

Muscular sense is attenuated when humans move

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1. Muscle receptors play an important role in our conscious perception of movement, but there are no published accounts of our ability to detect their signals during different motor tasks. The present experiments introduce a method to test muscular sense when humans move.
2. Muscle receptors were excited by an electrically induced twitch of the right extensor carpi ulnaris muscle. The muscle was stimulated via percutaneously inserted intramuscular electrodes or using surface stimulation through anaesthetized skin. Muscular sense was represented by the ability to detect the twitch and was compared between various tasks and stationary control trials.
3. Three hertz voluntary wrist movements significantly attenuated muscular sense to 37% of control. This velocity-dependent attenuation was present over a range of twitch amplitudes suggesting it does not simply reflect a masking of low intensity stimuli. Perceptual ratings of twitch amplitude during fast imposed passive movements were reduced by 40%, though this did not quite reach statistical significance. However, perceptual ratings of twitches evoked up to 2 s after the termination of the passive movements *were* significantly different from control.
4. Reaching with the stimulated, but not the contralateral, arm also significantly reduced muscular sense (to 40%).
5. Attenuation to 58% of control during cyclic stretching of the skin on the dorsum of the hand showed that signals from peripheral receptors may play a role. Attenuation prior to a single wrist flexion movement indicated that central sources can also contribute.
6. The results are consistent with current findings of a general attenuation of sensory feedback during movement and raise questions regarding the role of muscular sense in movement control.

Human 'muscular sense' refers to our remarkable ability to perceive the position and movement of our body segments without the aid of vision. Nearly a century ago Sherrington believed that this ability, now commonly referred to as kinaesthesia, originated primarily from sensory receptors located in skeletal muscle (Sherrington, 1900). These receptors, which also play other important roles in movement control, include the Golgi tendon organ and the muscle spindle. Muscle receptors are still thought to play a crucial, if not dominant, role in kinaesthesia (Goodwin, McCloskey & Matthews, 1972; Gandevia, 1996). Therefore, one might expect that, during movement, the neural pathways mediating muscle receptor signals would remain open to faithfully transmit this information through the central nervous system. However, some previous evidence suggests that this may not be the case. The amplitude of somatosensory evoked potentials (SEPs) recorded through the scalp arising from primarily cutaneous (Abbruzzese, Ratto, Favale & Abbruzzese, 1981; Rushton, Rothwell & Craggs, 1981) and muscle (Grunewald, Grunewald-Zuberbier, Schuhmacher, Mewald & Noth, 1984; Staines,

Brooke, Cheng, Misiasek & Mackay, 1997a) receptors is generally smaller during limb movements than in static conditions. While the size of these potentials may not correspond directly to conscious perception, the ability to detect signals from cutaneous receptors is certainly reduced during movement (Angel & Malenka, 1982; Milne, Aniss, Kay & Gandevia, 1988). Generally, cutaneous input has been equated to 'exteroception' (Edin, 1992), that is the signalling of external stimuli applied to the body, though mounting evidence indicates a significant kinaesthetic role as well (Edin, Essick, Trulsson & Olsson, 1995; Collins & Prochazka, 1996).

Muscle receptors play an important role in our conscious perception of movement (Sherrington, 1900; Goodwin *et al.* 1972; Gandevia, 1996), but there are no published accounts of our ability to detect their signals in different motor tasks and contexts. This represents a significant void in our knowledge regarding how sensory feedback is used to control movement. The present experiments introduce a method to test muscular sense when humans move.

METHODS

Nine subjects (7 male and 2 female) aged 26–50 years participated. All were informed volunteers with no history of neurological or skeletomotor disease. Experiments were conducted in accordance with the Declaration of Helsinki and the University of Alberta Hospitals Ethical Committee. Subjects were seated comfortably and were informed that the study was designed to investigate the way humans perceive sensations from the arm.

Muscle stimulation

Muscle receptors were excited by an electrically induced twitch of the right extensor carpi ulnaris muscle (ECU). The stimulus was delivered using a custom-made, constant-current stimulator which delivered a single, biphasic, 100 μ s pulse. The stimulation site was selected to provide the purest wrist extension, determined by visual inspection of the motor response to a 33 Hz train of suprathreshold stimuli.

