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REVIEW | *Control of Movement*

Age-related changes in leg proprioception: implications for postural control

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Henry M, Baudry S. Age-related changes in leg proprioception: implications for postural control. *J Neurophysiol* 122: 525–538, 2019. First published June 5, 2019; doi:10.1152/jn.00067.2019.—In addition to being a prerequisite for many activities of daily living, the ability to maintain steady upright standing is a relevant model to study sensorimotor integrative function. Upright standing requires managing multimodal sensory inputs to produce finely tuned motor output that can be adjusted to accommodate changes in standing conditions and environment. The sensory information used for postural control mainly arises from the vestibular system of the inner ear, vision, and proprioception. Proprioception (sense of body position and movement) encompasses signals from mechanoreceptors (proprioceptors) located in muscles, tendons, and joint capsules. There is general agreement that proprioception signals from leg muscles provide the primary source of information for postural control. This is because of their exquisite sensitivity to detect body sway during unperturbed upright standing that mainly results from variations in leg muscle length induced by rotations around the ankle joint. However, aging is associated with alterations of muscle spindles and their neural pathways, which induce a decrease in the sensitivity, acuity, and integration of the proprioceptive signal. These alterations promote changes in postural control that reduce its efficiency and thereby may have deleterious consequences for the functional independence of an individual. This narrative review provides an overview of how aging alters the proprioceptive signal from the legs and presents compelling evidence that these changes modify the neural control of upright standing.

balance; Ia afferents; muscle spindles; proprioception; upright standing

INTRODUCTION

Among hominid species, the natural bipedal erected posture is one of the most remarkable biomechanical characteristics of human beings. Upright standing in humans can be modeled as an inverted pendulum rotating around the ankle joint, with the intended equilibrium position being a slight forward tilt of the body, generating a gravity-driven instability. Because passive ankle stiffness cannot compensate for the forward-toppling torque (Loram and Lakie 2002), an active modulation of the neural drive to the motor neuron pools innervating the ankle plantar flexor muscles is necessary to adjust ankle stiffness. Its complexity (multijoint system) and its inherent instability (forward tilt of the body) make the upright standing posture a relevant model to study sensorimotor integration, as it requires managing multimodal sensory inputs to produce finely tuned motor output depending on the environment. The ability to maintain steady upright standing (referred to in this review as postural control) has long been considered an automatic task mainly controlled by spinal and brain stem structures. However, it is now clear that postural control also involves cortical area structures adjusting the motor commands as the state of the body and the environment change (Lephart et al. 1997). The sensory information used for postural control mainly arises from the vestibular system of the inner ear, vision, and proprioception (Peterka 2002). Because of the lower proprioceptive threshold for the perception of body sway during upright standing compared with visual and vestibular systems (Fitzpatrick and McCloskey 1994), proprioceptive inputs play a critical role in postural control (Doumas et al. 2008; Speers et al. 2002; Teasdale and Simoneau 2001; Van Impe et al. 2012).

In addition to revealing the capacity of the nervous system to face such a sensorimotor challenge, investigation of postural control also allows for determination of key factors for prevention and rehabilitation interventions. In this context, aging is accompanied by alterations in the proprioceptive system (Shaffer and Harrison 2007) that should contribute to changes in postural control (Anson et al. 2017; Horak et al. 1989).

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Considering the increasing percentage of the world population over the age of 60 yr, a better understanding of the effect of age on leg proprioception and its implications in postural control is of paramount relevance. Therefore, our main objective in this review is to provide an overview of how aging alters the proprioceptive signal from leg muscles and to put forward compelling evidence that these changes modify the neural control of upright standing.

LEG PROPRIOCEPTION IN POSTURAL CONTROL

Proprioception encompasses signals from mechanoreceptors—transducers that convert mechanical stimuli into action potentials—located in muscles, tendons, and joint capsules (proprioceptors); information from cutaneous mechanoreceptors (cutaneous stretch receptor) associated with tactile sensations is considered as additional sensory sources that complete proprioceptive inputs (Riemann and Lephart 2002). Proprioception plays a critical role in movement control by providing inputs to internal models that couple sensory signals and motor commands (Wolpert and Kawato 1998).

One important component of postural control is the ability to detect body sway that, in upright standing, mainly results in variations of leg muscle length induced by rotations around the ankle joint (Di Giulio et al. 2009; Fitzpatrick et al. 1994). Because of their in-series arrangement with muscle fibers, Golgi tendon organs are ideally located to encode variations in the force developed by the contracting muscle fibers and contribute to the senses of force and heaviness (Proske and Gandevia 2012). However, such anatomical position does not provide Golgi tendon organs with the possibility to encode changes in muscle length (Macefield 2005), thereby reducing their ability to provide relevant information on limb position and joint movement. Feedback from joint receptors appears to provide information restricted to extreme joint position (Macefield 2005) and is therefore unlikely to play a large role in postural control. Finally, cutaneous inputs from the plantar surface of the foot have very weak effects, if any, on postural control during unperturbed upright standing. A meta-analysis underscored that cooling the plantar surface of the foot had a very weak, nonsignificant, effect on upright standing (Hoch and Russell 2016). Accordingly, even though proprioceptive signals originate from multiple mechanoreceptors, there is a general agreement that muscle spindle receptors provide the primary source of proprioceptive information for postural control.

Furthermore, proprioceptive inputs trigger the rapid, automatic, and coordinated postural responses to unexpected movement of a support surface. In agreement, Stapley et al. (2002) suggested that the large afferent fibers (Ia afferents) are critical for the timing of automatic postural responses to ensure coordinated control of the body center of mass and balance after unexpected disturbances of the support surface. In contrast, the timing of automatic postural responses was unaffected by loss of vestibular information after bilateral labyrinthectomy, even when vision was absent (Inglis and Macpherson 1995). In addition, during a fall, individuals prepare for the impact based on sensory information, which would be mainly of proprioceptive origin at the fall onset (Le Goic et al. 2018). Therefore, alterations within the proprioceptive signal likely increase the risk of falls and impede the ability to reduce fall-related injury.

