. Force feedback linked single joint with two joint muscles in the quadriceps group, but these links were bidirectional unlike the unidirectional links in the triceps surae muscles (Nichols, 1999). In addition, we provide evidence that the excitatory pathway between the vastus and soleus muscles is substantial and is likely to influence interjoint coordination as well. These results extend our previous results and support our conclusion that short-latency, inhibitory force feedback links muscles that cross different joints and axes of rotation. In some cases, longer latency inhibition from VI to VL was also observed, suggesting a network of inhibitory mechanisms that is organized differently from the short-latency inhibition. This work
has appeared in a doctoral thesis (Wilmink, 1998), and preliminary data supporting these
conclusions have been published elsewhere (Nichols, 1994; Wilmink, et al., 1996; Wilmink, et
al., 1997).
METHODS

The results depicted in this study were drawn from experiments on twelve healthy adult cats of either sex (2 females and 4 males) weighing 3.25–6 kg. In most cases, the studies were conducted on both legs so each muscle was represented twice per preparation.

Surgery

Under deep anesthesia using isoflurane gas, an intercollicular decerebration was performed, removing all brain matter rostral to the transection. On both hind legs the muscles of the quadriceps and triceps surae were separated and their tendons were connected to individual clamps fixed to strain gauge myographs for the force measurements. Each myograph was mounted by way of a miniature universal joint to a linear slide. The universal joints maintained alignment between each muscle tendon and the moving slide. Muscle lengths were controlled using servo motors that moved the linear slides by way of flexible stainless steel cables clamped to the motor pulleys. The tendency of the cables to unwind and pull back amounted to less than 1 N and was compensated by unloading the slides with elastic bands. Position feedback was obtained from precision potentiometers mounted in line with the motor shafts. Up to four such actuators were available for these experiments.

The quadriceps muscles, vastus lateralis (VL), vastus medialis (VM), vastus intermedius (VI) and rectus femoris (RF), were separated in each leg in some preparations. During most surgeries it was possible to separate these muscles with little injury, but in some preparations it was necessary to sacrifice certain muscles in order to avoid damaging the adjacent muscle. For instance, VI merged in a complex way with both VL and VM in some cases. Also, the tendon of RF usually merged with VL and VM before inserting on the patella. As a result, VL was included in the study 11 times, RF and VI were included 10 times and VM 7 times. In some
experiments, the quadriceps group (Q) was subdivided into two groups based on articulation, namely, the vastus muscles (V) and RF. Similarly, the triceps surae group was divided into individual muscles, namely, medial gastrocnemius (MG), lateral gastrocnemius (LG) and soleus (S) muscles or in subgroups based on articulation, namely the gastrocnemius muscles (G) and S. In each leg the posterior tibial nerve was dissected, draped over a hook electrode and cut distally. Fixation of the leg was accomplished using rods ending in screws, which were inserted into the femur right below the hip and one just above the knee. Hip pins were used to immobilize the pelvis.

The crossed-extension reflex was evoked to recruit all of the muscles of the quadriceps and triceps surae groups. The contralateral posterior tibial nerve was stimulated using 40 Hz mono-phasic constant current pulses at two times reflex threshold. The initial length of each muscle was set by stretching the muscle until a passive tension of approximately 1 N was achieved. Data were acquired while the muscles were quiescent as well as when they were activated by the crossed-extension reflex. The stretches were trapezoidal in shape, with a rise- and fall time of 50 ms, amplitude of 2 mm, and a hold phase of 250 ms. Stretch velocity was therefore 40 mm/s. The amplitude of 2 mm was chosen to fall generally in the range of active lengthening during locomotion. The rise time of 50 ms was rapid enough to provide a sufficiently large pre-reflex force for reliable measurement of the intrinsic mechanical response of the muscle. This measurement was useful to detect the presence of mechanical artifacts.

Protocols

Three protocols were used to evaluate autogenic and heterogenic reflexes. In Protocol 1, one muscle, the donor, was stretched every 2-3 s during activation using the crossed-extension reflex. Another muscle, the recipient, was held isometrically (Nichols, 1999). Any heterogenic
reflex effects were detected by increases or decreases in force in the recipient. In Protocol 2, stretches of the recipient were performed in alternation with stretches of both donor and recipient as the force decayed (See Figure 1B). Two groups of records resulted from this protocol, namely, one with stretch of the recipient only, and one with stretch of both muscles. Heterogenic reflex effects were detected by changes in the magnitude of the reflexes in the recipient muscle on even-numbered trials. Force responses in the first group were purely autogenic, and responses in the second group consisted of autogenic and heterogenic components. These latter responses were therefore referred to as compound responses. Heterogenic effects present for protocol 2 but not protocol 1 would suggest that these effects are presynaptic. In Protocol 3, two muscles were stretched independently and then together (Figure 1A). In this case, each muscle served as both recipient and donor, resulting in three groups of responses. This protocol was used under quiescent conditions when a large number of trials were possible.

In selected cases, up to 150 µg strychnine was injected intravenously toward the end of the experiment to test whether inhibitory reflexes were likely to be mediated by glycinergic pathways (Bonasera and Nichols, 1994; Nichols, 1999). At the end of each experiment, the animal was euthanized with an overdose of sodium pentobarbital (100 mg/kg) injected intravenously.

A 486-based personal computer sampled the length and force channels (up to 8 total) at 500 Hz. The precision of data acquisition was 0.05 N for the force channels and 0.04 mm for the length channels. The same computer provided the servo amplifiers (PMI-Motion Technologies) with the length commands at a constant rate of 2048 Hz per channel through a dedicated 12-bit digital-to-analog conversion card.
Quantification of Reflex Effects

The data were analyzed according to the acquisition protocol (see above) using custom software written in Matlab (Mathworks®).

