Doctoral (PhD) Dissertation

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PSYCHOLOGICAL ASPECTS OF PROPRIOCEPTIVE ACCURACY

2022

EÖTVÖS LORÁND UNIVERSITY
FACULTY OF EDUCATION AND PSYCHOLOGY

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PSYCHOLOGICAL ASPECTS OF PROPRIOCEPTIVE ACCURACY

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Budapest, 2022

EÖTVÖS LORÁND TUDOMÁNYEGYETEM

ADATLAP a doktori értekezés nyilvánosságra hozatalához

I. A doktori értekezés adatai

A szerző neve: Horváth Áron

A doktori értekezés címe és alcíme: Psychological aspects of proprioceptive accuracy

A doktori iskola neve: Pszichológiai Doktori Iskola

A doktori iskolán belüli doktori program neve: Sport- és egészség-pszichofiziológia program

A témavezető neve és tudományos fokozata: Dr. Köteles Ferenc, DSc, egyetemi tanár

A témavezető munkahelye: ELTE PPK, Egészségfejlesztési és Sporttudományi Intézet

MTA Adatbázis-azonosító: 10064799

DOI-azonosító[1]:10.15476/ELTE.2022.119

II. Nyilatkozatok

1. A doktori értekezés szerzőjeként[2]

a) hozzájárulok, hogy a doktori fokozat megszerzését követően a doktori értekezésem és a tézisek nyilvánosságra kerüljenek az ELTE Digitális Intézményi Tudástárban. Felhatalmazom a Tanulmányi Hivatal ügyintézőjét Dávid Gergő-t, hogy az értekezést és a téziseket feltöltse az ELTE Digitális Intézményi Tudástárba, és ennek során kitöltse a feltöltéshez szükséges nyilatkozatokat.

b) kérem, hogy a mellékelt kérelemben részletezett szabadalmi, illetőleg oltalmi bejelentés közzétételéig a doktori értekezést ne bocsássák nyilvánosságra az Egyetemi Könyvtárban és az ELTE Digitális Intézményi Tudástárban;[3]

c) kérem, hogy a nemzetbiztonsági okból minősített adatot tartalmazó doktori értekezést a minősítés (……………….*dátum*)-ig tartó időtartama alatt ne bocsássák nyilvánosságra az Egyetemi Könyvtárban és az ELTE Digitális Intézményi Tudástárban;[4]

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[1] A kari hivatal ügyintézője tölti ki.

[2] A megfelelő szöveg aláhúzandó.

[3] A doktori értekezés benyújtásával egyidejűleg be kell adni a tudományági doktori tanácshoz a szabadalmi, illetőleg oltalmi bejelentést tanúsító okiratot és a nyilvánosságra hozatal elhalasztása iránti kérelmet.

[4] A doktori értekezés benyújtásával egyidejűleg be kell nyújtani a minősített adatra vonatkozó közokiratot.

d) kérem, hogy a mű kiadására vonatkozó mellékelt kiadó szerződésre tekintettel a doktori értekezést a könyv megjelenéséig ne bocsássák nyilvánosságra az Egyetemi Könyvtárban, és az ELTE Digitális Intézményi Tudástárban csak a könyv bibliográfiai adatait tegyék közzé. Ha a könyv a fokozatszerzést követőn egy évig nem jelenik meg, hozzájárulok, hogy a doktori értekezésem és a tézisek nyilvánosságra kerüljenek az Egyetemi Könyvtárban és az ELTE Digitális Intézményi Tudástárban.[5]

2. A doktori értekezés szerzőjeként kijelentem, hogy
a) a ELTE Digitális Intézményi Tudástárba feltöltendő doktori értekezés és a tézisek saját eredeti, önálló szellemi munkám és legjobb tudomásom szerint nem sértem vele senki szerzői jogait;
b) a doktori értekezés és a tézisek nyomtatott változatai és az elektronikus adathordozón benyújtott tartalmak (szöveg és ábrák) mindenben megegyeznek.

3. A doktori értekezés szerzőjeként hozzájárulok a doktori értekezés és a tézisek szövegének plágiumkereső adatbázisba helyezéséhez és plágiumellenőrző vizsgálatok lefuttatásához.

Kelt: Budapest, 2021.06.02

a doktori értekezés szerzőjének aláírása

[5] A doktori értekezés benyújtásával egyidejűleg be kell nyújtani a mű kiadásáról szóló kiadói szerződést.

Table of content

List of publications that the dissertation is based upon[6]

Horváth, Á. (2019). Propriocepció. In F. Köteles & E. Ferentzi (Eds.), *Tanulmányok az interocepcióról. Bárdos György professzor tiszteletére* (pp. 103–131). ELTE Eötvös Kiadó.

Horváth, Á., Ferentzi, E., & Köteles, F. (2019). Proprioceptive accuracy is not associated with self-reported body awareness, body competence, and affect. *Physiology International, 106*(4), 347–354. https://doi.org/10.1556/2060.106.2019.33

Horváth, Á., Ferentzi, E., Bogdány, T., Szolcsányi, T., Witthöft, M., & Köteles, F. (2020). Proprioception but not cardiac interoception is related to the rubber hand illusion. *Cortex, 132*, 361–373. https://doi.org/10.1016/j.cortex.2020.08.026

Horváth, Á., Ferentzi, E., Schwartz, K., Jacobs, N., Meyns, P., & Köteles, F. (2022). The measurement of proprioceptive accuracy: A systematic literature review. *Journal of Sport and Health Science*. https://doi.org/10.1016/j.jshs.2022.04.001

Horváth, Á., Vig, L., Ferentzi, E., & Köteles, F. (2021). Cardiac and Proprioceptive Accuracy Are Not Related to Body Awareness, Perceived Body Competence, and Affect. *Frontiers in Psychology, 11*. https://doi.org/10.3389/fpsyg.2020.575574

[6] Each co-author has granted permission for the given publication to be included in the current dissertation.

Other studies

Ferentzi, E., Bogdány, T., Szabolcs, Z., Csala, B., Horváth, Á., & Köteles, F. (2018). Multichannel investigation of interoception: Sensitivity is not a generalizable feature. *Frontiers in Human Neuroscience*, *12*, 223. https://doi.org/10.3389/fnhum.2018.00223

Ferentzi, E., Horváth, Á., & Köteles, F. (2019). Do body-related sensations make feel us better? Subjective well-being is associated only with the subjective aspect of interoception. *Psychophysiology*, *56*(4), e13319. https://doi.org/10.1111/psyp.13319

Horváth, Á., Ferentzi, E., & Köteles, F. (2019). A sportolás és a proprioceptív pontosság összefüggései. *Magyar Sporttudományi Szemle*, *2019*(3), 8–13.

Horváth, Á., Ferentzi, E., Ragó, A., & Köteles, F. (2022). The retention of proprioceptive information is suppressed by competing verbal and spatial task. *Quarterly Journal of Experimental Psychology*, 17470218221096251.

Horváth, Á., Köteles, F., & Szabo, A. (2021). Nocebo effects on motor performance: A systematic literature review. *Scandinavian Journal of Psychology*, *62*(5), 665–674. https://doi.org/10.1111/sjop.12753

Horváth, Á., Ragó, A., Ferentzi, E., Körmendi, J., & Köteles, F. (2020). Short-term retention of proprioceptive information. *Quarterly Journal of Experimental Psychology*, *73*(12), 2148–2157. https://doi.org/10.1177/1747021820957147

Acknowledgement

I would like to thank to my supervisors, Ferenc Köteles and Eszter Feretzi. I could not wish for a more supportive and motivating environment then they have created. To develop ideas and make scientific work with them was not only essential for professional development but was always a joy. I am grateful for their guidance and trust in every aspect of the work.

I am also thankful to all my colleagues I have worked with. Especially to the former and present members of the Ádám György Psychophysiology Research Group: Ádám Koncz, Barbara Csala, Benedek Tihanyi, Csilla Suhaly, György Bárdos, János Körmendi, Luca Víg, Orsolya Drozdovszky, Renáta Szemerszky, Tamás Bogdány, Zsuzsanna Dömötör, Zsuzsanna Szabolcs and Vera Gál. I am grateful for their help in the preparation and conduction of the studies. Their ideas and constructive criticism essentially contributed to the articles. I would like to thank to all my co-authors, who did irreplaceable job in the preparation of the manuscripts: Anett Ragó, Kristóf Schwartz, Michael Witthöft, Nina Jacobs, Pieter Meyns and Tibor Szolcsányi. I would like to thank to Henriett Ipacs and Orsolya Moravecz for their help in the conduction of the studies. I am also thankful to participants of the studies.

I could not have done this work without the support of my family. My mother and father always helped me and taught that with hard work I can achieve my goals. I would like to thank to my partner, Zita, for her patient, support, and love.

Aim of the dissertation

The goal of this dissertation is to shed more light on the association between proprioceptive accuracy and different aspects of healthy psychological functioning (such as affectivity, perceived physical competence, body awareness, feeling of body ownership), and to address methodological issues in proprioceptive accuracy measurement. This dissertation is based on four published studies, I will shortly introduce these after discussing the theoretical background. That will be followed by a general discussion of the findings.

