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TOPICAL REVIEW

What if muscle spindles were also involved in the sense of effort?

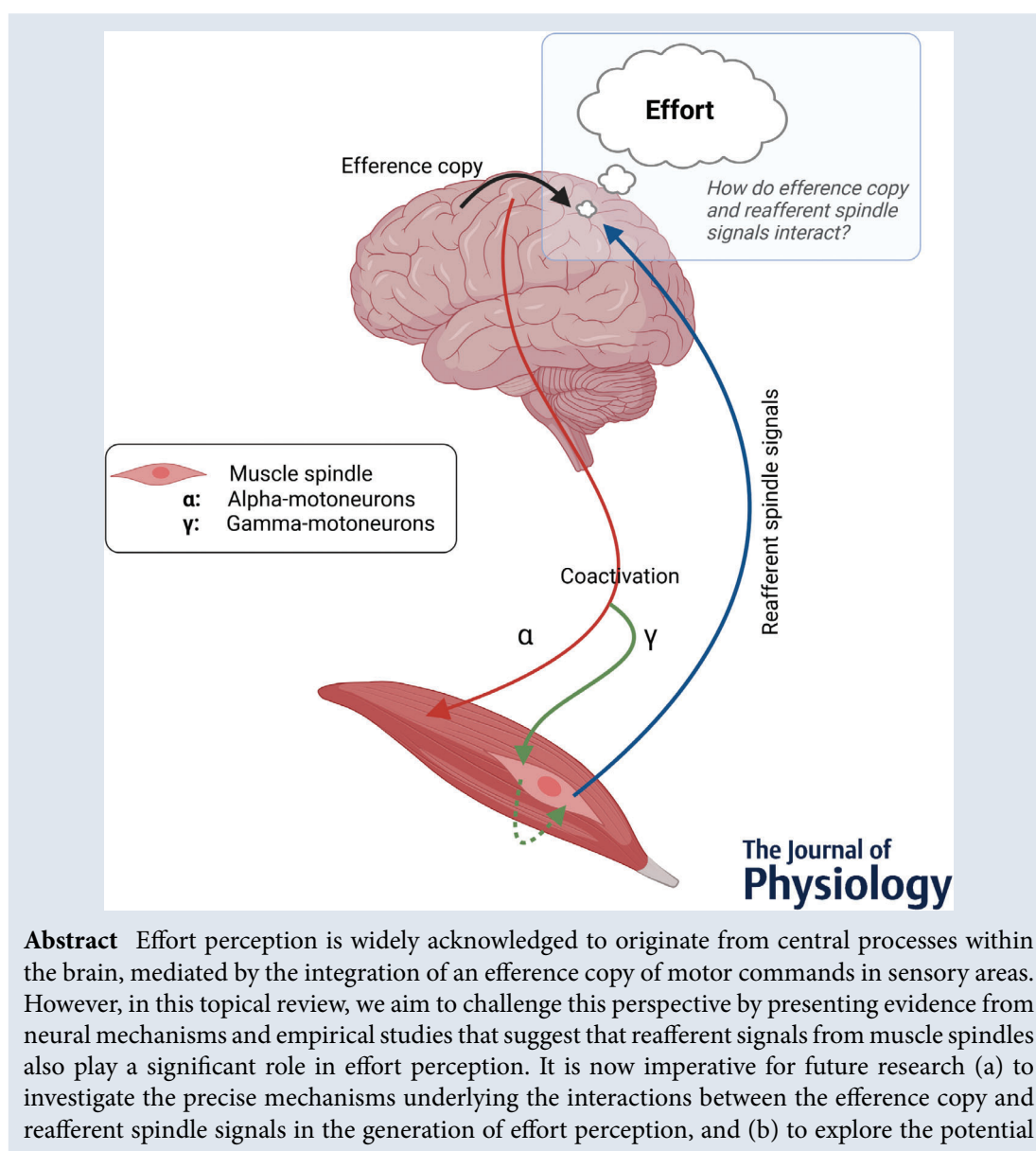
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for altering spindle sensitivity to affect perceived effort during ecological physical exercise and, subsequently, influence physical activity behaviours.

