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Factors Influencing Proprioception: What do They Reveal?

Fernando Ribeiro[1,2] and José Oliveira[2]
[1]*CESPU, Polytechnic Health Institute of the North, Physiotherapy Department*
[2]*University of Porto, Faculty of Sport, Research Centre in Physical Activity, Health and Leisure*
Portugal

1. Introduction

The term proprioception was coined in 1906 by the neurophysiologist Sir Charles Sherrington from the Latin "proprius," meaning "one's own," for sensory information derived from neural receptors embedded in joints, muscles, and tendons (Sherrington, 1906). Hence, proprioception was originally defined as "the perception of joint and body movement as well as position of the body, or body segments, in space"(Sherrington, 1906). Some years before, in 1880, Bastian introduced the term kinaesthesia, from the Greek "kinein" to move + "aisthēsis" sensation, to describe the role of the motor cortex in eliciting motor behaviors that coordinate specific and functionally appropriate somatosensory afferent patterns (Finger, 1994). Presently, "kinaesthesia" and "proprioception" are used practically synonymously to indicate the capability to appraise the configuration and movements of an organism's body parts.

At present, proprioception can be defined as the cumulative neural input to the Central Nervous System from specialized nerve endings called mechanoreceptors, which are located in the joint, capsules, ligaments, muscles, tendons, and skin (Carpenter, Blasier, & Pellizzon, 1998; Ribeiro & Oliveira, 2007; Voight, Hardin, Blackburn, Tippett, & Canner, 1996). Proprioception alludes to the perception of tension/force, body/joint movement, and limb relative position (Riemann & Lephart, 2002). Proprioception is generally divided in the sub modalities sense of tension (resistance), sense of movement, and joint position sense. Sense of resistance represents the ability to appreciate force generated within a joint. Sense of movement refers to the ability to appreciate joint movement, including the duration, direction, amplitude, speed, acceleration and timing of movements. Joint position sense determines the ability of the subject to perceive a presented joint angle and then, after the limb has been moved, to actively or passively reproduces the same joint angle. All three modalities can be appreciated consciously and unconsciously, contributing to automatic control of movement, balance, and joint stability, and thus being essential to carry out daily living tasks, walking, and sports activities (Riemann & Lephart, 2002).

Proprioceptive information is originated and perceived within an organism at the level of the mechanoreceptor, which are sensory neurons located in the muscle, tendon, fascia, joint capsule, ligament, and skin (Carpenter, et al., 1998; Voight, et al., 1996). The main

receptors contributing to proprioceptive information are located in muscle, tendon, ligament, and capsule, while those located in the deep skin and fascial layers are traditionally considered as supplementary sources. Mechanoreceptors, as specialized sensory receptors, transduce the mechanical events, in general deformation of their host tissues, as frequency-modulated neural signals to the Central Nervous System throughout afferent sensory pathways (Grigg, 1994). The role of the different mechanoreceptors in the construction of proprioception has been actively debated in the literature, although current knowledge indicates that proprioception is primarily signaled by muscle receptors, namely muscle spindles (Proske, 2005, 2006). In fact, joint receptors seem to play a minor role through the midranges of motion, being only sufficiently stimulated in end ranges of motion in order to contribute substantially to proprioception (Burgess & Clark, 1969; Burke, Gandevia, & Macefield, 1988; Clark & Burgess, 1975; Grigg, 1975). Similar to joint receptors, cutaneous receptors have been hypothesized to respond only at the end ranges of motion (Burke, et al., 1988). In contrast, muscle spindles have been almost unanimously described as able to provide potent afferent information across the entire range of motion (Burgess, Wei, Clark, & Simon, 1982; Macefield, Gandevia, & Burke, 1990). In summary, muscle mechanoreceptors afferent information, specially arising from muscle spindles, is paramount to the mediation of proprioception, while other sources of proprioceptive information, including cutaneous and joint mechanoreceptors, seem to be also important for determining the position of distal body segments and/or signaling limits of range of motion (Goble, Coxon, Wenderoth, Van Impe, & Swinnen, 2009; Proske, 2005, 2006; Proske & Gandevia, 2009). The sense of tension is provided by muscle mechanoreceptors, namely Golgi tendon organs (Proske, 2005).

The sensory inputs received from mechanoreceptors are integrated and appreciated at three distinct levels of the Central Nervous System: at the spinal level, at the brain stem, and at the higher levels of the Central Nervous System such as the cerebral cortex and cerebellum (Myers & Lephart, 2000). At the spinal cord, the axons conveying proprioceptive information can be controlled via descending commands from the brain stem and cortex through interneurons and neurons connecting with higher Central Nervous System levels. Hence, the supraspinal regions of the Central Nervous System also play a role in the modulation of the proprioceptive information that enters the ascending tracts. Most proprioceptive information travels to the supraspinal regions of the Central Nervous System by both the dorsal lateral tracts that convey the signals to the somatosensory cortex and the spinocerebellar tracts that terminate in the cerebellum. The spinocerebellar tracts exhibit the fastest transmission velocities in the Central Nervous System and are associated with nonconscious proprioception, while the dorsal lateral tracts are responsible for the conscious perception of proprioception (Riemann & Lephart, 2002). The spinal level can contribute to functional joint stability by providing direct motor responses in the form of reflexes. At the brain stem, afferent information is integrated with visual and vestibular inputs in order to control automatic and stereotypical movement patterns, balance, and posture. The higher regions of the Central Nervous System, such as the cerebral cortex and cerebellum, elicit the conscious awareness of proprioception, thus contributing to the voluntary movements (Myers & Lephart, 2000). The integration of the proprioceptive input at these levels of the Central Nervous System aims to coordinate body stability ahead of movement execution (feedforward) as well as to correct for velocity and timing errors during its execution (feedback) (Batson, 2009).

Overall, undeniable evidence exists highlighting the importance of proprioception for the generation of smooth and coordinated movements, maintenance of normal body posture, regulation of balance and postural control, and influencing motor learning and relearning. These important roles were demonstrated in several studies evaluating deafferented patients (Ghez, Gordon, & Ghilardi, 1995; Ghez & Sainburg, 1995). Their data showed that without proprioception, the onset of movement is delayed and trajectory formation is impaired and highly inaccurate.