General introduction[7]

Proprioception

Definition

To be able to effectively control our movements, we need information about the spatial position of our body, and the position of our limbs relative to each other. For this, we can rely on information from different sources: we can use information coming from outside the body (e.g. vision), but we can rely on information coming from within the body too. Even if we close our eyes, we are aware of the position of our limbs, we can touch the tip of our nose, and we do not have to watch our feet when walking. These skills require intact proprioception. The term came off from the Latin “proprius” (one’s own) and “perception” (perception) terms, and was introduced by Sherrington (1906), who defined it as the perception of our movements, based the information originating from within the body. The exact meaning of the concept has changed over the last more than 100 years, and to date, no uniform definition exists. Definitions are still inconsistent as to whether proprioception refers to the source of stimulus (the body/locomotor system itself, (e.g. Stillman, 2002), or whether the subject of the perception has to be the locomotor system too (e.g. Han et al., 2016). This often poses problems in interpreting research findings. Tasks requiring discrimination of the weight of different objects, or the degree of muscle tension illustrate well the inconsistency, as they are used as an indicator of proprioceptive accuracy in a number of studies (Chang & Lenzenweger, 2005; Sarnoch et al., 1997). However, several authors does not discuss these paradigms in their review of measurement methods, as their approach defines proprioception as the judging of the position and movement of different body parts (Han et al., 2016; Hillier et al., 2015). Balancing ability is also often associated with proprioception, but the role of visual and vestibular information can contribute to this ability to a high degree (Han, Anson, et al., 2015). While the deprivation of visual

[7] The General introduction is based on and contains translated parts of the following work: Horváth, Á. (2019). Propriocepció. In F. Köteles & E. Ferentzi (Eds.), *Tanulmányok az interocepcióról. Bárdos György professzor tiszteletére* (pp. 103–131). ELTE Eötvös Kiadó.

information is simple (by covering the eyes), deprivation of vestibular information is almost impossible.

Also, the terms of proprioception and kinesthesia show considerable overlap, as kinesthesia was originally defined as the perception of body movement by Bastian (1887), and the perception of movement and the position of the body is practically inseparable in both laboratory and natural conditions. For this reason, it can be argued that the two terms are synonymous (Han et al., 2016; Stillman, 2002). In some cases, however, proprioception is defined as the perception of the static position of the body, and kinesthesia as the perception of the movement of the body (Grob et al., 2002; Proske & Gandevia, 2012). In other cases, the perception of body position is termed "stasis", while the perception of the movement of the body is termed "kinesthesia", both of that considered as a subcategory of proprioception (Boisgontier et al., 2012).

In addition, there is disagreement as to whether proprioception is necessary a conscious process or not. Gallagher (2005) makes a distinction between proprioceptive information (not necessary conscious input), and proprioceptive awareness (conscious perception). It is also important to consider that both automatic and conscious aspect of proprioception and movement control relies not only on afferent information originating from the receptors of the body, but on efferent information, originating from the central nervous system (e.g. efferent copy of the motor command and sense of effort) too (Smith et al., 2009).

Here we define proprioception as the (conscious) perception of the information originating from the locomotor system and the skin, that may be modified by related efferent signals.

Role of afferent information

The receptors involved in proprioception are called proprioceptors. These are muscle spindles, that inform the central nervous system about the length and rate of muscle stretch, Golgi tendon organs, that process information about tension, and mechanoreceptors located in the joint capsules, ligaments and skin (Proske & Gandevia, 2012; Tuthill & Azim, 2018). This information got passed to the brain by the dorsal columns of the spinal cord and reaches the somatosensory regions of the cortex (Köteles, 2021).

As information originating from different sources are consistent with each other in natural conditions, it requires sophisticated methods to investigate the role of them separately. To illustrate this, we can think of flexing the elbow joint. The biceps muscle contracts, and the tendon connecting the muscle fibers to the forearm bone tighten, while the triceps muscle relaxes. In the joint capsule, the bone end is displaced, the skin on the back surface of the joint is stretched, while the skin on the inner surface is contracted. One method, selectively altering information from a given source, is muscle vibration. The eyes of the subject are covered, and the muscle and its associated joint are subjected to painless vibration of approximately 100Hz. Consequently, subjects will perceive a movement of their arm. The direction of movement corresponds to the displacement caused by the stretching of the muscle subjected to the vibration, meaning that when the triceps muscle is vibrated, arm flexion is perceived (Goodwin et al., 1972; Jones, 1988). By stretching the skin surface, it is also possible to induce the sensation of the arm moving in a consistent direction. If two pieces of information (i.e. muscle vibration and skin stretching) are consistent, the perceived displacement will be even greater. By combining the two methods, there can be a 40 degree difference between the perceived and the real flexion of the arm (Collins et al., 2005). In contrast, healthy individuals without visual information and manipulation can judge the position of their elbow joint with an order of magnitude average error of about 3-6 degrees (Goble, 2010).

In experimental situation, when proprioception is investigated, visual information is often deprived. However, in natural conditions, visual and proprioceptive information often get integrated. For example, if a light spot is attached to the finger of the participants in a dark room, and biceps muscle of the arm is subjected to vibration, the participants will see the light spot move in the direction corresponding to the perceived movement of the arm (Levine & Lackner, 1979). Visual information can be manipulated for example by placing a prism in front of the subjects' eyes, which alters the field of view, so visual and proprioceptive information become contradictory. When asked to judge the perceived position of their hands, participants typically consider both visual and proprioceptive information. However, visual information have typically a more dominant role (van Beers et al., 1999, 2002).

Role of efferent information

It is important to consider, that proprioception is not only affected by afferent information (originating from the receptors), but by efferent information (originating from the brain) too. To execute self-generated movements, the brain sends a motor command from the motor cortex via the anterior horn of the spinal cord via a-motoneurons, which contract muscles accordingly and execute the movement sequence. However, as the motor command may not be completely accurate, and the environmental may change, a correction may be necessary. The correction is possible via afferent feedback from the self-generated movement, that is called reafferent feedback. However, the processing of reafferent signal may take a relatively long time. For fast movements or for rapidly changing environmental conditions, a short-cut may be necessary to fasten up the process. A possibility is to use the motor command to predict the consequence of the movement before it occurs. That is called efferent copy of the motor command, or corollary discharge, and is then compared to the reafferent information (Miall & Wolpert, 1996).

Many empirical studies showed that efferent signals indeed play a role in proprioception. Gandevia and colleagues (2006) paralyzed and anaesthetized one arm of the participants. Then they were instructed to try to move their arm to a given direction and then determine the magnitude and the direction of the movement. Participants misperceived their arm moving to the intended direction. However, the ecological validity of this experiment is low, as participants were not provided any efferent information about their limbs (nor proprioceptive, nor visual). The study of Smith et al (2009) showed that even when proprioceptive afferent information is available, efferent information plays an important role. They temporarily paralyzed and covered, but not anaesthetized one arm of the participants. If then the arm was moved passively to a given position, they could judge the position relatively accurately. However, if they were instructed to try to move their arm to a particular direction, they felt that it had moved (which could not happen, as it was paralyzed). In a further experiment, only the vision of the arm was blocked, but no paralysis was used. Participants were asked to move their unseen hand, which was made impossible because of a mechanical block. However, they perceived a movement in the direction of the intention to move (Smith et al., 2009)

The role of efferent signals is also demonstrated by studies showing that perceived effort can modify the processing of proprioceptive information. In the study of Winter and colleagues (2005), a weight was hung on the arm of the participant. Consequently, the arm was perceived more flexed than it really was because the perceived effort and muscle contraction suggested that. Also, in the study of Allen and Proske (2006), the biceps muscle of the arm was fatigued with weight-bearing exercises. To hold the arm against the gravity requires more (flexing) effort. In line with that, the perception of the position of the arm was biased in the direction of the perceived effort.

Role of proprioception

Loss or damage of proprioception

The consequences of losing or damaging proprioception can tell us a lot about its importance in motor control. Some diseases can cause a loss of proprioception, for example sensory neuropathy, which often develops as a consequence of diabetes (Dyck et al., 1980). Brain injury or stroke can also cause the loss of proprioception (Sacks, 1985). In the absence of feedback from the proprioceptors, individuals are less able to control their movements effectively and are more uncoordinated even when visual feedback is available. Proper postural control is also damaged, and almost impossible without visual attention. Significant impairments in fine manipulation occur, which can make it impossible to write, for example. There are also serious impairments in tasks that require adaptation to constantly changing external conditions or judging the weight of different objects (Sainburg et al., 1993). Some disorders are associated with severe impairment, but not a complete loss of proprioception. Patients with Parkinson's disease, show a damaged proprioception, which is associated with postural problems and hypokinesia (Zia et al., 2000). Interestingly, dopamine therapy, that relieves symptoms, further reduces the accuracy of proprioceptive processing (O’Suilleabhain et al., 2001). Worse proprioceptive processing is also observed in dystonia, a disease characterized by involuntary muscle contractions, that interfere with the execution of movements. Improving proprioception may help to relief the symptoms of the disease (Avanzino & Fiorio, 2014; Rosenkranz et al., 2008). Optic ataxia and spatial hemineglect are also characterized by impaired proprioceptive ability (Blangero et al., 2007; Chokron et al., 2002).