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Abstract figure legend The perception of effort is intimately tied to the neural signals related to motor command magnitude. The efference copy has long been recognized as the primary signal that the brain processes to generate a sense of effort. However, recent evidence suggests that reafferent muscle spindle signals may also play a crucial role in effort perception, particularly through interactions with the efference copy. During voluntary contractions, alpha-motoneurons (innervating force-producing extrafusal fibres) and gamma-motoneurons (innervating intrafusal fibres) are coactivated. The fusimotor commands transmitted by gamma-motoneurons to intrafusal fibres are conveyed through muscle spindles to reach afferent fibres. Reafferent spindle signals thus provide feedback to the brain regarding the amount of fusimotor commands received by intrafusal fibres. While the precise mechanisms underlying the interactions between the efference copy and reafferent muscle spindle signals remain speculative, we propose that future research should focus on identifying these mechanisms to further our understanding of the generation of effort perception.

Introduction

Muscle spindles are encapsulated mechanoreceptors located within most skeletal muscles, parallel to extrafusal fibres. Estimated at approximately 50,000 in the human body (Banks, 2006), they are composed of intrafusal fibres which are innervated by sensory neurons (Ia and II afferents). What makes these mechanoreceptors unique in mammalian skeletal muscle is that they are also supplied by motor neurons, namely gamma motoneurons (which exclusively innervate intrafusal fibres) and beta motoneurons (which synapse with both extrafusal and intrafusal fibres) (Manuel & Zytynski, 2011). While muscle spindles are mainly considered to be muscle length-sensitive receptors informing the central nervous system (CNS) about muscle length and movement, recent studies show that their functions go well beyond this scope. While not an exhaustive list, muscle spindles have been shown to be fundamental to body ownership (Butler et al., 2017), to play a central role in realignment of fractured bones and regeneration of injured spinal cord axons (Kröger, 2018), to act as 'signal-processing devices' to enhance sensorimotor control (Dimitriou, 2022), and

to contribute to intramuscular force encoding in quiescent muscles (Blum et al., 2017). The aim of this short review is to provide evidence, based on experimental data and on their neurophysiological configuration, that they are also well-featured to be involved in effort perception.

The neural correlates of effort perception

In the context of physical activity, *effort perception* (synonymously called *sense of effort*, or *perceived exertion*) is usually defined as the phenomenological experience of invested physical resources in the task (Preston & Wegner, 2009). A longstanding debate has been ongoing in the fields of exercise physiology regarding the neural correlates of effort perception. Specifically, the debate has centred on the signals processed by the brain that generate the perception of effort. Two models have been proposed. The first model (peripheral model) posits that effort perception arises from the processing of afferent feedback conveyed through nociceptive and metaboceptive III and IV afferents originating from active skeletal muscles and organs (i.e. heart and lungs) (Hampson et al., 2001;

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St Clair Gibson et al., 2006). The other model (central model) suggests that effort perception is determined by the processing of a copy of the central commands generated within the brain (De Morree & Marcora, 2015; Marcora, 2009). A recent meta-analysis focused on studies investigating the effects of pharmacologically blocking III and IV muscle afferents on effort perception (Bergevin et al., 2022). The results discounted the role of afferent feedback from metaboceptive and nociceptive III and IV afferents and clearly showed that effort perception is determined by motor command-related signals. These findings are consistent with the observation that effort perception arises solely in the presence of voluntary motor commands (Pageaux, 2016). In contrast, the perceptions stemming from the integration of III and IV afferents (such as fatigue, pain, and discomfort) can be experienced in relaxed muscles (Pollak et al., 2014; Smirmaul, 2012).

