

# Cutaneous mechanisms of isometric ankle force control

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**Abstract** The sense of force is critical in the control of movement and posture. Multiple factors influence our perception of exerted force, including inputs from cutaneous afferents, muscle afferents and central commands. Here, we studied the influence of cutaneous feedback on the control of ankle force output. We used repetitive electrical stimulation of the superficial peroneal (foot dorsum) and medial plantar nerves (foot sole) to disrupt cutaneous afferent input in 8 healthy subjects. We measured the effects of repetitive nerve stimulation on (1) tactile thresholds, (2) performance in an ankle force-matching and (3) an ankle position-matching task. Additional force-matching experiments were done to compare the effects of transient versus continuous stimulation in 6 subjects and to determine the effects of foot anesthesia using lidocaine in another 6 subjects. The results showed that stimulation decreased cutaneous sensory function as evidenced by increased touch threshold. Absolute dorsiflexion force

error increased without visual feedback during peroneal nerve stimulation. This was not a general effect of stimulation because force error did not increase during plantar nerve stimulation. The effects of transient stimulation on force error were greater when compared to continuous stimulation and lidocaine injection. Position-matching performance was unaffected by peroneal nerve or plantar nerve stimulation. Our results show that cutaneous feedback plays a role in the control of force output at the ankle joint. Understanding how the nervous system normally uses cutaneous feedback in motor control will help us identify which functional aspects are impaired in aging and neurological diseases.

**Keywords** Cutaneous feedback · Force · Ankle dorsiflexion · Human

## Introduction

The sense of force is critical in our interactions with the physical environment. For example, we use an estimate of the amount of force applied to move an object (e.g., pushing a shopping cart) to determine whether it is heavy or light. Force perception depends on the interaction between peripheral feedback and central motor commands; perceived force magnitude can be biased by removing cutaneous feedback via anesthesia (Gandevia and McCloskey 1977a, b; Marsden et al. 1979), during fatigue (Jones and Hunter 1983) or after central lesions (Maschke et al. 2006; Simon et al. 2009).

The control of finger force output can be achieved to some extent in the absence of peripheral feedback, as demonstrated in a man with peripheral neuropathy (Rothwell et al. 1982). Patients with sensory neuropathy instead rely

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on visual feedback to maintain accuracy (Rothwell et al. 1982; Sanes et al. 1984). In order to achieve fine force resolution in finger control, cutaneous feedback must be properly integrated with central motor command (Henningsson et al. 1995, 1997). Besides the importance of cutaneous feedback in fine finger force control, less is known about the relevance of cutaneous afferents for controlling force at the ankle.

In the lower limbs, the effects of deafferentation via anesthesia suggest that the nervous system has the means to adjust the motor command to produce different levels of muscle activity without peripheral information, but cannot maintain the constant output over time (Gandevia et al. 1993). We therefore hypothesized that cutaneous feedback is normally used in ankle force control, and we predicted that force errors would increase with disruption of cutaneous feedback.

To investigate the importance of cutaneous feedback for ankle force control, we disrupted afferent signals from the foot using repetitive electrical nerve stimulation. The advantage of using electrical nerve stimulation, rather than anesthesia as in previous experiments, is that it could be turned on and off, enabling a quick switch between normal and altered cutaneous feedback conditions. Before testing the effects of electrical stimulation on ankle force control, we determined the effects of the stimulation on cutaneous and proprioceptive function by measuring touch and vibration thresholds. Repetitive stimulation of the peroneal nerve and plantar nerve increased touch thresholds on the foot dorsum and foot sole, respectively. Second, we found that absolute ankle dorsiflexion force errors increased during peroneal nerve stimulation without vision. The effect of stimulation was not observed in ankle position matching. The results suggest that ankle force control, like finger force control, depends on the integration of cutaneous afferents feedback.

## Methods

### Subjects

The study was approved by the local ethics committee of the Copenhagen region (Protokol nr. H-A-2008-029) and conformed to the *Declaration of Helsinki*. Twenty healthy subjects (7 females, 13 males; mean age  $\pm$  SD  $27 \pm 5$  year) were recruited from the University of Copenhagen campus. All subjects gave written informed consent prior to participation.