It was critical to these experiments that the twitch excite primarily muscle receptors. It is unlikely that the evoked twitch recruited a significant population of joint receptors as these tend to fire at the extremes of joint rotation (Burgess & Clark, 1969) and at high compression forces (Johansson, Sjolander & Sojka, 1991). However, it was clear that the electrical stimulation, though producing very small twitches, could excite some skin and hair follicle receptors. Two techniques were used to minimize or abolish this unwanted excitation of cutaneous receptors. (1) In four subjects the ECU was stimulated via fine intramuscular electrodes inserted percutaneously (Basmajian, 1974). (2) In five subjects the muscle was stimulated with surface electrodes (ConMed Versa-stim, 5 cm \times 3.5 cm) through locally anaesthetized skin. Anaesthesia was achieved by applying a thick layer of 2.5% lidocaine (lignocaine) cream (Emla) over the extensor surface of the forearm prior to an experimental session. This was covered with an occlusive dressing for 2 h. The extent of the anaesthesia was then tested using Semmes-Weinstein monofilaments (Bell-Krotoski & Tomancik, 1987). A thin layer of cream was left on throughout the experiment. This effectively abolished input from all but the deep pressure receptors for the duration of an experimental session (2–4 h). Any visible twitch-related skin movement was always well within the anaesthetized area.

Twitch amplitude was monitored using one or two 5 g accelerometers (Analog Devices) taped to the skin overlying the ECU to measure the evoked movement. Signals were AC coupled (first-order filter; corner frequency, 0.1 Hz) and low-pass filtered (second-order filter at 30 Hz). Peak-to-peak amplitudes were calculated over a defined latency after stimulus delivery. During the intramuscular stimulation experiments the electromyographic (EMG) activity associated with the twitch was also recorded using surface electrodes (Jason Electrotrace). The large stimulus artifact during the surface stimulation precluded useful EMG recording during those experiments.

Experimental protocol

Subjects indicated verbally each time they perceived the muscle twitch. Stimulus intensity was set at a level to evoke a twitch in the stationary arm which subjects could clearly perceive 100% of the time. Twitch amplitude varied between subjects from barely distinguishable to the human eye to clearly discernible; however, it rarely resulted in visible wrist movement. During the intramuscular stimulation experiments subjects were asked to report each time they clearly perceived a muscle twitch. For a given task, muscular sense was represented by the number of twitches identified divided by the total number delivered. During the

surface stimulation experiments, subjects reported twitch intensity on a subjective scale. Initially, they were presented with a series of twitches delivered at rest and told to 'calibrate' the intensity of the twitches as a numerical rating of 5. Subjects then reported the twitch intensity in whole numbers relative to this static rating. Muscular sense was represented by the mean numerical rating during a given task. Twenty twitches were evoked during a block of trials. One to eight blocks of trials were conducted for each task during which twitches were evoked randomly at intervals ranging from 2 to 10 s. Static control values were calculated from blocks ($n = 2$ –10) of trials interspersed throughout each experiment during which subjects remained relaxed and stationary. In all trials in which the wrist was stationary, twitches were evoked with the wrist at approximately 180 deg.

Tasks

Cyclic wrist movement. Muscular sense was examined during cyclic wrist movements in seven subjects. During all trials the forearm and hand were restrained to ensure that the movement was restricted to the wrist. Subjects were requested to report muscle twitches while making fast (3 Hz) or slow (1 or 1.5 Hz) voluntary flexion–extension movements of the right wrist (45 deg joint excursion) in time to a metronome. Muscular sense was also examined while subjects remained fully relaxed and movements were driven by a linear servomotor through a similar velocity and range of motion as the fast voluntary movements. In five subjects twitches were evoked 0.5, 1 or 2 s (3 subjects only) after the abrupt termination of these passive movements.

Muscular sense was examined during the 3 Hz voluntary wrist movements at three twitch amplitudes in five subjects. Stimulus intensity was adjusted to evoke a twitch which stationary subjects rated as approximately 2, 5 or 8, relative to twitches in previous trials. They then rated the twitch during a block of wrist movement trials at each of the three twitch amplitudes. Presentation order of the blocks was randomized across subjects.

Reaching. To investigate muscular sense during a more natural movement, which may be more reliant on feedback from muscle receptors, subjects ($n = 8$) were requested to reach out to touch or grasp a target in front of them from a starting position with the arm at rest beside them. Separate blocks of trials were conducted during which subjects performed the self-paced reaching movements with either the stimulated (ipsilateral) or the contralateral arm.

Skin stretch. The potential contribution from signals originating in the periphery was investigated using a skin-stretch technique developed in our laboratory (Collins & Prochazka, 1996). Small pieces of adhesive tape were stuck to the dorsum of the right hand distal and proximal to the metacarpophalangeal joints of all the fingers in five subjects. The skin was then cyclically stretched at 3 Hz to evoke discharges from these receptors mimicking those during fast finger movements.

