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Human muscle spindles are wired to function as controllable signal-processing devices

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Contents

Abstract

Muscle spindles are encapsulated sensory organs found in most of our muscles. Prevalent models of human sensorimotor control assume the role of spindles is to reliably encode the mechanical state of muscle i.e., muscle stretch. Here, I argue that the traditional view of the spindle as a basic mechanoreceptor is outdated. Spindle organs can be independently tuned by spinal γ motor neurons that receive top-down and peripheral input, including from cutaneous afferents. I propose that spindles under efferent control play a flexible and higher-level role, providing a unique service to the nervous system: that of a peripheral signal-processing device that helps augment and expedite sensorimotor performance. Recent studies with naturalistically active humans support such a role, showing that spindle tuning enables the independent preparatory control of muscle compliance, the selective extraction of information during implicit motor adaptation, and for segmental stretch reflexes to operate in joint space. A new model of human sensorimotor control is presented, viewing γ motor activity as an intermediate coordinate transformation that allows different descending and peripheral information to project onto a common spindle-based coordinate frame. Incorporation of advanced signal-processing at the periphery may well prove a critical step in the evolution of sensorimotor control theories.

Introduction

Most of our skeletal muscles contain a large collection of muscle spindle organs. Spindles are generally believed to be basic mechanoreceptors that encode muscle stretch and provide reliable and consistent information about the state of the spindle-bearing muscle. Previous work and more recent studies using genetic manipulation methods have added a great deal of knowledge about the molecular mechanisms of mechanotransduction (e.g., Kruse & Poppele, 1991; Bewick & Banks, 2015; Woo *et al.*, 2015). Spindles have been proposed to play a basic, low-level role in reflex motor control (Houk, 1976) and proprioception (Goodwin *et al.*, 1972), and their malfunction has been linked to impaired muscle coordination (Sainburg *et al.*, 1993). An interesting new proposition is that the mechanoreceptive part of spindles responds best to force-related variables, as shown in relaxed muscles (Blum *et al.*, 2017). Still, the role of muscle spindle organs in their entirety (i.e., of the mechanoreceptor under in vivo efferent control) has remained unclear and a matter of ongoing debate (e.g., Macefield & Knellwolf, 2018; Burke, 2021a, b; Dimitriou, 2021a, b).

In the relaxed muscle of the unengaged human, the characteristics of imposed muscle stretch are rather faithfully encoded by the signals of muscle spindle afferents. Specifically, there are two main types of muscle spindle receptors, the primary and the secondary, which give rise to the primary (type Ia) and secondary (type II) afferents, respectively (Boyd & Davidson, 1962). When imposing a ramp-and-hold stretch of the relaxed muscle, type Ia from this muscle are most responsive during muscle stretch, are sensitive to the rate of change of length (i.e., velocity), may encode static length but are silent during muscle shortening. That is, under passive conditions, primaries can be considered to have both a good dynamic and fairly good static muscle-length sensitivity, whereas type II from passive muscle represent good static length sensitivity but a poorer dynamic sensitivity (Edin & Vallbo, 1990a). These response patterns reflect the general view of spindles, which says that type Ia firing encodes static muscle length and the velocity of stretch, and type II encode static muscle length. However, unlike other types of peripheral mechanoreceptors, the spindle organs have their own motor supply in the form of γ motor ('fusimotor') neurons (Barker & Chin, 1961; Matthews, 1972). Despite their rich innervation, the general function of muscle spindles in sensorimotor control has remained unclear, particularly so in the context of naturalistic active movement.

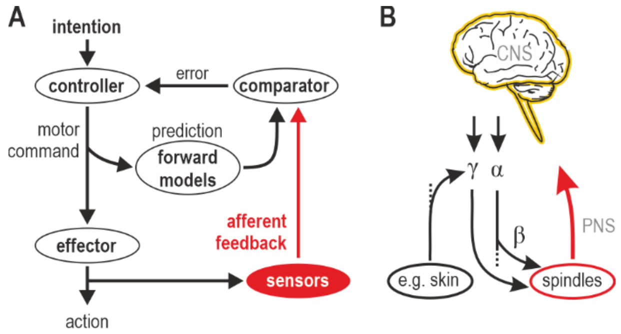

Figure 1. Human sensorimotor control and muscle spindle innervation
(A) One prevalent model of human sensorimotor control. Proprioceptors in muscle and skin are viewed as basic sensors, reliably encoding actual mechanical state in unimodal coordinates. Advanced (e.g., selective) processing of sensory signals is thought to occur only in the CNS. **(B)** The role of muscle spindles under naturalistic efferent control has remained unclear. Mammalian muscle spindles can be powerfully controlled by γ motor neurons. These lower motor neurons are subject to both top-down and peripheral control, including from cutaneous afferents.