2. Techniques to measure proprioception

Several different testing techniques to assess joint proprioception have been reported in the literature. Despite proprioception being generally assessed by measuring both joint position sense and the sense of limb movement (Hiemstra, Lo, & Fowler, 2001), all three conscious sub modalities of proprioception can be assessed. Due to their nature, it is imperative to differentiate the modality been assessed.

Joint position sense measures the accuracy of position replication and can be conducted actively or passively in both open, and closed kinetic chain positions (D. M. Hopper, et al., 2003; Magalhaes, Ribeiro, Pinheiro, & Oliveira, 2010; Pickard, Sullivan, Allison, & Singer, 2003; Skinner, Wyatt, Hodgdon, Conard, & Barrack, 1986; Stillman & McMeeken, 2001; Torres, Vasques, Duarte, & Cabri, 2010). It can be also assessed using contralateral or ipsilateral matching responses (Bouet & Gahery, 2000). The accuracy of joint position sense has been measured directly, using goniometers, potentiometers and video analysis systems (Figure 1), and indirectly using visual analog scales (Barrett, 1991; Dover & Powers, 2004; D. Hopper, Whittington, & Davies, 1997; Miura, et al., 2004; Ribeiro, Mota, & Oliveira, 2007; Stillman, McMeeken, & Macdonell, 1998; Torres, et al., 2010; Tripp, Boswell, Gansneder, & Shultz, 2004; You, 2005).

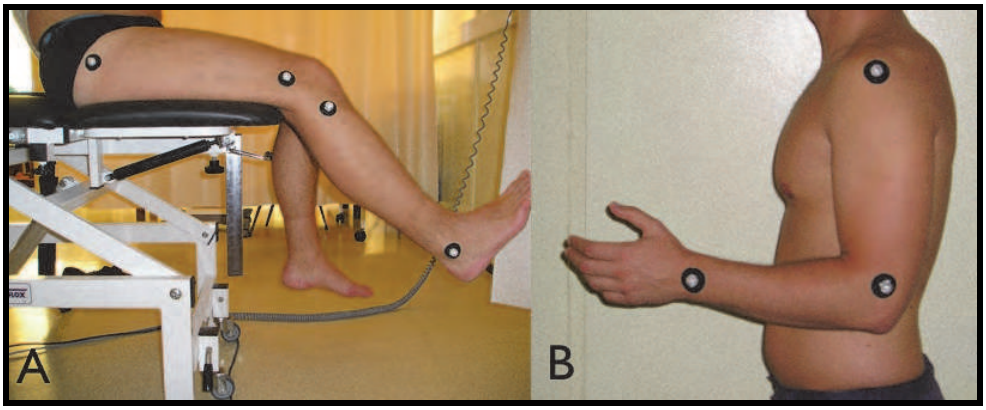

Fig. 1. Marker placement, according to four- (A) and three-point (B) model, for position sense assessment of individual joints using a video analysis system

The testing protocols usually comprise the definition of a target position that is identified and appreciated by the subjects, which are blindfolded. Then, the target position is reproduced passive or actively to the best of subjects' ability. Joint position sense is

generally reported as the absolute angular error, defined as the absolute difference between the target position and the estimated position, the relative angular error, defined as the signed arithmetic difference between a test and response position, and the variable angular error, commonly represented by the standard deviation from the mean of a set of response errors. Importance should be paid to the quite different methods of joint position sense assessment employed in the literature, which make difficult to establish comparisons among the studies.

Sense of limb movement is evaluated by measuring the threshold to detection of passive motion (Allegrucci, Whitney, Lephart, Irrgang, & Fu, 1995; Carpenter, et al., 1998; Lephart, Giraldo, Borsa, & Fu, 1996; Li, Xu, & Hong, 2008; Skinner, et al., 1986; Torres, et al., 2010). Threshold to detection of passive motion quantifies a subject ability to consciously detect movement, as well as, its direction and is often performed on some type of proprioception testing device such as an isokinetic dynamometer (Figure 2).

Fig. 2. The isokinetic dynamometer is used for assess joint position sense and sense of limb movement

In general, this procedure requires subjects to wear headphones, to be blindfolded to block visual input, and with a pneumatic sleeve to diminish tactile cues. The speeds used are slow, ranging from 0.5 to 2°/s, in order to target the slow-adapting mechanoreceptors (Riemann, Myers, & Lephart, 2002). The subject indicates (usually stops the device by pressing a "hold" button) when the passive movement is detected and the examiner records the amount of movement occurring before detection.

The sense of tension is assessed measuring the ability to reproduce torque magnitudes produced by a group of muscles (Riemann, et al., 2002; Torres, et al., 2010). The force-matching protocols are usually conducted without visual feedback and with low load, as the ability to reproduce force is associated with the recruitment of motor units and its firing frequency (Cafarelli, 1982). The difference between the target force and the torque produced is used to quantify the accuracy of sense of tension.

Despite different, all the above-mentioned proprioceptive testing methods rely on conscious appreciation of the mechanoreceptors input. Particular attention should be paid to several factors contributing to the wide variety of results reported in the literature, namely factors related with the testing device (eg, position of the patient with respect to gravity leading to different muscular actions during the reproduction movements), the assessment procedures (eg, angular positions, direction and speed of movement, ipsilateral or contralateral matching responses), and the study design (eg, experimental group compared with control group or bilateral comparison).

3. Factors influencing proprioception

A wealth of evidence exists pointing out several factors that induce transient or chronic changes in joint proprioception. In the following sections, we will focus the influence of aging, cryotherapy and acute bouts of exercise on proprioception.

3.1 Aging

A large body of evidence suggests that proprioceptive function declines during the aging process (Bullock-Saxton, Wong, & Hogan, 2001; Kaplan, Nixon, Reitz, Rindfleish, & Tucker, 1985; Pai, Rymer, Chang, & Sharma, 1997; Petrella, Lattanzio, & Nelson, 1997; Ribeiro & Oliveira, 2010; Skinner, Barrack, & Cook, 1984).