The final two tasks were designed to investigate the potential contribution from central sources. Twitches were evoked when subjects were stationary, thus at a time when there was no movement-evoked re-afference.

Counting. For this task, five subjects were requested to continuously count backwards from 100 in threes.

Reaction time. In the final task we investigated the time course of the gating of muscle sensation during the interval just prior to a single flexion–extension movement of the right wrist. Five subjects performed a simple reaction time task whereby two audible tones separated by 1 s provided the warning signal (WS) and the

response signal (RS) to initiate the wrist movement. In approximately 5% of the trials no RS was presented to minimize subject anticipation. In a similar percentage of the trials no stimulus was delivered to minimize anticipation of the twitch. In each subject, 120–160 twitches were delivered randomly in the interval between the WS and just after termination of the movement. Combined data from four to five blocks of ten twitches interspersed throughout these trials were used for the static control. For each subject the data were sorted, *post hoc*, into 50 ms bins based on the time of stimulus delivery relative to movement onset (not EMG onset) and averaged.

Data analysis

Visual inspection of the data collected using the two muscle stimulation techniques showed qualitatively similar results. Therefore, data from trials common to both experiments were combined for statistical analysis. The data were normalized to the appropriate static control trial. Changes in muscular sense were represented by per cent changes from the control levels. Statistical tests on combined data were conducted on the normalized values using Friedman’s one-way repeated measures on ranks (Friedman’s

ANOVA) followed by Student–Newman–Keuls *post hoc* multiple comparisons test to identify significant differences. Statistical analysis for tasks examined in the surface stimulation experiments only (tasks examined in only 5 subjects) and on all accelerometer data was conducted on the raw data using one- or two-way repeated measures analysis of variance (RM ANOVA) followed by *post hoc* multiple comparisons tests as above. Pairwise comparisons were made using Student’s paired *t* tests or Wilcoxon signed-rank tests when tests for normality or equal variance failed. Statistical significance was accepted when $P < 0.05$.

RESULTS

Twitch amplitude

The amplitude of the evoked twitch was monitored by accelerometers mounted over the muscle belly in all subjects and also by surface EMG recording in four subjects. Examples of the accelerometer signals during single trials are shown in the middle panels of Figs 1A and 4A during the wrist movement and reaction time tasks, respectively.

