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Muscle proprioceptive feedback can be adapted to the behavioral and emotional context in humans

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To interact with the external world, incoming sensory information informs us about situational changes that are of relevance to our behavior and we act upon these accordingly, be it in a produced movement or an internal reaction (e.g. an emotion, paying attention). Humans efficiently interact with their world and each other and to do this, a system is required to promote relevant sensory feedback to allow fast, accurate, and appropriate actions. We review findings from single unit recordings of muscle afferents that demonstrate the effects of the descending γ -fusimotor system on their activity. This includes changes in firing from cognitive and emotional influences, which we postulate can prepare the body for responsive and appropriate action to a change in environment.

We are frequently placed in different situations and the way our body reacts determines how we handle them. Humans are predisposed to react in certain ways (e.g. fight or flight) and these reactions are enriched by individual experience, resulting in constant adaptation and individual variability. To react appropriately, a feedforward system is ideal for efficiency, where the brain anticipates the best movement strategy suited to the situation. Muscle spindles (Box 1) are complex mechanoreceptors, which send afferent information to the central nervous system about muscle stretch, but they also have the particularity of being innervated by a sophisticated, descending, efferent system, called the (gamma) γ -fusimotor system (Fig. 1) [1]. This efferent signal can make the muscle spindle more or less sensitive to different parameters of a motor activity [2,3]. The existence of this efferent system to control muscle spindle sensitivity leads us to believe that its function is useful, such as proprioceptive adaptation during a movement in progress.

Box 1. Muscle spindles: These are mechanoreceptors that respond to changes in the stretch of a muscle. Primary type Ia sensory fibers are the most numerous (signaling the degree of change in muscle movement), there are less secondary type II fibers (signaling the length of the muscle), and Golgi tendon organs (type Ib, sensing muscle tension) are even rarer. These messages are processed centrally and add to our sense of proprioception (kinesthesia), providing us with a sense of body position and self-movement.

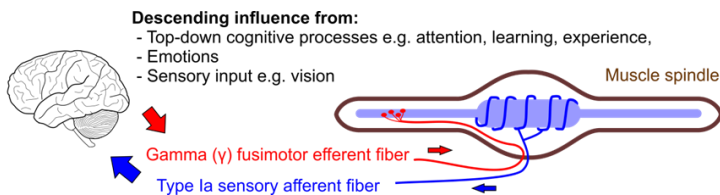


Figure 1. Schematic of how the γ -fusimotor drive influences the responses of muscle spindles. The descending influence of process such as cognition, emotions, and other senses (shown in red) can directly influence the static and/or dynamic sensitivity of muscle spindles via the selective control of static and/or dynamic γ -fusimotor efferents. The effect of this can be measured by imposing the exact same movement to a muscle under different conditions, as measured via single unit microneurography recordings from muscle afferents.

Researchers in the field of proprioception have investigated which conditions engage the fusimotor system. The technique of microneurography (Box 2), which permits direct recordings from human peripheral nerves and access to the messages emitted by single afferents, has provided many insights into proprioceptive feedback [4,5]. Researchers have asked whether the γ -fusimotor system allows a selective control of muscle spindle afferent sensitivity, which would allow us to adjust muscle proprioceptive feedback to the environmental context and the requirements of a motor activity [6].

Box 2. Microneurography: This technique of percutaneously accessing peripheral nerve fibers in awake humans. In single unit microneurography, a needle electrode is inserted through the skin and into a peripheral nerve, where recordings from individual fibers, typically afferents, can be distinguished. Stimuli can be applied to the body, while single unit activity is monitored to different interventions.

In animals, it has been demonstrated that sensitivity of muscle afferents can be modified by descending influences of the γ -fusimotor drive, where the central nervous system can 'set' the activity level independently [7]. Similar mechanisms have been investigated in humans, but only small effects of a descending drive have been found [8–10]. Most microneurographic recordings showed a coupling between muscle spindle activity and muscle

contraction (α - γ coactivation), which led to the conclusion that the fusimotor system functioned to compensate for the slackening of receptors during muscle shortening [2,11]. Although fully in agreement with this view of the role of the fusimotor system, microneurography work from our group, performed at the level of the leg, has provided evidence that this role is not exclusive, but that independent control of the γ -fusimotor system can also exist, which has opened the door to other functions of the muscle proprioceptive system [12–16]. We have found that it is imperative to control the environmental situation well and monitor the physiological state of the participant to ensure that these are stable, as during cognitive and emotional manipulation, a steady baseline is required. It is important for the participant to be comfortable in the environment and physiological signals of the participant (e.g. heart rate, electrodermal activity, electromyographic signals, see [13]) can be measured. These are useful during the whole microneurography processes, as fluctuations and high activity in these can indicate that the participant is not calm or comfortable, without having to continually explicitly ask them.

