Is muscle–tendon unit length a valid indicator for muscle spindle output?

Huub Maas[1] and Glen A. Lichtwark[2]

[1]*Research Institute MOVE, Faculty of Human Movement Sciences, VU University Amsterdam, the Netherlands*

[2]*School of Physiotherapy and Exercise Science, Griffith University, Gold Coast, Queensland, Australia*

Email: h.maas@fbw.vu.nl. and g.lichtwark@griffith.edu.au

An important role of feedback from muscle and cutaneous receptors is to regulate the magnitude and timing of muscle activity to satisfy the mechanical demands during locomotion (Rossignol *et al.* 2006). Such sensory information can be used to modulate the walking system of the central nervous system, but it is also suitable to compensate for acute mechanical perturbations via rapid spinal pathways. The latter is likely to be important during walking on uneven surfaces, preventing the body from getting off balance and in the worst case falling. This hypothesis was tested in a well-designed study by af Klint *et al.* (2008), who assessed changes in within-step activity of the triceps surae muscles during over-ground walking.

In this study, natural variations in ground surface were mimicked with small (i.e. ± 3 deg) slope changes of a robotic platform that was embedded in the walkway. Modulation of proprioceptive feedback as a result of an altered ground was assessed by changes in muscle–tendon unit (MTU) length, Achilles tendon force (ATF) and electromyography. MTU length was calculated using kinematic data of the ankle and knee joints as well as regression equations from the literature. ATF was assessed using a E-shaped buckle transducer externally clamped to the tendon. It was found that stepping on an inclined surface increased triceps surae activity as well as MTU length and ATF. The opposite occurred during steps on a negative slope. These results clearly show acute modulation of neural drive to the muscle. As the slopes were imposed in a random order, these compensatory responses most likely rely on within-step reflex pathways (through proprioceptive and/or cutaneous afferents) in contrast to feed-forward control. This significant finding opens the door for our understanding of which of the reflex pathways might be critical for maintaining stability during walking on uneven terrain.

Relating mechanical variables to potential feedback from peripheral afferents is a frequently used approach for studying the neural control of locomotion (specific references can be found in the extensive review of Rossignol *et al.* 2006). The role of length feedback is typically based on changes in MTU length, assuming constant gamma activation and presynaptic inhibition. Based on our experience with *in vivo* measurements of MTU and muscle fascicle length changes, we discuss the following question: Is MTU length a valid indicator of muscle spindle output? As the muscle spindles lie in parallel with the extrafusal skeletal muscle fibres, muscle fascicle length changes are more representative of the strains that muscle spindles 'sense'.

In the discussion, af Klint *et al.* (2008) state: 'The muscle–tendon length was directly changed by the inclination of the platform and concomitant changes in ATF were recorded. While these estimates are subject to error, the general pattern is most likely present at muscle fibre level.' However, MTU length changes can be profoundly different from fascicles length changes in triceps sureae muscles, as we have shown in humans (Lichtwark & Wilson, 2006) and cats (Maas *et al.* 2005). In cats, sonomicrometry has been used to measure muscle fascicle length during overground walking at various slopes. In the early stance phase during walking on a level surface and on a positive slope (25–100%, 14–45 deg), the muscle fascicles of medial gastrocnemius (MG) are consistently shortening while MTU length is increasing. Note that sensory information from this part of the step cycle (close to heel or paw contact) can still be used to alter muscle activity levels within the same step. The general pattern of length changes in MG fascicles and MTU is similar only during walking on a negative slope (−25% and −50%). Such MTU-fascicle similarity was found for all slope conditions in soleus (SO) muscle. Note that this muscle has a different architecture (parallel instead of pinnate, lower tendon-to-fibre length ratio) and crosses only one joint instead of two. Thus, the statement made by af Klint *et al.* (2008) is true for cat SO. However, the architecture of human SO muscle is markedly different from the architecture of cat SO. Therefore, a comparison with human data is needed.