Figure 1A represents one prevalent model of how a voluntary movement is controlled and monitored (Wolpert & Miall, 1996). In this model, a controller in the CNS turns the intention to move into a motor command that is sent to skeletal muscles that power the action. A copy of the motor command is sent to internal forward models that make predictions about the sensory consequences of this action. The action itself generates feedback from sensory receptors. If the movement progresses as intended, there should be no discrepancy between the internally predicted signal and actual sensory feedback. This framework views mechanoreceptors in muscle and skin as basic sensors that transduce physical stimuli into unimodal feedback signals, ignoring the independent motor supply to muscle spindles. However, in mammals, ~30% of spinal motor neurons are γ, which supply muscle spindles exclusively. These γ neurons can be controlled by descending commands and/or peripheral afferent input (Fig. 1B; see also following sections). The nervous system has clearly placed a premium on the control of muscle spindle signals at source. Given the renewed emphasis on proprioception in motor control and implicit adaptation of voluntary movement (e.g., Crevecoeur *et al.*, 2016; Scott, 2016; Tsay *et al.*, 2021), it is important to strive for a better understanding of how the most complex sensory organ outside of the special senses contributes to sensorimotor function.

Spindle tuning linked to skeletal muscle activation

The most popularized explanation for human spindle control is based on ‘α-γ co-activation’ (Vallbo, 1970). In this view, γ fusimotor neurons are activated virtually the same time as α motor neurons, in order to prevent spindles from falling slack during muscle contraction. Essentially, in this context, α-γ co-activation simply maintains the sensor operational, allowing it to keep functioning as a mechanoreceptor that encodes muscle stretch. This rather mundane fusimotor function is probably one reason why prevalent computational frameworks have ignored fusimotor control. Most support for a lack of independence between α and γ motor neuron activity has come from recording spindle afferent signals during isometric contractions or during unnaturally slow and restricted movements (e.g., Gandevia & Burke, 1985; Wessberg & Vallbo, 1995; Kakuda *et al.*, 1996). Moreover, co-activation of extrafusal (skeletal) and intrafusal (spindle) muscle fibers can be easily implemented through the more primitive beta neurons (Jami *et al.*, 1982; Emonet-Dénand *et al.*, 1992). β neurons are essentially just α motor neurons that branch out to innervate extrafusal and intrafusal muscle fibers. Both mammals and lower vertebrates have β motor neurons, but only mammals have γ motor neurons. The vast majority of efferent projections to spindles are from γ motor neurons. The independent γ motor supply must therefore represent an evolutionary advantage, realized through the ability to dissociate spindle control from the control of skeletal muscles, in cases where this dissociation is favorable to the organism (see following sections).

Nevertheless, α-γ co-activation can account for the increase in spindle afferent firing observed during isometric contraction of the spindle-bearing muscle (Edin & Vallbo, 1990b); β motor neurons can also contribute (Kakuda *et al.*, 1998). This increase in spindle firing is congruent with the known 'automatic' gain-scaling of short-latency stretch reflexes (SLRs), where reflex sensitivity is proportional to background activation of the homonymous muscle, as shown in postural tasks (e.g., Matthews, 1986; Pruszynski *et al.*, 2009). However, automatic gain-scaling alone cannot account for the modulation of SLR gains observed during movement (Dufresne *et al.*, 1980; Soechting *et al.*, 1981; Nakazawa *et al.*, 1997; Wallace & Miles, 1998). I have recently shown that spindle sensitivity to stretch can be positively related to the activity level of the spindle-bearing muscle, but also be negatively related to antagonist muscle activity (Dimitriou, 2014). That is, during continuous sinusoidal movements of a finger against different loads, spindle responsiveness to stretch was shown to depend on the balance of activity across an antagonistic muscle pair (hence joint dynamics), rather than activity in the spindle-bearing muscle alone (Fig. 2A). The negative relationship with antagonist activation is compatible with top-down reciprocal inhibition of fusimotor neurons, as shown in intercostal muscles of the cat (Sears, 1964).

