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profound implications for both the doctor–patient relationship and psychotherapy. In fact, the psychosocial context and the therapeutic act itself, along with verbally induced expectations of clinical benefit, may indeed induce specific changes in the patient's brain, thus placing the therapist–patient communication and psychotherapy into a therapeutic context which *per se* is capable of modifying the patient's brain.

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#### References

Benedetti F (2008). *Placebo effects: understanding the mechanisms in health and disease*. Oxford University Press.

Benedetti F, Colloca L, Torre E, Lanotte M, Melcarne A, Pesare M, Bergamasco B & Lopiano L (2004). Placebo-responsive Parkinson patients show decreased activity in single neurons of subthalamic nucleus. *Nat Neurosci* 7, 587–588.

Benedetti F, Lanotte M, Colloca L, Ducati A, Zibetti M & Lopiano L (2009). Electrophysiological properties of thalamic, subthalamic and nigral neurons during the anti-parkinsonian placebo response. *J Physiol* 587, 3869–3883. <http://jp.physoc.org/content/587/15/3869.long>

de la Fuente-Fernandez R, Ruth TJ, Sossi V, Schulzer M, Calne DB & Stoessl AJ (2001). Expectation and dopamine release: mechanism of the placebo effect in Parkinson's disease. *Science* 293, 1164–1166.

Zubieta JK & Stohler CS (2009). Neurobiological mechanisms of placebo responses. *Ann N Y Acad Sci* 1156, 198–210.

#### Swartz Prize

Horace Barlow from the Cambridge Physiological Laboratory has recently won the Swartz Prize for Theoretical and Computational Neuroscience. The Prize is awarded annually to:

an individual whose activities over a period of time have produced a significant cumulative contribution to theoretical models or computational methods in neuroscience, or to:

a person who has made a particularly noteworthy advance over the past several years in theoretical or computational neuroscience.

## Neuromuscular interaction during human walking: how do changes in muscle–tendon mechanics affect the motor control of walking?

Prolonged walking can increase the compliance of soleus tendinous tissues, which could ultimately impair the ability to recover from a sudden balance disturbance

When humans walk, muscle–tendon units in the legs are constantly subjected to length changes, which are distributed between the muscle and tendinous tissues within the muscle–tendon unit. These length changes can affect the activity of afferent receptors located in the muscle. One situation where this is particularly important is when encountering an unexpected balance disturbance during walking, such as a trip or stumble. In order to avoid falling, the central nervous system must be able to detect the disturbance and initiate a response, all in a matter of milliseconds.

### Investigating neural and mechanical behaviour simultaneously

A wealth of data have been presented investigating sensory feedback in humans during walking, and this has without question improved our understanding of human motor control. However, since many of the receptors that contribute to afferent feedback during walking are located in the muscle and tendinous tissues, it has become increasingly desirable to investigate the behaviour of these tissues, and to relate it to sensory feedback. One method that has facilitated experiments in this field is ultrasonography. Although this method is traditionally associated with fetal scanning, the last two decades have seen an adaptation to the methodology that has allowed the study of muscle and tendon length changes during dynamic movements. Although the method is naturally limited by the fact that it is 2-dimensional, it has nonetheless provided valuable information about muscle and tendon mechanics during movement.