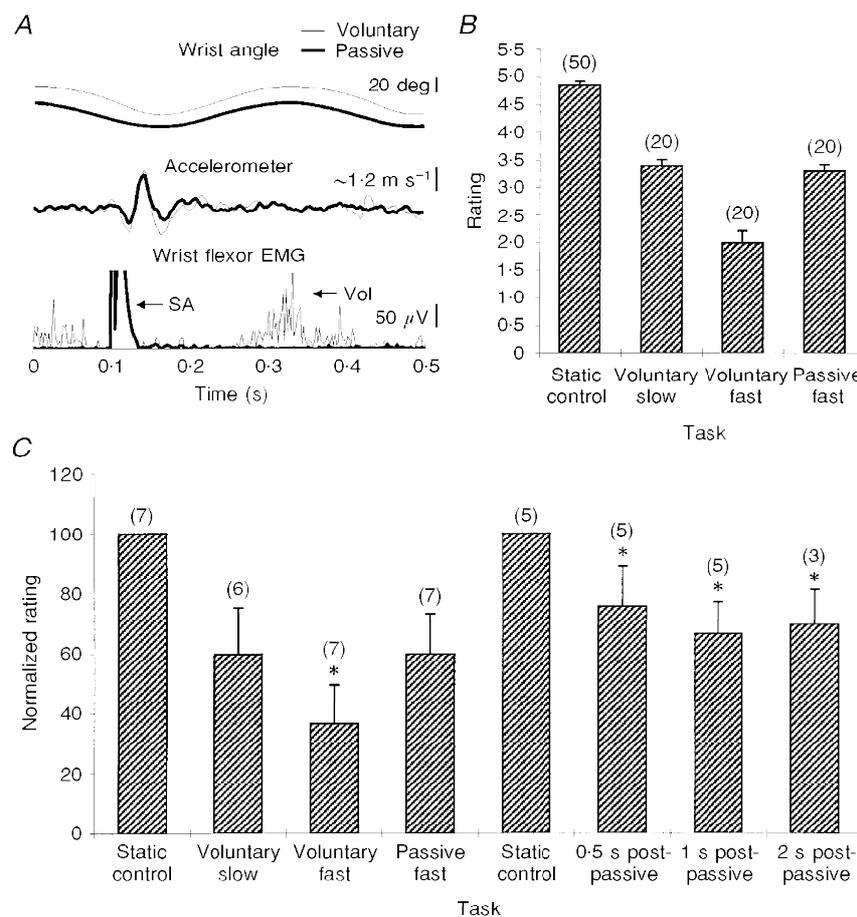


Figure 1. Attenuation of muscular sense by wrist movement

A, raw data for one subject during fast voluntary (thin line) and passive (thick line) movements. Wrist angle (flexion downwards), accelerometer signals and wrist flexor EMG are shown in the top, middle and bottom panels, respectively. Stimulus artifact and voluntary EMG activity are denoted by SA and Vol, respectively. B, mean rating of twitch amplitude for the subject in A. The number of muscle twitches contributing to each mean is given in parentheses. C, mean ratings across all subjects. The number of subjects contributing to each mean is given in parentheses. Asterisks denote significant differences from control. Error bars depict one standard error about the mean.

There were no significant differences across subjects in twitch amplitude between each movement task and its corresponding control trial as measured by either technique.

Cyclic wrist movement

Our first aim was to establish whether human muscular sense is attenuated during simple wrist movements. Figure 1A depicts raw data for one subject from the surface stimulation experiments during the fast voluntary and passive movements. The wrist angle, accelerometer signal and wrist flexor EMG activity are shown. The time of stimulus delivery for both movements is indicated by the large stimulus artifact in the EMG traces. This was followed by the evoked twitch seen in the accelerometer traces and then by a burst of EMG activity (in the voluntary movement trace only). Mean subjective ratings of twitch amplitude for this subject are shown in Fig. 1B. The wrist movements reduced muscular sense in this subject to 41, 70 and 68% of control for the fast and slow voluntary movements and the passive movements, respectively. Across all subjects, the fast voluntary movements reduced muscle sense to 37% of control, which was significantly different from the static control and both other movement conditions (Friedman's ANOVA; Fig. 1C). However, the reduction (to 60%) during the slow voluntary and the passive movements was not significantly different from control. In contrast, muscular sense was significantly attenuated 0.5, 1 and 2 s after the passive movement ended (RM ANOVA).

In general, throughout these experiments the results were consistent within subjects but quite variable between subjects. On only three occasions through all the

experiments in this study did a subject report a twitch when none was presented.

The effect of movement phase on the gating of ascending muscle afferent signals was investigated using the data from five subjects. Active and passive 3 Hz wrist movement trials were sorted according to the movement phase in which the twitch was delivered. Movements were divided into four phases. Flexion and extension phases were defined as those in which movements were in the appropriate direction and were through the mid-range of joint excursion (approximately ± 20 deg about the mean). The flexed and extended phases included the transitions in movement direction within approximately 15 deg of the corresponding maxima. There were no significant differences between twitch ratings at the different movement phases during either the active or passive movements (RM ANOVA). During active movements mean twitch ratings across subjects (± 1 s.e.m.) were 1.9 ± 0.8 , 2.0 ± 0.8 , 2.4 ± 0.8 and 2.6 ± 0.9 when the twitch was delivered during the flexion, flexed, extension and extended phases, respectively. Comparable twitch ratings during the passive movements were 2.1 ± 0.8 , 2.8 ± 0.9 , 2.5 ± 0.9 and 2.7 ± 0.8 .

Muscular sense was examined during the fast voluntary wrist movements at three twitch amplitudes. Raw data for one subject are shown in Fig. 2A. Across all subjects twitch perception was reduced to 65, 51 and 58% of the stationary control for the small, medium and large amplitude twitches, respectively (Fig. 2B). Statistical analysis (two-way RM ANOVA) identified a significant main effect of task and no significant interaction between task and amplitude. Multiple

