



Contribution of muscle proprioception to limb movement perception and proprioceptive decline with ageing

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Perception of self-body movements relies on multiple senses among which muscle proprioception plays a crucial role. However, estimating its specific contribution is challenging given the difficulty to stimulate the deep muscle spindles independently from the skin and other tissues. Recent advances in psychophysical and neuroimaging studies that allow targeting muscle proprioception reveal (i) its specific contribution with respect to touch and vision, (ii) the interplay between bimanual proprioceptive signals and (iii) the sensorimotor cerebral network associated with movement illusion. Moreover, they highlight in older adults a larger decline in muscle proprioception than touch, which goes with structural alteration of cortical gray matter and corpus callosum, and with increased inter-network connectivity. These findings underline the importance to address disruption of sense of movement for both diagnosis and rehabilitation.

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Introduction

In 1826 Sir Charles Bell described the existence of the 6th sense or muscle sense and its contribution to the perception of self-body movement [1]. Since then, electrophysiological studies in humans have clearly identified that

muscle spindles, widely scattered in the muscle belly, are extremely sensitive to muscle lengthening [2]. However, these proprioceptive mechanoreceptors are deeply embedded, which makes their access and specific stimulation challenging [3]. Classically, the role of muscle proprioception has been widely studied by assessing one's ability to detect or reproduce passive displacement of body segments that actually activates simultaneously both touch and muscle proprioception. However, touch also conveys kinaesthetic information. Indeed, just stretching [4] or brushing the skin [5,6] alone can create perception of illusory movements. Microneurographic studies further confirmed that cutaneous mechanoreceptors are sensitive to the velocity [7] and the direction [8] of passively imposed movements of a limb. In addition, a vast amount of studies have also demonstrated the kinaesthetic function of vision [6,9,10*]. The perception of the self-body movement, called kinaesthesia, is thus fundamentally multisensory.

Revealing the specific contribution of muscle proprioception to such a complex perception is critical and deciphering the corresponding proprioceptive brain network is challenging. This review presents recent insights into the specific contribution of muscle proprioception to kinaesthesia from studies that have disentangled proprioception and touch (vision being easily isolated), and from studies that investigated the interplay between bimanual proprioceptive feedback. The development of magnetic resonance imaging (MRI) compatible devices of stimulation has also allowed identification of the underlying brain network.

Of relevance, recent behavioral and neural evidence has shown that touch and muscle proprioception may not contribute equally to kinaesthesia across the lifespan and may be unequally affected with ageing. An important finding that underlies the need to specifically assess proprioceptive deficits to adapt personalized sensory training approaches for rehabilitation perspectives.

Contribution of muscle proprioception to kinaesthesia: what's new?

A loop on muscle proprioception specificity with respect to touch and vision

Perception of our own body movements is multisensory by nature. Seeing our moving limbs, feeling the skin stretching as well as muscles lengthening are all relevant information processed concomitantly by our central

nervous system (CNS) to optimize the resulting percept. The question of the reliability of each sensory input, and its weighting in the final percept may therefore arise.