Differences between the length trajectory of the muscle fascicles and the MTU arise due to the compliance of the elastic tissues that lay in series to the muscle (tendon and aponeurosis). In humans, the Achilles tendon is a very long structure relative to the fibres to which it attaches. As a result, the tendon stretches significantly during locomotion, which is thought to increase the muscle's efficiency. This has been demonstrated by measuring muscle fascicle length changes with B-mode ultrasound imaging. During steady speed walking on different slopes (level, 10% uphill and 10% downhill; 10% = 5.7 deg), the MG muscle fascicles have been shown to act relatively isometrically throughout the midstance period while the MTU is lengthening (Lichtwark & Wilson, 2006). Similar to the study of discussion (af Klint *et al.* 2008), the MTU length during stance under the different slope conditions changed significantly. However, no significant differences in the length trajectory of muscle fascicles were found. Although there are some limitations in accurately measuring length with ultrasound (due to probe and muscle movement and limited temporal resolution), this result is likely to be due to the finding that the Achilles tendon experiences significantly different strain patterns in the downhill, level and uphill conditions. No study has examined the fascicle length changes of SO muscle on different slopes; however, experiments on a level surface suggest that the muscle fascicle length trajectory more closely follows that of the MTU (Ishikawa *et al.* 2005). As in the cat, this is likely to be due to differences in muscle architecture, where the elastic tissues are much shorter relative to the muscle fibre length. The above results suggest that the potential role of length feedback is muscle dependent. Therefore, spindle output particularly from SO could be critically important for the compensatory response.

DOI: 10.1113/jphysiol.2008.165555

The study by af Klint *et al.* (2008) is unique in that the Achilles tendon force was estimated using an external clamp transducer. This demonstrated clear differences in the force production from the triceps surae muscle group as a result of small variations in foot orientation. Force differences imply differences in the strain of the Achilles tendon, which in turn suggests that muscle fascicle trajectory will be different under each condition. This is particularly pertinent when the tendon undergoes most of the length change of the MTU. Their Fig. 2 shows that stepping on an inclined surface yields higher MTU lengths of MG, but also higher ATF values and thus increased length changes of the in-series tissues. Thus, due to variation in ATF the muscle fascicles change length in a different fashion from that of the MTU. Therefore, it is difficult to judge from these results which of the reflex pathways might be responsible for modulating muscle activation.

In addition to the group of able-bodied subjects, effects of small unexpected slopes were also tested in one deafferented person (af Klint *et al.* 2008). In this case the inclined surface resulted also in this case in higher MTU lengths, but no increase in muscle activity was observed. Even though similar MTU length changes were observed as in the able-bodied subjects, this does not necessarily mean that the length trajectories of the muscle fascicles were equal as well. As mentioned above, this is for the most part determined by the ATF and the compliance of the in-series elastic tissues. ATF was not measured for this patient, but the reported ground reaction forces appear to show a different pattern. In addition, the compliance of the elastic elements can vary considerably across healthy individuals (e.g. due the effects of disuse, see Magnusson *et al.* 2008) and between different clinical populations (e.g. in cerebral palsy, post stroke). Even though there may be differences in muscle fascicle length changes, the results from the deafferented subject clearly support the role of afferent feedback in compensating for ground variations. This is an important finding in understanding how the human walking system maintains a stable gait in natural environments.

In conclusion, the study by af Klint *et al.* (2008) clearly demonstrates within-step modulation of neural drive to deal with small perturbations during gait and identified sensory input as major source of this modulation. However, it is difficult to isolate which sensory inputs might be primarily responsible partly because muscle fascicles often experience very different length change trajectories from the MTU. Further studies using ultrasonography in humans subjects and both sonomicrometry and afferent recording in animal subjects are needed to investigate the relationship between changes in muscle fascicle length, MTU length and afferent firing.

References

af Klint R, Nielsen JB, Cole J, Sinkjaer T & Grey MJ (2008). Within-step modulation of leg muscle activity by afferent feedback in human walking. *J Physiol* **586**, 4643–4648.

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 (2006). Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. *J Exp Biol* **209**, 4379–4388.

Maas H, Prilutsky BI & Gregor RJ (2005). In vivo fascicle length of cat medial gastrocnemius and soleus muscles during slope walking. In *XXth Congress of the International Society of Biomechanics*, pp. 90.

Magnusson SP, Narici MV, Maganaris CN & Kjaer M (2008). Human tendon behaviour and adaptation, *in vivo*. *J Physiol* **586**, 71–81.

Rossignol S, Dubuc RJ & Gossard JP (2006). Dynamic sensorimotor interactions in locomotion. *Physiol Rev* **86**, 89–154.

Acknowledgements

We would like to thank C. J. Heckman and Andy Cresswell for reading our manuscript and their constructive comments.