Participants were divided into three groups. In the first group of subjects ( $n = 8$ ), we tested tactile thresholds, force matching and position matching with transient nerve stimulation. In the second group of subjects ( $n = 6$ ), we

tested force matching with transient stimulation versus continuous nerve stimulation. In a third group of subjects ( $n = 6$ ), force matching was tested before and after lidocaine injection.

### Repetitive nerve stimulation

Repetitive nerve stimulation was administered with a constant current stimulator (DS7A, Digitimer, UK) that delivered 1 ms pulses at 80 Hz through two surface electrodes (2.5 cm PALS Platinum, Axelgaard, Denmark). Stimulation intensity was set at the radiating threshold for each subject. Radiating threshold for each subject was determined by increasing stimulation intensity until the subject perceived a tingling sensation on the skin that radiated to the great toe distal to the stimulation site. Radiating thresholds were determined separately for the foot dorsum and foot sole (peroneal nerve and plantar nerve stimulation, respectively). Two electrodes were placed in the front of the ankle approximately 3 cm apart to stimulate the medial cutaneous branch of the superficial peroneal nerve. To stimulate the medial plantar nerve (i.e., a branch of the tibial nerve), one electrode was placed below the medial malleolus and another was placed behind the medial malleolus. Stimulation was applied on the right foot.

### Touch and vibration thresholds

Sensory thresholds in two different modalities of touch, pressure and vibration, were measured using common clinical methods. Touch thresholds were measured using Von Frey monofilaments (20 piece Touch Test™ Sensory Evaluator, North Coast Medical). Areas tested included the foot dorsum, the plantar side of the great toe and heel on the right side. The monofilament was pressed on the skin surface for 1 s and then removed. Subjects were instructed to say “yes” when the pressure was felt. For each site, increasingly larger monofilaments were used until a single positive response was recorded. For monofilaments size 1.65 through 4.08, corresponding to 0.008–1 g in force, the touch was applied up to three times. For monofilaments size 4.17–6.65, corresponding to 1.4–300 g in force, the touch was applied only once. The force from the smallest monofilament to elicit a positive response was the touch threshold. All sites were first tested without stimulation. The foot dorsum was re-tested with peroneal nerve stimulation; the great toe and heel was re-tested with plantar nerve stimulation.

Vibration sensation on the right great toe was determined using Vibratron II device (Physitemp Instruments, New Jersey, USA), which consists of two separate vibrating rods (100 Hz). Only one rod vibrated at a time. A controller was used to switch which rod will vibrate and to

adjust the vibration amplitude (0–200 micron). On each trial, the subject pressed the right great toe against each rod in sequence for about 1 s, and then determined which of the two rods was vibrating. When switching between rods, the subject was instructed to be consistent in the location of the touch and the approximate force applied to the great toe. Vibration threshold was measured using a two-alternative forced-choice procedure (Arezzo et al. 1985). The vibration amplitude was decreased by about 10 % from trial to trial, until the subjects made the first incorrect choice. After the first error, each amplitude setting was repeated for a total of 3 trials. The next amplitude was decreased by 10 % if the subject was correct in two out of three trials, and increased by 10 % otherwise. The test was completed when the subject made a total of 5 errors. We noted the vibration amplitudes where the 5 errors were made and where the 5 lowest correct responses were made; the vibration threshold was then calculated as the average of these 10 values, excluding the highest and lowest values (Arezzo et al. 1985). The reproducibility of this method for measuring vibration threshold has a coefficient of variation between 17 and 20 % (Nasserri et al. 1998). The test was performed first without stimulation and then repeated with stimulation of the right peroneal and plantar nerves together.

#### Force matching

Subjects were seated in an upright position with the right foot attached to a pedal instrumented with a strain gauge force transducer. The knee and ankle angles were approximately 110° and 120°, respectively. To determine maximal voluntary contraction (MVC), subjects were instructed to exert maximal isometric ankle dorsiflexion force and hold it for approximately 2 s. The peak torque obtained across 3 trials was taken as the MVC.