Proprioception and the development of the self

The perception of our body is not only important from the perspective of motor control. By comparing the reafferent feedback and the efferent copy of the motor command, it is possible to determine whether a given change (e.g. the movement of a given body part) is self-generated or not (Straka et al., 2018; Wolpert & Flanagan, 2001). If the movement is self-generated, the difference between the predicted and the actual state of the body based on the motor program will be minimal (Blakemore et al., 2000). The separation of movements generated by the self or the environment is crucial for the separation of the environment and the self itself, and so in for the development of self-awareness (Tsakiris, 2010).

Proprioception also takes part in the development and maintenance of body schema. The body schema is a holistic representation of the body, an is mainly proprioceptive in origin, playing a major role in movement control (de Vignemont, 2010; Gallagher, 2005).

Proprioceptive feedback plays an important role in constantly experiencing our body as our own, or in other words, in the feeling of body ownership. This sensation can be experimentally modified. One of the most well-known and most frequently used paradigm is the rubber hand illusion, in which the arm of the person is covered and visually replaced with a rubber hand (Golaszewski et al., 2021; Ramachandran et al., 1995). If the artificial hand and the real hand are then stimulated synchronously (stroked with a brush at the same time on the same place). In doing so, visual, and haptic information suggests that the artificial hand belongs to the person, but proprioceptive information contradicts this, suggesting that the real hand belongs to the person (Ehrsson, 2020). Because of the stimulation, many of the participants have the subjective experience that the prosthetic hand became the part of their body, while their real hand lost, and when asked to position it, they typically show a drift towards the prosthetic hand. It is important to note that there are individual differences between in the extent to which participants experience the illusion (Tsakiris & Haggard, 2005). The third study of this dissertation will investigate the association between proprioceptive accuracy and the rubber hand illusion, also discussing its relevance for psychological functioning.

The role of proprioception in the development of emotions

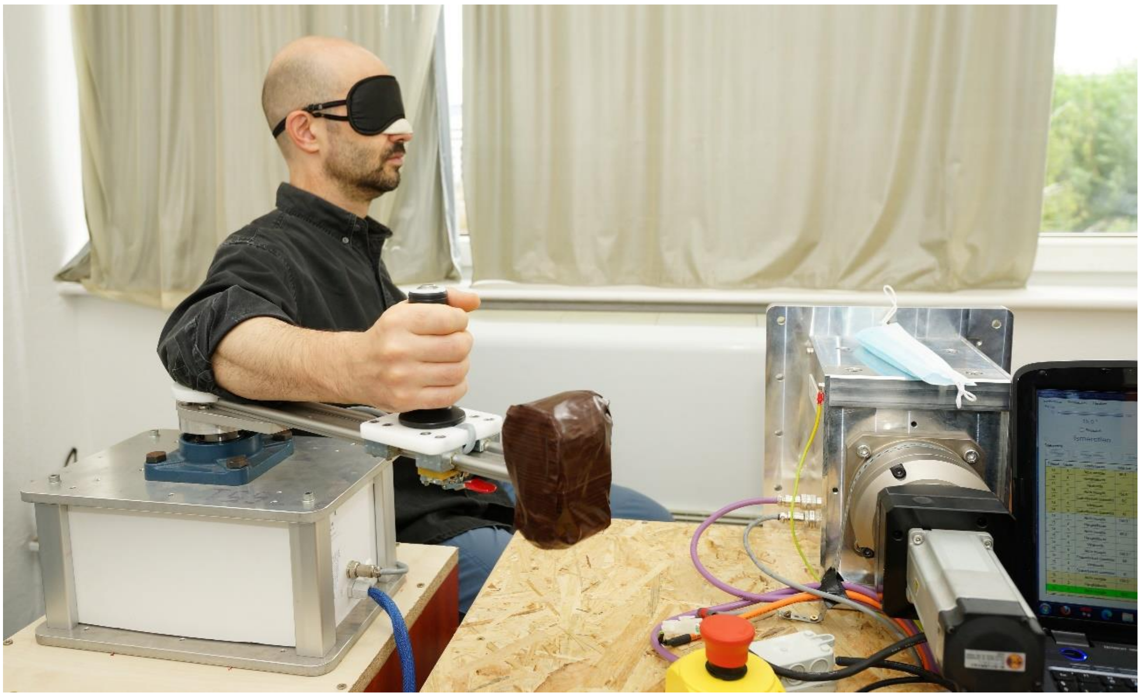
The internal state of the body and its perception is important in the development of emotional experience (Moors, 2009). In the context of proprioception, for example increased muscle tone reflects a state of readiness, which can be associated with unpleasant experiences, especially in the long term, such as experiencing tension or stress (Lundberg et al., 1994, 1999). Through relaxation of the muscles, the negative emotional experience can be reduced. This is the main aim of progressive relaxation (Jacobson, 1938). The goal of the method is to relax the muscles of a particular body parts as much as possible with the eyes closed, paying attention to each body part in turn. The aim of autogenic training (Schultz & Luthe, 1959) is also to create a relaxed state, where one of the first steps is to relax muscles across the body. These relaxation methods can also be used to reduce the anxiety level, and also heart rate and blood pressure (Kanji et al., 2006; Rausch et al., 2006). They can be easily applied without the need for special technical equipment but can also be complemented by biofeedback (Green et al., 1974), which provides the person with accurate and objective feedback about the physiological state of the body. For example, EMG (electromyogram) signals may be used to provide feedback about muscle tension (Sarnoch et al., 1997).

Proprioceptive accuracy

Definition of proprioceptive accuracy

There are individual differences in the ability to perceive proprioceptive information, that is called proprioceptive accuracy (Goble, 2010). It is determined by two main components: the quality of the sensory signal and the efficiency of the central nervous system processes (Ribeiro & Oliveira, 2007). Individual differences are thought to play an important role in the efficiency of movement control (Han, Waddington, et al., 2015). One of the most widely used technique is the Joint Position Reproduction test (Goble, 2010), where a given joint is moved to a target position, and after 3-4 seconds moved away, then the target position must be reproduced as accurately as possible by the participant (Figure 1.). In the ipsilateral version of the test, the same joint should be used, while in the contralateral version, the reproduction happens with the contralateral joint. The fourth study of this dissertation will give a detailed overview about the possible techniques and current state of the literature about proprioceptive accuracy and its measurement.

Figure 1. The custom-made motorized proprioceptor in our laboratory, that was used for most of our studies.



Factors affecting proprioceptive accuracy

Age

Proprioceptive accuracy shows an inversed "U" shaped relationship with age, with the best performers being young adults, while children and elderly people perform worse (Goble, 2010). For elderly people, it is an important question if the quality of afferent signals, or central processing deteriorates, or both factors are involved. The possible role of central processes is demonstrated by Boisgontier and colleagues (2012), who showed that old individuals performed worse than young individuals only when they had to perform a Stroop test while repositioning joint positions (Boisgontier et al., 2012). The authors concluded that elderly people show decreased proprioceptive performance if the proprioceptive task is relatively complex and/or the cognitive load is high, thus central processing play an important role in the deterioration of proprioceptive performance with older age (Boisgontier et al., 2012).

Laterality

There are differences in the proprioceptive performance of the dominant and the subdominant limb. For both left- and right-handed people, the non-dominant hand is characterized by better proprioceptive accuracy (Goble et al., 2009), whereas the dominant hand shows better performance under visual feedback (Goble & Brown, 2008). Goble and Brown (2008) explained that this is because in everyday life, the dominant hand typically manipulates objects with visual feedback, whereas the non-dominant hand performs supporting role with less visual feedback. Further studies (Han, Anson, et al., 2013) have also shown that the advantage in processing proprioceptive information in favor of the non-dominant limb is not only preferent for the upper limb (finger and shoulder) but also for the lower limb joints (ankle, knee). Another research shows that right and left-handed people perform differently when they have to judge the position of both hands at the same time. The performance of left handed people decreases to a greater extent when they have to judge the position of two fingers on both hands at the same time, compared to when they have to judge the position of only one finger (Han, Waddington, et al., 2013). The authors concluded that the difference is due to the greater hemispheric information flow in left-handed people, which resulted in a less efficient ability to separate information conveying the position of the two fingers (Han, Waddington, et al., 2013).

Physical activity and proprioceptive training

People who engage in regular physical activity have better proprioceptive ability (Ribeiro & Oliveira, 2011).The question of cause and effect is not entirely clear in every case. It can be assumed that physical activity increases accuracy (Ribeiro & Oliveira, 2010), but the possibility of selection also arises, especially in elite athletes (Han, Waddington, et al., 2015). There are exercises and trainings that were specifically designed to improve proprioceptive accuracy. Such programs typically involve exercises based on balance and coordination, where precise control of joint position is important (Aman et al., 2015). They have been shown empirically to improve accuracy in the knee joint in elite athletes (Pánics et al., 2008) and have also been shown to maintain the positive effects of development over the long term (Kynsburg et al., 2010). Proprioceptive development has also been shown to be effective in cases of knee osteoarthritis. In their study, Lin and colleagues (2009) divided the participants into three groups: one group received proprioceptive training and one group received strengthening training, while the control group received no intervention. At the end of the experiment, the group that received proprioceptive training showed better accuracy than the other two groups. It is important to note that a transfer effect was demonstrated for both dominant and non-dominant limb development, meaning that training the dominant knee also improved the accuracy of the non-dominant knee (El-Gohary et al., 2016).