1. The quiescent state

The quiescent runs, in which the background force was essentially constant, were acquired using protocol 3 and analyzed by superimposing the averaged autogenic with the averaged heterogenic plus autogenic (compound) force response for that muscle (Figure 1A). The difference in area under these force traces, in the interval from 10 ms after stretch onset until the end of the hold phase (see lowest panel in Figure 1A), was computed and normalized to the area under the autogenic force response. The 10 ms start time for this integration was chosen because reflex effects could not have begun before this time. For each muscle combination at least 10-15 complete runs of data were collected. Figure 1A shows the initial portion of a quiescent run and the resulting averaged responses as an example.

2. The activated state

The background force in all the activated muscles generally decayed during the crossed-extension reflex to levels observed during the quiescent state, over a time course of 10–60 seconds. Data were collected for 50 ms prior the onset of stretch using either protocol 1 or 2. The offline analysis program calculated an estimate of the baseline force for every force response, by computing a linear fit through the first and last 50 ms of data for every trial during data collection. The ‘force response’ is here defined as the difference between the force at the corresponding time points and the estimated baseline force. The force responses were measured
every 5 ms during the time course of the trial for the responses at all force levels. Therefore, each response measurement was associated with a time point and an initial force, as represented in the three dimensional plots (see below). For data collected using protocol 1, one group of responses of the recipient muscles resulted. For each of these time points, the relationships of the responses to background force were fitted using quadratic polynomials. The polynomials were plotted together for all time points in the form of three-dimensional surfaces with time and force as independent variables (Figure 8). Positive values on the vertical axis represent excitatory effects.

For data obtained using protocol 2, 2 groups of responses were obtained, namely, autogenic and compound (Figure 1B). Force responses at two particular time points, the end of the ramp (the ‘dynamic’ response, as shown in Figure 2A-C) and the end of the hold-phase (the ‘static’ response, as shown in Figure 2D) were used to represent early and late effects of heterogenic reflexes (Nichols and Koffler-Smulevitz, 1991). For each experimental run, these points were graphed against the initial force (force averaged over 5–45 ms prior to stretch) of the donor muscle (Figure 2), since force-related heterogenic effects are correlated mainly with force of the donor muscle (Bonasera and Nichols, 1994; Nichols, 1999). The points for the autogenic and compound responses were then fitted with second order polynomials (see Figure 2). Confidence intervals (95%) were also computed for polynomials corresponding to autogenic responses or for polynomials corresponding to both autogenic and compound responses. Heterogenic effects were detected by significant differences between the polynomials corresponding to autogenic and compound responses.

In some cases, the confidence intervals for a pair of polynomials were overlapping or the data points for the compound responses fell within the confidence limits for the autogenic
responses. In this sense the two polynomials were considered statistically indistinguishable for the range over which they overlapped. Overlapping confidence intervals were observed under two conditions. First, when the mean values were very similar, the overlapping confidence limits indicated that for that range that the results were statistically indistinguishable. Second, when the range of background forces was so narrow that the confidence intervals were very wide, even substantial differences in mean were not statistically distinguishable. In the latter cases, the data were not included in subsequent analysis. Mechanical artifacts caused by mechanical interactions between muscles were detected by apparent heterogenic effects that were observed 10 ms after the initiation of stretch (Bonasera and Nichols, 1996). Data in which these artifacts exceeded 5% of the autogenic response were rejected.

For each complete run using protocols 2 and 3, a number was calculated to express the amount of inhibition or excitation found for that muscle combination. For protocol 3, the force responses for each trial were calculated and integrated from 10–300 ms post stretch. The resulting integrated value for the compound responses was normalized to the integrated value of the autogenic reflex responses and translated into a percentage. For protocol 2, the area under the compound fitted line was normalized to the area under the autogenic fitted line and expressed as a percentage increase or decrease. A positive percentage indicated excitation (compound force response larger than autogenic force response), whereas a negative number indicated inhibition. The lines were not extrapolated beyond the last data point and the area under the fitted lines was computed, taking only those points in which both of the fitted lines have valid interpolated values.

Three-dimensional surfaces were also computed for the results using protocol 2. Compound and autogenic responses were measured every 5 ms as described above for the data
using protocol 1. Second order polynomials were again computed for the compound and autogenic responses at each time point plotted against the initial forces in the donor muscle. The polynomials corresponding to the autogenic responses were then subtracted from the polynomials corresponding to the compound responses. The polynomials corresponding to these differences were then plotted together to form surfaces (Figures 1-3). For the comparison of heterogenic effects from different muscles, the differences were normalized to the autogenic responses and therefore represent a percentage change due to the heterogenic input. The polynomials corresponding to the normalized differences were plotted together for all time points in the form of three-dimensional surfaces with time and force as independent variables (Figures 6, 7 and 9).

Measurement of latency

The latency of the heterogenic feedback was estimated in the following manner. Pairs of single force records of the recipient muscle from the autogenic and the compound responses were matched with respect to their initial force levels. After removing the baseline from these traces they were plotted superimposed together with the calculated difference between the two traces. The latter was used as an aid to identify the time at which the two force traces diverge. Force traces were plotted on a time-expanded scale, concentrating on the region between −10 and +60 ms relative to stretch onset (Figures 2C and 2D). For each run up to 8 matches were automatically generated. The time at which the force traces diverged was recorded in a database from which averages and standard deviations were calculated. For cases in which the diverging point could not be satisfactorily estimated, the corresponding time-point would not be included in the average. This procedure was taken for results from protocol 2 as well as from protocol 3.
and these results were pooled together in the database.
RESULTS

*Short-Latency Excitation Between Vastus Muscles*

The heterogenic reflex effects among the vastus muscles were mainly excitatory under both quiescent and active conditions. An example of the excitation between VL and VM is shown in Figure 1A for the quiescent condition. Stretch of either muscle alone evoked an excitatory response in the other, isometric muscle. When both muscles were stretched, both responses were significantly enhanced. These excitatory effects were also observed under active conditions (Figure 2A and B) and were little affected by force or time. The excitation from VL to VM was greater than the reverse in some preparations, but this asymmetry was not consistently observed and did not reach statistical significance across preparations (Table 1). Excitation between VI and VM was also consistently found, and the strength was observed to be greater in the direction VI to VM (Table 1).