During the force-matching task, subjects were instructed to maintain an isometric ankle dorsiflexion force equivalent to 10 % maximal voluntary contraction. Subjects watched a monitor displaying the target force represented as a horizontal cursor, and a trace of the actual force applied to the pedal. Each trial consisted of 3 epochs: 0–5 s (eyes opened, EO), 5–10 s (eyes closed, EC1) and 10–15 s (eyes closed, EC2). Electrical stimulation was applied at the same time visual feedback was removed (at 5 s). Subjects completed a total of 15 trials: 5 trials in each of the 3 stimulation conditions (no stimulation, right peroneal nerve and right plantar nerve) randomly.

#### *Effects of transient versus continuous stimulation*

We hypothesized that the nervous system may compensate for disrupted cutaneous feedback by using other sources of information (e.g., visual feedback, muscle afferents,

central motor commands) to recalibrate the force output. To test this, we compared the effects of disrupting cutaneous feedback via transient versus continuous peroneal nerve stimulation in subjects ( $n = 6$ ) who did not participate in the first set of force-matching experiments. In the former condition, stimulation was turned at the same time visual feedback was removed, so subjects never received feedback about their performance in the altered cutaneous feedback state. In the latter condition, subjects received feedback about their performance in the altered cutaneous feedback state before visual feedback was removed, and therefore had time to recalibrate the force output.

As before, the force-matching trial consisted of 3 epochs: EO (0–5 s), EC1 (5–10 s) and EC2 (10–15 s). Each subject completed 4 blocks of 5 trials (a total of 20 trials) in the same order: no stimulation was applied (e.g., removing visual feedback only) in *block 1*; peroneal nerve stimulation was applied starting at 0 s (e.g., disrupting cutaneous feedback before removing visual feedback) in *block 2*; no stimulation was applied in *block 3*; peroneal nerve stimulation was applied starting at 5 s (e.g., disrupting cutaneous feedback and visual feedback at the same time) in *block 4*. The effects of continuous versus transient repetitive electrical nerve stimulation were determined by comparing *blocks 2 and 4*. The purpose of *block 3* was to washout possible aftereffects from stimulation before re-test.

#### *Effect of nerve block with lidocaine*

A lidocaine experiment was done separately to determine the effects of blocking cutaneous afferents using anesthesia, which does not involve the possibility of activating central mechanisms via peripheral nerve stimulation. The force-matching task was tested in 6 naive subjects ( $n = 6$ ) before and after anesthetizing of the foot. Lidocaine (25 mg/ml) was injected around the ankle joint targeting the deep peroneal nerve, branches of the superficial peroneal nerve and the tibial nerve. Areas on the foot dorsum and foot sole were tested for sensation of light touch (i.e., short finger strokes). Complete anesthesia of the whole foot was obtained in two subjects. In the remaining subjects, lack of sensation was obtained in approximately 80–90 % of the plantar and dorsal sides of the foot, but complete anesthesia of the toes and the heel was not obtained. Another evaluation of light touch was done at the end to ensure that the anesthesia was effective throughout the experiment. The force-matching trial consisted of 3 epochs: EO (0–5 s), EC1 (5–10 s) and EC2 (10–15 s). Each subject completed 3 blocks of 5 trials (total of 15 trials): pre-lidocaine injection, post-lidocaine injection and post-lidocaine injection with peroneal nerve stimulation (starting at 5 s).

## Position matching

We tested whether cutaneous stimulation affected ankle position sense. Subjects were seated in an upright position with both feet placed in separate pedals allowing independent movement of the ankle joints. Ankle angles were measured using electrogoniometer bilaterally and recorded at 2 kHz. The rotational axis of each pedal was aligned to the rotational axis of the ankle. The knee angle was fixed at approximately 110°. The ankle angle was approximately 90° at the starting position. The experimenter rotated the subject's left ankle (dorsiflexion) from the starting position to a random position within normal range of motion. The rotation speed varied across trials in order to decouple the test position and the duration of rotation. While being blindfolded, the subject was asked to move their right ankle to match the left ankle angle position and hold it for approximately 2 s. Then, both ankles were lowered to the starting position separately. There were 60 trials in total: 20 random positions in each of the 3 stimulation conditions (no stimulation, right peroneal nerve and right plantar nerve). The stimulation was applied at the beginning of each trial and lasted for 5 s.