Certain conditions and manipulations may also affect proprioceptive accuracy in the short term. After warm-up, individuals are more accurate, whereas muscle fatigue impairs accuracy (Ribeiro & Oliveira, 2011). Some studies report a positive effect of kinesiology taping (Iris et al., 2010), while other studies have failed to find a significant effect (Bradley et al., 2009).

Attention and working memory capacity

Cognitive factors, such as attentional load and working memory capacity can also influence accuracy. Tasks that require mental effort and are performed simultaneously with proprioceptive accuracy can impair performance. A research by Yasuda and colleagues (2014) demonstrated that in young, healthy individuals, performing a difficult subtraction task (subtracting seven from random two-digit numbers) while reproducing ankle joint position impairs proprioceptive accuracy, whereas an easy subtraction task (subtracting three from random two-digit numbers) does not. The study by Han, Waddington and colleagues (2013) is also worth mentioning, where participants were asked to judge the position of either one finger at a time or two fingers on different palms at the same time. The performance deteriorated when people had to divide their attention between two fingers. To study the effect of working memory capacity, Goble and colleagues (2012) divided elderly individuals into two groups, one with low and one with high working memory span. The results showed that the effect of the concurrent task depends on working memory span. The group with relatively low working memory span deteriorated in performance because of the parallel task, while the group with relatively high working memory span did not. An important implication of this research is that a decline in proprioceptive ability in old age may be (at least partly) due to a decline in cognitive ability (Goble et al., 2012).

The relationship between proprioceptive accuracy and mental and physical well-being

Although Ferentzi and colleagues (2019) did not find a direct relationship between proprioceptive accuracy and global well-being, there are several findings suggesting that proprioceptive accuracy may be related to different aspects of physical and mental well-being.

Self-esteem

Perceived physical competence is associated with global self-esteem (Sági et al., 2012; Sonstroem & Morgan, 1989). It would be logical to assume that those with better proprioceptive accuracy can execute their movements more efficiently due to more accurate processing of feedback (Han, Waddington, et al., 2015), and thus have higher physical competence. This would mean, that better proprioceptive ability leads to more positive self-esteem. While we are not aware of any research that provides direct evidence of this, we do have indirect results. The relationship between physical competence and proprioceptive accuracy has been shown empirically: elite athletes with better proprioceptive ability generally achieve better results (Han et al., 2014; Han, Waddington, et al., 2015). In addition, it is also known that regular physical activity is positively associated with both self-esteem and proprioceptive accuracy (Ribeiro & Oliveira, 2010; Sági et al., 2012). Of course, many factors other than proprioceptive ability can contribute to physical competence, and perceived physical competence does not necessarily correspond to actual physical competence, this relationship might be more complex. The first and second study of this dissertation will give more insight about the relationship of proprioceptive accuracy and psychological factors, such as perceived body competence, body consciousness and affect.

Physical injuries

Several studies have established that worst proprioceptive accuracy predicts a higher chance of getting injured. Follow-up studies of athletes have shown that those with worse proprioceptive accuracy are more likely to suffer injuries (Cameron et al., 20r03; Payne et al., 1997). In addition, injuries can further reduce accuracy. For example, individuals who had a torn cruciate ligament in the knee had poorer proprioceptive ability compared to the control group, and the accuracy of their own injured leg was poorer than that of the uninjured (Relph et al., 2014).

Chronic neck and back pain

Chronic neck and back pain do not always occur as a cause of a specific reason (e.g. an accident). In these cases, along with psychosocial causes (such as stress and poor working conditions), the importance of poor posture is also raised (Andersson, 1999; Ariëns et al., 2001), in which proprioception may play a role.

A systematic review and meta-analysis about neck pain due to non-specific causes (Stanton et al., 2016) pooled the results of 13 studies on the topic. The overall conclusion of the study was that when reproducing neck positions, individuals with neck pain showed poorer ability when the task required moving the head. Since vestibular information may also play an important role in such procedures, it is questionable to what extent the difference in performance can be attributed to the role of pure proprioception. In some studies, to overcome this problem, the position of the neck had to be reproduced by moving the trunk. The authors reported on only two such studies, only one of which found a significant difference between the neck pain patients and the control group (Stanton et al., 2016).

A similar review was conducted for back pain due to non-specific causes, including 24 studies (Tong et al., 2015). The results showed that when participants were asked to determine joint positions by active movement, there was a difference between the affected and healthy populations, whereas there was no difference when passive movement was used. This may indicate that the impairment in proprioceptive processing for patients with back pain is specific to signals that are basically related to active motion (i.e., muscle spindle feedback, efferent signals). When measuring the detection threshold of passive movement, there was no difference between the two populations.

There has also been a review conducted on the beneficial effects of proprioceptive training for neck and back pain. However, after reviewing the results of 18 studies, the authors could not draw a clear conclusion on its effectiveness (McCaskey et al., 2014).

Fibromyalgia

Fibromyalgia is a chronic disease in which patients experience pain of unknown origin in various parts of their body. Symptoms often include sleeping complaints, fatigue, and cognitive problems (Wolfe & Häuser, 2011). The causes of the disease are not fully understood, but psychological factors are assumed to play a role in it (Eich, 2000). Others have identified several other possible causes, such as viral infection or altered neurotransmitter and endocrine function (Ablin et al., 2008). In the study of Akyol and colleagues (2013), fibromyalgia patients did not differ from healthy controls in their ability to reproduce knee joint positions. This finding was replicated by Ulus and colleagues (2013). That the relationship may be more complex is illustrated by the study by Bardal and colleagues (2016), who compared the performance of a fibromyalgia group with a healthy control group. In the task, participants were first asked to keep their upper arm (shoulder joint) immobile with visual feedback and then without visual feedback. In addition, they were also tested on shoulder joint position reproduction accuracy (passive adjustment, active reproduction with the same limb). The results showed, on the one hand, that fibromyalgia subjects without visual feedback show higher movement variability (worse performance) when they had to hold their arm motionless without visual feedback than the healthy control group, and on the other hand, proprioceptive accuracy was related to movement variability in the control group, but not in the fibromyalgia group. The results show that fibromyalgia patients are less able and less prone to rely on proprioceptive feedback.

Somatoform disorder

Somatoform disorder manifests itself as physical symptoms but is either due to psychological or unknown causes (Voigt et al., 2010). In a study by Scholz and colleagues (2001), participants were asked to tense their trapezius muscles to a certain level and then to rate the extent of this tension. People with somatoform disorder generally felt the degree of tension more intensely and were also able to judge it more accurately. The relationship with proprioceptive accuracy is likely to be shown only in cases of clinical severity of the disorder, as there is no relationship with proprioceptive accuracy for the non-clinical severity questionnaire score assessing susceptibility (Ratcliffe & Newport, 2016).

Schizophrenia

Rado (1953) was the first to suggest that one of the basic components of schizophrenia is a disturbance of proprioception (Arnfred et al., 2006). In a study by Rosenbaum and colleagues (1959), it was empirically shown that schizophrenics have poorer proprioceptive ability: patients group showed poorer weight discrimination ability compared to the healthy control group. Since then, a number of studies have been conducted with mixed results (Leventhal et al., 1982; Ritzler, 1977; Ritzler & Rosenbaum, 1974; Rosenbaum et al., 1965). One of the most recent studies was conducted by Chang and Lenzenweger (2005), who compared weight discrimination ability of the relatives of schizophrenics with the relatives of bipolar patients and people without a close relative with mental illness. The experiment involved comparing a standard weight of 200 g with 210 g or 220 g. The results showed that relatives of schizophrenics performed worse in terms of sensitivity. In addition, the strength of schizotypal traits was negatively associated with discrimination performance.

Schizophrenic patients, when hallucination, often misperceive a self-caused event as caused by an external agent (Kean, 2009). This suggests that there may be an error in comparing information about one's own movements from the receptors (reafferent) with information conveyed by the movement command (efferent copy) (Frith et al., 2000). One manifestation of this is that people with schizophrenia can tickle themselves to a greater extent than healthy individuals (Blakemore et al., 2000). The scientific explanation for the inability to tickle oneself is that there is a minimal mismatch between reafferent stimuli and information conveyed by the efferent copy (Blakemore et al., 2000). A correlation between schizotypal personality traits and the efficacy of self-induced tickling has also been demonstrated in a non-clinical population (Whitford et al., 2017). Also, it is important to highlight that people with the disorder experience a stronger rubber hand illusion. Thakkar and colleagues (2011) showed that schizophrenics report the illusion to be stronger, and show a greater degree of proprioceptive shift (perceived shift in hand position towards the rubber hand). These findings may indicate a more flexible body representation and a weaker sense of self, contributing to the development of psychotic experiences and hallucinations (Thakkar et al., 2011).