Muscle Proprioception

Muscle spindles are sensors that consist of intrafusal muscle fibers enclosed in a sheath, fusiform in shape (spindle), and arranged in parallel to the extrafusal muscle fibers, rendering them very sensitive to muscle length and its rate of change. Primary muscle spindle afferents, referred to as group Ia fibers, terminate in the annulospiral ending around the central part of the bag 1, bag 2, and chain intrafusal fibers. Secondary muscle spindle endings, referred to as group II fibers, supply the bag 2 and chain fibers (Proske and Gregory 2002) (Fig. 1). Although both primary and secondary endings act as stretch receptors, the primary ending has a higher dynamic sensitivity. Accordingly, the discharges of primary endings convey information about changes in muscle length and velocity, whereas those of secondary endings mainly carry information about changes in muscle length (McCloskey 1978). Muscle spindles, widely scattered in the muscle belly, are stretched when the muscle lengthens, which results in the generation of action potentials on afferent fibers that form synapses with alpha motor neurons and interneurons or convey proprioceptive information to the sensorimotor cortex and the cerebellum (Fig. 2*A*).

Gamma motor neurons provide motor innervation of intrafusal fibers to modulate the sensitivity of muscle spindles to muscle length changes. These neurons are termed "fusimotor" neurons (Matthews 2011), with γ dynamic and γ static fusimotor fibers. The fusimotor drive (gamma motor neurons), under the control of descending tract (Fig. 2*A*), is assumed to modulate the dynamic and static sensitivity of muscle spindles with the task requirements (Prochazka 1989). Beta motor neurons, which are smaller and less abundant than other motor neuron subtypes, innervate both intrafusal and extrafusal muscle fibers (Bessou et al. 1965).

Even though muscle spindles respond unidirectionally across the entire physiological range of movement (Burgess et al. 1982; Macefield et al. 1990), interpretation of the information conveyed by muscle spindle afferents from plantar flexor muscles during upright standing can be confounded by the fact that length changes of the muscle-tendon unit are transmitted indirectly via compliant tendinous tissue. On example of such potential bias is provided by the uncoupling between changes in the length of the muscle-tendon unit of gastrocnemius medialis and muscle fascicles, and presumably muscle spindles (Baudry et al. 2012; Loram et al. 2004). This suggests that the

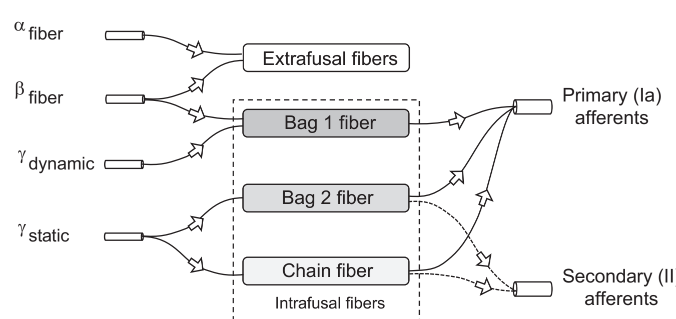

Fig. 1. Schematic representation of sensory and fusimotor innervation of the intrafusal fibers of a muscle spindle, with the exception of α fibers that only innervate extrafusal fibers, in contrast to β fibers that innervate both extrafusal and intrafusal (bag 1) fibers. Arrows indicate the direction of the impulse conduction. Sensory afferent axons Ia and II convey information to sensory neurons located in the dorsal root ganglia.

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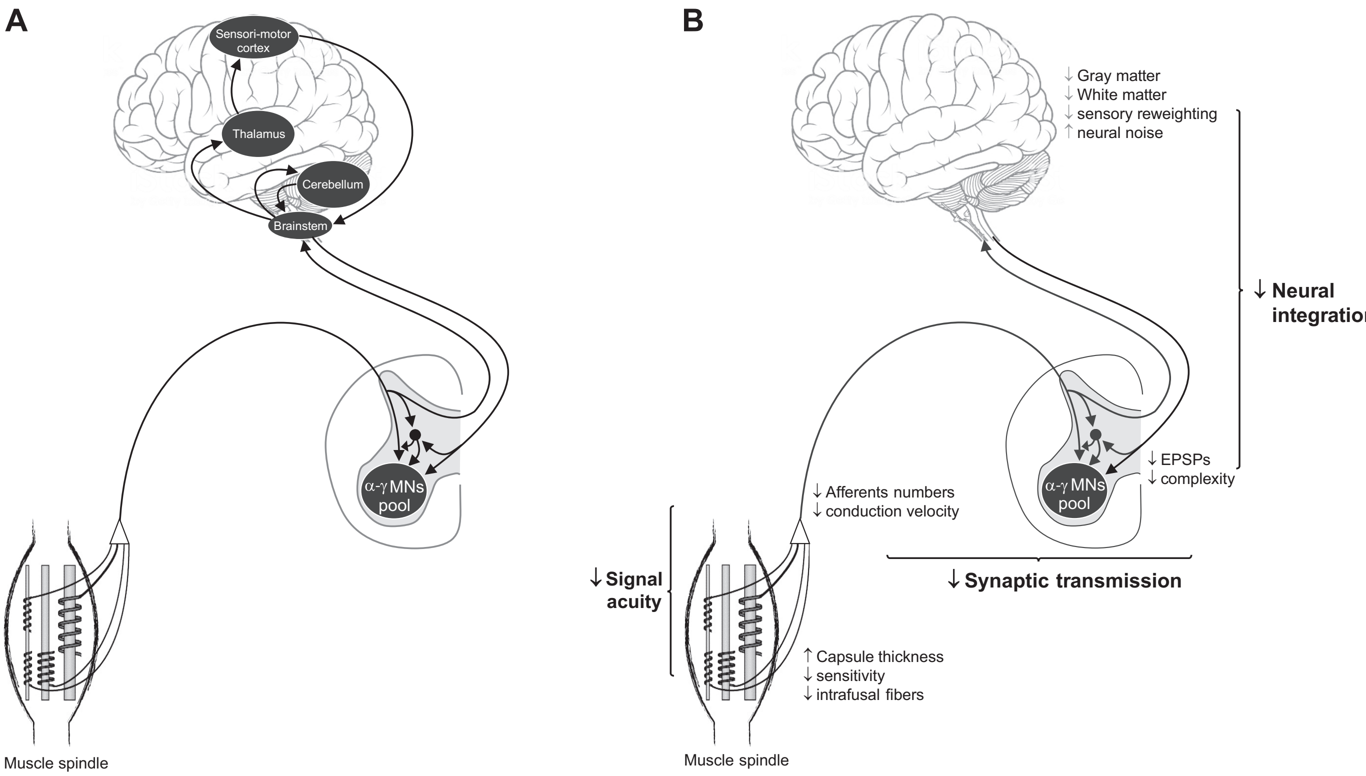