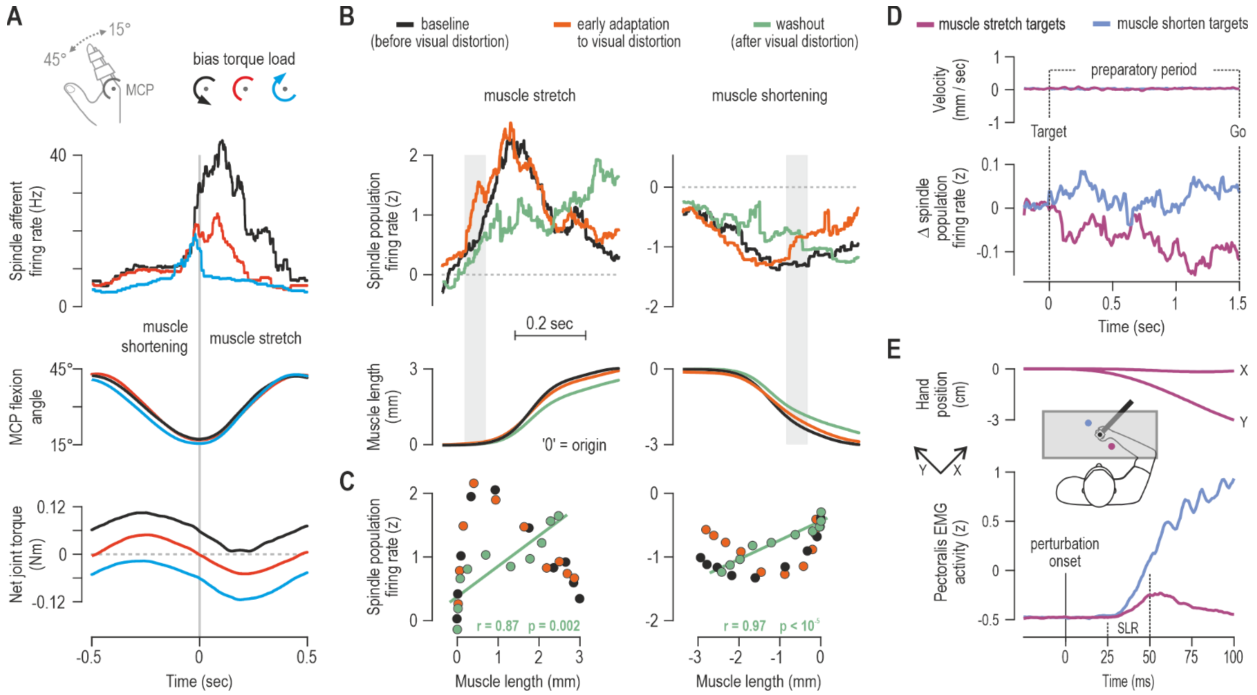

Figure 2. Human muscle spindle organs are not basic kinematic sensors
(A) Averaged responses of a representative spindle afferent from the common digit extensor muscle, during active sinusoidal movements of a single finger at 1Hz (adapted from Dimitriou, 2014). Movement was constrained to the metacarpophalangeal joint (MCP) and occurred under a flexion resistive or assistive torque load, or no external load. Standard classification tests identified the afferent as a typical spindle primary (i.e., 'type Ia'; see Fig. 2 in Dimitriou, 2014). Despite virtually identical finger flexion, spindle responses to stretch varied according to joint dynamics. **(B)** Averaged spindle afferent population responses and equivalent muscle length changes during the classic visuomotor rotation task (both 'B' and 'C' adapted from Dimitriou, 2016). Grey background bars highlight phases in early adaptation (orange) that differ substantially from baseline (black). **(C)** Correlating the signals shown in 'B' (down-sampled at 50 ms) confirmed a significant relationship in the washout stage. **(D)** Muscle velocity (null) and changes in spindle Ia responses before movement initiation in the classic instructed-delay reaching task with the hand. Ia firing rates from extensor muscles were lower when preparing movement to visual targets associated with stretch of the spindle-bearing muscle (purple). 'D' and 'E' are adapted from Papaioannou and Dimitriou (2021). **(E)** Averaged signals across participants; experiments using a robotic manipulandum showed a congruent goal-directed tuning of stretch reflexes, including at the short-latency epoch ('SLR') in cases where the homonymous muscle was not heavily loaded before perturbation. Color coding as in 'D'.