The deterioration of proprioception throughout the human lifespan has deleterious repercussions on motor coordination and balance (Shaffer & Harrison, 2007). Colledge et al. (1994) investigated the relative contribution of vision, proprioception, and vestibular system to the balance of different aged groups and reported that all aged groups rely more on proprioception than on vision for the maintenance of balance. This is exacerbated in subjects older than 80 years, in who the disruption of proprioceptive input seems to be a major determinant of quantitative balance performance (Camicioli, Panzer, & Kaye, 1997). In fact, impaired lower limb proprioception has been associated with balance deficits (Horak, Shupert, & Mirka, 1989; Lord & Ward, 1994; Manchester, Woollacott, Zederbauer-Hylton, & Marin, 1989; Woollacott, Shumway-Cook, & Nashner, 1986), which have, in turn, been associated with a higher incidence of falls (Lord, Rogers, Howland, & Fitzpatrick, 1999; Overstall, Exton-Smith, Imms, & Johnson, 1977; Sorock & Labiner, 1992; Tinetti, Speechley, & Ginter, 1988). Furthermore, decreased proprioception could lead to abnormal joint biomechanics during functional activities that over a period of time could result in degenerative joint disease (Skinner, 1993).

Proprioception acuity in the elderly has been extensively determined through cross-sectional studies comparing sense of position (Table 1) and/or limb movement in different age groups (Goble, et al., 2009; Ribeiro & Oliveira, 2007).

Among the first studies determining the effects of aging on proprioception are those performed by Kokmen and colleagues (1978) and Barrack and colleagues (Barrack, Skinner, & Cook, 1984; Skinner, et al., 1984). Skinner et al. (1984) compared knee proprioception under passive movement (threshold to detection of joint motion and the ability to reproduce passive knee positioning) between old and young subjects and found better proprioception in the young group. Similarly, Kaplan and colleagues, in 1985, determined the age-related changes in knee joint position sense using two techniques that required active movement, ipsilateral and contralateral matching repositioning, and observed reduced proprioception in older subjects. Interestingly, the source of acuity errors could be different for ipsilateral and contralateral matching. The contralateral matching limits the influence of eventual decreased memory abilities, as it relies greatly on interhemispheric communication, although the proprioceptive performance in this procedure could be influenced by decreased integrity of the corpus callosum or proprioceptive deficits in the contralateral leg (Goble, et al., 2009). A recent study, conducted by Ribeiro & Oliveira (2010), encompassing 129 subjects (69 older male adults aged 72.2 ± 5.0 years, and 60 young male adults aged 20.6 ± 3.0 years) and evaluating knee position sense with an open kinetic chain technique and active positioning also concluded that age has deleterious effects on position sense.

The different assessment methods employed in the above-mentioned studies and the different joints evaluated led to a wide range of acuity values, hence precluding the determination of normal values for elderly position sense acuity. Indeed, the methods used to assess position sense could have a direct influence in the acuity results. For instance, (i) active reproduction of joint position is more functional and accurate than passive reproduction (Bennell, Wee, Crossley, Stillman, & Hodges, 2005; Pickard, et al., 2003); (ii) weight bearing closed kinetic chain assessments enhance the position matching acuity (Bullock-Saxton, et al., 2001); and, (iii) target positions located farther from the starting joint position seem to increase the matching errors (Adamo, et al., 2007; Kaplan, et al., 1985). Despite using different methodological procedures, it is important to note that in general the direction of results allows to reach a similar conclusion: a significant deterioration of joint position sense is observed with advancing age.

Fewer studies have been conducted determining the effects of age on sense of movement in comparison with sense of position. Notwithstanding, they also clearly indicate that sense of movement is less accurate in old age subjects. In fact, studies conducted in the metacarpophalangeal and metatarsophalangeal (Kokmen, et al., 1978), knee (Barrack, et al., 1983; Skinner, et al., 1984), and ankle (Gilsing, et al., 1995; You, 2005) joints collectively highlight that the threshold to detection of passive motion increase with advancing age. In one of these studies (Skinner, et al., 1984), the decline in the acuity to detect passive motion was estimated to be, on average, 0.068^{o} per year of adult life.

The mechanisms of proprioception deterioration with aging involve both central and peripheral nervous system changes. At the peripheral level, studies using animals and humans have shown anatomical and physiological age-related changes in several mechanoreceptors (Shaffer & Harrison, 2007). Aging changes the muscle spindles function by: (i) decreasing dynamic and static sensitivities (Miwa, Miwa, & Kanda, 1995); (ii) decreasing the total number of intrafusal muscle fibers and nuclear chain fibers per spindle (Kararizou, Manta, Kalfakis, & Vassilopoulos, 2005; Liu, Eriksson, Thornell, & Pedrosa-

Author	Joint	Assessment Procedures				Results (AAE)	
		Matching responses	Matching movement	Weight bearing	Target angle	Old	Young controls
Adamo, Martin, & Brown, 2007	Elbow	I	Active	No	10° 30° 60°	3.3° 4.6° 5.5°	1.6° 3.3° 4.0°
		C	Active	No	10° 30° 60°	3.8° 5.1° 6.6°	2.2° 4.5° 6.0°
Pickard, et al., 2003	Hip	I	Active (outer) Active (inner) Passive	No	20° 20° 20°	~2.2° ~1.8° ~2.4°	~2.2° ~1.8° ~2.4°
Ribeiro & Oliveira, 2010	Knee	I	Active	No	40°–60°	9.4 ± 4.3°	4.7 ± 2.7°*
Tsang & Hui-Chan, 2003	Knee	I	Passive	No	3°	4.0 ± 3.4°	–
Petrella, et al., 1997	Knee	I	Active	Yes	10°–60°	4.6 ± 1.9°	2.0 ± 0.5°*
Kaplan, et al., 1985	Knee	C	Active	No	15° 30° 70°	5° 5° 8°	3° 3° 4°
Barrack, Skinner, Cook, & Haddad, 1983	Knee	I	Active	No	5°–25°	4.6°	3.6°*
Verschueren, Brumagne, Swinnen, & Cordo, 2002	Ankle	I	Passive	No	10°	2.7°	2.2°*
You, 2005	Ankle	I	Active	Yes	2°–38°	2.6 ± 0.8°	1.4 ± 0.6°*
Lord, et al., 1999	Toe	C	Active	No	–	1.6°	–