(Figure 1 near here)

Excitation was also observed between VL and VI (Table 1) but in the case of the reflex from VI to VL, the net excitation resulted from a balance between early excitation and late inhibition (Figure 2E-G). The excitation was marginally significant for the dynamic time point (Figure 2E), became larger following termination of the ramp, and then gave way to inhibition later during the hold phase (Figures 2F and 2G). Excitatory effects were found in 7 preparations, and the late inhibition was observed in 4 of these cases. In the remaining 3 cases, inhibition was suggested by declining excitation during the hold phase, and in one case the reflex remained excitatory with no decline throughout the hold phase.
The latencies of the excitatory reflexes among the vastus muscles were sharply defined (Figures 2C and 2D) and ranged between 18.6 and 20.8 ms, in agreement with the short-latency reflexes observed for other muscles in the cat hindlimb (Bonasera and Nichols, 1994; Nichols and Houk, 1976; Nichols, et al., 1999) and with the distribution of monosynaptic excitation for the quadriceps muscles (Eccles, et al., 1957). It was not possible to estimate the latency of the late inhibition from VI to VL, but the fact that this inhibition did not suppress short-latency excitation at high forces (Figure 2G) indicates that it was slower than other types of force-dependent inhibition (Nichols, 1999).

Mixed Excitation and Inhibition Between Vastus and Rectus Femoris Muscles

Heterogenic feedback from all vastus muscles included inhibitory and weak excitatory components. The inhibition was often present under quiescent conditions, often increased with initial force and could overcome the short-latency excitation. The strength of the inhibition is illustrated in Figures 3A, where the static response of RF is plotted against the initial force of the VI, the donor muscle. The inhibition was evident during the ramp, but also increased substantially during the hold phase (Figure 3B), suggesting a second component of inhibition. This later inhibition from VI was large enough to cancel the autogenic response of RF. The inhibition from VL and VM to RF was only marginally significant and weaker than that from VI and was in no case sufficient to cancel the autogenic response of RF (Figures 4A and 4B).
The reflexes from RF to V were similarly distributed. The strongest inhibition was found to extend from RF to VI. This inhibition increased with force and suppressed the short-latency excitation at higher forces (Figure 3C). The inhibition from RF to VL and VM was weaker and not strong enough to suppress the autogenic reflexes of these muscles (Figures 4C and 4D). These inhibitory reflexes could also be observed in some cases under quiescent conditions.

Evidence was obtained that the inhibition was sensitive to strychnine as is the case for reciprocal inhibition (Nichols and Koffler-Smulevitz, 1991) and force-dependence inhibition in other muscle groups (Bonasera and Nichols, 1994; Nichols, 1999). In one preparation, strychnine was injected intravenously in increments up to a total of 150 µg. The inhibition from RF to VL was reduced progressively with each additional dose (data not shown). The inhibition was reduced by approximately 80% after the final increment had been delivered.

**Latencies of heterogenic excitation and inhibition**

The statistical results of the analyses of latencies are summarized in Table 2. This table includes measurements for both excitation and inhibition for the activated as well as the quiescent runs. The table only contains the shortest latencies observed among the quadriceps muscles. We did not attempt to estimate the longer latencies because the departures were much less distinct. The data in Figure 3B suggest two phases of inhibition, but it was not possible to calculate the onset of the longer latency. Even though inhibition from VM to RF could be observed when comparing force traces at the end of the hold-phase, the excitation was usually stronger earlier in the response, making an estimate of the latency of inhibition difficult. Latencies were compared using a 2-way ANOVA. The excitatory and inhibitory pathways from RF to VL, RF to VM and VI to RF have
indistinguishable latencies (P<0.05). Latencies for excitation and inhibition were different only for RF to VI and for VL to RF (P<0.05).

Heterogenic reflexes from Quadriceps to Individual Triceps Surae Muscles

Following the investigation of heterogenic reflexes within Q, we studied the reflexes between Q and TS. Among the triceps surae muscles, the non-sagittal components of torque differ significantly (Lawrence and Nichols, 1999; Lawrence and Nichols, 1999; Lawrence, et al., 1993). In the case of the quadriceps, the vastus lateralis (VL) and vastus medialis (VM) muscles pull in different directions on the patella, but exert little non-sagittal torque on the tibia due to the patellar mechanism (Abelew, et al., 1996). We tested whether these mechanical complexities were represented in the strengths of heterogenic reflexes between individual quadriceps and triceps surae muscles. Figures 4E and 4F show that both VL and VM exert force-dependent inhibition on LG. Similar analyses were performed for all muscle combinations. There were no significant asymmetries attributed to the identity of the recipient or of the donor muscle. Since torque direction did not appear to have a major influence on the pattern of inhibition, we performed the remainder of the experiments on muscle groups defined by articulation, namely the single joint S and V, and the two joint G and RF.