Fig. 2. *A*: schematic illustration of the spinal and ascending pathways conveying proprioceptive information. Arrows indicate the direction of flow of the neural information. *B*: effects of aging on the proprioceptive system. Morphological changes in muscle spindles and parent afferent fibers decrease the acuity of the proprioceptive signal. The combination of changes in afferent fibers and spinal network alters the efficacy of synaptic transmission of proprioceptive volleys from muscle spindles. Spinal and supraspinal changes alter the neural integration of the inputs from muscle spindles. EPSPs, excitatory postsynaptic potentials; MNs, motoneurons; ↑, increase; ↓, decrease or alteration.

plantar flexor muscles may not be the main contributors to proprioceptive signals during upright standing. In contrast, the tibialis anterior, which is mainly quiescent in standing, could provide more relevant proprioceptive inputs. Di Giulio et al. (2009) and Day et al. (2013) indicated that changes in the length of fascicles of tibialis anterior were tightly coupled with changes in sway position. Further investigations revealed that muscle spindles in the human tibialis anterior encode fascicle length of parent muscles during passive length changes (Day et al. 2017). In agreement, Aniss et al. (1990) already showed that muscle spindle afferents from the tibialis anterior can provide information on backward sway direction.

Nonetheless, a recent study (Peters et al. 2017) investigating the coding of ankle angle and velocity by human calf muscle spindles indicated that activity of muscle spindle afferents reflected passive ankle movements at frequencies and amplitudes similar to those recorded during upright standing. Even though voluntary contraction of calf muscles reduced spindle sensitivity to such ankle movements, Peters et al. (2017) showed that muscle spindles remained sensitive enough to provide valuable sensory feedback for postural control. Furthermore, in an elegant study, Blum et al. (2017) underscored that muscle-tendon force and its first time derivative predicted the transient instantaneous firing rate of muscle spindles in anesthetized cats. This suggests that signal from muscle spindles could be involved in coding force variations within the muscles, such as those associated with mechanical perturbations of the body. For an up-to-date review on this topic, the reader is invited to read Proske and Allen (2019).

Relevance of Leg Proprioception in Postural Control

The significant role of leg proprioception in postural control is highlighted in patients with polyneuropathies that compromise proprioception. Such individuals exhibit greater center of pressure excursions compared with control subjects (Bergin et al. 1995). Similar observations were reported for patients with diabetic peripheral neuropathy. In response to a translation of the support surface, diabetic patients showed a delayed onset of muscle activity and an impaired ability to scale torque magnitude to both the velocity and amplitude of surface translations (Inglis et al. 1994). The role of muscle spindles in postural control was also assessed experimentally by altering the proprioceptive signal. This can be done, for example, by using pneumatic cuffs around limbs to progressively block action potential propagation in afferent axons. When the cuffs were placed bilaterally at the ankle level, the imposed ischemia had relatively little influence on upright standing. When the cuffs were placed above the knee, however, ischemia increased antero-posterior excursion of the center of pressure, indicating that leg proprioceptors are more relevant to postural control than stretch-sensitive receptors of the sole of the foot and proprioceptive signals from foot muscles (Knellwolf et al. 2019; Mauritz and Dietz 1980). Muscle proprioception can also be altered by vibrating tendons, which activates muscle spindle primary endings and produces a sensation of displacement of the associated body segment (Burke et al. 1976; Goodwin et al. 1972; Roll and Vedel 1982). When a person stands upright with his/her eyes closed, the vibration of the

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Achilles tendons generates a backward shift of the center of pressure to counteract the illusion of falling forward (Eklund 1972). An opposite response occurs when vibration is applied to the distal tendon of the tibialis anterior muscle (Kavounoudias et al. 1999). Eysel-Gosepath et al. (2016) observed a greater excursion of the center of pressure during Achilles tendon vibration compared with a situation in which subjects closed their eyes, suggesting that muscle proprioception is more important for postural control than vision in healthy young adults. Furthermore, the backward lean observed during Achilles tendon vibration was sustained after the cessation of tendon vibration and accompanied by trunk extension, posterior tilt of the pelvis, and flexion of the hips and knees (Thompson et al. 2007). These results indicate that prolonged perturbation of proprioceptive input from leg muscles modifies the perception of the body's vertical position that alters postural control.

Overall, these different approaches underscore the key role of leg proprioception in postural control. Changes in postural control observed in older adults could therefore reflect, in part, alterations in muscle spindles and their neural pathways.

AGE-RELATED CHANGES IN PROPRIOCEPTION

Aging is associated with numerous changes in the neuromuscular system (Hunter et al. 2016; Shaffer and Harrison 2007) that are accompanied by a general decline in motor performance, as reflected in a decrease in maximal muscle force (Frontera et al. 1991) and force control accuracy (Baudry et al. 2010; Tracy and Enoka 2002), and an increase in center of pressure excursions during unperturbed upright standing (Abrahamová and Hlavačka 2008; Laughton et al. 2003; Nagai et al. 2011; Van Impe et al. 2013). From a clinical point of view, it is worth noting that the decrease in postural control is associated with an increased risk of falling (Horak 2006; Maki et al. 1994). Alterations in muscle spindles and their afferents, along with the integration of the signal at the supraspinal level, have been shown to influence proprioceptive perception and postural control in older adults (Goble et al. 2011, 2012).

Muscle Spindles

As shown in Fig. 2*B* and described below, aging alters both the structures and the functioning of the proprioceptive system.

Morphology and innervation. Swash and Fox (1972) reported an increase in the capsular thickness of muscle spindles with age in postmortem human muscles, accompanied by a slight decrease in the mean number of intrafusal muscle fibers, whereas Kararizou et al. (2005) reported that the diameter of the spindles decreases with age. Liu et al. (2005) reported an age-related decrease in the total number of intrafusal muscle fibers and chain fibers in postmortem human muscle spindles, whereas no difference was observed for the bag fibers. In addition, Kim et al. (2007) showed that in aged rats primary endings lost their typical annulospiral configuration, becoming tapered and irregular in shape. A comparable alteration was not observed for secondary endings.