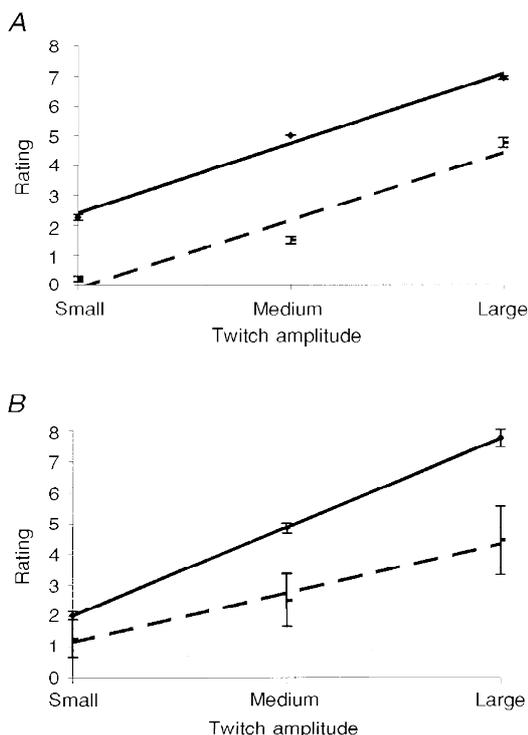


Figure 2. Effect of wrist movement on muscular sense at three twitch amplitudes

Mean rating of small, medium and large amplitude twitches for one subject (A) and across all five subjects (B) during 3 Hz voluntary wrist movement (■) and stationary controls (◆). Dashed and continuous lines depict the best-fit lines for the movement and stationary trials, respectively. Error bars depict one standard error about the mean.

comparisons tests showed that the difference between tasks (i.e. static *versus* movement) was significant at all three twitch amplitudes.

Reaching

Reaching with the arm being stimulated totally abolished the perception of muscle twitches in one subject (Ipsilateral reach in Fig. 3A) and reduced twitch perception to 40% of control values across all subjects, which represented a significant attenuation on both control and contralateral reaching values (Friedman's ANOVA; Fig. 3B). The contralateral reaching task reduced twitch perception to 13% of control in the subject in Fig. 3A. However, in five of the other seven subjects twitch perception remained within 5% of the static control value and muscular sense was not significantly attenuated from control during this task (Fig. 3B).

Skin stretch

Cyclic stretching of the skin on the dorsum of the hand reduced the ratings of twitch perception to 19% of control in the subject in Fig. 3A. Muscular sense was significantly reduced to 58% of control across all subjects (paired *t* test; Fig. 3B).

Counting

To test whether the attenuation of twitch perception was a non-specific attentional mechanism, we asked subjects to count backwards in threes from 100. Against expectations, this did not result in significant reductions in perceptual ratings. Thus in Fig. 3A, the mean rating was reduced to 94% of the corresponding static control in one subject, but across subjects muscular sense was not significantly reduced from control (Wilcoxon signed-rank test; Fig. 3B).

Reaction time

Raw data from a typical reaction time trial are presented in Fig. 4A. The wrist angle, accelerometer signal and the wrist flexor EMG are shown. During this trial the muscle twitch was delivered 116 ms (at the time labelled SA in EMG trace) prior to wrist movement.

Attenuation of muscle sense prior to movement was seen in all five subjects. Mean twitch ratings for one subject are shown in Fig. 4B. Statistical analysis across all subjects showed that the attenuation was significant throughout the preparation to move (RM ANOVA; Fig. 4C). Over the six bins during the interval up to 100 ms before movement