Using an innovative experimental approach, Villamar and colleagues (Villamar *et al.*, 2021) have very recently tested the hypothesis that SLR sensitivity during movement can be explained by the balance of activity across agonist and antagonist muscles. The observed changes in SLR sensitivity during ballistic elbow movements did reflect the net background activity across agonist and antagonist muscles. Moreover, the relative impact of agonist and antagonist activity on SLR gain were "remarkably similar" to the coefficients generated by the aforementioned spindle study. Taken together, the afferent and stretch reflex results suggest that spindle tuning is at least partly responsible for shaping SLR gains during sinusoidal and ballistic movements under different loads. The 'antagonistic' mode of control demonstrates that spindle sensitivity to stretch does not only reflect the state of the homonymous muscle. The spindle response to a physical stimulus (i.e., the mechanoreceptor signal) can be modulated or 'processed' according to the contractile state of the spindle-bearing muscle and its antagonists. In the context of sinusoidal and ballistic single-joint movement, primary spindles do not seem to function as reliable unimodal sensors encoding muscle stretch or joint rotation (Fig. 2A). Rather, by integrating mechanical stimulation and fusimotor commands, spindles help augment volitional motor control according to the prevalent dynamics around a single joint. That is, spindle tuning based on muscle activation balance (i.e., reciprocal control) enables even segmental reflex contribution from single muscles to occur in 'joint space'. Future research will determine whether spindle tuning can also reflect multi-joint dynamics.

Independent tuning of muscle spindles in active contexts

As described in the previous section, spindle sensitivity can reflect muscle activation in isometric and movement tasks where differential muscle loading is the defining variable feature. However, neither 'α-γ co-activation' nor 'antagonistic muscle balance' can justify the need for an independent fusimotor system. α-linked fusimotor activity could be carried solely by β efferents. So why have we and other mammals evolved γ motor neurons? What are the benefits for sensorimotor performance? With existing methodologies, it has proven virtually impossible to systematically record from human γ motor neurons. Only one study claims to have directly recorded from single γ efferents of immobile humans (Ribot *et al.*, 1986). However, recording from individual spindle afferents using microneurography is a feasible and even preferable alternative, because γ neurons supply spindles exclusively, and the spindle organ acts as an integrator of input from mechanoreception and multiple fusimotor fibers (Matthews, 1972). Therefore, one way to address the questions above is to record spindle afferent signals during naturalistic movement in fundamental sensorimotor tasks.

One such task involves implicit motor adaptation to a visual distortion (i.e., the classic visuomotor rotation). In a recent study, participants used their right hand to perform this task while spindle afferent signals were recorded from wrist extensor muscles (Dimitriou, 2016). The observed adaptation behavior was stereotypical for this type of task: an exponential curve could be fitted to movement direction error in the early adaptation stage and in 'washout' (the stage where participants gradually re-adapt to removal of the visual distortion). Despite fundamentally similar muscle kinematics across all stages of the task, there was a dissociation in spindle population signals as a function of task stage. Specifically, compared to baseline, there was an increase in primary muscle spindle sensitivity in early adaptation (Fig. 2B), suggesting a similar increase in stretch reflex gains. In the washout stage, spindle afferents (Ia and II) stopped encoding velocity and were instead 'linearized' with respect to muscle length (Fig. 2BC, green). That is, spindle signals were tuned to hand position only during washout, possibly for facilitating the relevant update of internal models. It appears the fusimotor system can enable spindle signals to shape primarily according to kinematic or kinetic/dynamic variables (e.g., Fig. 2BC vs. 2A), according to the nature of the motor task. Despite the specific benefit of spindle control in the visuomotor rotation task, the results demonstrate that the fusimotor system is a contributor in implicit motor adaptation. Here, the mechanoreceptive signal was tuned both according to the need to adapt and the congruency between haptic and visual coordinate frames.

By applying whole-arm perturbations at the different stages of the implicit adaptation task, a follow-up study produced equivalent results concerning stretch reflex modulation, including evidence that SLR tuning reflects individual rates of implicit adaptation (Dimitriou, 2018).