The perception of effort is thus thought to be determined by the level of neural resources deployed to activate the muscles involved in a physical task (Smirmaul, 2012). For instance, when lifting objects of increasing load, effort perception, as assessed by rating of perceived exertion scale, increases in direct proportion of the magnitude of the centrally generated motor command that activates the muscles (de Morree et al., 2012). Furthermore, in the case of sustained isometric muscle contractions performed at a constant force level, as neuromuscular fatigue sets in, the participant's ratings of perceived exertion increases while the muscle force remains constant (Souron et al., 2020). In this situation, Golgi tendon organs, which are sensitive to muscle tension (Jami, 1992), are unlikely to be responsible for the perception of effort since the muscle force is held constant. Instead, the increase in perceived effort is likely to be due to the recruitment of additional motor units to compensate for neuromuscular fatigue, resulting in an increased 'sensation of innervation' (von Helmholtz, 1867). This example further reinforces the notion that effort perception is derived from motor command-related signals, while also indicating that mechano-sensations arising from tendon receptors are not a contributing factor in effort perception.

From a neurophysiological perspective, it is hypothesized that a copy of the central motor commands (so called efference copy), which arises in premotor cortical regions, particularly the premotor cortex (Christensen et al., 2007) or the supplementary motor area (Zénon et al., 2015), is integrated in sensory regions of the brain to indicate the level of effort being exerted (Gandevia, 1982). This mechanism is supported by research demonstrating that altered cortical activity in these premotor regions affects effort perception. For instance, studies have shown that caffeine ingestion, which reduces activity in premotor cortical regions, is linked to a reduction in the rating of perceived

exertion scores during voluntary isometric contractions despite comparable levels of muscle activation (De Morree et al., 2014). Additionally, decreasing neural activity in the supplementary motor area using repetitive transcranial magnetic stimulation protocols has been demonstrated to reduce ratings of perceived effort scores during handgrip tasks and to facilitate effort-based decision-making (Zénon et al., 2015). These findings are interpreted as a decrease in the efference copy that is processed by sensory regions of the brain. This mechanism is also supported by studies in deafferented subjects who can accurately perceive weight and force despite the total absence of feedback from muscle and tendon proprioceptors (Lafargue et al., 2003; Luu et al., 2011). To do so, these patients would use motor command signals, that is an effort perception originating in a purely central manner.

In deafferented patients, there is evidence supporting the use of a sense of effort derived from efference copy signals to indirectly perceive force and weight. This has led to the hypothesis that similar mechanisms are at play in healthy participants. In the field of kinesiology, effort perception is usually assessed with bilateral weight or force matching tasks. That is, one reference limb is voluntarily contracted at a target force level with the help of visual feedback while the contralateral indicator limb attempts to reproduce, in blind conditions, the force perceived in the reference limb. In such a situation, participants can use signals from a vast variety of receptors located in the skin, tendon organs and muscle spindles (Proske & Gandevia, 2012). When the reference or the indicator limb is weakened by neuromuscular fatigue (Carson et al., 2002; Weerakkody et al., 2003) or pharmacologically induced paralysis (Gandevia & McCloskey, 1977), participants tend to overestimate the force produced with their weakened muscles, leading to a lower force production in that limb. This was interpreted as participants matching weights or forces predominantly based on motor command signals (i.e. the efference copy). In other words, participants seem to intuitively use a sense of effort to judge weight and force, rather than a sense of muscle tension originating in Golgi tendon organs (McCloskey et al., 1974).