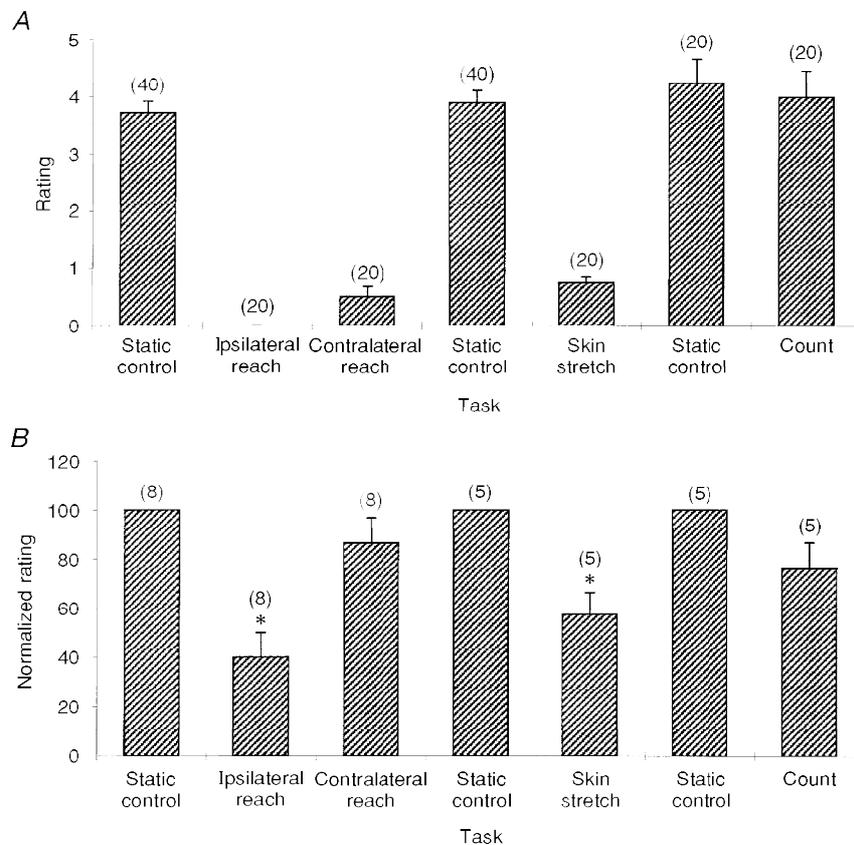


Figure 3. Attenuation of muscular sense during other tasks

A and B, mean twitch rating for one subject and across all subjects, respectively. In each graph the appropriate static control rating precedes the corresponding experimental trial. The number of muscle twitches and subjects contributing to each mean, respectively, is given in parentheses. Asterisks denote significant differences from control. Error bars depict one standard error about the mean.

onset muscular sense was reduced on average to 72% of control. Each of these bins was significantly attenuated from control but they were not significantly different from each other. Twitch perception then fell to 38% of control 50–99 ms before movement and to 15% during the final 50 ms before movement. Each of these two bins was significantly different from all preceding bins. Twitch perception remained significantly attenuated during and after movement, compared with the static control.

DISCUSSION

Sensory feedback from receptors located in skeletal muscle has long been thought to underlie our conscious perception of movement (Sherrington, 1900; Goodwin *et al.* 1972; Gandevia, 1996). The present experiments reveal that our ability to detect this feedback is reduced just before, during and after simple hand movements and that the attenuation arises from both peripheral and central sources. The results