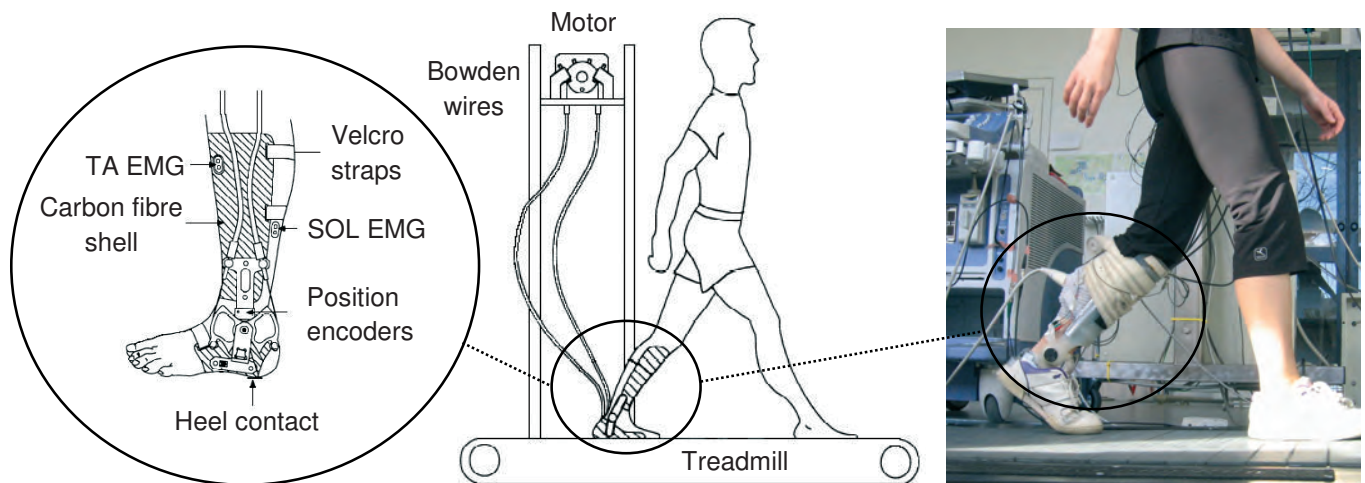


Neil Cronin.

### Neuromuscular interaction during walking: what happens when we walk for a long time?

It has previously been shown that after a 1 h period of repeated passive stretching of the human ankle extensor muscles, the compliance of the tendinous tissues (outer tendon and aponeuroses) increases (Avela *et al.* 2004). If the same phenomenon were present during walking, increased tendinous tissue compliance could affect the firing behaviour of sensory receptors within the muscle–tendon unit, such as the muscle spindles. These receptors are thought to make an important contribution to muscle activation during normal walking, as well as in response to an unexpected balance disturbance (Sinkjaer *et al.* 2000). Therefore, changes in tendinous tissue compliance could affect the motor control of human walking.

We recently sought to examine whether changes in tendinous tissue compliance were indeed evident during human walking in a group of 11 young, healthy adults (Cronin *et al.* 2009). Subjects walked on a treadmill for 75 min with a portable robotic actuator attached to the ankle joint. This device is capable of eliciting rapid ankle dorsiflexion perturbations during the stance phase of walking (Fig. 1). Full details of the device are presented



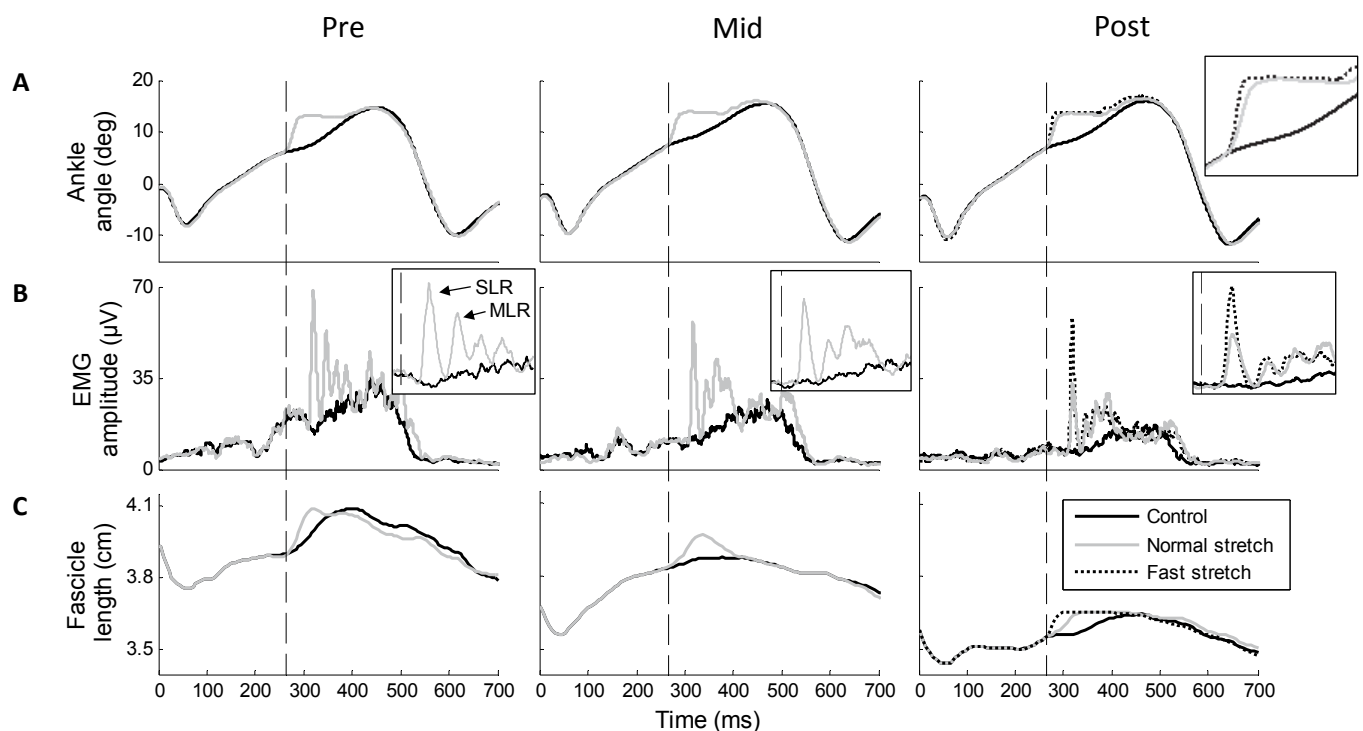
**Figure 1.** Schematic of the robotic actuator that was used to elicit rapid dorsiflexion perturbations during walking. This device was combined with surface EMG and ultrasonography. A fully instrumented subject is shown in the right panel.