1-Evidence for an independent gamma drive in subjects at rest

a. Recordings from single γ -fusimotor neurons

Our first data on the fusimotor system were obtained by the direct recording of γ -fusimotor neurons in subjects at rest [16], where we showed that these efferents were activated by factors such as cognitive, behavioral, and environmental interventions. This was in contrast to the skeletomotor extrafusal muscle efferents, which could be clearly distinguished during movements and were not influenced by such top-down factors. We also observed that when γ -fusimotor activity was triggered, the subject could voluntarily stop it by seeking a deep state of physical and mental relaxation. This showed the importance of controlling the relaxation of the subject, since if the gamma system was already activated because the subject was alert (e.g. interested in the experimental approach), any test maneuver would not increase the γ -fusimotor activity relative to the control situation in a clear or true manner (see [17,18] for further information about experimental controls), although data modeling can also aid in accounting for descending influences under active conditions [19,20]. However, these recordings were rare and it took 5 years to collect data from the 6 γ -fibers presented in the paper. Communication with other microneurographers at the time revealed they had occasionally also encountered similar neurons. Characteristically, these neurons did not respond to sensory stimulation, and demonstrated intermittent behavioral changes with no clear cause. Due to the challenges in finding such activity and the difficulty in testing the neuron, it was not feasible to pursue our questioning of the influence of the γ -fusimotor system using direct γ -efferent recordings. Rather, as muscle spindle afferents are readily recorded, we sought to infer γ -activity through their influence on muscle spindles.

b. Recordings from single muscle spindle afferents during cognitive processes

By taking particular care of the mental state of the participants, we subsequently showed an increase in the responsiveness of muscle spindle primary endings to movement in resting subjects performing mental computation [21]. It was unlikely that these changes could be attributed to changes in muscle sympathetic activity, despite a direct sympathetic innervation of intrafusal muscle fibers [22], since muscle spindle firing is not influenced by a strong and sustained physiological activation of muscle sympathetic outflow [23]. Rather, we postulated that switching from a relaxed state to an active mental state triggers a γ -fusimotor drive independent of the α -motoneuron drive. Beyond this general excitatory effect, the question remained as to whether there could be a modulation of the static and/or

dynamic parameters of muscle proprioceptive feedback in the regulation of movements.

To answer this question, we investigated whether muscle proprioceptive sensitivity changed in a situation where the subject was asked to close their eyes and focus their attention on an imposed movement, in order to recognize it, as compared to a control situation where they did not pay attention to the movement [15]. We imposed movements in the shape of cursive letters because they are sufficiently complex to engage the subject's attention, but were easy to name once recognized. The neural response of muscle spindles to the same movement describing a letter was highly reproducible in the control condition; however, the afferent responses were modified when the subject paid attention to the movement to recognize it (Fig. 2A). The observed changes suggested that primary muscle spindle endings behaved like secondary endings. We interpreted this 'secondarization' as a means to facilitate the coding of the shape of the movement that would facilitate the task of recognizing letters. In all, the percentage of correct recognized movements increased when changes in muscle spindle sensitivity were observed. Thus, the γ -fusimotor drive seemed to adapt to select the most relevant muscle proprioceptive information according to the task.

It was postulated that such spindle sensitization could also be the result of an aspecific effect, such as arousal, which could condition the receptivity of the whole organism to surrounding stimuli. We therefore extended this research and asked the subject to pay attention either to the speed of ramp movements of their foot or to its final position reached [14]. We observed changes in muscle afferent firing when participants attended to the velocity or amplitude, reflecting dynamic and static gamma activation, respectively. These results support the view that γ -fusimotor control is not an aspecific effect but results from a task-specific event and allows the parametric control of muscle spindle feedback to fit task requirements.

c. Recordings from single muscle spindle afferents during emotional processes

It is not only cognitive processes that can engage the γ -fusimotor drive, but emotions can influence the feedback gained from muscle afferents. Emotions can evoke strong reactions that profoundly influence our bodies and modulate our preparedness to move [24], where pleasantness typically facilitates approach and unpleasantness primes withdrawal. The emotion derived from a situation can impact on the timing of movements [25], where unpleasant situations are particularly salient [26,27]. Recently we recorded muscle afferent activity [13], while changing the participant's emotional state through listening to happy, sad, or neutral-emotional music. Muscle afferent firing in response to passive ankle movements was modified by the emotional context, especially for the induced sad emotion, where the muscle spindle dynamic response increased (Fig. 2B). This effect could be seen in the change in the depth of modulation of muscle afferent firing over each condition (i.e. the maximum minus the minimum firing rate), where in the sad condition, there were typically marked pauses between the sinusoidal movements that were not present in the neutral condition. This was supported by behavioral findings showing that under the same conditions, kinesthetic acuity was also affected by emotional state, where it was improved during imposed sadness [28]. Our findings are also congruent with those obtained using transcranial magnetic stimulation, showing that corticospinal excitability is increased when listening to emotional music [29]. The specific effect of emotions that we demonstrated may be exploited therapeutically, such as for priming movements in patients with depression, by listening to sad music and it is clear that emotions should be taken into account during movement investigations, especially as emotion is already known to shape our perception in vision and audition [30].