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Study 1: Proprioceptive accuracy is not associated with self-reported body awareness, body competence, and affect

Abstract

Purpose: Proprioception plays an essential role in motor control and in psychological functioning: it is the basis of body schema and the feeling of body-ownership. There are individual differences in the processing accuracy of proprioceptive stimuli. Although proprioceptive acuity plays an important role in physical competence, there are contradictory findings concerning the role it plays in healthy psychological functioning. The current study aims to shed more light on this association.

Material and methods: 68 young adults participated in our study. We estimated proprioceptive acuity by the reposition accuracy of elbow joint positions. We tested both dominant and non-dominant hand with two different versions of Joint Position Reproduction Test. Perceived physical competence, body awareness, and affectivity were assessed using questionnaires (Physical Competence scale of Body Consciousness Questionnaire, Somatic Absorption Scale, and Positive and Negative Affectivity Schedule, respectively).

Results: No significant association between proprioceptive acuity and body-awareness, perceived body competence, and positive and negative affect was found.

Conclusion: Proprioceptive acuity, measured in the elbow joint, does not play a substantial role in body-awareness, perceived body competence, and affect.

Keywords: Proprioception, proprioceptive accuracy, physical competence, body awareness, affect

Introduction

Based on our proprioceptive sense, we are able to assess the relative position of our body parts, our posture, and the tightness of our muscles, even in the absence of visual stimuli (Sherrington, 1906). This ability relies on signals coming from mechanoreceptors located in the muscles (muscle spindles), tendons (Golgi organs), ligaments and skin (Proske & Gandevia, 2012). Beyond the aforementioned static sensations, proprioception plays an essential role in motor control. It provides the central nervous system with afferent information about the actual position and state of various parts of the sensorimotor system, which helps it to maintain muscle tone, body posture, and seamless movements to achieve the desired state (Prochazka, 2011).

The majority of the aforementioned processes is automatic and does not require attention or conscious effort. To some extent, we are also able to sense the position of joints and muscle tone consciously (Gallagher, 2006); however, there are considerable individual differences in the processing of proprioceptive stimuli, for example, with respect to its accuracy (Han et al., 2016).

A number of methods has been developed to measure various aspects of proprioceptive acuity or accuracy. Concerning the position of the joints, one of the most widely used tests is Joint Position Reproduction Test (Goble, 2010). In this test, the task of the participants is the reproduction of the target position of a given body segment without visual feedback. The test starts with placing the reference body part from starting position into the target position. After that, in ipsilateral condition, the body part is moved back into the starting position, and the participant is asked to reproduce the target position with the same limb. In contralateral condition, however, the reference limb stays in the target position, and the reproduction occurs with the contralateral limb (Goble, 2010).

Proprioceptive acuity plays an important role in various aspects of physical competence. For example, it is associated with higher level of sport performance (Han et al., 2014; Han, Waddington, et al., 2015), and reversely associated with the number of sport injuries (Cameron et al., 2003; Han, Anson, et al., 2015; Parkhurst & Burnett, 1994; Payne et al., 1997) Beyond motor control, proprioception also impacts psychological functioning. One of the first steps in the development of the self is the differentiation between the body and the environment. In this progression, it is fundamental to implement and recognize self-generated movements (Jeannerod, 2003). This is possible by comparing proprioceptive afferent signals with corollary discharge, which is the predicted state of the body based on the efferent copy of motor command (Miall & Wolpert, 1996; Wolpert & Flanagan, 2001). Proprioception yields the basis of body schema, which is a complex representation of the body that operates mainly on a not conscious level, and gives rise to motor control and cognition (Gallagher, 2006). Proprioceptive information may also play a role in the formation of emotions. For example, muscle tone increases in stressful situations (Lundberg et al., 1994), and the systematic relaxation of the muscles can in turn reduce anxiety (Rausch et al., 2006).

A number of studies demonstrates the positive association between proprioceptive processing and healthy psychological functioning. Worse than average acuity is associated with schizophrenia (Chang & Lenzenweger, 2005; Rosenbaum et al., 1959, 1965) and fibromyalgia (Bardal et al., 2016). Higher acuity is not always associated with positive conditions, however; for example, somatoform patients are more precise than healthy controls when they have to judge their muscle tone (Scholz et al., 2001). There are also studies that report no association between proprioceptive processing and the severity of sub-clinical or clinical mental illnesses (Akyol et al., 2013; Leventhal et al., 1982; Ratcliffe & Newport, 2016; Ritzler, 1977; Ritzler & Rosenbaum, 1974; Ulus et al., 2013).

Theoretically, consciously accessible proprioceptive abilities, for example physical performance or the perception of the position of the body and its parts might interact with and contribute to the self-concept in multiple ways. First, those with higher levels of dispositional body-focused attention (aka body awareness) might realize and correct errors between expected and actual body positions more readily which leads to higher proprioceptive accuracy over time. Second, proprioceptive accuracy contributes to better physical performance and perceived body competence. Finally, the latter positively affects self-esteem (Sonstroem & Morgan, 1989), which is associated with higher levels of positive affect and lower levels of negative affect (Watson et al., 1988; Watson & Clark, 1984).

The current study aims to assess the assumed associations between proprioceptive accuracy and high-level psychological constructs. It was expected that proprioceptive accuracy is positively associated with body awareness (Hypothesis 1), perceived body competence (H2), and positive affect (H3), and reversely associated with negative affect (H4).

Materials and Methods

Participants

A priori power analysis for a medium level association ($r = 0.3$, one-tailed, $\alpha = 0.05$, and $1-\beta = 0.80$) indicated $n = 67$ as minimum necessary sample size (G*Power v3.1.9.2; (Faul et al., 2007). Participants of the study were undergraduate university students ($n = 68$, age: 21.1±1.49 yrs, 52.9% female, 92% right-handed); they participated in the study for partial course credit. Most of them attend in regular (although not elite level) sport activity, they spent 9±5.014 hours a week with sport training in average. The study was approved by the Research Ethics Committee of the university; all participants signed an informed consent form before participation.

Questionnaires

To assess body awareness, participants filled out the Somatic Absorption Scale (SAS) (Köteles et al., 2012). The questionnaire was developed to measure non-pathological tendency to monitor body processes. It contains 19 items, for example "When I watch TV or a movie, I am very aware of my bodily reactions". Two from the 19 items are reversed. Participants have to rate statements on 5-point Likert scale. Higher final scores on the scale indicate higher level of bodily awareness. In this study, Cronbach alpha value was 0.794, showing adequate internal consistency.

Body competence was measured by the Physical Competence subscale of the Body Consciousness Questionnaire (BCQ-PC) (Miller et al., 1981). This scale consists of 4 questions concerning various aspects of perceived physical competence, for example: "I'm better coordinated than most people". Higher values mean higher level of perceived competence. Internal reliability, measured by Cronbach-alpha was sufficient, with a value of 0.779.

Positive and Negative Affectivity Schedule (PANAS) (Gyollai et al., 2011) was used to measure affect. This questionnaire was developed to measure the current (state) or general (trait) emotional state of the person. We have used trait instruction in our study. The questionnaire consists of 10 items to measure positive affect, for example enthusiasm, and 10 items to measure negative affect, e.g nervousness. Participants have to rate how often they feel the given emotional state on a five-point Likert scale. Higher total scores refer to higher level of positive and negative affect, respectively. Cronbach-alpha of the positive scale was 0.876, and 0.920 of the negative scale in this study, both indicating a high level of internal consistency.

Proprioceptive measurements

We used the Joint Position Reproduction Test (Goble, 2010) to measure proprioceptive acuity. We measured the position of the elbow joint and tested both dominant and non-dominant hand of the participants with the two above-described versions (i. e. ipsilateral and contralateral conditions) of the test. Overall, four tests (each with five trials) were performed: ipsilateral dominant (ID), ipsilateral subdominant (IS), contralateral dominant

(CD), and contralateral subdominant (CS). In each case, participants were in a seated position with the elbow placed on a rotatable board at shoulder height, eyes closed and covered. Before each trial, the arm of the participant was fully stretched (starting position), then it was moved in the target position. In ipsilateral condition, the arm was moved back to the starting position, and the participant's task was to reproduce the target position by actively moving the same arm. In contralateral condition, the reference arm stayed in the target position, and the reproduction happened with the contralateral arm. We used 5 target positions: 150, 120, 90, 60 and 30 degree. The positions were presented in a random order. We could measure the position of the elbow joint with a precision of ±1 degree. Proprioceptive accuracy in each test was calculated as the absolute value of the average difference between the degree of the target and reproduced position; higher scores refer to lower levels of accuracy. Internal consistency was in the acceptable domain (i. e. Cronbach's alpha above 0.65) for two tests out of four (ID: 0.557, IS: 0.677, CD:0.659, CS:0.603).