Looking at the innervation of muscle spindles, an early study (Swallow 1966) performed on human cadavers (aged between 16 and 82 yr) reported that in the anterior tibial nerve of the foot the total number of nerve fibers drastically decreased with age, with a significant decrease in the proportion of large fibers in the older subjects. As Ia afferents are the largest peripheral axons, this suggests an age-related decrease in the amount of muscle spindle afferents, especially the Ia afferents. More recently, Vaughan et al. (2017) confirmed in mice that proprioceptive sensory neurons degenerate with aging and that this degeneration starts earlier than atrophy of the intrafusal muscle fibers.

Sensitivity. When investigating the static and dynamic sensitivities of muscle spindle primary endings, Miwa et al. (1995) reported a lower discharge frequency in response to muscle stretch (dynamic sensitivity) in aged rats, whereas the static sensitivity did not exhibit an age-related effect. Kim et al. (2007) also observed a loss of dynamic sensitivity. The dampening of muscle spindle sensitivity seen with aging may be accounted for by the morphological changes discussed above.

During tendon vibration, the repetitive activity of Ia afferents decreases the Hoffmann reflex amplitude, which assesses the net excitatory input of group I afferents onto spinal motor neurons. However, Burke et al. (1996) reported that tendon vibration has less of an effect on the Hoffmann reflex in older compared with younger adults. Age-related changes in the effectiveness of the synaptic transmission through pre- and postsynaptic mechanisms likely contribute to these observations. The deleterious morphological changes of aged muscle spindles that decrease the dynamic sensitivity of muscle spindles could also reduce the vibration-related muscle spindle activity. In agreement, Chung et al. (2005) reported weaker and slower reflex-induced muscle force generation in response to Achilles tendon tap in old compared with young adults.

Signal Integration

Signal integration is referred to here as the summation, gating, and modulation of varying combinations of excitatory and inhibitory synaptic inputs distributed throughout the central nervous system.

Conduction velocity. Conduction velocity (Boxer et al. 1988; Kim et al. 2007) and axon diameter shift in the direction of slower speeds and smaller axons, abolishing differences between primary and secondary endings with aging (Kim et al. 2007). Combined with the reduction in the conduction velocity of motor axons (Morales et al. 1987), the decrease in conduction velocity of Ia afferents should contribute to increasing the latency of reflex responses originating from the muscle spindle pathway. In support of this assumption, the latency of the Hoffmann reflex in the soleus (Baudry et al. 2015; Sabbahi and Sedgwick 1982; Scaglioni et al. 2003) and stretch reflex evoked in the tibialis anterior muscle increases with age (Klass et al. 2011).

Spinal synaptic integration. When looking at the integration of the muscle spindle signal at the spinal level, one should consider the spinal interneuron networks. Terao et al. (1996) demonstrated that the number of small neurons in the intermediate zone of the ventral horn decreased with aging. As those small neurons are thought to be mostly interneurons, these results suggest a decreased complexity in the spinal network that may alter the integration of the afferent signal. In addition, older cats exhibit longer rise time and half-width of the Ia excitatory postsynaptic potentials (EPSPs) compared with younger cats, accompanied by a lesser rate of rise of EPSPs

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(Boxer et al. 1988; Chase et al. 1985). The smaller rate of rise of Ia-induced EPSPs in old cats likely decreases their efficacy to promote motor neuron discharge (Fetz and Gustafsson 1983).

The age-related reduction in the effectiveness of the Ia afferents to activate motor neurons could also be influenced by changes in Ia presynaptic inhibition. Butchart et al. (1993) suggested a decrease in Ia presynaptic inhibition as inferred from a smaller reduction in soleus Hoffmann reflex in response to tendon vibration in older adults. In contrast, Morita et al. (1995), in the same muscle, suggested an increase in Ia presynaptic inhibition in older adults based on the reduced facilitation of the Hoffmann reflex to a conditioning stimulation applied on heteronymous Ia afferents. Finally, when Ia presynaptic inhibition was assessed with two complementary Hoffmann reflex conditioning techniques, the amount of Ia presynaptic inhibition did not differ between young and older adults in forearm (extensor carpi radialis) and leg (soleus) muscle (Baudry et al. 2010; Baudry and Duchateau 2012). These divergent results do not speak in favor of a change in Ia presynaptic inhibition with aging but may reflect a decrease in the number of Ia afferents and/or in their conduction velocities.

Supraspinal integration. Although little is known about the role of aging in the integration of the proprioceptive signal at the supraspinal level, there is evidence that older adults experiencing mobility impairment are more likely to have underlying alterations in the structure and function of the brain (Kilgour et al. 2014).

STRUCTURAL CHANGES. Efficient integration of different sensory inputs in the brain might be compromised because of age-related declines in white (Abe et al. 2002; Sullivan and Pfefferbaum 2006) and gray (Good et al. 2001; Kalpouzos et al. 2009) matter integrity. In agreement, fractional anisotropy, a measure of white matter integrity, of frontal and fronto-occipital tracts was predictive of postural performance in older but not young adults (Van Impe et al. 2012). The decrease in brain gray matter thickness in pre- and postcentral gyrus areas (Good et al. 2001; Salat et al. 2004), which are related to the sensorimotor regions of the brain, may also result in poorer proprioceptive integration. Furthermore, neuronal loss in the pallidum, a relevant region for postural control, has been associated with difficulties in holding the semitandem standing position (Rosano et al. 2007), a position that likely requires greater proprioceptive inputs compared with normal bipedal (hip width) foot position (Sarabon et al. 2013). Similarly, age-related decline in the brain stem structure partly accounts for the decline in postural control (Boisgontier et al. 2017).