## Data analysis

The Wilcoxon signed-rank test was used to compare touch and vibration thresholds between the stimulation ON and OFF conditions. An alpha-level of 0.05 was used as the statistical significant criterion for all comparisons.

In the force-matching task, error was calculated as the mean absolute difference between actual and target force during three epochs: 3–5 s (eyes opened, EO), 5–10 s (eyes closed, EC1) and 10–15 s (eyes closed, EC2). A two-way

repeated measures ANOVA with the factors epoch (EO, EC1, EC2) and stimulation (no stimulation, peroneal nerve, plantar nerve) was used to compare force error. When the ANOVA yields a significant effect, post hoc analysis comparing the means against the control value (EO, no stimulation) was performed with a Dunnett's test.

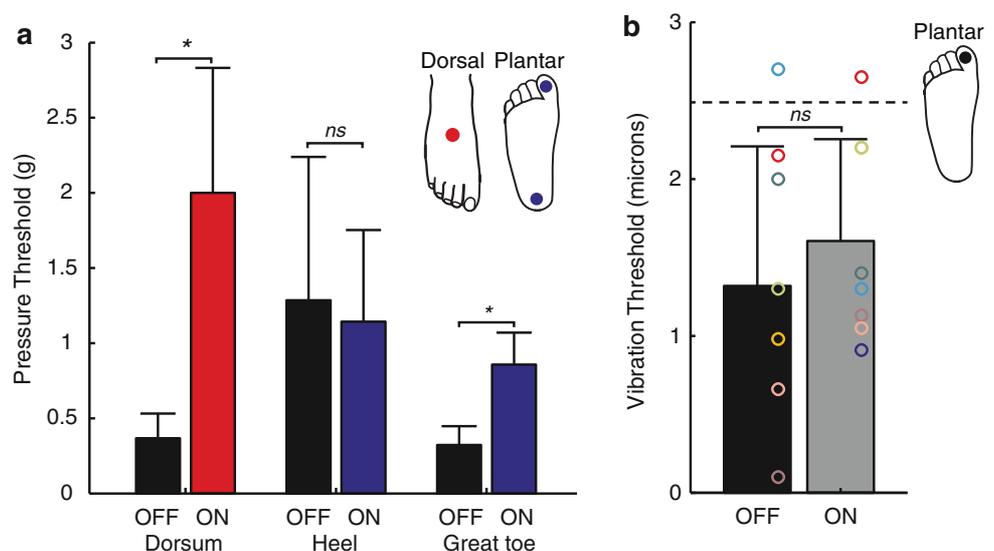
In the angle-matching task, error was calculated as the absolute angular difference between the actual (left) ankle and the reported (right) ankle. The mean position was taken from the hold period, determined using the velocity of the right ankle joint. Sometimes, subjects made one or two small adjustments after the first stop. In such case, the final position was taken from the last hold period. Subjects always reached the final position before the end of the 5-s trial. A one-way repeated measures ANOVA with the factor stimulation (no stimulation, peroneal nerve, plantar nerve) was used to compare position error.

## Results

### Touch threshold

Touch sensation was impaired with repetitive stimulation of the superficial peroneal and medial plantar nerves (Fig. 1a). Peroneal nerve stimulation increased touch threshold on the foot dorsum ( $P = 0.02$ ). Plantar nerve stimulation increased touch threshold on the great toe ( $P = 0.02$ ), but not the heel ( $P = 0.8$ ). This corresponded to an increase in monofilament size from 3.61 to 4.31 for the foot dorsum and from 3.61 to 4.08 for the great toe. This demonstrated that peroneal nerve stimulation and plantar nerve stimulation impaired cutaneous sensation in the foot dorsum and foot sole, respectively.