Procedure

Participants filled out the Hungarian versions of the questionnaires online at home, the latest the day before the proprioception measurements. The order of the questionnaires was the same for every person, i.e.; PANAS, SAS and BCQ-PC. The assessment of proprioceptive acuity was conducted in the laboratory of the university. Participants were asked to wear comfortable clothes, not to conduct hard physical exercise, and avoid the use of any psychoactive drugs, including caffeine and alcohol 12 hours before the experiment. We have randomized the order of the 4 proprioceptive measurements to avoid the effect of learning or fatigue. Participants were seated in a chair with adjustable height. We could also adjust the length of the rotatable board to achieve a standard position for the Joint Position Reproduction Test: upper arms were parallel with the ground and with the line of the upper body. During the task, only the elbow joint moved.

Statistical analysis

Statistical analysis was conducted using the JASP v0.9.0.1 software (JASP Team, 2019). As Shapiro-Wilk test indicated significant deviation from normality for several variables, hypotheses were tested using Spearman correlation. As direction of associations was inherent part of our hypotheses, one-tailed significance tests were used. To avoid inflation of Type 1 error due to high number of independent analyses, accepted level of significance were set to 0.05/16 = 0.003 (Bonferroni correction). Beyond the widely used frequentist method, we also used the Bayesian approach to evaluate our hypotheses. In Bayesian statistics, the probability of an alternative hypothesis compared to the null hypothesis is calculated thus the major caveats of the frequentist statistics (e.g. issues with Type I and II error) can be avoided. If the so-called Bayes index (BF_{10}) is smaller than 1, the null hypothesis is more probable than the alternative hypothesis (Kline, 2013).

Results and Discussion

Results

Descriptive statistics of the assessed variables are presented in Table 1.

Table 1. Descriptive statistics of the assessed variables

Variable	M±SD	Minimum	Maximum
Proprioceptive error (ipsilateral dominant)	6.40±3.794	0.00	19.00
Proprioceptive error (ipsilateral subdominant)	5.13±4.359	0.00	20.00
Proprioceptive error (contralateral dominant)	5.71 ±3.758	0.00	17.00
Proprioceptive error (contralateral subdominant)	5.34±3.454	0.00	12.00
Body awareness(SAS)	61.62±8.513	45.00	86.00
Body competence (BCQ-PC)	14.51±3.005	9.00	20.00
Positive affect (PANAS-P)	37.09±6.093	18.00	50.00
Negative affect (PANAS-N)	18.82±7.461	10.00	38.00

Note: For proprioceptive error, higher values refer to lover levels of acuity; Abbr.: SAS: Somatic Absorption Scale, BCQ-PC: Body Consciousness Scale - Physical Competence Subscale, PANAS-P: Positive and Negative Affectivity Schedule - Positive Affectivity subscale, PANAS-N Positive and Negative Affectivity Schedule - Negative Affectivity subscale

Frequentist correlation analyses revealed no significant correlation between proprioceptive error and any of the assessed psychological constructs (for details, see Table 2).

Bayesian analysis supported this conclusion, as all BF_{10} values are below 1 (Table 3.).

Table 2. Correlations (Spearman rho coefficients) between variables; frequentist approach

	Proprioceptive error (ipsilateral dominant)	Proprioceptive error (ipsilateral subdominant)	Proprioceptive error (contralateral dominant)	Proprioceptive error (contralateral subdominant)
Body awareness (SAS)	-0.069; p = 0.287	0.031; p = 0.600	0.002; p = 0.506	0.020; p = 0.564
Body competence (BCQ-PC)	0.139; p = 0.870	0.080; p = 0.739	0.055; p = 0.673	-0.051; p = 0.341
Positive affect (PANAS- P)	0.026; p = 0.582	-0.072; p = 0.282	0.027; p = 0.587	0.000; p = 0.500
Negative affect (PANAS - N)	-0.019; p = 0.561	0.268; p = 0.014	0.075; p = 0.271	-0.097; p = 0.784

Note: One-tailed significance, Bonferroni-corrected level of significance is 0.003; Abbr.: SAS: Somatic Absorption Scale, BCQ-PC: Body Consciousness Scale - Physical Competence Subscale, PANAS-P: Positive and Negative Affectivity Schedule - Positive Affectivity subscale, PANAS-N Positive and Negative Affectivity Schedule - Negative Affectivity subscale

Table 3. Correlations (Kendall's tau coefficients) between variables; Bayesian approach

	Proprioceptive error (ipsilateral dominant)	Proprioceptive error (ipsilateral subdominant)	Proprioceptive error (contralateral dominant)	Proprioceptive error (contralateral subdominant)
Body awareness (SAS)	-0.009; BF_{10} =0.141	0.037; BF_{10} =0.230	-0.008; BF_{10} 0.143	0.030; BF_{10} 0.215
Body competence (BCQ-PC)	0.080; BF_{10} =0.418	-0.032; BF_{10} =0.115	0.068; BF_{10} =0.349	0.036; BF_{10} =0.288
Positive affect (PANAS- P)	0.031; BF_{10} =0.216	0.003; BF_{10} =0.159	0.004 ; BF_{10} =0.161	-0.055; BF_{10} =0.098
Negative affect (PANAS - N)	-0.023; BF_{10} =0.197	-0.061; BF_{10} =0.317	0.069; BF_{10} =0.088	0.187; BF_{10} =0.047

Note: One-tailed significance; Abbr.: SAS: Somatic Absorption Scale, BCQ-PC: Body Consciousness Scale - Physical Competence Subscale, PANAS-P: Positive and Negative Affectivity Schedule - Positive Affectivity subscale, PANAS-N Positive and Negative Affectivity Schedule - Negative Affectivity subscale

Discussion

Contrary our hypotheses, no association was found between indicators of proprioceptive acuity with respect to the elbow joint and perceived body awareness (H1), body competence (H2), and positive and negative affect (H3 and H4, respectively).

We hypothesized that a higher level of dispositional body awareness leads to greater attention to proprioceptive signals, which is associated with higher proprioceptive accuracy. Our findings do not support the existence of this relationship. According to previous studies that showed positive association between physical activity and proprioceptive acuity (Goble, 2010; Ribeiro & Oliveira, 2011), proprioception can be improved by physical activity, but apparently not by body related attention.

While proprioceptive accuracy is associated with physical performance in elite athletes (Han et al., 2014; Han, Waddington, et al., 2015), we found no association between proprioceptive accuracy and perceived body competence in our study. The explanation might be the difference between the samples (elite athletes vs. sport-oriented university students), or that objective and subjective body competence may not completely overlap. The results show that proprioceptive acuity does not play a role in perceived physical competence.

According to our hypothesis, more accurate processing of proprioceptive signals is associated with more effective implementation of movements, which results in higher level of self-efficacy and self-esteem (Sonstroem & Morgan, 1989), and in higher level of positive, and lower level of negative affect. In contraction of this assumption, we found no correlation between affect and proprioceptive acuity. Empirical evidence, however, indicates that the condition of the locomotor system has an important role in emotional processing. According to Cacioppo and colleagues (1993), contraction of arm extensor muscles activates the avoidance system, as demonstrated by faster processing of negative words or more negative judgement of neutral stimuli, while the contraction of flexor muscles activates the approach system, which is associated with faster processing of positive words, or more positive judgement about neutral stimuli (Cacioppo et al., 1993; Neumann & Strack, 2000). Our results show that proprioceptive acuity does not play such a relevant role in experiencing negative or positive emotions to make a trait-level difference between people in affectivity.

Limitations

Generally speaking, the proprioceptive acuity of the elbow joint does not necessarily represents a general proprioceptive ability, as proprioceptive accuracy measured in different joints does not correlate (Han et al., 2013; Waddington & Adams, 1999).

Regarding the question of the ecological validity of our assessments, we have to note that while Joint Position Reproduction test requires conscious effort, in our everyday life proprioception works in a close to automatic way in most of the time (Gallagher, 2006). The two processes (i.e. conscious and automatic) might not completely overlap or relate. Empirical evidence also shows that body-focused attention has a negative impact on physical performance, presumably because of the disruption of automatic processes (Wulf, 2013).

Low Cronbach alpha, measured in the half of the tasks, also represents a limitation of our study. It may be the result of proprioceptive acuity measured in the elbow joint being a non-unidimensional construct, as the accuracy can vary depending on the spatial position, and on the magnitude of the movement (Goble, 2010).

Conclusion

Although proprioception plays a fundamental role in motor performance and in psychological functioning, proprioceptive acuity, measured in the elbow joint was not associated with perceived body-awareness, body competence, and affectivity.

Acknowledgments

This research was supported by the Hungarian National Scientific Research Fund (KH 130319).