d. Recordings from single muscle spindle afferents during multisensory processes

The effect of the γ -fusimotor system can be seen when unisensory, as compared to multisensory, information is received. For example, we found

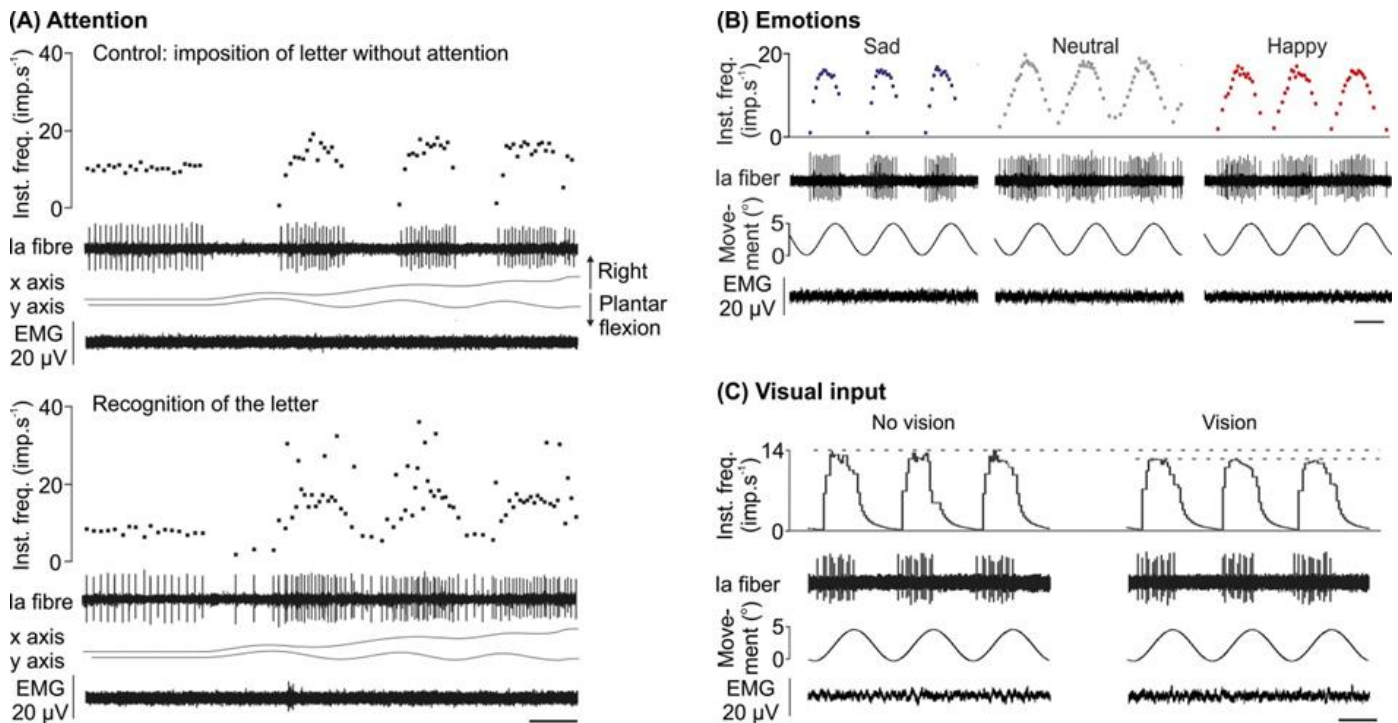


Figure 2. Examples of situations where there is a descending influence from the γ -fusimotor drive, as shown by changes in muscle afferent activity to imposed movements of the foot. (A) The imposition of a letter as a 2D movement without the participant paying attention (top) and when the participant was instructed to pay attention to the movement to attempt to recognize the letter (bottom). The muscle afferent response was more variable during recognition. Adapted from Hospod et al (2007) [15]. (B) Sinusoidal movements of the foot were imposed during listening to sad, neutral or happy music, to induce the corresponding emotion. During sad music, the depth of modulation (change in instantaneous firing frequency) was increased, as well as clear silences (lack of spontaneous activity) between sinusoids. Adapted from Ackerley et al (2017) [13]. (C) Sinusoidal movements of the foot were imposed when the participant either closed their eyes or watched their foot move. The depth of modulation (change in instantaneous firing frequency) was decreased when the participant had combined proprioceptive and visual input. Adapted from Ackerley et al (2019) [12]. All microneurography recordings were from Ia muscle spindle afferents originating in the extensor digitorum longus muscle of the leg. Horizontal scale bars = 1 s.