**Fig. 1** Touch and vibration thresholds. **a** Group-average touch thresholds are plotted for stimulation ON and OFF conditions. Areas of the skin tested are illustrated in the inset. **b** Group-average vibration thresholds are plotted for stimulation ON and OFF conditions. Horizontal dotted line represents 2 SD above the mean of normal values reported in the literature (Arezzo et al. 1985). Colored circles represent individual subjects. Error bars represent group standard errors (SE). Asterisk indicates  $P < 0.05$ ; ns not significant (color figure online)



**Fig. 2 Force matching.** **a** Group-average absolute force error across time epochs (EO, EC-1, EC-2) with no stimulation (black), peroneal nerve stimulation (gray) and plantar nerve stimulation (white). *Bottom, shaded area* represents period without visual feedback. *Dotted line* begins and ends at the time of stimulation onset and offset, respectively. **b** Group-average absolute force error with no stimulation (black), continuous stimulation (light gray) and transient stimulation (dark gray) of the peroneal nerve stimulation. **c** Group-average absolute force error pre-lidocaine (black) and post-lidocaine with no stimulation (light gray) and peroneal nerve stimulation (dark gray). *Colored dots* represent individual subjects. *Error bars* represent group SE (color figure online)

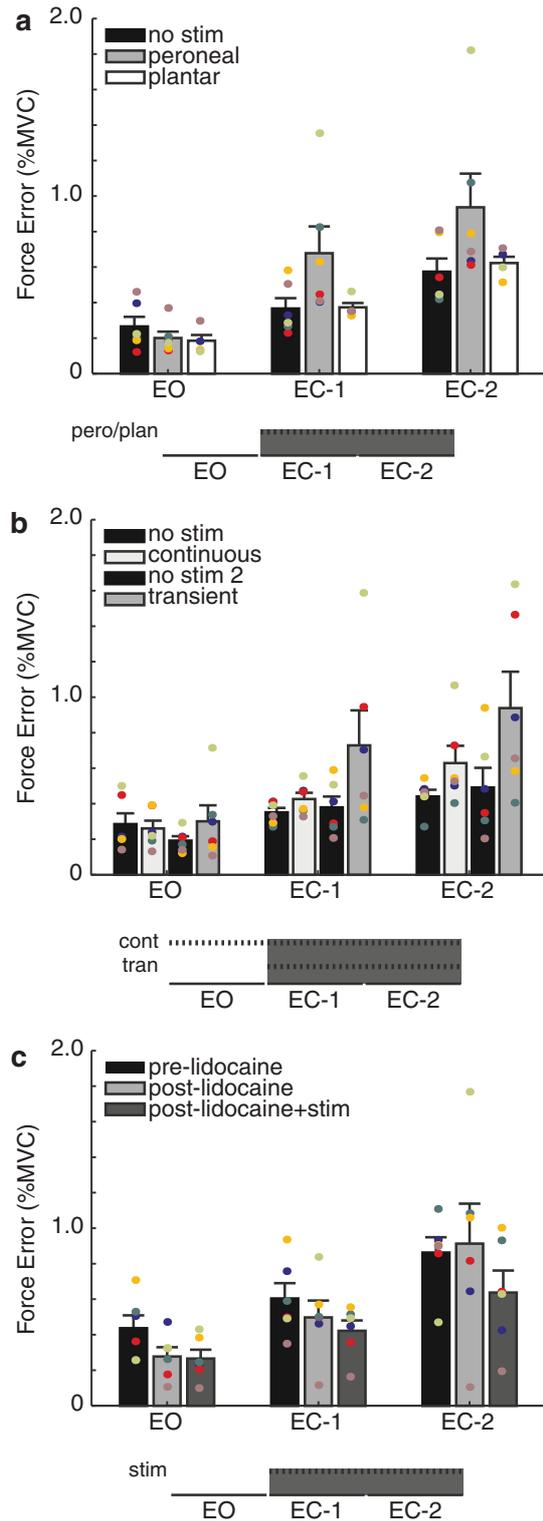
Vibration threshold

Repetitive electrical nerve stimulation did not have a robust effect on vibration sensation. The group-average vibration threshold increased approximately 20 %, but the effect was not statistically significant (Fig. 1b,  $P = 0.4$ ). Group-average vibration thresholds measured with and without stimulation were both within the range of normal values reported in the literature (Arezzo et al. 1985). Therefore, repetitive electrical nerve stimulation did not significantly impair vibration sensation.