Table 1. Summary of joint position sense results from studies in the elderly.
AAE – absolute angular error; C – contralateral; I – ipsilateral; * significantly better acuity in young vs. old subjects ($p<.05$)

Domellof, 2005; Miwa, et al., 1995; Swash & Fox, 1972); (iii) increasing spindle capsule thickness (Kararizou, et al., 2005; Liu, et al., 2005; Miwa, et al., 1995; Swash & Fox, 1972); (iv) deteriorating the spinal presynaptic inhibition pathways (Burke, Schutten, Koceja, & Kamen, 1996); and, (v) denervation due to spherical axonal swellings, expanded motor end plates, and group denervation atrophy (Swash & Fox, 1972). Cutaneous receptors, such as Meissner and Pacinian type corpuscles, also undergo structural modifications including a decrease in number and mean density of receptors per unit of skin area (Bolton, Winkelmann, & Dyck, 1966; Iwasaki, Goto, Goto, Ezure, & Moriyama, 2003). Changes in the number and morphology of joint mechanoreceptors, particularly in Ruffini, Pacinian and Golgi-tendon type receptors, are also reported in literature (Aydog, Korkusuz, Doral, Tetik, & Demirel, 2006; Morisawa, 1998). In addition to these peripheral modifications, the decline in proprioception as result of the aging process could be also consequence of changes in the Central Nervous System. Indeed, inadequate processing of proprioceptive input could be determined by numerous changes at central level, including decreased conductive function in the somatosensory pathways (Tanosaki, Ozaki, Shimamura, Baba, & Matsunaga, 1999), decreased grey matter in postcentral gyrus (Quiton, et al., 2007), progressive loss in the dendrite system of the motor cortex (Nakamura, Akiguchi, Kameyama, & Mizuno, 1985; Scheibel, Lindsay, Tomiyasu, & Scheibel, 1975), decline in the number of neurons and receptors, and neurochemical changes in the brain (Masliah, Mallory, Hansen, DeTeresa, & Terry, 1993; Pakkenberg & Gundersen, 1997; Strong, 1998). Central Nervous System alterations could also induce alterations in muscle spindle sensitivity, as supraspinally mediated changes in the gamma drive to the muscle spindle could have a direct effect on its sensitivity (Mynark, 2001).

3.2 Cryotherapy

Cool, in the form of cryotherapy, is one of the therapeutic modalities most extensively used in the treatment of acute and chronic injuries. Cryotherapy modalities comprise the application of ice (for instance crushed ice) (Oliveira, Ribeiro, & Oliveira, 2010), cold water immersion (Costello & Donnelly, 2011), commercially available cooling pads, and liquid cooling solutions (Leite & Ribeiro, 2010) aiming to reduce tissue temperature, metabolism, inflammation, pain, vasodilatation, and symptoms of delayed-onset muscle soreness. A number of studies have focused the effects of cryotherapy on proprioception (Costello & Donnelly, 2011; Dover & Powers, 2004; D. Hopper, et al., 1997; LaRiviere & Osternig, 1994; Oliveira, et al., 2010; Ozmun, Thieme, Ingersoll, & Knight, 1996; Uchio, et al., 2003; Wassinger, Myers, Gatti, Conley, & Lephart, 2007) and reported conflicting results (Table 2). Cryotherapy modalities varied from single joint ice-bag application to lower limb water immersion and durations ranging, in general, from 15 to 30 minutes. The ice bag modality was applied over the joint in all studies, with one study (Oliveira, et al., 2010) applying the ice bag also over the skeletal muscle. In general, the studies performed in this field assessed proprioception by measuring sense of position in different joints, including shoulder, knee, and ankle. All the studies (Dover & Powers, 2004; Thieme, et al., 1996; Wassinger, et al., 2007), but one (Oliveira, et al., 2010), using an ice bag application found no deleterious effect of cryotherapy on proprioception. Wassinger et al. (2007) applied an ice bag, filled with 1500 g of cubed ice, to the shoulder joint for 20 minutes and assessed active sense of position while standing in 2 target positions, 90^{o} of shoulder flexion to 20^{o} flexion and 20^{o} of flexion to 90^{o} of flexion. The authors found no differences in joint position sense after the ice application, but the results were reported in centimeters of vertical displacement, making those hard to interpret and compare with the literature.

Author	Joint	Cryotherapy application			Proprioception assessment	Results (AAE)	
		Modality	Local	Duration		Before	After
LaRiviere & Osternig, 1994	Ankle	Water immersion	Leg immersion to a distance of 4 cm distal from the knee joint line	20 min	Active JPS	3.8±2.0	3.7±2.3
Thieme, Ingersoll, Knight, & Ozmun, 1996	Knee	Ice bag	Knee joint	20 min	Active JPS	N/A	N/A
Hopper, et al., 1997	Ankle	Water immersion	Immersion to a depth of 5 cm above the medial malleolus	15 min	Active JPS	2.4°	2.9°*
Uchio, et al., 2003	Knee	Cooling pad	Knee joint	15 min	Active JPS	4.8±1.6°	6.5±2.1*
Dover & Powers, 2004	Shoulder	Ice bag	Shoulder joint	30 min	Active JPS – IR Active JPS – ER	4.5±2.8° 2.9±1.6	4.1±2.1° 3.8±2.2°
Oliveira, et al., 2010	Knee	Ice bag	Quadriceps muscle Knee joint	20 min 20 min	Active JPS Active JPS	4.7±3.0° 4.6±2.9°	6.9±4.8* 6.8±4.7*
Costello & Donnelly, 2011	Knee	Water immersion	Immersion to the level of the umbilicus	30 min	Active JPS: ~35° ~55° ~75°	 4.5±3.3° 2.9±2.7° 3.0±1.9°	 5.4±2.5° 5.6±3.1° 3.2±2.9°

Table 2. Summary of studies examining the effects of cryotherapy on proprioception. AAE – absolute angular error; ER – external rotation; IR – internal rotation; JPS – joint position sense; min – minutes; * significantly worse proprioception after cryotherapy application ($p<.05$)

The studies (Costello & Donnelly, 2011; D. Hopper, et al., 1997; LaRiviere & Osternig, 1994) using water-immersion cryotherapy protocols found similar results for lower limb proprioception. Indeed, despite using different immersion durations (15, 20 and 30 minutes), depths, and water temperatures (14º, 4º, 5º, respectively), and assessing different joints (ankle and knee), they reported no changes in position sense after water immersion (Costello & Donnelly, 2011; LaRiviere & Osternig, 1994) or have questioned the clinical significance of the changes (D. Hopper, et al., 1997).