Inhibitory Reflexes from Triceps Surae to Quadriceps Muscles

Stretch of either S or G resulted in inhibition of both V and RF (Figure 5). Excitatory effects were minimal or absent for all time points. The inhibition did not occur in temporally distinct components, but instead increased smoothly with time. To examine how heterogenic pathways from different donor muscles were integrated, combinations of donor muscles were stretched.
The responses of RF to the stretch of the triceps surae muscles were less than the sum of the inhibitory responses from S and G (Figure 5, A-C). The averaged percentage inhibition for both donors was -38%, while the sum of the two effects from S and G was 44%. Figure 5, D-F shows the heterogenic effects measured within one preparation from muscles of the triceps surae muscles onto the vastus muscle group (V). Stretch of S had an average inhibitory effect of 15% and of G, 26%. Stretch of both triceps surae groups led to an approximately summed inhibition of 44% (Figure 5C). This analysis was also performed at different time points with the same overall result (data not shown) and seems to hold true across the range of initial forces, indicating approximately linear summation of heterogenic feedback from S and G to V. In the accumulated data across preparations, nearly linear summation was observed for the vastus and quadriceps muscles, but not for RF alone. Given the large contribution of forces from V to the quadriceps group, the approximately linear summation of inputs from the triceps surae muscles to quadriceps muscles was probably due largely to the contribution of the vastus muscles. Nonlinear summation would be expected on the basis of cable properties (Burke, 1967; Rall, et al., 1967), but the factors that would affect the degree of linearity for the interactions investigated here are unknown.

The inhibition from the TS to the vastus muscles did not depend on the background force (Fo) of the donor to the same extent as did the inhibition to RF. This result could indicate that the inhibition for this muscle combination was not force dependent and did not arise from Golgi tendon organs. An alternative explanation is that the inhibition was from Golgi tendon organs.
but that the threshold to V was lower than for the inhibition to RF. It has been noted (Nichols, 1999) that when the threshold of force dependent inhibition from G to S is low, the inhibition achieves a maximum at low forces and therefore becomes independent of Fo. The data in Figure 5 is consistent with this explanation, since the inhibition of V in response to the stretch of G or the combined triceps surae muscles is large at low forces. In general, G contributed more inhibition to the quadriceps muscles than S (Figure 5).

**Heterogenic reflexes from quadriceps to the triceps surae muscles**

The heterogenic feedback from Q to S included excitation as well as inhibition. At low initial force, the excitation from V to S achieved substantial levels during the plateau (Figure 6A). This excitation occurred in two distinct phases, the first of which appeared with a latency of approximately 20 ms (Figure 6A). This excitation declined and was replaced by inhibition as force increased, although evidence of the excitatory component could still be discerned at high forces (Nichols, 1999). In the case of RF to S (Figure 6B), no excitation could be detected, in agreement with previous studies showing excitatory reflexes only between single joint extensors (Eccles and Lundberg, 1958). Inhibition appeared within 20 ms and increased during the plateau phase of the ramps up to approximately 125 ms following stretch. When RF and V were stretched together (Figure 6C), the excitatory and inhibitory components summed approximately linearly at low forces. At higher forces, the inhibitory components summed less than linearly.

(Figure 6 near here)

The inhibition from Q to G was purely inhibitory (Figure 6, D-F). The combined
percentage inhibition across preparations showed that the inhibition from the combined quadriceps muscles was no greater than the contributions of either RF or the vastus muscles. When the force responses were recorded from the combined triceps surae muscles (Figure 7), the heterogenic feedback was predominantly inhibitory as expected. The excitatory component from V to S was evident as a more rapid recovery of force in Figures 7A and 7C.

(Figure 7 near here)

The above analysis provided a description of the interactions between heterogenic inputs and the stretch reflex. These interactions could, in principle, include postsynaptic influences on motoneuron excitability as well as presynaptic effects of the heterogenic feedback on autogenic reflex gain and tonic sensory input. To determine whether the heterogenic input had an effect on the recipient motor neurons that was independent of autogenic reflexes, we stretched the donor muscles and measured the responses in the isometric recipient muscles (Protocol 1). Similar patterns of excitation and inhibition were observed when S and G were constrained isometrically, thereby minimizing autogenic reflexes (Figure 8). Combinations of excitation and inhibition were received by S from V, while the other heterogenic reflexes contained predominantly inhibitory components that increased with background force and declined with time (Figure 8, panels B – D). The inhibition was not evident at low initial forces since the isometric muscle was generating little or no force. As background force increased, the inhibition was not limited by the background force itself, indicating that the apparent force dependence did not result from saturation to zero net force. Another feature of the isometric responses was that the magnitudes of the inhibition were smaller than in the case of trials using Protocol 2. This difference was
likely to be due in part to the greater level of motor unit recruitment when the recipient muscle
was stretched. The inhibition of a population of larger motor units would have resulted in a
larger decrease in force than in the case of the isometric recipient muscle. However, a
contribution from presynaptic inhibition could not be excluded. A major role for postsynaptic
inhibition, however, was supported by the strychnine sensitivity of this inhibition (see above).

(Figure 8 near here)

During the second extension phase or E2 of the step cycle, the ankle and knee joints flex
and therefore all extensor muscles spanning these joints undergo stretch (Goslow, et al., 1973).
The hip joint does not yield, so all four quadriceps muscles presumably undergo similar length
changes. To investigate the influence these heterogenic reflexes associated with the triceps surae
and quadriceps muscles could potentially exert during this yield phase, the heterogenic input to
each muscle group was evaluated by using the remaining muscles as donors, which were
stretched simultaneously (Figure 9) according to protocol 2. The stretch amplitude of 2 mm used
in this study was similar to the magnitude of active lengthening during E2 for forward walking
(Goslow, et al., 1973). Although the extent of inhibition in intact animals is not known, the net
effects observed in this experiment illustrated (1) the extent to which excitatory and inhibitory
influences can potentially compete and (2) the relative influence of heterogenic inputs from local
and more distant muscles.