However, as pointed out by Luu et al. (2011), the results of these experiments cannot be fully explained by this efference copy-based central model because a weight lifted with a muscle group weakened by 50% of its initial force capacity feels significantly less than twice as heavy. This led authors to assume that some peripheral signals, especially from muscle spindles, could contribute to matching weights during a bilateral matching task using the thumbs. To test their hypothesis, the researchers administered curare, a paralyzing drug with dissociative pharmacokinetic effects on extrafusal and intrafusal fibres. Specifically, curare has a delayed paralyzing effect on

intrafusal fibres due to a diffusion lag within the capsule of the muscle spindles compared to extrafusal fibres. Therefore, at a certain point in time, while extrafusal fibres were recovering from paralysis, intrafusal fibres remained completely paralyzed. When the paralysis of intrafusal fibres surpassed that of extrafusal fibres, resulting in a decreased spindle responsiveness to gamma drives and lower-than-expected reafferent spindle signals, participants underestimated the weight lifted by their weakened muscles. They observed similar results after the thumb was fatigued with a high force contraction and with a low force contraction associated with vibration, that is protocols aimed at desensitizing muscle spindles. While deafferented subjects perceived the object as heavier (consistent with them using the centrally derived motor command), normal subjects' objects felt the same or lighter. These outcomes are the opposite of what is expected if participants used the efference copy to match weights. The authors thus concluded that the unloading of muscle spindles, which resulted in lower-than-expected firing rates in fusimotor-driven afferents, accounted for this weight underestimation. To further corroborate these results, Brooks et al. (2013) replicated some parts of Luu et al.'s experiments at the elbow flexors and showed that desensitizing muscle spindles indisputably decreased weight and force perception, although to a lesser extent. It is noteworthy that even strong advocates of the central model hypothesis acknowledge the involvement of fusimotor-driven afferents in the perception of effort (de Morree et al., 2012).

Mechanisms accounting for a potential implication of muscle spindles in effort perception

While the results of these two studies suggest that manipulating spindle afferents alters weight and force perceptions, we argue that those results are accounted for, at least in part, by a direct implication of muscle spindles in effort perception. As mentioned above, unless clearly instructed to match muscle tensions, participants naturally match effort, that is motor command signals rather than afferent information from tension-sensitive Golgi tendon organs. In this sense, Monjo et al. (2018) conducted a study in which participants performed voluntary unilateral isometric contractions of elbow flexors at controlled force and rated their perceived effort using the CR10 scale (Borg & Kaijser, 2006). The contractions were performed both before and after a 10-min vibration protocol designed to desensitize muscle spindles. Muscle contractions were perceived as requiring less effort following the vibration protocol (Monjo et al., 2018). It is worth mentioning that the counterpart of muscle spindle desensitization is a decreased afferent facilitatory support to homonymous

motoneurons (Macefield et al., 1991). To compensate for the lower support, increasing central command is necessary, which should result in increased effort perception if the only source of effort perception is the efference copy. Such outcomes then support the evidence of an important contribution of muscle spindle afferents to effort perception.

However, what mechanisms could explain that muscle spindle afferents provide effort cues? As pointed out above, effort perception only arises when a *voluntary* motor command is produced, that is when an efference copy is generated and, by association, when the fusimotor system activates intrafusal fibres through alpha-gamma coactivation. During voluntary isometric contractions, the firing rate of spindle afferents increases compared to the relaxed state (Prochazka, 1996; Wilson et al., 1997). This increase suggests that gamma drives are conveyed through muscle spindles to reach afferent fibres, providing feedback to the brain regarding the amount of fusimotor commands received by intrafusal fibres. To put it differently, the increase in afferent firing rate driven by gamma drives informs the brain about the strength of fusimotor commands. Former microneurographic studies have found that firing rates in afferent units increased in proportion to voluntary isometric contraction magnitude, up to 30% of maximal contraction with a discharge rate of approximately 30 Hz (Macefield et al., 1991; Vallbo & Hulliger, 1982). Currently the technical limitations of microneurography do not allow testing this linear relationship over the entire range of contraction intensities. However, muscle spindle endings have been shown to be driven harmonically up to 500 Hz with tendon vibration in cat preparations (Brown et al., 1967), suggesting that afferent firing does not saturate at high levels of contraction intensities.