Force matching

Subjects could normally maintain a constant force in the absence of visual feedback. However, the absolute dorsiflexion force error increased when cutaneous feedback was disrupted during peroneal nerve stimulation. Group data showed a significant difference in absolute force error across stimulation conditions (Fig. 2a). Repeated measures ANOVA showed a significant effect of epoch ( $F[2,10] = 25, P < 0.001$ ), stimulation ( $F[2,10] = 4.4, P = 0.04$ ) and interaction between epoch and stimulation ( $F[4,20] = 3.7, P = 0.02$ ) on the force errors. Post hoc analysis showed that force errors increased during the eyes-closed epochs, EC1 ( $P < 0.05$ ) and EC2 ( $P < 0.001$ ), with peroneal nerve stimulation. There was no significant effect of plantar nerve stimulation, suggesting that it was not a general effect of repetitive nerve stimulation. The results suggest that disrupting cutaneous input from the foot dorsum via peroneal nerve stimulation, but not by plantar nerve stimulation, impaired the ability to estimate dorsiflexion force output.

The mean force was also analyzed in order to determine whether there was consistent over-estimate or under-estimate of force across trials, which would indicate that the stimulation biased cutaneous feedback, rather than disrupting it. Repeated measures ANOVA showed no significant effect of epoch ( $F[2,10] = 0.06, P = 0.9$ ) or stimulation ( $F[2,10] = 2.4, P = 0.2$ ) on the mean ankle force produced. This suggests that the stimulation did not amplify the



cutaneous afferent signals, which would have caused a consistent over-estimate of force (and thus a decrease in force output when the peroneal nerve was stimulated during the matching task).

### Transient versus continuous stimulation

In a separate group of subjects, we compared the effects of transient stimulation versus continuous peroneal nerve stimulation. The purpose was to test whether subjects compensate for disrupted cutaneous feedback by using visual feedback.

Group data showed a significant difference in absolute force error across stimulation conditions (Fig. 2b). A two-way repeated measures ANOVA showed a significant effect of epoch ( $F[2,10] = 24, P < 0.001$ ) and stimulation ( $F[3,15] = 4.4, P = 0.02$ ) on the force errors. The interaction effect was non-significant ( $F[6,30] = 2.3, P = 0.06$ ).

The results showed that sudden, but not continuous, disruption of cutaneous feedback had a significant effect on force performance. This suggests that the nervous system has the capability of using efferent signals and afferent feedback other than cutaneous afferents to control ankle force output, when sufficient information is provided for the recalibration (see “Discussion”).

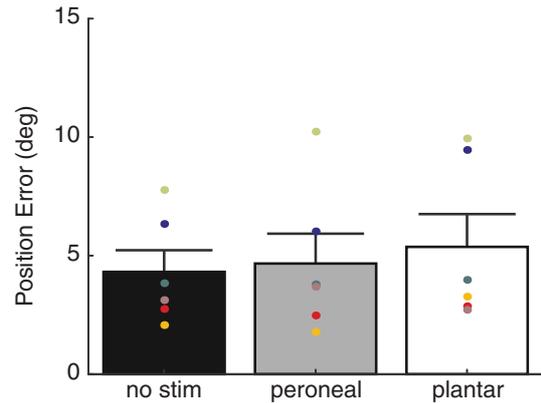
### Lidocaine experiment

The force-matching task was tested in another group of subjects before and after anesthesia of the foot. The purpose of this experiment was to verify our findings using another method that does not involve the possibility of activating central mechanisms via peripheral nerve stimulation.

Group data showed no significant difference in absolute force error across the three conditions: pre-lidocaine, post-lidocaine, post-lidocaine with stimulation (Fig. 2c). Repeated measures ANOVA showed a significant effect of epoch ( $F[2,10] = 36, P < 0.001$ ). The effects of condition ( $F[2,10] = 2.0, P = 0.2$ ) and interaction between epoch and condition ( $F[4,20] = 0.8, P = 0.5$ ) were not significant.