(Figure 9 near here)
The responses of S to stretch of the other three muscle groups consisted of excitatory components from V and G, and inhibitory components from G and Q (Figure 9A). In contrast, G received only net inhibition (Figure 9B; Figure 6). The known excitatory feedback from S to G may have reduced the onset of inhibition at low force and contributed to the recovery of force at longer times. The strong inhibition from the triceps surae to the vastus muscles was reflected in the profound and long-lasting inhibition resulting from the stretch of all three donors (Figure 9C). The excitation from RF was evident at low forces and early in the responses, but rapidly gave way to the large inhibitory influences from the three donors. The heterogenic inputs to RF were characterized by greater excitation and less inhibition than to the vastus muscles (Figure 9D). The substantial excitation most likely arose from the combined excitation from V. The net inhibition onto both V and RF remained larger during the hold phase than onto S and G, indicating the potential strength of force feedback from TS to Q.
DISCUSSION

We found consistent patterns of rapid excitatory and inhibitory feedback among the quadriceps and triceps surae muscles in intercollicular decerebrate animals. The distribution of these reflexes was similar to the organization of rapid feedback within the triceps surae muscle group, with two interesting differences that may be related to the greater disparity in function between members of the quadriceps muscles compared to members of the triceps surae group.

Mechanisms of heterogenic excitation

The patterns of excitation that we observed are generally consistent with the findings of Eccles and coworkers (Eccles, et al., 1957) on monosynaptic Ia connections in anesthetized animals and provide some additional details concerning these projections. In the latter study, VL and VM were grouped together as the vastus muscle. The vastus muscle was linked strongly to crureus muscle (VI) and both vastus and crureus muscles were linked weakly to RF. Our results confirm this weighting and add further detail since the four muscles were individually examined. The strongest excitatory feedback was found in the linkages among the vastus muscles. Strong pathways linked VL to VM, although the strongest excitation was in the direction VL to VM in some preparations. Strong excitation was also found from VI to VM. The weakest excitatory pathways within the vastus group were found to converge onto VI. Weaker still were the excitatory linkages between each vastus muscle and RF. These results indicate that the vastus muscles form a strong synergistic group with non-uniform synaptic weights. The only instance of heterogenic excitation across joints was found between V and S. A monosynaptic pathway from the vastus intermedius to S has been demonstrated electrophysiologically (Eccles et al., 1957). The present results indicate that this pathway is sufficiently strong as to be evident in the
reflex interactions among multiple muscles (Figure 10).

**Mechanisms of heterogenic inhibition**

Rapid heterogenic inhibition was distributed in a manner that was largely complementary to the distribution of excitation. This inhibition was absent among the vastus muscles, but present in the interactions between each vastus muscle and RF and between the quadriceps and triceps surae muscles. Only in the case of heterogenic reflexes from V to S was inhibition found to parallel excitation. The inhibitory reflexes among the quadriceps muscles were organized in a similar manner to the pattern previously observed for the triceps surae muscles (Nichols, 1994; Nichols, 1999), except that inhibition was bi-directional between V and RF. The lack of inhibition from VL and VM to VI along with previous motor unit studies (Dacko, et al., 1996), allows us to reject the hypothesis that the inhibition is organized according to motor unit type.

The latencies of rapid excitation and inhibition were not significantly different. They were all in the range of 16-25 ms, which compare favorably with previous estimates (Bonasera and Nichols, 1994; Nichols and Houk, 1976). As argued previously (Nichols, 1999), these latencies are consistent with pathways from group I and group II receptors. The similarity in distribution between the heterogenic excitation reported here and the monosynaptic pathways among the quadriceps muscles (Eccles, et al., 1957), suggests that the excitatory reflexes are dominated by pathways from group Ia afferents.

The force dependence of most of the rapid inhibitory reflexes observed here suggests that pathways from Golgi tendon organs play a prominent role in these linkages, although some contribution from group II pathways cannot be excluded. It is possible that longer latency components were present as well. Inhibition tends to develop slowly under similar conditions
(Nichols, 1999), so resolution of later components is difficult. The inhibitory response from VI to RF (Figure 4) appeared to comprise a short-latency and a stronger, longer latency component, but it was not possible to identify this later component as a separate reflex. For the case of VI to VL, the inhibition was present in only some preparations and comprised only a longer latency component. This late inhibition occurred with latency in the range of 80-100 ms and could have been mediated by afferents in the group III or IV range. This inhibition had the magnitude and time course of clasp-knife inhibition, but was distributed more locally than clasp-knife inhibition in cases of spinal injury (Cleland and Rymer, 1990; Nichols and Cope, 2001). In the case of spinal injury, the magnitude of clasp-knife inhibition is greatest in certain extensor muscles (Nichols and Cope, 2001), but it does project to most extensor muscles including the muscle of origin. In the present case, the long latency inhibition was observed to arise only from VI and project to VL and RF, but not to VM or itself. The present results suggest that, if the long-latency inhibition from VI to RF and VL does indeed arise from group III and IV afferents, that the associated interneurons have more specific and localized distributions than those associated with the clasp-knife reflex.

As was the case for the triceps surae muscles, the inhibitory actions observed among the quadriceps muscles were prolonged (Hayward, et al., 1988; Nichols, 1999). The inhibition did not decline rapidly during continued application of the stimulus as has been observed in the case of electrical stimulation (Heckman, et al., 1994; Lafleur, et al., 1993; Zytnicki, et al., 1990). Instead, the inhibition remained strong for the duration of the stretch (250 ms) and in some cases was strong enough to reduce the force response of the recipient muscle to zero (Figure 4B).