Another well-studied experimental paradigm is the instructed-delay reach, where there is a delay between a target cue and a 'Go' signal to move. This delay is designed to investigate movement preparation. Having a long-enough preparatory delay improves the overall quality of movement and cuts down on reaction time (Rosenbaum, 1980; Ghez *et al.*, 1997; Sutter *et al.*, 2021). Preparatory cortical activity correlates well with parameters such as movement direction/extent and visual target location (Tanji & Evarts, 1976; Weinrich *et al.*, 1984; Kurata, 1993; Shen & Alexander, 1997). It was initially suggested that preparatory cortical activity represents a subthreshold version of the activity seen during movement, but more recent work suggests that preparation sets an initial neural state that somehow facilitates the subsequent movement (Churchland *et al.*, 2010). In a recent study (Papaioannou & Dimitriou, 2021), we demonstrate goal-directed tuning of muscle spindles and stretch reflex gains during movement preparation. Specifically, despite no differences in kinematics or surface EMG during preparation, type Ia firing rates were lower when preparing to reach targets associated with stretch of the spindle-bearing muscle (Fig 2D). These findings are congruent with recent reports of preparatory modulation in the primary somatosensory cortex (Ariani *et al.*, 2021; Gale *et al.*, 2021), but suggest that such preparatory changes in the CNS may be partially due to processing altered afferent signals, rather than exclusively reflect internally-generated commands or priming.

We also found a strong positive relationship between type Ia firing during late preparation and time-to-peak velocity during reaching, suggesting that spindle preparatory tuning has a substantial impact on the subsequent voluntary movement (Papaioannou & Dimitriou, 2021); every additional unit increase in Ia firing rate involved a 3 ms delay in attaining peak velocity during movement. This relationship can be understood in terms of the spindle's role in stretch reflexes. By independently modifying spindle gains, the fusimotor system can affect the degree of reflex muscle stiffness during movement execution, without affecting contractile muscle force during preparation. Accordingly, additional experiments implicating whole-arm perturbations confirmed that preparatory differences in type Ia responses reflected a congruent goal-directed tuning of stretch reflex gains, including at SLR latencies (Fig. 2E). Decreasing the level of reflex stiffness in a goal-appropriate manner facilitates the execution of planned reaching movements. Muscle afferent (reflex) feedback contributes significantly to force generation, about a third of volitional contraction (Hagbarth *et al.*, 1986; Gandevia *et al.*, 1990), regardless if the contraction is maximal or not (Macefield *et al.*, 1993). Future work will determine whether spindle tuning helps control muscle compliance across different tasks (such as object interception), and further clarify how muscle loading interacts with independent tuning of spindles.

Nevertheless, in planned voluntary reach, spindle responses to stretch can be locally adjusted (or 'processed') according to the intention to move in a particular direction (Fig. 2D). That is, tuning of human spindles can reflect specific goals within a behavioral context (reaching), which represents a finer degree of spindle modulation than tuning according to behavioral context or type of task, as previously and more recently suggested (Prochazka *et al.*, 1985; Ribot-Ciscar & Ackerley, 2021). One study found no evidence of a selective effect on fusimotor neurons when anticipating the need to make a contraction that would oppose an imposed movement of the foot at the ankle (Burke *et al.*, 1980). However, our 2021 study was the first to implicate true reaching intention and action. In this case, the intention to perform a voluntary goal-directed movement may be necessary for engaging independent fusimotor control.

Moreover, there may be a large degree of functional specialization in the fusimotor control of upper vs. lower limbs. Admittedly, most of what we know concerning muscle spindle structure and fusimotor function has come from work with cats (e.g., Barker, 1948; Matthews, 1972; Hulliger, 1984), and many inferences we currently make concerning human fusimotor control would have been impossible without this work. For example, such research has shown that there are two independently controlled groups of γ motor neurons, ‘static’ and ‘dynamic’, with the latter innervating only primary muscle spindles (Matthews, 1962). In active cats, fusimotor and spindle activity has been mostly examined in the context of locomotion (see e.g., Prochazka, 1996). Equivalent data during human locomotion are lacking due to methodological limitations. One prominent line of work suggests that cat spindles are not basic length detectors, but instead are independently controlled in a predictive manner in order to modulate the function of spinal central pattern generator (CPG) circuits during locomotion (Ellaway *et al.*, 2015). A similar fusimotor support of human bipedal locomotion may occur, although it is currently unclear whether CPG networks exist in the human spinal cord (Minassian *et al.*, 2017).