The static sense of limb position as well as the dynamic sense of limb movement have been generally investigated by passively moving a joint. Participants have to either match the imposed joint displacement (ipsilateral matching task or simultaneous contralateral matching) or detect the occurrence of movement. Healthy young adults can accurately reproduce angular displacements (e.g. 0.2° mean matching error at the ankle level for a target angle of 10° , [11]) and detect passively imposed movements (e.g. a mean threshold detection of 1.8° for passive wrist movement at $40^\circ/\text{s}$, [12]). However, cutaneous mechanoreceptors are activated concomitantly with the muscle spindles during passive limb displacements. Other studies rather used muscle tendon vibration known to specifically stimulate muscle spindle endings. Roll and Vedel [13] showed that a mechanical vibration applied to a muscle tendon increases the activity of muscle spindle endings with primary afferents Ia responses linearly proportional to the vibration frequency up to 80 Hz. The proprioceptive message generated by tendon vibration is interpreted by the CNS as an actual lengthening of the stimulated muscle, which gives rise to an illusory movement perception. Although skin mechanoreceptors are also activated by a mechanical vibration, it is generally accepted that kinesthetic illusions induced by the vibration of muscle tendons are mainly proprioceptive in origin since anesthetizing the cutaneous zone to which the vibrator is applied does not alter the perceptual effect [14]. In addition, based on actual recordings of muscle spindle responses evoked by passive foot movements, complex patterns of vibration have been elaborated and gave rise to the corresponding illusory sensation of movement, including two-dimensional illusions of movements such as writing a cursive letter [15]. This highlights the relevance of tendon muscle vibration as a means of studying the specific role of muscle proprioception in the fine coding of movement trajectories. In addition, muscle proprioceptive stimulation can be combined with visual or tactile stimulation to investigate the integrative co-processing of multimodal information for kinaesthetic purposes. Recent studies showed that, the weighting of the proprioceptive signal is not constant in multisensory integration, but may vary depending on which sensory modalities are available to assess the on-going movement [9], its velocity [5], or the individual sensory preferences [16]. For example, touch can override muscle proprioception for perceiving relatively slow hand movement rotations and vice versa [5]. But, in case of a visuo-proprioceptive conflict, the resulting perception may rely on visual or proprioceptive feedback depending on individual sensory preferences [16]. Neurophysiological and neuroimaging studies have provided compelling evidence that multisensory mechanisms occur at several

stages of the central nervous system including association cortices but also primary cortices, historically considered as unisensory areas (see review [17]). In these brain regions, sensory reweighing might be driven by the respective reliability of different sensory sources. This hypothesis is sustained by the fact that level of activity in the parietal cortex is modified as the reliability of the visual stimulus changes in an audio-visual spatial detection task [18], as well as that of the primary somatosensory cortex in a visuotactile shape identification task [19]. Moreover, multisensory interactions can also have an impact at the peripheral level as adding visual information has been found to reduce muscle-related firing during passive movement, probably via descending commands by fusimotor efference. This decrease in muscle spindle sensitivity may reflect a re-weighting of the two sensory cues in favor of the visual source [20].

A complex intra-modal integration for self-body perception: the example of bimanuality

Another complex picture of the role of proprioception in kinaesthesia can be drawn when focusing on the integration of proprioceptive feedback arising from different limbs. This question is especially relevant given how frequent are bimanual gestures in our daily life [21]. The temporal and spatial synchronisation of bilateral homologous muscle activation sequences attests of a very efficient motor coupling mechanism (for review, see Ref. [22]). More recently, a case study argues that bimanual coupling also requires bimanual integration of proprioceptive feedback. Indeed, in a patient with a cerebral lesion causing an unilateral central proprioceptive loss, the emergence of bimanual coupling is prevented despite a preserved motor intentionality and planning [23^{*}]. This finding echoes previous results showing that contralateral proprioceptive feedback can also influence involuntary arm movements: for example, the speed of an involuntary arm flexion following sustained, isometric contraction, that is, the Kohnstamm effect, is modulated by contralateral proprioceptive feedback [24]. Indeed, the higher is the mechanical vibration frequency applied to the triceps tendon of one arm, simulating an arm flexion of that arm, the faster is the contralateral Kohnstamm effect. Several studies have suggested that such bimanual coupling exists also at the perceptual level. For example, manipulating the proprioceptive signal from one arm using vibration stimulation can alter the perceived position of the contralateral arm [25]. Furthermore, kinaesthesia as well is built on the integration of bilateral proprioceptive information. Using the mirror illusion, that is, the reflection of a moving hand in a mirror positioned in the sagittal plane that creates an illusion of symmetrical bimanual movement, Chancel and collaborators *et al.* [26] showed that masking the muscle proprioceptive afferents of the reflected arm, by co-vibrating antagonistic muscles, reduced the velocity of the illusory displacement of the hidden arm. The same group showed that the arm