The strychnine sensitivity of this inhibition indicates that it is largely postsynaptic and glycinergic. Previous mechanographic studies have shown that many of the intermuscular
pathways evaluated under similar conditions are also strychnine sensitive. These reflexes include reciprocal inhibition between the tibialis anterior and soleus muscles (Nichols and Koffler-Smulevitz, 1991), force-dependent inhibition between the gastrocnemius and soleus muscles (Nichols, 1999) and force-dependent inhibition between the gastrocnemius and flexor hallucis longus muscles (Bonasera and Nichols, 1994). There is evidence that there are linkages mediated by presynaptic inhibition between Q and TS in the cat (Misiaszek and Pearson, 1997) and between hip, knee and ankle in the human (Brooke and McIlroy, 1985). Our data from both isometric and stretched recipient muscles do not exclude a role for presynaptic inhibition, but the accumulated evidence including the response to strychnine supports the hypothesis that postsynaptic inhibition does constitute an important component of the inhibition.

Although the inhibitory reflexes are most likely to be mediated largely by postsynaptic mechanisms, the possibility that they arise from recurrent pathways rather than proprioceptive pathways must also be addressed. The distribution of recurrent inhibition is generally organized to link muscles involved in stereotyped movements and locomotion (Hamm, et al., 1987; Turkin, et al., 1998). However, the effects of recurrent inhibition on motoneuron firing appear to be rather subtle (Lindsay and Binder, 1991) and not great enough to affect static gain (Maltenfort, et al., 1998). It is therefore unlikely that recurrent inhibition could produce a substantial inhibitory response. Finally, in animals selectively deprived of effective proprioceptive feedback by the reinnervation of muscles, force-dependent inhibition is absent along with stretch reflexes from the reinnervated muscles (Cope, et al., 1994). We conclude that the rapid, force dependent components of inhibition observed within and between the triceps surae and quadriceps muscles in the decerebrate cat result from actions of Golgi tendon organs.
Role of heterogenic feedback in postural regulation

Available evidence indicates that short-latency feedback is distributed according to architectural features of the musculoskeletal system (Eccles, et al., 1957; Nichols, 1994). Short-latency excitation links muscles that cross the same joint and that pull in approximately the same direction. Our results and those of Eccles et al. (Eccles, et al., 1957) indicate that the vastus muscles form a strong synergistic group, and that these muscles are only weakly linked to RF. Although the vastus muscles pull in different directions on the patella, the patellar mechanism redirects the forces of all the quadriceps muscles into a nearly pure line of pull on the patella (Abelew, et al., 1996).

The non-sagittal forces on the patella do have important functions within the knee joint mechanism, however. Deviations in patellar tracking can result in damage to the articular surfaces. Since VL and VM are the two muscles exerting large components of non-sagittal forces on the patella, these muscles are potentially very important for the correct tracking of the patella. The greater mass and potential force production of VL compared VM (Sacks and Roy, 1982) suggests that some mechanism other than similarity of mechanical properties might contribute to balancing the forces of these muscles on the patella. In some preparations, we found heterogenic excitation to be stronger in the direction VL to VM. This non-uniformity in heterogenic excitation complements the disparity in intrinsic properties and could result in equalizing the stiffnesses of the two muscles, resulting in balanced pull on the patella. The inhibitory pathway from VI to VL could further improve patellar tracking since VM does not appear to receive this inhibition. We therefore suggest that the vastus muscles function as a group to perform the task of knee extension and the associated heterogenic reflexes reinforce the stiffness of this muscle group. This interpretation is consistent with previous ideas and results.
concerning the reflex interactions of synergistic muscles (Eccles, et al., 1957; Lloyd, 1946) if the organizing principal is based on global action of the muscles on the joint rather than the individual lines of action of the muscles.

The weakness of the excitatory reflexes between each vastus muscle and RF observed here as well as in the electrophysiological studies of Eccles and coworkers (Eccles, et al., 1957) provides insights into the functional significance of short latency or monosynaptic excitatory reflexes. It might be concluded that the weakness of these pathways is associated with the dissimilar activation patterns of RF and the vastus muscles (Engberg and Lundberg, 1969; Rasmussen, et al., 1978). Similarly, it has been suggested that the pattern of monosynaptic Ia connections is correlated with muscular “synergies” in motor coordination (Caicoya, et al., 1999; Eccles and Lundberg, 1958).

Application of this argument to other muscle groups, however, leads to a different interpretation. The triceps surae muscles are often considered to be close synergists, and they exchange non-uniform but strong excitation (Eccles, et al., 1957). These muscles are activated during the stance phase at all speeds of locomotion (Rasmussen, et al., 1978) but become somewhat functionally dissociated at higher forces and higher speeds of locomotion (Fowler, et al., 1993; Walmsley, et al., 1978). These patterns are consistent with the strong Ia connectivity among the triceps surae muscles. However, the activation patterns diverge during stimulation of the caudal cutaneous sural nerve (Hagbarth, 1952; Labella, et al., 1989; Siegel, et al., 1999). A similar dissociation between Ia linkage and patterns of activation has been noted for the long toe flexors (Bonasera and Nichols, 1994; Dum, et al., 1982; O'Donovan, et al., 1982). Patterns of muscular activity during either voluntary movement or responses to cutaneous stimuli are clearly not restricted by these pathways.
In view of these and other data, it has been suggested that short-latency excitation contributes to the coordination of muscles during responses to postural disturbances rather than to patterns of voluntary activation (Nichols, 1994; Nichols, et al., 1999). In the case of triceps surae, monosynaptic inputs from all three muscles enhance the stiffness of LG and MG, and therefore strengthen the coupling between ankle and knee. In the case of the quadriceps, the coupling between knee and hip is not as strongly enhanced by reflex excitation of RF from the vastus muscles. During locomotion in the cat, the knee and ankle joints remain closely in phase throughout the step cycle, but the hip follows a somewhat different trajectory (Goslow, et al., 1973) in support of this interpretation. For example, the hip does not yield with the knee and ankle during the E2 phase of locomotion. These differences in coordination during the loading response correspond to the differences in strength of excitatory feedback in the two muscle groups.