In fact, Hopper et al. (1997) questioned if a 0.5° difference in ankle joint position sense following 15 minutes of ice bath immersion would be clinically relevant. Surenkok et al. (2008) investigated the effects of cold spray (ethyl chloride) application to the knee (until volunteers reported a feeling of cold) and a cooling pad (in two sessions 1-week apart) on passive knee joint position sense and concluded that both methods negatively affected position sense; despite these results, the efficacy of superficial applications of cryotherapy such as cold spray to decrease deep tissue sufficiently to elicit a reduction in proprioception is questionable (Costello & Donnelly, 2010). Moreover, the felling of cold could vary from individual to individual, and thus temperature decrease could not be uniform in all the subjects. Interestingly, Uchio et al. (2003) found a statistically significant decrease (1.7°) in knee joint position sense after 15 minutes of cooling, but reported position sense normalization at 15 minutes postcooling.

The authors reporting changes in proprioception after cryotherapy almost unanimously suggested the reduction of nerve conduction velocity, as the rationale for the observed decrease in proprioception. Indeed, a study reported an average reduction of 33 % and 17 % in nerve conduction velocity when the skin temperature was reduced to 10° C and 15 ° C, respectively, which relates to a 0.4 m/s decrease in nerve conduction velocity for each 1° C fall in skin temperature (Algafly & George, 2007).

In summary, the number of studies showing an increase in joint position sense error after cryotherapy is similar to the number of studies reporting no changes. Due to the limited number of investigations and the inconsistency of its results, which likely resulted from the methodological differences, the influence of cryotherapy on proprioception is still to be clearly ascertained. Since cryotherapy is a common therapeutic modality used in several settings, its impact on proprioception needs to be clearly determined in order to ensure its safety use before exercise without increasing the risk of injury due to inadequate proprioception and consequently impaired motor control.

3.3 Acute bouts of exercise

In this section we aim to discuss results of studies assessing the acute effects of pre-participation warm-up exercises and strenuous exercise inducing muscle fatigue on proprioception. The hypothesis underlying these studies is based on the proposition that if muscular mechanoreceptors were the most important afferent information contributors for proprioception, it would be expected that changes in the functional state of the muscle would have repercussions on proprioception acuity.

3.3.1 Pre-participation warm-up exercise

Warm-up exercise is acknowledged to have beneficial effects on athletic performance by reducing muscle stiffness, ameliorating the viscous elastic functioning of structures surrounding the joints, increasing neural conduction and velocity, and metabolic efficiency

(Bishop, 2003; Fradkin, Zazryn, & Smoliga, 2010). The general purposes of warm-up exercise are to increase muscle and tendon suppleness, muscle temperature, and blood flow to the periphery, and to enhance movement coordination (Fradkin, et al., 2010).

Since proprioception plays a vital role in the conscious and unconscious sensations, automatic control of movement, and motor coordination, improving proprioception in the course of warm-up might reduce the risk of injury and improve movement accuracy (Thacker, et al., 2003). Notwithstanding, few studies (Bartlett & Warren, 2002; Bouet & Gahery, 2000; Magalhaes, et al., 2010; Subasi, Gelecek, & Aksakoglu, 2008) investigated the impact of warm-up exercises on proprioception (Table 3). Indeed, the theoretical relation between warm-up, proprioception and reduced risk of sport injuries seems to be clearly established, however few studies determined the effect of pre-participation warm-up exercise on proprioception in athletes (Bartlett & Warren, 2002; Magalhaes, et al., 2010).

Regardless of using different warm-up protocols and assessment procedures to measure proprioception, the overall conclusions of all of the above-mentioned studies indicate an augment on joint proprioception after warm-up. Bouet and Gahéry, in 2000, tested the hypothesis that the accuracy of knee position sense would be better as the muscles worked under better conditions. The investigation involved 32 healthy subjects and comprised the assessment of knee position sense in two tasks (intramodal: using the contralateral leg, and crossmodal: using a scheme of a leg on a screen) with two ways of positioning (active and passive) before and after a moderate exercise consisting of pedaling during 10 minutes on a cycle ergometer. The results showed an improvement in position sense after warm-up only with the intramodal protocol combined with active positioning of the reference leg.

Bartlett and Warren (2002) evaluated the effects of a standardized four-minute duration warm up, consisting of jogging and stretching exercises, on passive knee position sense in 12 rugby players. The authors concluded that after a period of stretching and gentle exercise knee proprioception is improved, indicating an increase in sensitivity of proprioceptive mechanisms associated with the ligaments around the knee. More recently, Subasi et al. (2008) designed a study to determine the effects of different warming up periods on passive knee joint position sense of 30 healthy subjects. The 30 subjects were randomly distributed into a control (n = 10) and two exercise (each with n = 10) groups, which performed warm-up exercises of different lengths (5 and 10 minutes). Interestingly, the authors found that the 10-minute warm-up exercise period induced greater improvement in proprioception than the 5-minute warm-up period.

From the above-mentioned studies, only one (Magalhaes, et al., 2010) assessed proprioception, namely knee joint position sense, in closed kinetic chain, a procedure more close to the demands of sport and/or the exercises used in programs of proprioceptive training. The authors assessed knee joint position sense before and immediately after a warm-up program through active repositioning in open kinetic chain and closed kinetic chain in ten young amateur karatekas. Results showed that the warm-up program enhanced knee joint position sense only in closed kinetic chain.