Recordings from humans have also suggested a more predictive role for spindle signals. In one paper, we correlated spindle population responses recorded during block-grasping and key-pressing with muscle velocity occurring at the same time as the recorded afferent signal, and velocity observed at different points into the future (Dimitriou & Edin, 2010). The closest relationship was between afferent firing rate and velocity ~150ms after the spindle signal. This result meant that muscle spindles fulfilled all three neurophysiological criteria for identifying a forward sensory model (Wolpert & Miall, 1996): spindle inputs were the current state of the system (mechanoreception) and an efferent command (β or α-γ), and spindle output predicted the future kinematic state. However, later studies showed that the spindles’ ‘predictive’ capacity does not hold across tasks. For example, if anything, the opposite results should have been observed in preparatory modulation (e.g., Fig. 2D), and suddenly adding a new external load did not significantly alter the predictive capacity of spindles during the initial cycles of sinusoidal movement (Dimitriou, 2014). To identify forward sensory models, one could perhaps add a fourth criterion stating that forward models should make worse predictions in novel contexts.

Peripheral afferent control of fusimotor neurons

Prominent theories of spindle and fusimotor control have not incorporated the possibility of substantial afferent influence on fusimotor neurons. Peripheral (‘reflexive’) input to γ neurons, including from cutaneous afferents, has been mainly demonstrated using electrical nerve stimulation in anaesthetized cats (Appelberg *et al.*, 1977; Johansson & Sojka, 1985; Johansson *et al.*, 1986). These findings reinforce the idea that pools of γ motor neurons should be considered as an integrative system able to combine sensorimotor ‘apples and oranges’ i.e., descending commands and peripheral multisensory information.

A functional degree of peripheral multisensory integration -such as for dexterous object manipulation- may be possible at the level of the spindle as a result of afferent control of γ neurons. This hypothesis is compatible with evidence of ‘multimodal’ signals (tactile-proprioceptive) already in area 3a of the somatosensory cortex (Kim *et al.*, 2015). However, so far, cutaneous stimulation has been shown to have a limited impact in two studies of spindle afferent activity in passive humans at rest (Aniss *et al.*, 1990; Gandevia *et al.*, 1994). But afferent control of spindle sensitivity may prove stronger or more easily unmasked in the active individual (e.g., due to higher background tonus). The specific functional advantage of having such afferent connections is currently unclear. One previous study has demonstrated edge-orientation processing in tactile neurons as a function of their receptive fields (Pruszynski & Johansson, 2014). However, in this case, cutaneous afferent signals were bound to the characteristics (edge-orientation) of the ‘adequate’ physical stimulus. In contrast, muscle spindle output can potentially be modulated according to the characteristics of a physical stimulus in another modality (e.g., cutaneous), via efferent control. Although top-down control alone supports the notion that spindles are best viewed as flexible signal-processing devices rather than basic mechanoreceptors (Fig. 1B & Fig. 2), the possibility of substantial peripheral control of fusimotor neurons adds another layer of support to this proposition.

Concluding remarks

I propose that spindle organs are controllable pieces of peripheral hardware whose primary function is to augment and expedite sensorimotor performance, rather than encode stretch. The fusimotor neurons controlling spindles can integrate multisensory peripheral input and top-down commands (which can also reflect sensory events, e.g., in vision; Fig. 2D). It is reasonable to think of fusimotor activity as an intermediate coordinate transformation enabling different information sources to project onto a common spindle-based coordinate frame (Fig. 3). Such dimensionality reduction may potentially simplify motor control without limiting performance. A more flexible and central role for spindles justifies the premium placed on their control by the nervous system (i.e., ~30% of lower motor neurons are γ). Such a role is also compatible with the seemingly large number of parameters found to correlate closely with motor and premotor neural activity, and with models that claim the motor cortex essentially operates in 'proprioceptive' coordinates (Adams *et al.*, 2013).