BRAIN ACTIVATION. Several elements support age-related changes in brain activation in relation to upright standing. As observed during nonpostural motor tasks, (Heuninckx et al. 2005, 2008), older adults exhibit increased activity in somatosensory cortices (right postcentral gyrus) during motor imagery of upright stance compared with young adults (Zwergal et al. 2012). Similarly, Mouthon et al. (2018) reported a greater activity in the supplementary motor area, motor area, premotor cortex, and putamen of older adults during motor imagery of upright standing in various conditions compared with young adults. This engagement of additional cortical areas most likely reflects a compensatory mechanism for age-related sensorimotor decline (Heuninckx et al. 2008; Reuter-Lorenz and Lustig 2005). Changes in brain neurochemistry that occur with aging can also induce motor deficits (for a review, see Seidler et al. 2010). Serotonin concentration, for example, is lower in older compared with young adults, especially in the cingulate cortex and the putamen (Gottfries 1990). Interestingly, Goble et al. (2012) reported a positive relation between the sense of joint position—which mainly rests on muscle spindle inputs (Proske and Gandevia 2012)—and the neural activity in the right putamen. Reduced brain activation in this region in response to proprioceptive stimulation could reflect a loss of proprioceptive integration in older adults. In this vein, Piitulainen et al. (2018) reported that cortical processing of the proprioceptive signal is altered by aging. Furthermore, Ozdemir et al. (2018) indicated that impairments in perceptual processing of sensory signals contribute to prolong muscle response delays during perturbed upright standing in older adults.

One potential consequence of these structural and functional changes is an increase in neural noise within the sensorimotor system that may impair the neural signal (Cremer and Zeef 1987; Kail 1997; Mozolic et al. 2012). The neural noise hypothesis rests on the assumption that the effective signal-to-noise ratio decreases (Cremer and Zeef 1987) because of increased spontaneous/baseline neural spiking activity (Hong and Rebec 2012), which disrupts the fidelity of neural signals. A lower signal-to-noise ratio should require greater processing that may partly explain the greater brain activation observed in older adults. When considering the decrease in sensitivity and transmission of the proprioceptive signal due to age-related alterations in muscle spindles and their neural pathways (see above), an increase in neural noise should further challenge the integration of proprioceptive signals and contribute to decreasing the relevance of the proprioceptive signals for postural control in older adults.

HOW IMPAIRED LEG PROPRIOCEPTION CHANGES POSTURAL CONTROL IN OLDER ADULTS

The alterations in muscle spindles and their neural pathways with aging encompass among other mechanisms decreases in the sensitivity, acuity, and integration of the proprioceptive signal. The framework of the potential links between age-related changes in leg proprioception and postural control in older adults is synthetized in Fig. 3 and further discussed below.

Behavioral Aspects

Different approaches were used to investigate whether age-related changes in proprioception are associated with reduced postural control. Relevant for the following discussion is the fact that in most of the studies mentioned, an increase in body sway amplitude (assessed through kinematics of the center of mass), center of pressure excursions (assessed by ground reaction forces), or trunk acceleration (assessed through accelerometers) are assumed to underscore alterations in postural control. However, recent advancements in postural control bring forward that increased excursions of the center of mass or pressure in older adults can be interpreted as a positive adaptation to ensure that sensory inputs exceed the thresholds for detection and enhance the sensory information available to the central nervous system (Carpenter et al. 2010; Rajachandrakumar et al. 2018). Along these lines, the increase in body sway or center of pressure excursions may reflect an increase in

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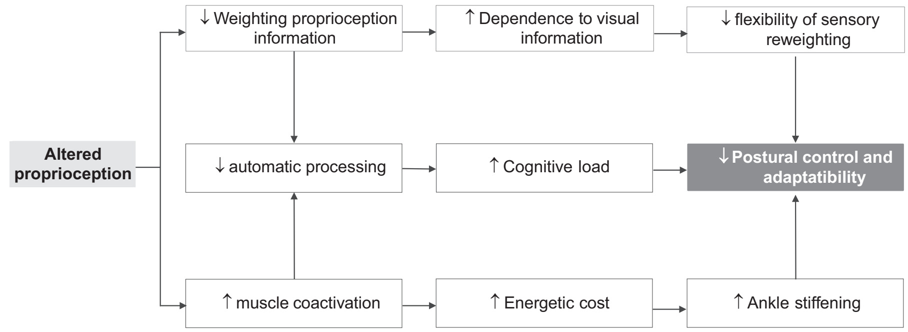

Fig. 3. Framework of how age-related alteration of leg proprioception changes postural control and its adaptability. ↑, increase; ↓, decrease or alteration.

sensory thresholds (reduced sensitivity) and/or reduced integration capacity. Nonetheless, regardless of the interpretation and the metrics used, these changes are evidence of an overall decline of the postural system that likely rests, in part, on a decreased ability to detect body sway.

An interesting approach to assess the age-related changes in proprioception during upright standing consists of using tendon vibration of plantar flexor muscles (see *Relevance of Leg Proprioception in Postural Control*). Most studies report a lesser influence of Achilles tendon vibration on postural control in older compared with young adults (Ehsani et al. 2018; Hay et al. 1996; Nakagawa et al. 1993; Penzer et al. 2015; Pyykkö et al. 1990; Quoniam et al. 1995; Toosizadeh et al. 2018). For example, Pyykkö and colleagues (Pyykkö et al. 1990) assessed a proprioceptive ratio that merely represents the weight assigned to ankle proprioceptive signals to regulate postural control. The ratio was calculated between sway velocities during baseline stance (no vibrating stimulus) and during Achilles tendon vibration at 80 Hz, with both baseline and vibration conditions being performed with eyes closed. The greater quotient in older (0.84) than younger (0.51) adults indicates that tendon vibrations have less of an effect on postural control in older adults. Using another approach, Penzer et al. (2015) assessed postural control before and after long-duration Achilles tendon vibration (1 h, 80 Hz). The 1-h tendon vibration altered postural control in young but not older adults. The decreased effect of vibration with aging suggests a lesser reliance on leg proprioception for postural control in older adults. The lower vibration-induced postural perturbation observed in older adults can also reflect, at least in part, a decreased sensitivity of muscle spindles to vibration (see *Sensitivity*).