movement illusion can survive longer after the participant's vision was occluded if the initially seen arm kept moving instead of becoming still [27[•]]. These last two studies suggest that the kinaesthetic mirror illusion is not solely visual in origin but results from a combination of both visual and proprioceptive signals from the two arms. Giroux *et al.* [10[•]] recently confirmed these results using a virtual reality adaptation of the conventional mirror paradigm, highly convenient to separate visual inputs from other body signals. In this 'virtual' mirror paradigm, the participant sees an avatar from a first-person perspective through a virtual reality headset. It was found that the kinesthetic illusions evoked by the movement of the avatar's left or right arms were much stronger when this visual stimulation was combined with the actual passive movement of the participant's opposite arm. This result confirms that the mirror illusion, often considered a prototypic visual illusion, involves bilateral proprioceptive-somaesthetic signals that interact with the visual signals and reinforce the kinaesthetic effect. In a broader perspective, the importance of bilateral integration of proprioceptive afferents should be more considered, notably in the examination of bimanual coordination. For example, Monteiro *et al.* [28] observed bimanual motor impairment in the elderly; however, the proprioceptive component of this impairment is yet to be investigated.

Proprioceptive acuity in older adults

The global population ageing promotes studies on age-related declines in sensorimotor performance and the specific contribution of proprioception decline [29]. Studies focused mainly on the effect of ageing on proprioceptive acuity by assessing lower limb's perception of position. Their findings are controversial as they show both impaired and unaffected joint position sense in older participants [11]. Few studies focused on the lower limb's sense of movement using velocity discrimination tasks and detection tasks of passive movements. These passive movement paradigms revealed an alteration of kinaesthesia with ageing [11,12], but they recruit both cutaneous and muscle receptors, each of which gives rise to kinesthetic information. Interestingly, recent studies used tendon vibration and a textured disk rotating under the participant's hand to induce illusions of hand rotations from a proprioceptive or a tactile origin, respectively. They showed that the ability of older adults to discriminate the velocity of proprioceptive illusions were more affected than that of tactile illusions, suggesting a larger functional deficit in muscle proprioception than touch in healthy adults aged 65 years and over [30,31]. The authors also stressed the importance of developing tasks that can separate proprioceptive and tactile deficits in the evaluation of position sense and thus may clarify inconsistent findings in the literature. Furthermore, a better understanding of physiological impairment of muscle proprioception may also help the development of targeted

interventions for disorders showing disruption of the sense of movement [32]. For example, a specific proprioceptive training based on mechanical vibrations can prevent cortical disruption in the sensorimotor brain network due to a limb immobilization [33] and facilitate sensory processing in patients with Parkinson's disease [34[•]].

The proprioceptive brain network

Not a pure sensory but a sensorimotor network

Functional MRI (fMRI) studies have investigated perception of own body movements by examining brain activation during imposed passive movements. The development of MRI-compatible vibrators allowed specific exploration of the proprioceptive brain network. Since the pioneer study by Naito *et al.* [35], further studies identified brain activations associated with vibration-induced illusory movements of the wrist [36–38,39^{••},40] or the ankle [41,42]. All these studies converge to show that the sensory proprioceptive stimulation activates the primary somatosensory cortex, the inferior parietal lobules and insula, but also motor-related areas including the primary motor cortex, the supplementary motor area, the premotor cortex, the basal ganglia (striatum) and cerebellum, as well as the inferior frontal gyrus. Of relevance, awareness of illusory body movement seems rather linked to the frontoparietal activation [40,42]. This result is in line with the crucial role of the inferior parietal lobule in multisensory representation of the body [37,43] and the sense of ownership of one's body [44]. By contrast, the velocity of illusory movement is correlated with activation level in motor-related areas [36]. By implementing multivariate approaches and more complex stimulation protocols, one could further dissociate the respective involvement of each part of the proprioceptive network in the coding of different movement features (e.g. direction, speed) but also the integration of multi-joint or even multi-segmented movements.