Since the testing blocks were not randomized, change in performance from the first to the second block is the sum of the effects of lidocaine and practice time. If subjects learned to perform better over time, the effect of practice time may mask the effect of lidocaine. While that is possible, we showed above that errors increased in *Block 4* when transition stimulation was applied. This suggests that, if present, the effects of lidocaine were smaller compared to transition stimulation. Lidocaine, like continuous stimulation, did not significantly decrease force accuracy since subjects had time to recalibrate the force output using visual feedback.

The results verified that peroneal nerve stimulation had no effect on force errors after blocking cutaneous feedback with lidocaine injection, suggesting that the effect of nerve stimulation on force output could be attributed to disruption of cutaneous afferents.



**Fig. 3** *Position matching.* Group-average mean ankle error with no stimulation (*black*), peroneal nerve stimulation (*gray*) and plantar nerve stimulation (*white*). *Colored dots* represent individual subjects. *Error bars* represent group SE (color figure online)

### Position matching

Repetitive electrical nerve stimulation did not affect performance in the position-matching task. Group-average data showed that position error is about 4° (Fig. 3). Repeated measures ANOVA found no significant effect of stimulation ( $F[2,10] = 1.9, P = 0.2$ ) on absolute position error. This suggests that repetitive electrical nerve stimulation impaired force estimation, but not position estimation.

### Discussion

We have demonstrated that repetitive electrical nerve stimulation could be used to disrupt cutaneous sensory function. Stimulation at 80 Hz increased touch threshold on the foot dorsum by about fourfold. When cutaneous feedback was disrupted using repetitive electrical nerve stimulation, ankle force errors increased in the force-matching task. This suggests that subjects normally relied on cutaneous feedback to control force output. With continuous stimulation, but not transient stimulation, subjects were able to compensate for the disrupted cutaneous information with the available visual feedback. Finally, when peroneal nerve stimulation was applied after lidocaine injection, there was no additional effect on force performance. This suggests that the effect of nerve stimulation on force output was attributed to decreased cutaneous sensory function.

The extent of sensory disruption caused by repetitive electrical nerve stimulation was determined by measuring touch and vibration perception thresholds. During stimulation, subjects perceived a “tingling” sensation that resembles the “flutter vibration” and “sustained pressure” sensations reported during microstimulation of rapidly adapting and slowly adaptation cutaneous afferents (Ochoa and

Torebjörk 1983; Vallbo et al. 1984; Macefield et al. 1990). Our results showed that touch thresholds increased during stimulation, indicating that it was more difficult to perceive mechanically applied pressure on the skin in the presence of the electrically induced sensation. Stimulation did not have a robust effect on vibration thresholds. Vibration sense may be affected to a lesser extent compared to pressure sense because of differences in firing properties and location of the mechanoreceptors and central processing of the sensory afferents. It is also possible that higher stimulation frequencies (>80 Hz) may be required to disrupt vibration (100 Hz) thresholds.

### Force control

Previous studies have shown that the perception of weight can be biased after removing cutaneous feedback by anesthesia (Gandevia and McCloskey 1977a, b; Marsden et al. 1979). The changes in weight perception reflected the corresponding changes in the agonist and antagonist muscle activity after anesthesia (Marsden et al. 1979), rather than the relative contributions of stretch reflex and central motor commands to motoneurons (Gandevia and McCloskey 1977a, b). Thus, the size of central commands cannot entirely account for the perception of force, indicating that afferent feedback mechanisms must also play a role in assessing the force output.

The role of afferent feedback in force control has been studied by examining the ability to maintain a constant force in deafferented patients—they were able to maintain a constant force with visual feedback, but the force output drifted shortly after visual feedback was removed (see Fig. 15 from Rothwell et al. 1982). The variability in the force output may come from multiple sources, including variability in the centrally generated motor command and motor noise (Jones et al. 2002). This suggests that afferent feedback is necessary to recalibrate force output. However, the role of specific afferents is unclear because inputs from cutaneous, joint and muscle afferents are all removed in these patients.