Therefore, because the perception of effort arises from signals related to motor command magnitude, muscle spindles are perfectly wired to inform the brain of the fusimotor command magnitude they receive from gamma neurons. When intrafusal fibres are unloaded through paralysis or desensitized by muscle vibration, firing rates of fusimotor-driven afferents are lower than expected from the fusimotor command such that effort perception decreases at some contraction intensities.

There remain, however, some conundrums regarding how fusimotor-driven afferents integrate in effort perception. Namely, are they the only effort perception generator in healthy individuals? Do they interact with the efference copy? In the field of sensorimotor control, the internal model theory posits that every motor command is associated with an expectation of the sensory outcomes that should stem from the resulting movement. More precisely, the integration of the efference copy within forward internal models, in addition to its role in effort perception, would allow predictions of the sensory

consequences of the movement (Wolpert & Flanagan, 2001). By combining this outflow signal with the incoming sensory feedback, forward models would provide a more reliable estimation of the state of the body compared to feedback alone (Bhanpuri et al., 2013). Putting effort perception within this framework, the efference copy would provide a central sensory signal of effort, to be compared with a peripheral sensory effort signal carried by fusimotor-driven afferents. An unloading or a desensitization of muscle spindles would therefore inform the CNS that the motor command issued to the muscles (signalled through fusimotor-driven afferents) is lower than expected from the efference copy, decreasing the sense of effort. Although speculative, it would be interesting to investigate such mechanisms during psychophysical studies associated with neuroimaging techniques. This would also allow clarification of the neural operations and brain correlates underlying effort perception.

Implications for kinaesthesia

During voluntary contractions, the discharge of spindle afferents is influenced by both changes in muscle length (i.e. *exafference*) and fusimotor activity (i.e. *reafference* or fusimotor-driven afferent firing) (Proske & Gandevia, 2012). Therefore, at a given muscle length, action potential frequency in spindle afferents is higher during a voluntary contraction. However, it has been shown that the sense of position was not altered when comparing a passively vs. a voluntarily contracted limbs (Ansems et al., 2006), suggesting that the CNS can distinguish exafferent from reafferent spindle afferents. While the underlying mechanisms remain speculative, they have been proposed to involve forward model operations that would predict, based on the efference copy, the fusimotor-driven afferents expected from the voluntary contraction. This operation would allow dissociating exafferent from reafferent information to maintain an accurate kinaesthesia (see Figure 16 in Proske & Gandevia, 2012). Because spindle unloading could generate a decoupling between the efference copy and spindle reafference, this may disturb these operations and alter both effort perception and kinaesthesia. Future research should focus on that point to unravel these processes.

Concluding remarks and perspectives

Here, we propose that muscle spindles can calibrate effort perception based on forward model-mediated processes involving interactions between efference copy and spindle reafference. Up to now, the research conducted on the role of muscle spindles in the sense of effort are bilateral or unilateral isometric matching tasks focused on small

muscle groups. Accordingly, current studies probably do not account for the neuropsychological mechanisms of effort perception during ecological whole body dynamic exercises such as cycling or running. More research is therefore needed to precisely identify the role of fusimotor-driven afferents in effort perception, especially during such exercises. To that end, the development of muscle spindle electromyography (Partanen et al., 2022) associated with progress in high-density electromyographic techniques seems promising. According to Cheval and Boisgontier (2021), the current lack of physical activity in high-income countries may be due in part to people's natural preference for activities associated with low effort perception. To address this issue, exploring the effects of stimulation techniques intended to reduce the perception of effort during physical activities, such as manipulating spindle sensitivity (Monjo et al., 2018) or premotor cortical area activity (De Morree et al., 2014; Zénon et al., 2015), is promising. This approach could also benefit individuals with conditions like chronic fatigue syndrome, which can make voluntary movements feel more difficult than they actually are (DeLuca, 2005).

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Additional information

Competing interests

The authors declare no conflict of interest.

Author contributions

Both authors contributed to the conception or design of the work and drafting the work or revising it critically for important intellectual content. Both authors have approved the final version of the manuscript and agree to be accountable for all aspects of the work. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed

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