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CROSSTALK

Comments on CrossTalk50: There is/is not much to gain from the independent control of human muscle spindles

The control of muscle spindle sensitivity to rehabilitate movements

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The hypothesis that fusimotor neurons are independently controlled in humans is an idea that we have supported for many years, which includes the demonstration of changes in muscle spindle activity in fully relaxed participants and therefore in the complete absence of alpha activity (for review see Ribot-Ciscar & Ackerley, 2021). The observed effects are subtle, as found under ecological conditions, such as with learning or emotions, which is in opposition to the massive and synchronous recruitment of muscle afferents with reflex protocols.

This capability of humans to specifically control muscle spindle sensitivity is probably responsible, at least partly, for motor improvements induced by proprioceptive training, such as when a participant's hand is passively moved to reproduce a movement trajectory (Wong *et al.* 2012). Therefore, this capability opens perspectives in terms of rehabilitation where any manoeuvre liable to reinforce the role of proprioceptive feedback, by precise adjustments of muscle spindle sensitivity, may be used as movement re-education. As an example, proprioceptive training that consists in focusing attention to vibration-induced kinaesthetic illusions appears a simple means to improve the processing of muscle proprioceptive inputs in Parkinson's disease patients (Ribot-Ciscar *et al.* 2017).

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Additional information

Competing interests

We declare we have no competing interests.

Why do we have muscle spindles?

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It is unfortunate that both debaters chose to focus on short latency, segmental reflexes. Most of the terminal arbourizations of spindle afferents contribute to ascending tracts via brainstem to cortical and cerebellar destinations, where they account for most of posture sense and kinaesthesia (Goodwin *et al.* 1972). Similar to any sense organ, maximizing information over a wide dynamic range of self-generated postures and movements despite a limited range of noisy spike rates is a challenge best met by dynamic adjustment of sensor gain (Loeb, 1984). The numbers of spindle afferents in the muscles of the body correlate well with the psychophysical accuracy of posture and movement perception and the impact of errors on uncertainty of end-effectors (Scott & Loeb, 1994). This is most obvious in axial muscles of the head and neck, which have the highest numbers (Voss, 1971; Amonoo-Kuofi, 1983) of the most elaborated spindles (Richmond & Corneil, 2001) in the body but essentially no segmental stretch reflexes (Richmond & Loeb, 1992). As David Burke points out, the length, mass and slowness of human musculoskeletal systems make short latency stretch reflexes less useful, and hence less prominent, than in cats and monkeys. But knowing where your feet are with respect to your head is even more important when you are tall (Tjell, 2001). Computing posture from multiarticular muscles with task-specific fusimotor programs is complicated, suggesting that it must be learned. Overtrained monkeys achieved similar dynamic range in Ia afferent firing for large movements that stretched or shortened their active or passive parent muscles (Schieber & Thach, 1980). Why did they bother? Can humans afford to ignore this?

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Additional information

Competing interests

None declared.

Evidence for independent control of fusimotor and skeletomotor neurons is not convincing

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Based on microneurographic recordings of spindle afferents from intact human subjects, Dimitriou has proposed that it is advantageous for the central nervous system (CNS) to impose independent control of fusimotor neurons to allow targeted regulation of reflex function. We have two major concerns with this analysis.

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Our first concern is that the experiments cited do not directly show that fusimotor activation and skeletomotor neuron activation are decoupled in the muscle that is about to be stretched. In other words, the prevailing view of muscle spindle control (e.g. Edin & Vallbo, 1990), which links fusimotor and skeletomotor activation as part of a consistent coactivation strategy, is not shown to be incorrect. The reduced spindle afferent discharge could easily be part of a generalized reduction in motor activation and not a selective reduction in fusimotor drive.

Second, and more generally, managing fusimotor and skeletomotor activation separately adds to the complexity of motor control, because the CNS would need to track movements, not based simply on voluntary command and afferent feedback, but in full knowledge of what different afferent signals were describing. It is potentially harder to regulate limb motion when key muscle afferent signals may have different meanings (because of varying fusimotor input).

The simplest argument remains that muscle spindles are able to maintain receptor afferent discharge because skeletomotor and fusimotor input work together to facilitate that function. We do not need them to be independently controlled. In this regard we side with David Burke's position.

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Additional information

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None declared.

A fusimotor role for proprioceptive reweighting in a multisensory context

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Muscle proprioception is a key sensory modality for perceiving our own body movements, but it is not the only one. Many studies have provided evidence that vision also contributes to kinaesthesia (Blanchard *et al.* 2013). Spatio-temporally congruent visual and proprioceptive cues can optimise and enhance movement perception, which can be predicted in a Bayesian framework (Van Beers *et al.* 2002; Reuschel *et al.* 2010). Although multisensory integration is generally thought to rely on a weighted combination of different sensory information, the mechanisms underlying this sensory weighting have not yet been fully elucidated and primarily investigated at the highest level of the central nervous system (Klemen & Chambers, 2012). By modulating the sensitivity of muscle spindles, the fusimotor drive is a good candidate to change the relative weight of proprioceptive information by directly facilitating or depressing movement encoding. Ackerley *et al.* (2019) recently found that proprioceptive signals from a passive foot displacement change depending on whether or not the participant sees their foot moving. The relative increase of muscle afferent firing observed in the no vision condition may reflect a proprioceptive weighting increase presumably due to a change in fusimotor drive. Similarly, Jones *et al.* (2001) described a decrease in muscle afferent firing rate during incongruent muscle afferent and visual feedback, which was interpreted as a strategy for resolving bi-sensory conflict. Therefore, the fusimotor drive could play a key sensory role by reweighting proprioceptive information using a direct modulation of muscle mechanoreceptors in ecological and naturalistic multisensory contexts.

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None declared.

Both sides support the resolution

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The resolution of the debate is 'There is much to gain from the independent control of human muscle spindles'. Opposing the resolution, Dr Burke acknowledges that fusimotor drive in humans is partly independent of alpha motoneuronal activation, but he concludes that 'there is little evidence that this is a mechanism for changing the gain of stretch reflexes'. Even if he is right in doubting the evidence (e.g. Horslen *et al.* 2018), it is insufficient to refute the resolution. He goes on to say: 'It is conceivable that selective changes in fusimotor drive play an important role in kinaesthesia.' 'An important role' sounds a lot like 'there is much to gain'.

Dr Burke also feels that 'the field has been hampered by the belief that everything functions as in the cat and that we would see this if only we could study humans behaving like cats'. This alludes to the proposal that because it has not been possible to study spindle firing in humans in as wide a range of motor tasks and contexts as in cats and monkeys, this might explain why task- and context-dependent changes in fusimotor effects in humans have seemed relatively weak. It is worth remembering that animal recordings were the first to indicate that alpha–gamma coactivation did not keep spindle afferents firing during muscle shortening and that ensemble spindle firing signalled muscle length changes. These findings were subsequently confirmed in human neurography. In fact, the field might have moved along more quickly had it been possible to study muscle spindle firing in humans behaving like humans.

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Additional information

Competing interests

None declared.

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