The improvement of proprioception induced by pre-participation warm-up exercise involves exercise-related changes in both central and peripheral components of proprioception. At peripheral level, warm-up exercises may have positive impact on the function of muscular mechanoreceptors by improving the visco-elastic properties of muscular tissue, enhancing oxygenation, increasing nerve-conduction rate, and increasing body temperature due to vasodilatation (Bishop, 2003).

Author	Warm-up exercises	Warm-up duration
Bouet & Gahery, 2000	One-leg pedaling on a cycle ergometer without any imposed cadence and intensity	10 min
Bartlett & Warren, 2002	Jogging Stretching exercises (muscle group not specified)	4 min
Subasi, et al., 2008	Jogging (Protocol 1 – 2:30 min; Protocol 2 – 5 min) Stretching exercises Quadriceps muscle Hamstring muscle Gastrocnemius muscle	Protocol 1 – 5 min Protocol 2 – 10 min
Magalhaes, et al., 2010	Jogging and jumps Jogging end to end Backward running Forward running Jumping crossing the legs Skipping exercise Stretching exercises Quadriceps muscle Hamstring muscle Gastrocnemius muscle	10 min

Table 3. Summary of the warm-up procedures

At the level of Central Nervous System, warm-up exercises may also contribute to better proprioception by changing corollary discharges, likely involved in position sense (McCloskey & Torda, 1975), and/or fusimotor commands and, therefore, muscle spindle sensitivity (Bouet & Gahery, 2000).
Collectively, the available evidence supports that proprioceptive acuity is increased by pre-participation warm-up exercises.

3.3.2 Exercise-induced muscle fatigue

Per opposition to pre-participation warm-up exercises, high intensity exercise inducing muscle fatigue is associated with reduction of muscle force, joint range of motion and joint stability, and with clumsiness in movements demanding high levels of accuracy (Brockett, Warren, Gregory, Morgan, & Proske, 1997; Howell, Chleboun, & Conatser, 1993; Paschalis, et al., 2007; Proske, et al., 2003; Saxton, et al., 1995).
Fatigue is defined as an exercise-induced reduction in the ability of a muscle to generate force or power due to peripheral and/or central factors, related with an increase in perceived exertion, which can be defined as the intensity of subjective effort, strain, discomfort or fatigue sensation that one feels during exercise (Gandevia, 2001). The effects of exercise-induced muscle fatigue on joint proprioception have been extensively investigated in the last decades (Allen & Proske, 2006; Brockett, et al., 1997; Carpenter, et al., 1998; Forestier & Bonnetblanc, 2006; Forestier, Teasdale, & Nougier, 2002; Givoni, Pham, Allen, & Proske, 2007; Ju, Wang, & Cheng, 2010; Lattanzio, Petrella, Sproule, & Fowler, 1997;

Lee, Liau, Cheng, Tan, & Shih, 2003; Miura, et al., 2004; Myers, Guskiewicz, Schneider, & Prentice, 1999; Paschalis, et al., 2008; Paschalis, et al., 2007; Ribeiro, et al., 2007; Ribeiro, Santos, Gonçalves, & Oliveira, 2008; Ribeiro, Venâncio, Quintas, & Oliveira, 2011; Saxton, et al., 1995; Skinner, et al., 1986; Torres, et al., 2010; Tripp, et al., 2004; Vila-Cha, et al., 2011; Walsh, Hesse, Morgan, & Proske, 2004) (Table 4).

The majority of studies investigating the effects of exercise-induced fatigue on proprioception have been conducted in the knee joint. Sense of position, using active ipsilateral matching responses, has been the sub modality of proprioception mainly assessed.

The great majority of these studies induced muscle fatigue with laboratory protocols, often performed in an isokinetic dynamometer and involving isolated joint movements and muscle groups. The use of the information arising from laboratory studies is frequently difficult. Particularly in athletes, the use of exercise protocols that mimic the demands of sporting activity could have the advantage of reproducing more specifically the changes in neuromuscular control and proprioception observed in sport settings. Few studies have been conducted so far assessing changes in proprioception induced by sporting activity (Ribeiro, et al., 2008) or laboratory protocols replicating sporting activities (Tripp, et al., 2004). This issue is particularly relevant for athletes, as reduced proprioceptive acuity is an acknowledged risk factor for sport injuries (Barrack, Skinner, & Buckley, 1989). Additionally, it has been suggested that the higher number of injuries sustained during the last third of practice sessions or matches could be correlated with fatigue-induced alterations in lower limb neuromuscular control and joint dynamic stability due to changes in joint proprioception (Hiemstra, et al., 2001).

In general, the several studies performed in this field (Table 4), enrolling different populations (young and old-age subjects, male and female) and using distinct methodology in different joints, have demonstrated proprioceptive deficits, namely on joint position sense, as a consequence of exercise-induced muscle fatigue. The repercussions of muscle fatigue on elderly proprioception deserve singular interest, as altered proprioceptive input due to fatigue could result in deficits in neuromuscular and postural control, leading to increased risk of falls and consequently increasing the risk of osteoporotic fractures.

It has been theorized that muscle fatigue may impair the proprioceptive acuity by increasing the threshold of muscle spindle discharge and disrupting afferent feedback. Indeed, a plausible mechanism to explain the decrease in proprioception observed after fatiguing exercise could be the augmented intramuscular concentrations of several metabolites and inflammatory substances, which in turn have a direct impact on the discharge pattern of muscle spindles and alpha–gamma coactivation (Pedersen, Lonn, Hellstrom, Djupsjobacka, & Johansson, 1999; Pedersen, Sjolander, Wenngren, & Johansson, 1997). The direct impact of fatigue on the discharge patterns of muscle spindles was observed in an animal study (Pedersen, et al., 1997). In brief, in the fatigued muscle the nociceptors are activated by the end metabolic products (including bracykinin, arachidonic acid, prostaglandin E2, potassium, and lactic acid), which were produced during the previous muscular contractions. These metabolites and/or inflammatory substances within the muscle during fatiguing exercise modify the proprioceptive input by increasing the threshold for muscle spindle discharge (Djupsjobacka, Johansson, & Bergenheim, 1994; Djupsjobacka, Johansson, Bergenheim, & Wenngren, 1995; Pedersen, et al., 1997). On the other hand, changes in alpha/gamma co-activation or in alpha motoneuron activation induced by fatigue would alter muscle spindle excitability through stretch (Marks & Quinney, 1993). The decrease in proprioceptive acuity after fatiguing exercise may also be explained, at least partially, by changes in the central processing of proprioceptive signals, in result of Central Nervous System fatigue processes. It was reported that central fatigue may reduce the accuracy of motor control and interrupt voluntary muscle-stabilizing activity to resist imparted joint forces (Miura, et al., 2004).