elsewhere (Andersen & Sinkjaer, 2003). By combining this method with ultrasonography and surface electromyography (EMG), it was possible to examine changes in both muscle fascicle length and muscle activation in the soleus muscle throughout an exercise protocol.

Rapid stretches were imposed at the ankle joint at three time intervals representing the early,

mid and late phases of the 75 min walking protocol (Pre, Mid and Post, respectively). Between the Pre and Post intervals, the amplitude and velocity of fascicle stretch both decreased considerably (by 46% and 59%, respectively; mean values across all subjects), as did short and medium latency stretch reflex amplitudes (by 33 and 25%, respectively) in response to a constant external perturbation.

Furthermore, in response to a faster perturbation elicited at the Post interval, the amplitude of the short latency component and the velocity of muscle fascicle stretch both recovered to pre-exercise values (Fig. 2). These findings clearly show that when perturbations were elicited at the Post interval, the stretch was not transmitted as effectively to the muscle fascicles, and thus to the muscle spindles.



**Figure 2.** Neural and mechanical stretch responses from one representative subject at the Pre, Mid and Post intervals. A, mean ankle trajectory ( $n = 28$ ); B, SOL EMG activity ( $n = 28$ ); C, fascicle length ( $n = 3$ ). Dashed vertical lines represent the onset of the rapid perturbations. The enlarged insets are not shown to scale, but are intended to highlight the individual traces more clearly. SLR and MLR, short and medium latency stretch reflex, respectively.

This would explain why short and medium latency stretch reflex amplitudes decreased, as they are at least partly mediated by type Ia and type II afferents, respectively, both of which originate in the muscle spindles. At the Post interval, we also observed a decrease in fascicle length at the point of ground contact and immediately prior to the onset of the perturbation, as well as a smaller fascicle length change throughout the stance phase. Concurrently, the range of joint motion at the ankle during walking was unchanged throughout the study. Taken together, these findings provided strong evidence for an increase in the compliance of tendinous tissues after walking in the human soleus muscle–tendon unit.

Interestingly, during normal unperturbed walking, a general decrease in ongoing soleus muscle activity was observed ('Control' traces in Fig. 2). This may be an indication that the increased tendinous tissue compliance led to a decrease in the ongoing sensory feedback from muscle receptors, which is known to contribute to muscle activity during unrestrained walking (Sinkjaer *et al.* 2000). As with the responses to perturbations, this is probably due to the fact that the stretch stimulus reaching the muscle fascicles (and receptors) decreased after the walking protocol.