The observed distribution of inhibitory force feedback indicates that the underlying pathways do not serve to modulate strength of contraction of anti-gravity muscles in a global and uniform manner. In addition, inhibitory force feedback does not appear to interfere with the coactivation of antigravity muscles. Instead, the non-uniform pattern of these pathways suggests a role in governing interjoint coordination (Nichols, et al., 2002). The force feedback between the triceps surae and quadriceps groups parallels mechanical linkages of biarticular muscles between ankle and knee joints. Dorsiflexion of the ankle causes a mechanically mediated flexion moment at the knee through the gastrocnemius muscles and a neurally mediated decrease in knee extensor moment due to inhibition of the quadriceps muscles (Nichols, et al., 1999). Both mechanical and neural effects tend to distribute the perturbation between these joints and equalize the impedances of the two joints. The previously described inhibition from the
gastrocnemius to soleus muscles (Nichols, 1994) promotes this coupling of ankle and knee by suppressing the responses of the uniarticular soleus muscle in favor of the biarticular gastrocnemius muscles. The bilateral inhibition between the rectus femoris and vastus muscle can be interpreted as reducing the coupling between hip and knee, which action is consistent with the more independent motions of these two joints during locomotion (Goslow, et al., 1973).

Cross joint excitatory feedback observed during these studies was also non-uniform in that it was essentially uni-directional from the vastus to the soleus muscles. This linkage does not parallel mechanical linkages between knee and ankle, because forced flexion of the knee would lead to an enhancement of the extensor moment at the ankle rather than the reduction that would accompany unloading of the gastrocnemius muscles. This pathway would also tend to accentuate differences in impedances of the two joints rather than equalize them (Nichols, 1994). This action would be potentially disruptive of coordination if the pathway were to extend from the soleus to vastus muscles, but excitation in this direction was either small or masked by inhibition in these studies (see above). In the observed case of a proximal distal projection, the action would be to enhance the mechanical contributions of the lighter, more distal segments to the net response of the limb to gravitational loads in a manner that would depend upon the extent of yielding of the knee. We suggest that the excitatory pathways that project distally among uniarticular muscles compensate for the large proximal to distal gradient in the masses of limb segments (Hoy and Zernicke, 1985).

The more prolonged actions of inhibitory force feedback over those of excitatory length feedback have implications for the dynamics of postural responses. The issue of stability has recurred in the literature and is potentially most critical in the presence of feedback (Prochazka, 1996; Rack, 1981). The necessity for stretch reflexes to have low gain is often cited. A more
contemporary idea is that the gain of stretch reflexes automatically decreases due to the history-dependent properties of muscles and muscle spindle receptors (Lin and Rymer, 2000). A neglected idea (Granit, 1950) states that the inhibitory effects of force feedback could help stabilize the limb in the face of potentially destabilizing stretch reflexes. The impedance of the whole limb would depend upon the summed effects of length and force feedback (Houk, 1979; Nichols and Houk, 1976), but the different time courses of the two kinds of feedback would favor higher compliance and enhanced coupling between limb segments following an initially stiff response. These effects of force feedback would, in principle, become more important at higher forces.

State dependence

During locomotion, the pathways described here apparently become integrated with widespread excitation from oligosynaptic linkages from muscle spindle receptors and Golgi tendon organs (Pearson, 1995). It has been claimed that inhibitory force feedback is actually replaced by positive force feedback (Prochazka, 1996), but this exclusion has not been demonstrated for all muscle groups and behavioral conditions. During fictive locomotion, group I excitation evoked by stimulation of muscle nerves extends from triceps surae muscles to other muscles within that group as well as to quadriceps muscles (Angel, et al., 1996; Guertin, et al., 1995). Excitatory actions in the direction quadriceps to triceps surae, however, were often small or inhibitory (Guertin, et al., 1995). In a study of locomotion in premammillary decerebrate cats (Whelan, et al., 1995), electrical stimulation of nerves from vastus lateralis and intermedius muscles evoked responses in the triceps surae muscles of variable sign. Studies utilizing intermuscular stimulation in standing, intact animals (Pratt, 1995) showed variable inhibitory and
excitatory feedback for muscles in the triceps surae group. In view of the variability of these results and the variety of experimental conditions and preparations, the issue of exclusivity of these pathways remains unclear. Recent mechanographic data suggest that group I excitation during locomotion is predominantly autogenic, while heterogenic force feedback remains inhibitory (Ross, in press; Ross, et al., 2002). In most of the quoted studies, mixed effects were noted. Indeed, the presence of competing pathways from skin and muscle proprioceptors during normal movement would seem to be the normal mode of operation (Duysens, et al., 1992; Lundberg, et al., 1987). In the intercollicular decerebrate cat, inhibitory force feedback does not interfere with the coactivation of antigravity muscles, but can serve to coordinate responses among them (Nichols, et al., 2002). This coordinating system could co-exist with excitatory pathways that globally modulate the level of force of the antigravity apparatus.

ACKNOWLEDGMENTS

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Tables
Table 1: Magnitudes of heterogenic reflexes among the vastus muscles in percentage change. For each animal a mean value for each interaction was generated. These means were pooled across the preparations and median and ranges are given in this table.

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<th>VL</th>
<th>VM</th>
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<td>10.3</td>
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<td>Range</td>
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<td>-</td>
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<td>4</td>
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Table 2. **Latencies of heterogenic pathways for quadriceps muscles.** Latencies were measured from the onset of stretch to the departure of the compound response from the autogenic response (see Methods). Mean and standard deviations are reported with the sample size bracketed.