Here, we disrupted cutaneous afferents using peripheral nerve stimulation. The advantage of using electrical nerve stimulation is that we could quickly switch between normal and altered cutaneous feedback conditions, which could not be done using anesthesia. Ankle dorsiflexion force errors increased after sudden disruption of cutaneous feedback in the foot dorsum via peroneal nerve stimulation, suggesting that subjects were unable to rely on central signals (e.g., efferent copy) and other sensory feedback (e.g., changes in muscle length and tension) to recalibrate the force output in this situation.

Another possibility is that stimulation increased the amplitude of the cutaneous afferent signal, which the nervous system would interpret as an increase in pressure (i.e.,

pushing harder). Thereby, subjects should under-shoot when the dorsum is stimulated and over-shoot when the sole is stimulated. We think this is unlikely because the mean force output did not show consistent changes across trials when the stimulation was applied.

Providing visual feedback during repetitive electrical nerve stimulation improved the ability to maintain force output accurately. During continuous peroneal nerve stimulation, subjects were able to maintain the target force after visual feedback was removed. This suggests that the nervous system may rely on other available inputs (e.g., central commands, muscle spindle) to recalibrate force output under the circumstances.

The phenomenon of sensory weighting has been demonstrated in the estimation of position during reaching; the nervous system can dynamically weight and combine multiple sources when sufficient information about their accuracy is known (Beers et al. 1996; Ernst and Banks 2002). The nervous system appears to optimize the weights of different sensory modalities (e.g., vision, proprioception) in order to minimize the variance of the final estimate of position (Ernst and Banks 2002). Here, we showed that the nervous system might also vary the way it integrates efferent and afferent signals to form estimates of force output.

### Position control

We found no effects of repetitive electrical nerve stimulation on the perception of ankle joint position. This does not imply that cutaneous input has no contribution to the sense of position. The effects of peroneal nerve and plantar nerve stimulation were felt on the skin of the foot, and therefore, we did not expect a profound effect on position sense at the ankle joint. Other studies have suggested that cutaneous input likely contributes to position sense because anesthesia impairs movement detection in the thumb (Gandevia and McCloskey 1976) and ankle joint (Lowrey et al. 2010). Moreover, microneurographic studies suggest that cutaneous afferents can potentially encode position information about hand (Edin and Abbs 1991), knee (Edin 2001) and ankle (Aimonetti et al. 2007) movements. Cutaneous input may also have a role in biasing position sense at extreme joint positions where the skin is most stretched (Fuentes and Bastian 2010).

### Functional relevance

Ankle dorsiflexion is an important function during walking, allowing the toes to clear the ground during the swing phase of walking. Insufficient activation of the tibialis anterior muscle in persons post-stroke and children with cerebral palsy is related to particular gait deficits (e.g., foot drop). One training approach using a resistive ankle-foot

orthosis has been proposed that could promote increased activation in ankle dorsiflexion muscles during walking (Blanchette et al. 2011). The training paradigm is based on trial-and-error adaptation that acts to account for predictable perturbations (Lam et al. 2006; Choi and Bastian 2007; Blanchette and Bouyer 2009). We hypothesize that unexpected contact force on the foot dorsum may be an important error signal driving motor adaptation, and we are currently investigating whether disruption of cutaneous feedback via stimulation of the foot dorsum or foot sole alters adaptation to ankle torque perturbations during walking. If cutaneous feedback contributes to ankle torque correction, it may be possible to augment the training effects using cutaneous feedback.

## Conclusion

In conclusion, we have shown that the nervous system uses cutaneous feedback in combination with other inputs to estimate force about the ankle control. In this study, we showed that electrical stimulation of peripheral nerves disrupted cutaneous afferent information and decreased accuracy in ankle force control. Future studies will be necessary to further understand how somatosensory signals influence motor learning. Understanding how the nervous system combine and use various inputs will help us identify which functional aspects are impaired in aging and neurological diseases and how to assist these populations.

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