However, other studies reported no age effect or greater vibration-induced perturbations in older adults (Abrahámová et al. 2009; Brumagne et al. 2004; Ito et al. 2018; Maitre et al. 2013). Abrahámová et al. (2009) reported greater vibration effects on postural control in older adults for tendon vibration. Remarkably, the greater effects of vibration were accompanied by differences in postural strategy (body stiffening) adopted by older adults in response to vibration. These results suggest that responses to vibration may depend on postural strategy, a strategy that can be influenced by the level of force that has to be produced by the plantar flexors to maintain upright standing. Indeed, vibration effects decreased in contracted muscles (Ansems et al. 2006; Eklund 1972; Goodwin et al. 1972; McCloskey 1973). This may be particularly relevant when considering the greater activation of plantar flexor muscles in older compared with young adults during upright standing (Billot et al. 2010). In addition, other studies showing greater postural perturbation in older adults in response to vibration used vibration frequency of ≤60 Hz. As vibration effects increase with frequencies (Roll and Vedel 1982), low vibration frequencies may have limited the effects of vibration in young adults, thereby reducing the age-related difference in vibration-induced postural perturbation. Furthermore, low-frequency vibrations (<60 Hz) maximally activate Meissner's corpuscles (Martin and Jessel 1991) and can perturb sensory weighting between cutaneous stretch receptor and muscle proprioceptors (Pavailler et al. 2016) more in older adults who experience altered proprioceptive processing. Overall, if the use of tendon vibration tends to indicate a lesser contribution of leg proprioception to postural control in older compared with young adults, further work is needed to draw a definitive conclusion.

Another relevant approach to highlight the influence of altered leg proprioception in postural control is to investigate the relation between postural control and the integrity of the proprioceptive system. Along this line, Lord et al. (1991) searched for a relation between joint position sense and postural control in a sample of 95 older adults (mean age: 82.7 yr). The authors found that poor joint position sense was associated with larger body sway. With a bigger sample (550 women, aged between 20 and 99 yr), Lord and Ward (1994) confirmed that proprioception was a predicting factor of postural control in standing on a firm surface with eyes closed. Deshpande et al. (2016) investigated the relation between ankle joint proprioception, measured as the threshold for perception of passive movement that is generated by primary endings of muscle spindles, and postural control in a population-based sample across the adult life span ($n = 790$). The authors reported that poor proprioception was consistently associated with poor postural control, with proprioception acuity decreasing with age. By using multivariate kinematics and joint torque measurements during dynamic posturography, Speers et al. (2002) found that the increase in body sway amplitude with age was partly related to an increase in sensory noise that reduces the ability to detect small body motions through proprioceptive signals. Recently, Anson and colleagues (2017) assessed the relations between visual, vestibular, and proprioceptive functions and age with postural sway in 366 subjects aged between 20 and 103 yr. Multiple linear regressions indicated that proprioceptive function was the best predictor of sway area, whereas age per se was not a consistent predictor of sway characteristics. Accordingly, the authors concluded that loss of peripheral sensory function explains much of the age-related decrease in postural control. Together, these results underscore that age-related impairments in detection and processing of proprioceptive signals alter postural control.

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Neural Aspects

Increase in coactivation of lower limb muscles. To adjust the mechanical properties of a limb, the central nervous system can simultaneously coactivate agonist and antagonist muscles around a joint. Increasing the level of coactivation augments joint impedance (Hogan 1984) and thereby provides better joint mechanical stability. Antagonist coactivation may also counteract, or at least mitigate, responses to external perturbations and forces due to limb dynamics and gravity (Finley et al. 2012). The nervous system can therefore utilize a feedforward strategy relying on antagonist coactivation rather than feedback mechanisms, especially short-latency reflex responses, to increase ankle stability during unperturbed upright standing.

Compared with young adults, older adults maintain upright standing with a greater coactivation level between the plantar flexors and dorsiflexors of the ankle, especially when upright standing or sensory conditions are challenged (Baudry and Duchateau 2012; Benjuya et al. 2004; Donath et al. 2015; Melzer et al. 2001). Furthermore, previous work (Baudry and Duchateau 2012; Nagai et al. 2011) reported that muscle coactivation was significantly higher in older adults exhibiting poorer postural control. The increase in coactivation in older adults partly reflects a compensatory mechanism to changes in proprioception (Manchester et al. 1989; Nagai et al. 2011). In agreement, greater coactivation was observed in deafferented patients than in healthy subjects (Sainburg et al. 1995). Moreover, age-related alterations in peripheral sensory perception contribute to increase antagonistic leg muscle coactivation (Ortega and Farley 2015). The level of coactivation has also been inversely associated with the amount of Ia presynaptic inhibition of muscle spindle afferents converging onto soleus motor neuron pools during upright standing (Baudry and Duchateau 2012), suggesting that reductions of Ia afferent input onto soleus are associated with a greater level of coactivation. However, if coactivation may reflect a strategy of stiffening and freezing the lower legs to control upright standing (Benjuya et al. 2004), it could be inefficient to improve postural control (Latash 2018), and thereby uselessly increases the energetic cost of postural control. Associated with the fact that a greater reliance on feedforward strategies would decrease automatic processing of postural control (Finley et al. 2012), the increase of coactivation in response to age-related alterations in leg proprioception may not be an efficient strategy for postural control.

Increased dependence on visual information. As the information carried by each sensory source is weighted depending on the current functional state of the source, the postural task, and the context in which it is performed, the most reliable sensory inputs are emphasized and the less reliable inputs are weakened. A decrease in the reliability of proprioceptive information should be compensated, therefore, by upweighting another sensory source such as visual information. This assumption is supported by experimental data obtained in situations in which sensory conflict was generated through bilateral Achilles tendon vibration and contrasting visual flow (Kabbaligere et al. 2017). The results indicated a sensory reweighting process directly proportional to the relative reliability of the cues. In this study, the reduced weighting of the proprioceptive cues was compensated by visual cues. Along these lines, declines in peripheral sensory perception with aging have been involved in elevated reliance on visual feedback (Franz et al. 2015; Jeka et al. 2010). In agreement, numerous studies underscore that older adults tend to rely more upon their visual input than other sensory systems to control upright standing (Borger et al. 1999; Simoneau et al. 1999; Wade et al. 1995; Yeh et al. 2014). However, less work has focused on the potential link between such an increase in the relevance of visual inputs and impairment in proprioceptive input. Sundermier et al. (1996) investigated the influence of visual flow from a moving visual surrounding on postural control in young adults, healthy older adults, and older adults with balance problems. The group of older adults with balance problems had greater center of pressure excursions when changing the visual flow, indicating an overreliance on visual cues for posture control. The authors suggest that this greater reliance on visual cues reflects borderline somatosensory deficits, as this group had subclinical indications for somatosensory impairments and brain changes. With another experimental approach, Haibach et al. (2009) reported greater postural motion in older compared with young adults in response to the oscillation of a virtual moving room. In this experiment, older adults had an increased egomotion (increased body sway in response to visual scene motion) but a decreased vection (decreased perception of movement) in response to visual scene motion. The authors claim that the reduction in proprioceptive inputs that accompanies aging leads to an increased amplitude of body sways before people perceive visual scene motion, reflecting somehow a greater reliance on visual information. Furthermore, Eikema and colleagues (Eikema et al. 2012) indicated that older adults show less sensory reweighting in quiet standing because of a greater visual field dependence. An additional parameter that should lead to greater reliance on visual information in relation with poorer proprioceptive input could be muscle weakness. Indeed, individuals with lower limb weakness rely more on vision to detect and stabilize their body sway than people with strong lower limb muscles (Butler et al. 2008). This may be explained by the fact that the increase in muscle activation required to maintain upright standing with aging (Billot et al. 2010) may reduce the proprioceptive acuity (Proske et al. 2000; Wise et al. 1998; see also *Behavioral Aspects*). It is noteworthy that strategies incorporating visual information induce delayed and less accurate fall avoidance responses, in contrast to adaptative strategies based on proprioceptive information (Vouriot et al. 2004).