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Study 2: Cardiac and proprioceptive accuracy are not related to body awareness, perceived body competence, and affect

Abstract

Interoception in the broader sense refers to the perception of internal states, including the perception of the actual state of the internal organs (visceroception) and the motor system (proprioception). Dimensions of interoception include (1) interoceptive accuracy, i.e., the ability to sense internal changes assessed with behavioral tests, (2) confidence rating with respect to perceived performance in an actual behavioral test, and (3) interoceptive sensibility, i.e., the self-reported generalized ability to perceive body changes. The relationship between dimension of cardioceptive and proprioceptive modalities and their association with affect are scarcely studied. In the present study, undergraduate students (N = 105, 53 males, age: 21.0±1.87 yrs) filled out questionnaires assessing positive and negative affect (Positive and Negative Affect Schedule), interoceptive sensibility (Body Awareness Questionnaire), and body competence (Body Competence Scale of the Body Consciousness Questionnaire). Following this, they completed a behavioral task assessing cardioceptive accuracy (the mental heartbeat tracking task by Schandry) and two tasks assessing proprioceptive accuracy with respect to the tension of arm flexor muscles (weight discrimination task) and the angular position of the elbow joint (joint position reproduction task). Confidence ratings were measured with visual analogue scales after the tasks. With the exception of a weak association between cardioceptive accuracy and the respective confidence rating, no associations between and within modalities were found with respect to various dimensions of interoception. Further, the interoceptive dimensions were not associated with state and trait positive and negative affect and perceived body competence. In summary, interoceptive accuracy scores do not substantially contribute to conscious representations of cardioceptive and proprioceptive ability. Within our data, non-pathological affective states (PANAS) are not associated with the major dimensions of interoception for the cardiac and proprioceptive modalities.

Keywords: proprioception, cardioception, interoceptive accuracy, interoceptive sensibility, affect, body awareness

Introduction

Interoception refers to the processing of information originating from within the body (Cameron, 2002). Originally, it was a synonym for visceroception; later, the inclusion of somatosensory and proprioceptive information was also proposed (Vaitl, 1996; Ceunen et al., 2016; Berntson et al., 2018). The current paper applies this broad approach to interoception. Thus, conscious aspects of interoception include body sensations associated with emotions, awareness of non-emotive body processes and the perception of the actual state of the locomotor system.

The recently accepted conceptualization of conscious aspects of interoception describes at least two major dimensions (Ceunen et al., 2013; Garfinkel, Seth, et al., 2015; Garfinkel & Critchley, 2013). Interoceptive accuracy (IAc or sensitivity) refers to the acuity of perception of internal changes and states as assessed by behavioral methods. Its self-report counterpart, i.e., the perceived performance in an a behavioral test of acuity, is called confidence. Finally, the perceived general ability to sense body changes is called interoceptive sensibility (IS) or awareness in the literature. Empirical evidence shows that the association between these three dimensions of cardiac interoception is weak or non-existing (see below).

It is worth noting that there is an inconsistency in the literature with respect to the concept of interoceptive sensibility. Unfortunately, it is not clear which questionnaires should be used to assess the dispositional aspect of interoceptive sensibility. Garfinkel, Seth and colleagues (2015) recommend the Body Awareness Scale of the Body Perception Questionnaire (Porges, 1993).The Body Awareness Questionnaire (Shields et al., 1989) and the Multidimensional Assessment of Interoceptive Awareness (Mehling et al., 2012) have been also used in the literature (Meessen et al., 2016; Ferentzi et al., 2019). Although the former does not make a distinction between visceroception and proprioception, whereas the latter includes only visceroceptive modalities, a recent study indicated a substantial overlap between the two constructs (Ferentzi et al., 2020).

Concerning the emotional experience, the primary importance of visceroception has been suggested by many authors (James, 1884, 1890; Lange, 1885; Damasio, 1994), whereas others emphasize the role of the somatosensory system (Darwin, 1872; Tomkins, 1962, 1981; Izard, 1971). These models assume the causal role of interoceptive information in the development of affective experience thus they are called peripheral theories of emotion. Central theories do not suppose such a causal link (Cannon, 1927, 1931; Davis, 1989; LeDoux, 1990; Oatley & Johnson-laird, 1987; Panksepp, 1982, 1991); still, they accept that emotions are typically characterized by peripheral changes that prepare the organism for the behavioral response. As a proportion of these changes, both visceral and somatosensory, may reach conscious awareness, an association between the emotional experience and the perception of body changes can be explained by central theories too.

Cardiac response plays a central role in the physiological component of emotional reactions, as they are usually characterized by an increased energetic demand (Lacey & Lacey, 1978). It is widely assumed that, in line with the tenets of peripheral theories of emotion, the accuracy of perception of cardiac activity, dubbed cardioceptive accuracy, contributes to the emotional experience (Pollatos et al., 2005; Wiens et al., 2000). On the other hand, a more intense emotional reaction (e.g., if it is accompanied by sympathetic activation) can improve the perception of heartbeats (Fairclough & Goodwin, 2007; O'Brien et al., 1998; Schandry et al., 1993). Empirical studies revealed a positive association between the intensity (arousal) component of emotions and cardioceptive accuracy (Wiens et al., 2000; Barrett et al., 2004; Herbert et al., 2007, 2010; Pollatos, Herbert, Matthias, et al., 2007; Pollatos et al., 2005). Also, improved cardiac accuracy was found to be related to the actual level of anxiety in a number of studies (Schandry, 1981; Ludwick-Rosenthal & Neufeld, 1985), whereas no such associations were reported in others (Pollatos, Herbert, Kaufmann, et al., 2007; Werner et al., 2013). From a theoretical point of view cardioceptive confidence may also contribute to the affective experience. For example, manipulated feedback on heart rate was enough to intensify the emotional reaction (Valins, 1966, 1967). Even more intriguingly, if actual and perceived heart rate did not correspond, the latter influenced the perceived level of arousal (Kerber & Coles, 1978; Parkinson, 1985; Thornton & Hagan, 1976; Woll & McFall, 1979).

Proprioceptive information is also assumed to play a substantial role in the formation of emotional experience. According to different theories (for a review, see Moors, 2009), somatic and/or motor changes, modulated by cognitive processing, are cornerstones of the arising of affective feelings. On the one hand, changes in the musculoskeletal system can modulate the emotional experience. Shafir and colleagues

(2015) showed that different affective feelings can be evoked by specific, complex movement patterns. Power posing may also change the affective experience; hovewer results with respect to behavioral (more risk-taking) and hormonal responses (i.e. increased testosterone and decreased cortisol level) are controversial (Carney et al., 2010; Ranehill et al., 2015; Simmons & Simonsohn, 2017). In the same vein, EMG activity increases in many muscles and muscle groups in stressful situations (Lundberg et al., 1994; Wahlström et al., 2002; Krantz et al., 2004; Luijcks et al., 2014), and it is possible to reduce stress and anxiety through relaxation techniques (e.g. progressive relaxation, autogenic training), which operate (at least partially) through the systematic relaxation of muscles (Kanji et al., 2006; Rausch et al., 2006). Finally, Cacioppo and colleagues (1993) showed that the activation of arm flexor muscles activates the approach system, which biases the judgement of neutral stimuli to the positive direction. By contrast, activation of arm extensors stimulates the avoidance system, resulting in the opposite effect. Neuman and colleagues (2000) drew a similar conclusion in a categorization task. Overall, these findings support the idea that the actual state of muscles can impact the emotional experience.

Based on the aforementioned role of proprioceptive information in the formation of the affective experience, it is logical to assume that, similar to cardioceptive information, individual differences in the accuracy of processing of proprioceptive information (aka proprioceptive accuracy) are related to differences in emotional processing. In accordance with this assumption, alterations in processing and integration of proprioceptive input can be associated with pathological conditions. For example, a greater reliance on proprioception during the completion of a motor task is associated with impairments in imitation and empathy in autism spectrum, and attention deficit *hyperactivity* disorder (Gao et al., 2019). In fibromyalgia, however, patients were found to be less reliant on proprioceptive information than healthy controls (Bardal et al., 2016). Also, decreased proprioceptive accuracy was found in chronic pain (Tsay et al., 2015) and schizophrenia (Rosenbaum et al., 1959, 1965; Leventhal et al., 1982; Chang & Lenzenweger, 2005). In contrast, somatoform disorders are accompanied by higher proprioceptive accuracy (Scholz et al., 2001). It is also important to note that an emotionally intense state, e.g., the high level of stress, decreases proprioceptive accuracy (Şenol et al., 2018). However, not all studies confirmed the aforementioned relationships, there are null findings too, for example with respect to schizophrenia (Ritzler, 1977;

Ritzler & Rosenbaum, 1974), fibromyalgia (Akyol et al., 2013; Ulus et al., 2013), and chronic pain (Tsay et al., 2015). Moreover, Horváth and colleagues (2019) found that there is no association between trait affect and proprioceptive accuracy, as assessed with the Joint Position Reproduction test in the elbow joint. Additionally, proprioceptive accuracy was not correlated with body awareness - a construct that overlaps with interoceptive sensibility (Ferentzi et al., 2020) - and perceived body competence (Ferentzi et al., 2017; Horváth et al., 2019).

When investigating the role of interoceptive accuracy, it is a fundamental question whether individual characteristics in information processing established in one modality (e.g. cardioception) can be generalized to other modalities (e.g. proprioception). Ferentzi and colleagues (2018) reported no association between modalities of interoception. A significant association was found only between measures within the same modality for three visceroceptive modalities (i.e. pain threshold and tolerance, gastric fullness and unpleasantness, and the intensity and unpleasantness of bitter taste), but there was no association between the two included measures of proprioceptive accuracy (ipsilateral and contralateral version of the joint position reproduction test in the elbow joint). These and other results (Garfinkel et al., 2017) show that interoceptive accuracy cannot be generalized across interoceptive modalities.