Functional brain changes with ageing

In recent decades, neuroscience of ageing studies have been interested in new MRI approaches to evidence structural and functional brain changes across the lifespan [45]. In particular high field MRI studies showed focal reduction in gray matter and white matter volumes in older brains [46] and demonstrated that cortical morphological changes are good predictors of age [47], whilst fMRI studies focused on the age-related cognitive and sensorimotor declines (for review see Ref. [48]).

So far, sensorimotor studies mainly concentrated on motor decline with ageing. Recently, two groups have conducted complementary research on age-related kinaesthetic impairment both using muscle tendon vibrations, one at the level of the lower limb [41,49] and the other one at the level of the upper limb [39^{••}]. They both showed that vibrations in older adults recruit the same proprioceptive network as in young adults. In addition,

Goble *et al.* showed that the structural alteration of cortical gray matter due to ageing correlated with a decrease of activation in the corresponding brain regions [41], and with a decrease in ankle proprioceptive acuity [49]. By comparing illusions of hand movement induced by either a muscle vibration or a tactile stimulation, Landelle *et al.* [39**] showed that age-related brain activation only decreased in the proprioceptive condition. In particular, the latter authors observed that older adults exhibited a less-lateralized pattern of activity in the primary sensorimotor cortices and slower proprioceptive illusions than young adults. These functional brain changes are probably underpinned by a decline of the peripheral proprioceptive system [50], structural alterations in the corpus callosum [51] and modifications of inhibitory processes [52*] together. By comparing the resting-state connectivity between older and young adults, recent studies provide evidence of an increase in inter-network connectivity with ageing, which is generally interpreted as a decrease in the segregation of distinct networks [53]. Nevertheless, the older adults might take advantage of some of such extended connections, as increasing the strength of connectivity between the sensorimotor cortex and the lower parietal lobule was found to be positively correlated with proprioceptive acuity [39**]. Altogether, these findings provide convincing evidence of an unequal central alteration of the different sensory systems with age, resulting in a larger decline in muscle proprioception than touch for kinaesthetic perception. Age-related deterioration also occurs at the peripheral level with an alteration of structural properties (increase in the thickness of the capsules), reduced density and decrease in the number of intrafusal fibers in human muscle spindles as well as an alteration of peripheral nerve conduction (see reviews [54,55]). However, the relative deterioration of cutaneous versus proprioceptive system at the peripheral level remains to be investigated.

Conclusions

Multisensory integration is a key process underlying perception of body positions and body movements. In contrast to perception of the external world, perception of one's own body is a rather complex process to study considering that (i) numerous sensory (but also motor) signals are involved, (ii) these signals are highly dependent on each other and therefore difficult to disentangle, and (iii) some of the sensory receptors, deeply embedded in the body organs, are difficult to target specifically. Within the last decade, new techniques and paradigms, including virtual reality designs, MRI compatible stimulators, but also brain imagery tools to study network connectivity, have allowed us to make substantial advances in our understanding of the behavioral and neural mechanisms involved in the perception of body movements and their decline with age. Among those advances, one must underline the novel results on the involvement of bilateral proprioceptive signals in motion

perception, the larger impairment of muscle proprioception with ageing than touch, but also the increased inter-network connectivity in elderly. The latter one might be a helpful brain plasticity mechanism that temporarily compensates the age-related decline of peripheral and central sensory systems. All these insights stress the importance of examining muscle proprioception independently from other senses for both a better understanding of intra- and inter-modal integration processing and their cerebral substrates for kinaesthesia, as well as for clinical perspectives toward development of targeted rehabilitation protocols.

Conflict of interest statement

Nothing declared.

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