A critical examination of these results, however, raises two comments. First, previous work on manual (Boisgontier et al. 2014) and postural (Berard et al. 2012; Eikema et al. 2012; Jeka et al. 2010; O'Connor et al. 2008) tasks suggests that older adults may experience more difficulty in suppressing unreliable visual cues. In addition, Bugnariu and Fung (2007) showed that aging alters the interaction of the somatosensory and visual systems in the control of balance and the ability to resolve sensory conflicts. These elements may challenge the interpretation that greater visually evoked postural responses purely reflect an increased reliance on vision to control upright standing in older adults. Second, the general decrease in postural control when visual inputs are distorted or occluded may indicate that poor proprioception cannot compensate for changes in visual conditions. If such an assumption nuances an increased reliance on visual information due to impaired proprioception per se, it nevertheless indicates that altered propri-

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oception makes older adults more dependent on visual information to control upright standing (Lord and Ward 1994), thereby reducing the flexibility of the sensory reweighting process (Jeka et al. 2010; Wade et al. 1995). Overall, most studies point to an upweighting of visual information to compensate for age-related impairments in leg proprioception.

Increase in controlled processing of upright standing. Motor control ranges from totally controlled processing that involves basal ganglia-cortical loops (Jacobs and Horak 2007) to automatic processing involving spinal and brain stem networks (Honeycutt et al. 2009). An alteration in proprioceptive input from muscle spindles likely reduces the efficacy of the automatic processing, thereby increasing the controlled processing and the cognitive load associated with postural control. In agreement, proprioception loss, as observed in deafferented patients, leads to an increase in the cognitive resources needed to perform even simple movements (Ingram et al. 2000). Accordingly, older adults increase the attentional resources dedicated to postural control, as revealed by the dual-task paradigm (Baudry and Gaillard 2014; Berger and Bernard-Demanze 2011; Boisgontier and Nougier 2013; Gaillardin and Baudry 2018; Rankin et al. 2000; Teasdale and Simoneau 2001; Woollacott and Shumway-Cook 2002).

Additional elements in favor of a shift to a more controlled process are provided by transcranial magnetic stimulation (TMS), which allows one to assess changes in the excitability of the motor corticospinal pathways that encompass cortical and spinal motor neurons as well as spinal interneurons with task requirements (Petersen et al. 2003). For example, the motor evoked potential elicited in the soleus by TMS increased from seated or supported bipedal posture to normal bipedal posture (Soto et al. 2006; Tokuno et al. 2009), and motor evoked potential amplitude was greater in old compared with young adults during upright standing (Baudry et al. 2014a). Furthermore, when the excitability of the corticomotoneuronal pathway, which provides a more direct access to cortical excitability, was assessed, older adults also exhibited greater corticomotoneuronal excitability than young adults during upright standing (Baudry et al. 2014b). Interestingly, a positive association between corticomotoneuronal excitability and soleus muscle activity indicates that the individuals who activated the soleus muscle to a greater extent were those who had greater corticomotoneuronal excitability. This should be considered in regard to the opposite relation between Hoffmann reflex amplitude and soleus muscle activity during upright standing (Baudry 2016; see below) and to the fact that large muscle activity may alter the proprioceptive signal. The silent period observed in response to TMS, reflecting the excitability of intracortical inhibitory networks (Orth and Rothwell 2004), was depressed in older adults during upright standing, thereby suggesting a decrease in intracortical inhibition (Baudry et al. 2015). To go further in the modulation of intracortical inhibitory circuits, Papegaaij et al. (2016) investigated the age-related changes in motor cortical activity during nonpostural and postural contractions with varying levels of postural challenge by TMS-induced electromyography depression. Even though age does not affect the motor control strategy of modulating motor cortical activity with increasing postural challenge, the motor cortical modulation appears at a lower task difficulty with increasing age. These results likely reflect a more controlled processing of upright standing that may be in part due to changes in muscle spindle afferent signals (Heuninckx et al. 2004, 2005). In agreement, a recent study suggested that impaired proprioception contributes to alter the cortical control of upright standing in older adults (Ozdemir et al. 2018).

The amplitude of the Hoffmann reflex is depressed in the soleus during normal bipedal posture compared with seated or supported bipedal posture (Koceja et al. 1993; Tokuno et al. 2009) and from stable to unstable upright standing conditions (Earles et al. 2000). When measuring the amplitude of the Hoffmann reflex in seated and upright standing conditions in individuals aged between 19 and 76 yr, with the soleus background activity being matched between the two positions, Baudry et al. (2015) observed a decrease in Hoffmann reflex amplitude from seated to standing regardless of age. However, the reduction in Hoffmann reflex amplitude induced by upright standing increased with age, more so in individuals over the age of 60 yr compared with younger individuals. Because subjects had similar levels of habitual physical activity, such results cannot be explained by an age-related increase in sedentary lifestyle that could induce a more pronounced decrease in Hoffmann reflex amplitude (Chalmers and Knutzen 2000). One interpretation of the greater posture-related decrease in Hoffmann reflex amplitude with aging could rest on a reduced ability of the proprioceptive system to provide an appropriate signal to activate leg muscles. This should reduce the automatic processing associated with upright standing.