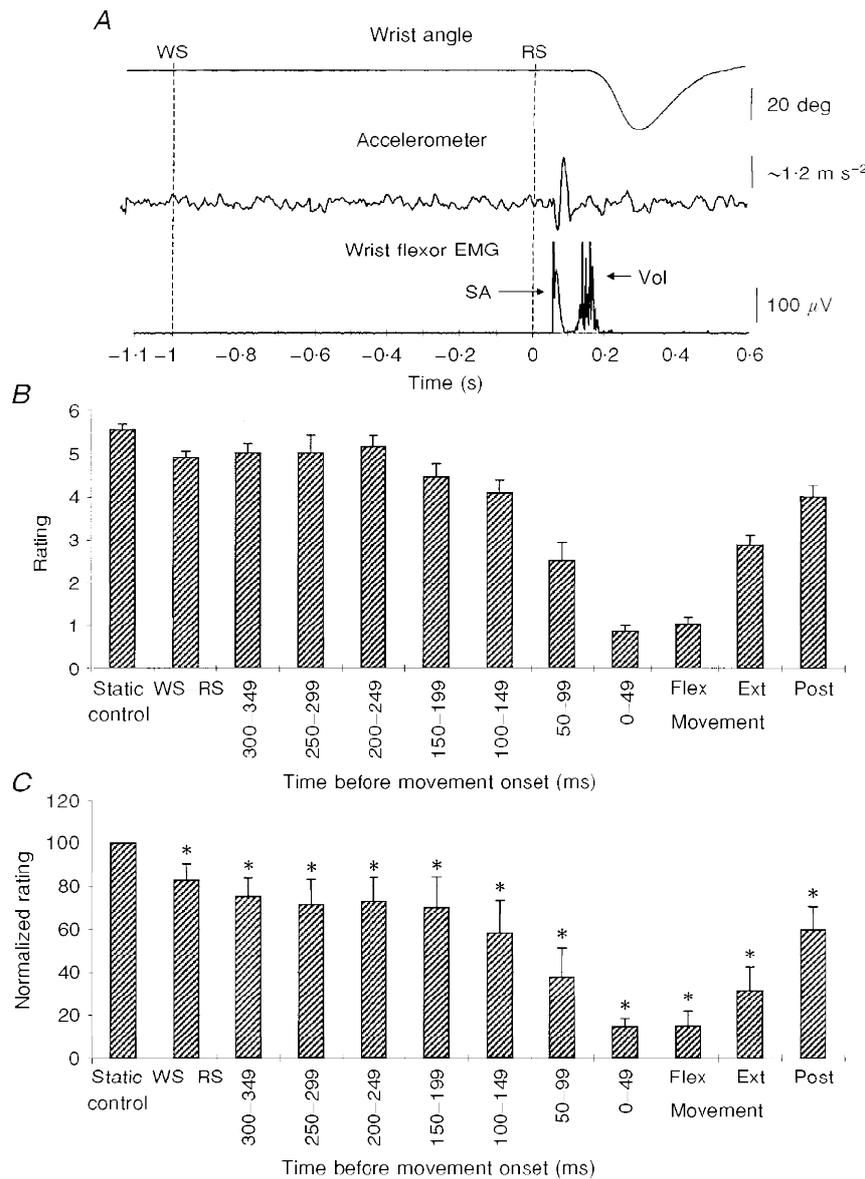


Figure 4. Attenuation of muscular sense before movement

A, raw data from a typical trial showing wrist angle (flexion downwards), accelerometer signal and wrist flexor EMG in the top, middle and bottom panels, respectively. This trial shows the warning signal (WS) followed 1 s later by the response signal (RS) after which the subject responded with a single flexion–extension movement at the right wrist. Stimulus artifact and voluntary EMG activity are denoted by SA and Vol, respectively. B, mean rating of twitch amplitude, relative to movement onset, for one subject. C, mean rating of twitch amplitude across all five subjects. Asterisks denote significant differences from control. Error bars depict one standard error about the mean. Flex, flexion; Ext, extension; Post, post-movement.

are consistent with current findings of a general attenuation of sensory feedback during movement (Prochazka, 1989; Brooke, Cheng, Collins, McIlroy, Misiaszek & Staines, 1997) and raise questions regarding the role of muscular sense in the control of movement.

Our results were not simply due to differences in the amplitude of the evoked twitch between tasks or signals evoked in non-muscular receptors by the muscle twitches. Two methods were used to monitor the constancy of twitch amplitude. Accelerometers mounted over the muscle belly recorded the mechanical event and, when possible, surface EMG recorded the electrical event. The amplitude of the evoked twitch, as measured by both techniques, was not significantly different between the various movement tasks and the corresponding static control. Two methods were used to avoid or minimize cutaneous receptor excitation. The first method bypassed most of these receptors by stimulating the muscle with percutaneous electrodes. The second method utilized a topical anaesthetic cream. The twitches were very small and localized within the muscle belly, so it is unlikely that joint receptors were activated.

Muscular sense was significantly attenuated (to 37% of control) during fast voluntary wrist movements compared with stationary controls (Fig. 1C). This effect was velocity dependent as these ratings were significantly lower than those during similar slow movements. Surprisingly, the reduction during fast passive movements (to 60%) was not significantly different from control. Significance may have been attained if more subjects had been tested or if the passive movements involved more than one joint. In contrast, perceptual ratings of twitches evoked 0.5, 1 and 2 s after the termination of the passive movements were significantly attenuated. The extent of the attenuation was not dependent on the phase of the movement in which the twitch was evoked during either the fast voluntary or passive movements. The attenuation during the fast voluntary movements was present over a range of twitch amplitudes (Fig. 2). This shows that the attenuation is not the result of a masking of low intensity stimuli as has been suggested for attenuation of the conscious perception of cutaneous signals (Chapman, Bushnell, Miron, Duncan & Lund, 1987).

The perception of muscle receptor input was attenuated in the simple movements described above. We thought that this may change during skilled tasks that are more reliant on proprioceptive feedback such as reaching to a target. There is increasing evidence that ascending afferent signals can be selectively gated according to their relevance to the task at hand (Knecht, Kunesch, Buchner & Freund, 1993; Chapman, Tremblay & Ageranioti-Belanger, 1996; Staines, Brooke, McIlroy & Peritore, 1997b). Surprisingly, in our experiments muscular sense was still attenuated while subjects reached with the arm being stimulated. Reaching with the contralateral arm did not have this effect

suggesting that the attenuation is specific to signals from the moving limb. During preliminary experiments muscular sense remained close to static control values in two subjects during the demanding task of threading a needle.

What is the source of the sensory attenuation we observed? Our results provide evidence that both signals from peripheral receptors excited by the movement itself and central structures can play a role. The attenuation during cyclic stretching of the skin on the dorsum of the hand (Fig. 3B) indicates a powerful role for cutaneous receptors in gating muscle receptor signals to the brain. Such cutaneous receptors are known to be rhythmically active during movements of the fingers (Edin & Abbs, 1991).