Author	Joint	Sample	Exercise protocol	Proprioception assessment	Results
Saxton, et al., 1995	Elbow	12 subjects (6 female)	50 eccentric contractions of the forearm flexors	Sense of tension and active JPS (contralateral and ipsilateral matching)	Both parameters decreased when using contralateral matching
Brockett, et al., 1997	Elbow	13 subjects (7 female)	120 contractions at 20% of MVC	Sense of tension and active JPS (contralateral matching)	Decrease in sense of tension and JPS
Walsh, et al., 2004	Elbow	18 subjects (4 female)	2 protocols: 200-250 E or C contractions at 30% of MVC	Active JPS (contralateral matching)	Both protocols decreased JPS
Allen & Proske, 2006	Elbow	15 subjects (7 female)	Lifting a weight of 30% of MVC with elbow flexors until exhaustion	Active JPS (contralateral matching)	Decrease in JPS
Carpenter, et al., 1998	Shoulder	20 subjects (9 female)	C/C contractions of shoulder rotators until a PT drop of 50%	TTDPM of humeral rotation	Decrease of 73% in sense of movement
Lee, et al., 2003	Shoulder	11 male subjects	C/C contractions of external and internal rotators until a peak torque drop of 50%	Active and Passive JPS	Decrease in active but not in passive JPS
Skinner, et al., 1986	Knee	11 male subjects	3.75-mile run and exercise	Passive JPS and TTDPM	Decrease in JPS; no changes in TTDPM
Lattanzio, et al., 1997	Knee	16 subjects (8 female)	3 cycling protocols to maximal exhaustion	Active JPS	Decrease in JPS
Miura, et al., 2004	Knee	27 male subjects	2 protocols: local load and general load	Active JPS	Only general load decreased JPS
Ribeiro, et al., 2007	Knee	16 old-age male subjects	30 C/C contractions of the knee muscles	Active JPS	Decrease in JPS
Ribeiro, et al., 2008	Knee	17 young male athletes	Volleyball match (90 min duration)	Active JPS	Decrease in JPS

Author	Joint	Sample	Exercise protocol	Proprioception assessment	Results
Ribeiro, et al., 2011	Knee	40 male subjects	2 protocols: 30 C/E contractions of the knee extensors or flexors	Active JPS	Decrease in JPS on both protocols
Torres, et al., 2010	Knee	14 male subjects	E knee flexors contractions at 60% of PT until exhaustion	Active JPS, sense of tension, and TTDPM	Decreased acuity in all parameters
Forestier, et al., 2002	Ankle	8 male subjects	Isometric contractions of ankle flexor at 70% of MVC	Active JPS (contralateral matching)	Decrease in JPS
Forestier & Bonnetblanc, 2006	Ankle	10 male subjects	Isometric contractions of ankle flexor at 70% of MVC	Active JPS (contralateral and ipsilateral matching)	Decreased JPS only when using contralateral matching

Table 4. Experimental evidence of the effects of exercise-induced muscle fatigue on joint proprioception. C - concentric; E - eccentric; JPS - joint position sense; MVC - maximum voluntary contraction; PT - peak torque; TTDPM - threshold to detection of passive motion.

Some authors, whose exercise protocols included eccentric contractions, have given as a reason for the proprioceptive deficits the exercise-induced muscle damage. In spite of this, it is pretty unlikely that the damage of muscle mechanoreceptors was the underlying cause of the changes observed, as studies using animal models revealed that, per opposition to extrafusal fibers, a series of eccentric contractions do not have any effect on intrafusal fibers of muscle spindles (Gregory, Morgan, & Proske, 2004) or on tendon organs (Gregory, Brockett, Morgan, Whitehead, & Proske, 2002).

4. Effects of regular physical activity and exercise on proprioception

It is widely acknowledged that regular physical activity and exercise generate an impressive collection of favorable effects in many physiologic systems. However, a pertinent question to be formulated is to whether physical activity performed on a regular basis is able to attenuate the age-related decline in proprioception?

The answer to this question is of crucial importance, since the only strategy that seems to retain/regain joint proprioception in old age subjects is regular physical exercise. The decline in proprioception in older adults, especially in lower limbs, is of great concern for several reasons: first, older adults rely more on proprioception than on vision (Colledge, et al., 1994); second, decreased proprioception has been related with disturbances in balance, which consequently increase the susceptibility to injurious falls (Lord, et al., 1999; Sorock & Labiner, 1992); and, third, decreased proprioception could lead to abnormal joint biomechanics during functional activities, which in turn could lead to, over a period of time, degenerative joint disease (Skinner, 1993).

Despite not consensual, the majority of studies pointed out the beneficial effect of regular physical activity and exercise on lower limb proprioception of older adults (Li, et al., 2008;

Petrella, et al., 1997; Pickard, et al., 2003; Ribeiro & Oliveira, 2010; Schmitt, Kuni, & Sabo, 2005; Tsang & Hui-Chan, 2003; Xu, Hong, Li, & Chan, 2004). Petrella et al. (1997) evaluated the influence of regular physical activity on proprioception by measuring knee joint proprioception among young volunteers and active and sedentary elderly volunteers. The authors reported significant differences between young (mean, 2.01 ± 0.46°) and active-old (mean, 3.12 ± 1.12°; $P < 0.001$), young and sedentary-old (mean, 4.58 ± 1.93°; $P < 0.001$), and active-old and sedentary-old ($P < 0.03$). Identical results were reported by Pickard et al. (2003), who found no differences when comparing hip joint position sense between sedentary-young and active-aged subjects (75 ± 6 years old). Some studies have also demonstrated a positive impact of Tai Chi, a Chinese mind-body exercise that puts a great emphasis on the exact joint position and direction, on proprioception, namely knee position sense (Tsang & Hui-Chan, 2003) and knee and ankle sense of movement (Li, et al., 2008; Xu, et al., 2004). More recently, Ribeiro and Oliveira (2010) tested the hypotheses that knee position sense declines with age and that regular exercise can attenuate that decline. The authors conducted a cross-sectional study encompassing 69 older and 60 young adults divided in four groups (exercised-old, N = 31; non-exercised-old, N = 38; exercised-young, N = 35; non-exercised-young, N = 25) according to chronological age and exercise practice in the past year and reported that compared to their non-exercised counterparts, exercised-old subjects exhibited better sense of position. Moreover, the proprioceptive acuity of exercised-old subjects was similar to non-exercised young subjects (Figure 3).