† No instances were found in which the short latency inhibition from VM to RF was strong enough compared to the short latency excitation to evaluate the latency of the reported heterogenic inhibition.

‡ Excitation was in all instances stronger than the inhibition, therefore the latency of inhibition could not be measured, but was consistently larger than the excitation reported for this muscle combination.

<table>
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<td>VL</td>
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<td>20.8 ± 3.1 (14)</td>
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<td>Inh.</td>
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<td>-</td>
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<td>Inh.</td>
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Figures
Figure 1. **Illustration of experimental protocols and data analysis.**

A) Portion of data from VL and VM are shown using protocol 3. Filled markers (● = VL; ■ = VM) indicate autogenic response and open markers (○ = VL; □ = VM) designate force responses due to autogenic plus heterogenic reflexes (compound responses). Bottom two graphs are averaged responses for both muscles, with the standard deviations shown on each curve in dotted lines. The responses that remain unmarked are the isometric force responses of the recipient muscle that result from stretching the donor muscle. Baseline forces were subtracted. The vertical dashed lines indicate the limits for integration (10 to 300 ms following initiation of the ramp).  

B) Force responses of RF using protocol 2 during a crossed-extension reflex. The donor muscle was VI. The surface shown in the bottom panel displays the excitation (positive deflection on z-axis) as a function of time and the initial force (Fo) of the donor muscle. The excitation was computed by subtracting the quadratic polynomials fitted to specific time points of the autogenic responses from corresponding polynomials fitted to the compound responses (see Methods). Muscles were stretched from 50–100 ms after which they were held at constant length from 100 to 350 ms.
Figure 2. **Heterogenic excitation among the vastus muscles.**

A) Dynamic responses are shown for interaction from VL to VM. The autogenic (●) and compound (○) dynamic responses to 2 mm stretches were fitted with quadratic polynomials and 95% confidence limits. The inset shows two force traces of VM at matched starting levels. The solid line represents autogenic response and the dotted line represents the compound force response to 2 mm length change. Major tick marks on inset are 5 N apart. **B)** Same as A with interaction from VM to VL. **C)** and **D)** Time expanded views of overlapping force traces from insets of A) and B), respectively, to better estimate latencies of heterogenic reflexes. **E)** Same as Fig. 2A, with dynamic response shown for interaction from VI to VL, as indicated in inset. **F)** Same as A, but with static interaction shown for same preparation. These data indicate that the reflex response was dominated first by excitation and then inhibition. **C)** A surface, computed as shown in Figure 1, showing the transition from excitation during the beginning of the stretch phase to inhibition towards the end of the hold phase and the force dependence of the inhibition. The vertical axis refers to absolute differences between the compound and autogenic responses.
Figure 3. Heterogenic reflexes between vastus intermedius and rectus femoris muscles.

A) Force dependence of inhibition from VI to RF, showing static responses. B) Two force traces of RF in response to a 2 mm stretch. The solid trace is the autogenic response, whereas the dotted trace the compound response. Tick marks indicate 5 N. The time scale shown is 500 ms. C) 3-D plot for the reflex effects from RF to VI, showing mixed excitation and inhibition. The vertical axis refers to the absolute difference between compound and autogenic responses.
Figure 4. Examples of inhibitory reflexes among the quadriceps and triceps surae muscles.

All plots depict the static responses of recipient muscles plotted against the initial forces in the donor muscles. Points corresponding to autogenic reflexes (?) are fitted by quadratic polynomials with confidence limits. Points representing compound responses (?) are fitted by quadratic polynomials (dashed lines). Panels A-D depict reflexes between vastus and rectus femoris muscles. Panels E and F illustrate force dependent reflexes between VL or VM and LG.
Figure 5. **Summation of heterogenic reflexes from the triceps surae to the quadriceps muscle groups.** Each panel shows plots of static responses versus initial force for autogenic (?) and compound responses (?) of the indicated muscles. The points were fitted using quadratic polynomials with 95% confidence limits. In panels A and D, the confidence limits for the two groups were substantially overlapping, so the limits for the autogenic responses only are shown for clarity. Negative numbers on the lower right of each panel indicate the percentage inhibition due to the heterogenic effects. Contributions of individual triceps surae muscles to compound responses of RF are shown in panels A-C and to V in panels D-F.
Figure 6. **Heterogenic reflexes from the quadriceps to subgroups of the triceps surae muscles.** These three dimensional plots show the percentage increase (excitation) or decrease (inhibition) of compound responses over autogenic responses. The plots were created from differences between the quadratic polynomials fitted to compound and autogenic responses at 5 ms intervals throughout the responses. The resulting surfaces show the dependence of heterogenic reflexes on force and time. The reflexes from the quadriceps muscle group and its components to the soleus muscle (S) are shown in panels A-C, and to the gastrocnemius muscles (G) in panels D-F.
Figure 7. **Heterogenic reflexes from the quadriceps muscles to the triceps surae muscle group.** The plots were constructed similarly to those shown in Figure 6, and show the contributions of subgroups of the quadriceps onto the triceps surae muscle group.
Figure 8. **Heterogenic reflexes from subgroups of the quadriceps muscles to subgroups of the isometric triceps surae muscles.** These plots show the dependence of isometric force in response to stretch of the donor muscles (Protocol 1) on force and time. Responses of S are shown in panels A and B, and responses of G are shown in panels C and D.
Figure 9. **Heterogenic reflexes from combinations of three muscle groups.** These plots are similar to those shown in Figures 6 and 7. They show the combined heterogenic reflexes from three of the four muscle subgroups onto the fourth to illustrate the predicted effects in the intact limb.