that when participants were not able to see their foot move, muscle afference was slightly increased, as compared to when participants had congruent proprioceptive and visual information (Fig. 2C) [12]. Similarly, when proprioceptive information from a moving hand was coupled with incongruent visual information, proprioceptive sensitivity was reduced to resolve bi-sensory conflict [31]. Along the same lines, we would predict that in a rubber-hand illusion paradigm [32], the embodiment of the fake hand is accompanied by a decrease in muscle afferent inputs due to a decrease in the γ -fusimotor drive, which counterpart would be to give more weight to the visual information of touching the plastic hand, but this remains to be explored. The specific contribution of muscle proprioceptive signals to body ownership has been recently demonstrated where grasping an artificial finger induced a sense of ownership of it [33], as well as the influence of cognitive and environmental factors on brain process from these sensory inputs [34].

2-Independent gamma motor control for purposeful movements adapted to the situation

The work summarized above and visualized in Figure 2 demonstrates the existence of an independent, top-down control of the γ -fusimotor system, since all changes have been shown in the resting subject, without concurrent α -activity. Note that stronger modulation may have been predicted from animal work, but it has always been an intriguing observation that muscle spindle firing rates are much lower in humans than in animals [35]. For example, the fusimotor-induced increase in human spindle discharge during isometric contraction may be ~15 times lower in humans than in awake cats [36,37]. Such differences may therefore be present in the influence of the fusimotor system on muscle spindle sensitivity and small changes in muscle spindle sensitivity may nevertheless have a significant effect on proprioception. This was the case during listening to sad music [13,28] and during noise-induced increases in the variability of the spindle discharge [38], both showing improved movement sense.

The selective and differential γ -fusimotor system that controls muscle spindle sensitivity is likely activated to adapt muscle proprioceptive feedback during voluntary motor activities. Although it is not easy to infer γ -activity from the recording of spindle endings in the active subject, a number of observations provide evidence of this. The finding that humans can finely-control muscle proprioceptive feedback through an optimized fusimotor drive is in line with the idea that proprioceptive training can improve motor performance [39]. There are also many studies showing that somatosensory factors play a major role in the process of learning, particularly at the early stage of motor skill acquisition [40–42]. In a direct way, Dimitriou showed an increase in the firing of muscle spindle afferents during a visuomotor task, reflecting a γ -fusimotor control that adjusted the muscle proprioceptive system in motor learning [20]. In a comparable visuomotor rotation task, other authors found a decrease in spindle firing [31], probably because of differences in experimental procedures, but both studies strongly suggest the presence of independent fusimotor control. Further, during simple block grasping with the thumb and finger, muscle afferent activity has been shown to better relate to the future muscle state, rather than the current state, demonstrating that an uncoupling of fusimotor and skeletomotor control would enable muscle spindles to work as a forward sensory model to predict the future kinematic activity of its muscle [19]. It is probable that focused movement training can increase proprioceptive acuity, which has been shown to be predictive of sport performance in elite athletes, such as dancers [43]. Our capacity to tune muscle proprioceptive feedback by optimizing gamma drive could also be a means to restore altered motor function [for a review, see 44].

In conclusion, it is clear that muscle proprioceptive feedback can be modulated by the γ -fusimotor drive, to adapt behavior to the current situation. Although few studies have been performed in this area, especially due to the difficulty in accessing muscle afferents under controlled environmental conditions, the evidence shows that both cognitive and emotional factors, as well as input from other senses, play a role in modifying the descending drive to influence muscle receptor sensitivity. This feedforward drive therefore allows the rapid and efficient adaptation to a change in situation that can help prepare the body for responsive and appropriate action.

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CRedit authorship contribution statement:

Edith Ribot-Ciscar: Conceptualization, Writing – review & editing, Visualization. Rochelle Ackerley: Conceptualization, Writing - review & editing, Visualization.

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Papers of particular interest, published within the period of review, have been highlighted as: *of special interest **of outstanding interest

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The study showed that muscle afferent activity is altered when attention is modulated, demonstrating the effect of the γ -fusimotor system. The majority of primary Ia muscle afferents changed when the participant was asked to focus on a pattern-recognition task of an imposed movement, showing that the body can up-regulate sensory muscle signals to aid in environmental demands.

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