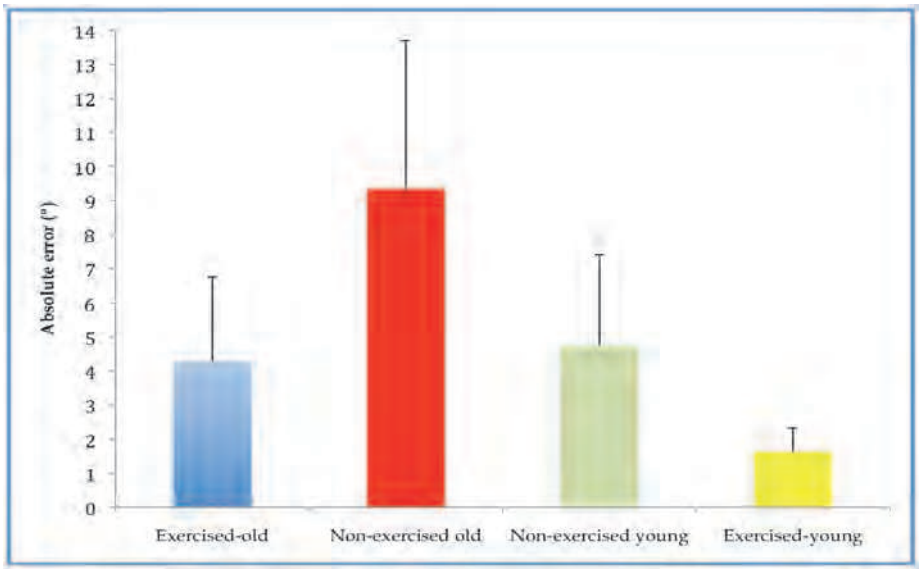

Fig. 3. Positive effects of regular physical exercise on knee joint position sense (adapted from Ribeiro & Oliveira, 2010)

Several mechanisms could be pointed towards to explain the positive impact of regular physical activity and exercise on joint proprioception. It is not surprising that being central and peripheral components of proprioception implicated in the age-related decline on proprioceptive function, they are also both potentially related to its improvement.

Physical exercise does not change the number of mechanoreceptors (Ashton-Miller, Wojtys, Huston, & Fry-Welch, 2001), but induces morphological adaptations in the muscle spindle (Hutton & Atwater, 1992). There are muscle spindle adaptations on a microlevel, the intrafusal muscle fibers could show some metabolic changes, and on a more macrolevel, the latency of the stretch reflex response decrease and the amplitude increase (Hutton & Atwater, 1992).

At central level, regular physical activity and exercise is able to change proprioception through the modulation of the muscle spindle gain and the induction of plastic modifications in the Central Nervous System. During physical activities an increase in the muscle spindle output through the ϒ route is observed, which facilitates the cortical projection of proprioception. Thus, by increasing the output of the muscle spindle over time, it is possible to induce plastic changes in the Central Nervous System, such as increased strength of synaptic connections and/or structural changes in the organization and numbers of connections among neurons (Ashton-Miller, et al., 2001). These plastic changes in the cortex would modify the cortical maps of the body over time, increasing the cortical representation of the joints and leading to enhanced joint proprioception (Ashton-Miller, et al., 2001).

5. Summary

In summary, this chapter highlighted the evidence that aging, cryotherapy, and exercise-induced fatigue have deleterious effects on joint proprioception, while moderate exercise or warm-up exercise enhances proprioceptive acuity. Additionally, it seems that regular physical activity and exercise play an undeniable role in the preservation of proprioceptive function.

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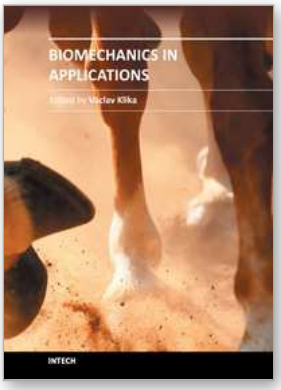

Biomechanics in Applications

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During last couple of years there has been an increasing recognition that problems arising in biology or related to medicine really need a multidisciplinary approach. For this reason some special branches of both applied theoretical physics and mathematics have recently emerged such as biomechanics, mechanobiology, mathematical biology, biothermodynamics. The Biomechanics in Application is focusing on experimental praxis and clinical findings. The first section is devoted to Injury and clinical biomechanics including overview of the biomechanics of musculoskeletal injury, distraction osteogenesis in mandible, or consequences of drilling. The next section is on Spine biomechanics with biomechanical models for upper limb after spinal cord injury and an animal model looking at changes occurring as a consequence of spinal cord injury. Section Musculoskeletal Biomechanics includes the chapter which is devoted to dynamical stability of lumbo-pelvi-femoral complex which involves analysis of relationship among appropriate anatomical structures in this region. The fourth section is on Human and Animal Biomechanics with contributions from foot biomechanics and chewing rhythms in mammals, or adaptations of bats. The last section, Sport Biomechanics, is discussing various measurement techniques for assessment and analysis of movement and two applications in swimming.

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InTech Europe
University Campus STeP Ri
Slavka Krautzeka 83/A
51000 Rijeka, Croatia
Phone: +385 (51) 770 447
Fax: +385 (51) 686 166
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中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

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