Together, these different approaches and viewpoints emphasize the impact of age-related deterioration of proprioception on postural control, as synthesized in Fig. 3. Because the aging process cannot be stopped, future research should be oriented to interventions designed to limit alterations of the proprioceptive system. Without being exhaustive, we highlight in the next section some promising approaches, going from basic behaviors (nontargeted physical activity) to more sophisticated interventions (augmented sensory feedback), that may counteract the aging process of proprioception and its consequences on postural control.

PERSPECTIVES

As postural control and gait contribute to healthy aging (Lara et al. 2013), it thereby requires maintaining the capacity of the proprioceptive system because, as developed in the previous sections, impaired proprioception is associated with poor postural control in older adults (Anson et al. 2017; Deshpande et al. 2016; Goble et al. 2011; Lord et al. 1991; Toledo and Barela 2010). The following approaches appear to be promising to preserve proprioceptive function and postural control with aging.

Regular physical activity has been proposed to attenuate the decline in proprioception in older adults (Adamo et al. 2009; Ribeiro and Oliveira 2010; Petrella et al. 1997). For example, by comparing young, active older, and sedentary older adults, Petrella et al. (2017) observed a decrease in proprioception with age but brought forward the positive role of regular activity to attenuate this decline. In addition to maintaining proprioceptive acuity, Maitre et al. (2013) indicated that regular physical activity may preserve the ability to reweight sensory sources for a better use of sensory information. These studies indicate that nontargeted physical activity can preserve

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proprioceptive acuity and postural control in older adults and suggest that regular exercise may represent a strategy to reduce the incidence of poor proprioception with aging. However, this approach does not allow for the determination of a link between specific exercises and improvement in proprioception. In fact, there is only limited evidence on the trainability of the proprioceptive sense and the extent to which improvements in proprioceptive function impact postural control. Because the acquisition or learning of a motor skill relies in part on proprioception, numerous interventions were called proprioceptive training even if they did not directly isolate the contribution of improved proprioceptive acuity to postural control. To overcome such an issue, Aman et al. (2015) suggested defining proprioceptive training as an intervention that specifically targets proprioception and evaluates improvement in proprioception and its impact on sensorimotor function. In this context, using a robotic exoskeleton coupled with a virtual visual environment to induce proprioceptive-motor learning, Elangovan et al. (2018) reported improvement in wrist position sense acuity and spatial movement accuracy in an untrained, discrete wrist-pointing task in healthy older adults and parkinsonian patients. More related to postural control, a creative dance program that emphasized body awareness and postural control improved knee joint position sense, knee kinesthesia, and arm positioning in older adults (Marmeleira et al. 2009). Interestingly, a recent meta-analysis points toward positive effects of long-term Tai Chi practice on ankle proprioception in older adults (Zou et al. 2019), while Tai Chi has been largely documented to improve balance (Chen et al. 2012). Other interventions using exergames, which combine physical exercise and gaming (active video game exercises), have shown improvements in balance, mobility and strength (van Diest et al. 2013) along with proprioception in older adults (Sadeghi et al. 2017). One advantage of exergames is that they may be more enjoyable and thereby should increase adherence to the intervention (Valenzuela et al. 2018). It has been hypothesized that these types of interventions positively influence proprioception through enhancements of the sensitivity of proprioceptive sensors and cortical reorganization, which improves central processing of proprioceptive information (Han et al. 2015).

Another approach consists of augmented sensory feedback, defined here as the addition of sensory cues via auditory, tactile, or visual modalities to provide relevant information about posture. In 1978, Wannstedt and Herman were among the first to show that augmented sensory feedback could improve postural control in hemiparesis patients (Wannstedt and Herman 1978). Since then, various methods have been used, showing some relevant effects on proprioception and postural control (Sienko et al. 2018). For example, healthy older adults who trained with augmented sensory feedback showed a greater increase in reliance on vestibular inputs after training than a group who performed balance exercises alone (Bao et al. 2018). In this study, participants performed balance exercises with or without vibrotactile sensory augmentation. These results suggest that augmented sensory feedback can be used as a rehabilitation tool targeting postural control by reweighting the sensory sources to control upright standing. However, another study showed no overall benefit of balance training in healthy older adults when training was performed both with and without multimodal (vibrotactile, auditory, and visual) augmented sensory feedback (Lim et al. 2016).

An interesting emerging approach of augmented sensory feedback rests on applying mechanical or electrical noise over the limbs (Ribot-Ciscar et al. 2013). This approach relies on a stochastic resonance phenomenon (Chow et al. 1998) that is assumed to enhance detection, transmission, and discrimination of sensory signals by the addition of mechanical or electrical noise (McDonnell and Abbott 2009; Moss et al. 2004). For example, Ribot-Ciscar et al. (2013) indicated that ankle movement sense could be improved by adding an optimal level of mechanical noise to ankle muscle-tendon unit through random vibration. The authors suggested that mechanical noise may constitute a means of improving postural stability in subjects with sensory deficits. Similarly, electrical noise stimulation applied over the knee or leg muscles improved proprioception and postural control in young and older adults (Gravelle et al. 2002; Toledo et al. 2017).

If these different approaches to limiting the impact of aging on leg proprioception and its effects on postural control are very promising, the heterogeneity of the interventions, subject characteristics, and outcome measures does not allow for definitive conclusions on their usefulness and specific recommendations. Future studies are therefore warranted to optimize such interventions in the context of postural control in older adults.

CONCLUSIONS

Our objective was to provide a comprehensive review of how advancing age changes leg proprioception and to put forward evidence that these changes modify the control of upright standing in older adults. Several lines of evidence indicate that leg proprioception is altered with aging, and these alterations encompass among other mechanisms decreases in the sensitivity, acuity, and integration of the proprioceptive signal. The impact of these alterations on postural control is reflected in greater body sway and excursions of the center of pressure, a decrease in the relevance of the proprioceptive signal for postural control, an increase in antagonist coactivation, a greater reliance on visual information, and less automatic control of upright standing. These changes contribute to decrease the flexibility of the postural system and would ultimately impair postural control and the adaptative capacity to face changes in internal or external conditions (Fig. 3). Nonetheless, specific interventions may improve postural performance through changes induced with the proprioceptive system, although future work should document the characteristics of such interventions.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

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AUTHOR CONTRIBUTIONS

M.H. and S.B. prepared figures; M.H. and S.B. drafted manuscript; M.H. and S.B. edited and revised manuscript; M.H. and S.B. approved final version of manuscript.

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