Consistent information about actual limb position and movement is also necessary, but vision (e.g., Sarlegna & Sainburg, 2009), joint and cutaneous signals can contribute to proprioception and kinesthesia (Collins & Prochazka, 1996; Collins *et al.*, 2005). This is also supported by the proposed model (Fig. 3). Interestingly, it is known that direct electrical stimulation of single joint and cutaneous afferents evokes appropriate sensations, but stimulation of single spindle afferents does not lead to any conscious sensations in the absence of movement (Macefield *et al.*, 1990). Tendon vibration (artificial spindle stimulus) of the unseen limb can lead to illusory perception of physically impossible limb configurations, and seeing the vibrated limb actually attenuates illusory motion (Lackner & Taublieb, 1984). If spindles are not routinely

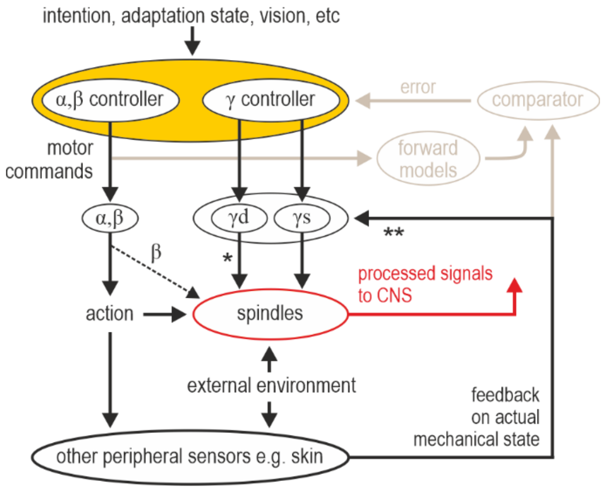

Figure 3. Advanced signal-processing at the level of muscle spindle organs
In addition to descending commands to skeletal muscles and an efferent copy to forward models (Fig. 1A), there can be independent descending control of γ dynamic ('γd') and γ static ('γs') spinal motor neurons. The vast majority of efferent projections to spindles are from γ motor ('fusimotor') neurons, but there is also some β supply (indicated by the thinner dashed line). Fusimotor control can affect spindle output in the absence of mechanical stimulation (i.e., muscle stretch), but fusimotor activity can also shape spindle responses to direct mechanical stimulation arising from own action or the external environment. '*': γd project only to primary muscle spindles, allowing for differential control of primary and secondary muscle spindles. Electrophysiological studies in mammals have also demonstrated multisensory afferent convergence onto fusimotor neurons. '**': The specific impact of afferent control of fusimotor neurons has not been determined yet in the active human, and may well vary across body segments e.g., stronger in the hand and/or the foot. In this model, joint and cutaneous receptors (and vision) provide consistent/reliable information about actual bodily state, and potentially so do spindles, e.g., if they are predominantly affected by direct mechanical stimulation (as in the case of the passive, unengaged individual). But here, fusimotor activity represents an intermediate coordinate transformation that allows different descending and peripheral information to project onto a common spindle-based coordinate frame. So far, spindle tuning has been shown to facilitate load compensation in joint space, the selective extraction of information during motor adaptation, and the independent preparatory adjustment of muscle compliance before goal-directed reaching (Fig. 2).

tasked with providing a consistent representation of muscle state (i.e., not tasked with encoding the actual sensory consequences of action), spindle tuning can instead emphasize the flexible facilitation of concurrent or future action. Here, I have outlined recent evidence that spindle tuning enables the independent preparatory control of muscle compliance, the selective extraction of information during implicit motor adaptation, and for segmental stretch reflexes to operate in joint space. The complete spindle repertoire remains to be revealed. Achieving a comprehensive account of spindle contribution will likely prove a decisive step towards better understanding of core sensorimotor principles.

Open questions

1. Does the nervous system tune muscle spindles according to multi-joint dynamics?
2. Beyond planned reaching, does independent tuning of spindles help control muscle compliance across different tasks (e.g., object interception)?
3. In terms of task-relevant flexibility, how different is the tuning of primary and secondary muscle spindle receptors?
4. Given the peripheral afferent input to fusimotor neurons, does cutaneous stimulation have a significant impact on spindle responses in the active human? What are the benefits for sensorimotor performance e.g., in terms of rapid and dexterous manipulation of objects?
5. Is there substantial functional specialization in spindle control across human upper and lower limbs (e.g., in the degree of cutaneous modulation), and if so why?
6. Which brain areas and descending pathways are involved in fusimotor control during e.g., movement preparation?

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Competing interests statement

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