There was also evidence for attenuation of a central origin. Muscular sense was significantly attenuated during active hand movements, compared with that during kinaematically similar passive movements (Fig. 1). The additional attenuation may reflect centrally mediated effects added to any existing attenuation which may have been laid down from peripheral receptors excited by the movement. Muscular sense was also attenuated throughout the preparation to perform a single flexion–extension movement at the wrist (Fig. 4). This attenuation, which was evident as long as 350 ms prior to movement onset, occurred before any movement-evoked re-afference could have been elicited, though an increase in muscle spindle firing due to preparatory fusimotor set cannot be ruled out. It also seems unlikely that the attenuation was due to a suppression of the memory of twitch perception by the subsequent movement-evoked sensory activity, given the long time course of the effect. The marked increase in the attenuation over the final 100 ms before movement is also likely to have been of central origin. This pattern of pre-movement gating is reminiscent of that of some spinal reflexes (Pierrot-Deseilligny & Lancert, 1973; Riedo & Rugg, 1988) and SEPs (Starr & Cohen, 1985; Staines *et al.* 1997a) arising from receptors in the leg and may originate from the motor cortex (Jiang, Chapman & Lamarre, 1990).

We do not believe that our finding of a movement-related attenuation of muscle sense is due simply to a non-specific reduction in attention. First, we demonstrated that some of the attenuation can arise from cutaneous feedback not associated with motor preparation. Also, we were unable to demonstrate significant attenuation while subjects counted backwards, a task requiring considerable cognitive attention. During the whole-arm reaching movements, the effect was specific to the arm being moved and was not generalized to both limbs. Further evidence that the attenuation was specific to the performance of movement was the large increase in attenuation over the final 100 ms before movement onset.

Our experiments show that the ability to detect signals from muscle receptors is attenuated during various movement tasks. To what extent does this reflect the normal processing

of ascending muscle afferent signals? Admittedly, the afferent volley evoked by our muscle twitch is artificial and unlikely to occur in an identical form during natural movements. Recently it has been shown that the ability to detect a small, passively applied, movement during a voluntary contraction is also attenuated (Wise, Gregory & Proske, 1998). Though skin sensations were not excluded, these results are consistent with our findings regarding the gating of sensory signals of purely muscle receptor origin. In our experiments, the attenuation was present the first time a twitch was presented during movement and therefore is not the result of a gradually developing active gating of an unwanted signal. Instead, we feel that the results reflect the normal attenuation of anticipated afferent signals. SEP studies have shown that the gating of ascending pathways can be modified according to the relevance of the ascending information (Knecht *et al.* 1993; Staines *et al.* 1997*b*). The extent to which such control is exerted over the pathways to the centres of conscious perception is not known.

Previous work has confirmed a major role for muscle receptors in the conscious perception of movement (Goodwin *et al.* 1972; Craske, 1977; McCloskey, Cross, Honner & Potter, 1983). There is evidence that stationary human subjects may occasionally perceive action potentials from even single muscle receptors in the hand (Macefield, Gandevia & Burke, 1990). However, our results suggest that the ability to perceive these signals is significantly attenuated before, during and after movement. How can we reconcile these findings? First, the sheer magnitude of movement-related sensory input from the periphery should be stressed. During feline locomotion the net input from muscle receptors of a single limb may reach 0.7 million impulses per second (Prochazka & Gorassini, 1998). Under static conditions, this input is far less. Attenuation prior to and during movement may therefore serve to keep the overall input to the central nervous system at manageable levels. In this respect, the control of muscle sense is comparable to the selective gating of ascending cutaneous signals during movement (Angel & Malenka, 1982; Milne *et al.* 1988), which appears to be related to the focusing of attention to relevant inputs (Rushton *et al.* 1981; Chapman *et al.* 1996). The attenuation of muscular sense probably occurs at many levels of the nervous system including the sensory receptors themselves, as a result of control signals emanating from the nervous system.

Our results are consistent with the idea of a general attenuation by spinal and supraspinal mechanisms of peripheral signals during movement (Prochazka, 1989; Brooke *et al.* 1997). In our experiments the attenuation was most evident during large, rapid movements. In tasks requiring fine manipulation involving small, slow movements, muscular sense probably remains closer to static control levels. A technical analogy would be the automatic gain control used in electronic amplifiers to suppress large signals.

We conclude that the conscious perception of signals from muscle receptors is attenuated during movement. This may prevent saturation of the central nervous system by the massive barrage of re-afference generated during movement. The extent to which the nervous system gates the different sensory modalities in the same way, or differentially, depending on the sensory demands of the task at hand, requires further exploration.

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