### What are the functional implications?

Based on data obtained with ultrasonography, it is known that when a muscle–tendon unit changes length, the actual length changes of the muscle and tendon components may be uncoupled (e.g. Ishikawa *et al.* 2005). In this context, the increase in tendinous tissue compliance that we have observed could enable the muscle fibres to contract relatively slowly (Lichtwark & Wilson, 2008), whilst the larger tendinous tissue stretch during the stance phase would facilitate the storage of elastic energy in the tendinous tissues. This could potentially increase the efficiency of the soleus muscle–tendon unit.

However, this raises an interesting series of questions. What happens in the other muscle–tendon units of the lower limb? If muscle activation decreases in soleus, how does the central nervous system compensate in order to maintain the same movement pattern? Furthermore, if the amplitude of stretch reflexes decrease after a sustained period of walking, and these responses are important for recovery from unexpected balance disturbances (Sinkjaer *et al.* 2000), are the responses to such disturbances compromised after prolonged walking? As the soleus muscle is just one of the plantarflexors, it is possible that activation of other synergistic muscles increases in response to decreased soleus activation. Indeed, this kind of neural compensation has been reported after higher intensity fatiguing exercise (Akima *et al.* 2002). This is a matter of ongoing study in our laboratory, and the results will help us to understand how the central nervous system adapts to time-dependent changes in muscle–tendon mechanics.

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### References

- Akima H, Foley JM, Prior BM, Dudley GA & Meyer RA (2002). Vastus lateralis fatigue alters recruitment of musculus quadriceps femoris in humans. *J Appl Physiol* **92**, 679–684.
- Andersen JB & Sinkjaer T (2003). Mobile ankle and knee perturbation. *IEEE Trans Biomed Eng* **50**, 1208–1211.
- Avela J, Finni T, Liikavainio T, Niemela E & Komi PV (2004). Neural and mechanical responses of the triceps surae muscle group after 1 h of repeated fast passive stretches. *J Appl Physiol* **96**, 2325–2332.
- Cronin NJ, Ishikawa M, Af Klint R, Komi PV, Avela J, Sinkjaer T & Voigt M (2009). Effects of prolonged walking on neural and mechanical components of stretch responses

in the human soleus muscle. *J Physiol* **587**, 4339–4347.  
<http://jp.physoc.org/content/587/17/4339.long>

Ishikawa M, Komi PV, Grey MJ, Lepola V & Bruggemann GP (2005). Muscle-tendon interaction and elastic energy usage in human walking. *J Appl Physiol* **99**, 603–608.

Lichtwark GA & Wilson AM (2008). Optimal muscle fascicle length and tendon stiffness for maximising gastrocnemius efficiency during human walking and running. *J Theor Biol* **252**, 662–673.

Sinkjaer T, Andersen JB, Ladouceur M, Christensen LO & Nielsen JB (2000). Major role for sensory feedback in soleus EMG activity in the stance phase of walking in man. *J Physiol* **523**, 817–827.

### Brown coats or white?

In Edinburgh in the late 1940s students wore white (or, more accurately 'off-white') lab coats for practical classes as did most of the technicians. Mr Marshall, the histology wizard, chose grey but I didn't encounter many brown coats till I arrived at the (then) Institute of Animal Physiology at Babraham. Here they were worn by animal house and workshop staff, and by the indispensable heavy-duty handy men – occasionally termed 'heavy-handed duty men' from their propensity to slosh distilled water about the lab while delivering it in winchesters from the central still.

Babraham's first Director Ivan de Burgh Daly favoured white coats for himself and the rest of the scientific staff, despite having worked with W. M. Bayliss. In his Bayliss–Starling Memorial Lecture, Daly said that Bayliss 'always wore his brown overall, which had seen better days, in the laboratory, and as long as I knew him it did not seem to change. I imagine therefore that the memo to be found in one of his notebooks which runs "Overalls, 35 inches, price 4s. 3d. [21p] post free" supplied by a firm in Newcastle, was a reminder in the event of an emergency which never emerged'.

I de Burgh Daly (1967) The Bayliss–Starling Memorial Lecture. *J Physiol* **191**, 1–23.