With respect to joint-related proprioceptive accuracy, a number of measurement paradigms were developed (Han et al., 2016). Studies investigating the association between different tests in one joint (Barrack et al., 1984; Grob et al., 2002; Jong et al., 2005; Elangovan et al., 2014; Li et al., 2016; Niespodziński et al., 2018; Yang et al., 2020) consistently report that accuracy is test-specific. The same conclusion can be drawn with respect to cardioception: accuracy scores obtained by heartbeat discrimination methods that use forced-choice methods and methods that use heartbeat tracking (i.e. counting) typically show no or only weak associations (Pennebaker & Hoover, 1984; Weisz et al., 1988; Phillips et al., 1999; Schaefer et al., 2012; Hart et al., 2013; Schulz et al., 2013; Michal et al., 2014; Garfinkel, Seth, et al., 2015; Garfinkel, Tiley, et al., 2015; Forkmann et al., 2016; Ring & Brener, 2018). Moreover, proprioceptive measurement methods can be conducted with respect to different joints; Han et al (2013) and Waddington and Adams (1999) revealed that accuracy, assessed with the same paradigm (active movement extent discrimination apparatus) is joint-specific, and only the same joints of the left and right side of the body show an association. The actual exertion (or tension) of muscles represents another proprioceptive modality; a fundamental difference is that activation of the muscles is controlled by a feed-forward mechanism thus the efferent information plays a similarly important role in the processing of the actual state as the afferent input (Miall & Wolpert, 1996; Cullen, 2004). Further, joint-related acuity primarily relies on receptors located in the joints (Ruffini end organs), whereas muscle-related accuracy is impacted by afference from receptors in the muscles (muscle spindles) (Batson, 2009; Jha et al., 2017).

Interoceptive sensibility, the self-reported dimension of interoception, appears to be independent of interoceptive accuracy for healthy participants (e.g. Ehlers et al., 1995). In another study, accuracy and sensibility were associated among high performers in both applied heartbeat perception tasks, i.e., the mental tracking and the discrimination task (Garfinkel, Seth, et al., 2015). The authors interpret their results as a dissociation of the assessed dimensions of interoception which was replicated by others regarding the mental tracking task (Forkmann et al., 2016; Meessen et al., 2016). A weak positive association between cardioceptive accuracy and sensibility was found in another study (Köteles, Éliás, et al., 2020). Besides heartbeat perception, interoceptive sensibility with respect to respiration has been also investigated and the dissociation between accuracy and sensibility was confirmed (Garfinkel et al., 2016). In the field of proprioception, however, sensibility has not been assessed to date.

The major goal of the present study is to shed more light on the associations within and between the dimensions of cardioception and two modalities of proprioception, i.e., the sense of joint position and muscle tension. We also wanted to explore the associations between affect and the behavioral and self-report measures of these modalities.

The following hypotheses were tested. First, accuracy and sensibility show a weak positive association within the same modality (H1). Second, accuracy and sensibility between modalities are independent of each other (H2). Third, cardioceptive accuracy and sensibility are associated with affect, whereas proprioceptive accuracy and sensibility are not (H3). Finally, we assumed that proprioceptive accuracy and sensibility would not be associated with perceived body competence and body awareness (H4).

Materials and Methods

Participants

A priori sample size calculation for r = 0.3, α = 0.05 (one-tailed), 1-β = 0.9 indicated a minimum required sample size of N = 92 (Faul et al., 2007). Participants were undergraduate students of Eötvös Loránd University (N = 105, 53 males, age: 21.0±1.87 yrs, 95 right handed). Participants consuming alcohol and/or taking psychoactive drugs within 8 hours before the experiment, and those with severe injury/disability of the arm were excluded. Participation was rewarded with partial course credit. Joint Position Reproduction test was missing for 9 individuals due to technical problems. The study was approved by the Research Ethics Committee of the university. Before participation, everyone signed an informed consent form.

Behavioral measures

Proprioceptive accuracy - Joint Position Sense

Joint Positions Sense was assessed with a version of the Joint Position Reproduction Test (JPR) (Goble, 2010), where participants had to reproduce elbow joint positions We tested the non-dominant arm of the participants. Participants were blindfolded, seated, and asked to keep a standard posture (upper arms parallel with the ground and in line with the body). During the measurement, they placed their upper arm on a rotatable lever, which was connected to a motor, and made possible the accurate (±0.1 degree) measurement and movement of the elbow joint. They had to hold a handle and keep their hand on a button. 180 degree indicated fully extend elbow. From starting position, the machine moved the arm of the participant to the target positions with a speed of 12 degree/sec. After spending 4 seconds there, the device moved back the lever to the starting position. After 1 second, the lever started to move again, with a speed of 8 degree/sec. The task of the participants was to press the button, when they felt that their arm reached the target position. Following this, the lever moved the arm back to the starting position again and a new trial begun. The starting position was always 160 degree, while the target position changed from trial to trial. Overall, 9 trials were conducted, with nine different target positions (150, 135, 120, 105, 90, 75, 60, 45 and 30 degree). Every target position was presented once; the order of presentation was randomized. To calculate the accuracy of Joint Position Reproduction, an error score (i.e. the difference between the target and the reproduced position (i.e. the difference between the target and the reproduced position) was calculated for each trial. Outliers above and below two standard deviation were removed and missing values were imputed by using the fully conditional specification (MCMC) and linear regression model options of SPSS v20 software. To determine accuracy, we used two error scores: constant and variable error (Schutz & Roy, 1973; Boisgontier et al., 2012; Goble et al., 2012). Constant error is the mean of the error scores and shows the magnitude and direction of the systematic distortion in position judgements. Negative values of constant error score indicate bias towards the inside direction, whereas positive values indicate bias towards the outside direction. Internal consistency of constant error was acceptable (Cronbach's alpha: 0.751). Variable error is the standard deviation of the error scores and shows the inconsistency of judgements (i.e. higher variable error shows higher level of inconsistency.

Proprioceptive accuracy - Weight Discrimination

To assess weight discrimination ability, participants had to compare the weight of two objects (Chang & Lenzenweger, 2005). These objects were glass bottles filled with water, identical in shape and size. During the measurement, participants eyes' were covered; they had to keep a standing posture, keep their left upper arm next to their body, and their lower arm in a flexion of approximately 90 degree.

Overall, 32 comparisons were made. The weight of one of the presented bottles was always 200 g. In one half of the trials (16), the other bottle was 200 g (identical pairs), while in the other half (16), it was 215 g (different pairs). The presentation order of the pairs and that of the bottles within pairs were randomized. Participants had to hold every bottle for 8 seconds, verbally judge if they were the same weight or one was heavier. For heavier judgements, it also had to be indicated which weight was heavier. Weight discrimination ability was calculated by dividing the number of correct trials by the number of all trials.

Cardioceptive accuracy

Cardioceptive accuracy was assessed with a mental heartbeat-counting paradigm (Schandry, 1981). Participants had to count their heartbeats silently, while sitting on a chair, with their hands on their laps. They were explicitly encouraged to count if they had the lightest heartbeat sensation in any part of their body but were also asked not to count if they did not have any sensation. After a practice trial, which lasted for 15 seconds, 3 test trials of different lengths (25, 35 and 50 sec) were conducted. The test trials were presented in a randomized order. The number of heartbeats were recorded with the NeXus recording system (NeXus Wireless Physiological Monitoring and Feedback: NeXus-10 Mark II, Version 1.02; BioTrace+ Software for NeXus-10 Version: V201581; Mind Media BV, Herten, the Netherlands). For every interval, an accuracy score was calculated as: 1 - |(HB recorded - HB counted)/ HB recorded |. For every individual, the scores of the three intervals were averaged to calculate cardioceptive accuracy. Internal consistency of the Schandry task was high (Cronbach's alpha = 0.906).

Questionnaires and questions

Confidence ratings

After every task (Joint Position Sense, Weight Discrimination, Cardioceptive accuracy), participants' subjective judgement about their performance (“*How do you think you performed in this test?*”) was recorded. For this purpose, they had to indicate their perceived performance on a 10cm-long, vertical visual analog scale. The anchor points were "*The best possible*" and "*The worst possible*". We measured the distance of the crossed part of the line from the bottom of the visual analog scale in millimeters. Higher values indicate higher levels of confidence.

Interoceptive sensibility - Body Awareness

Body Awareness Questionnaire (BAQ) measures the self-reported sensitivity to bodily processes, and the ability to anticipate bodily reactions (Shields et al., 1989; Köteles, 2014). Participants have to answer 18 questions on 7-point Likert-scales (e.g. "I notice distinct body reactions when I am fatigued"), where higher scores mean higher levels of body awareness (except one reversed item). Internal reliability in this sample was good (Cronbach's α = 0.848).

Body Competence

Body Competence was assessed with the Body Competence Scale of Miller's Private and Public Body Consciousness Questionnaire (Miller et al., 1981). The scale consists of four questions (e.g. "*I'm better coordinated than most people*"), rated on a 5-point Likert scale. Higher values indicate higher levels of perceived physical competence. Internal consistency of the scale in this study was good (Cronbach’s α= 0.835).

Affect

We used the Positive and Negative Affect Schedule (PANAS) to asses affect (Watson, 1988; Gyollai et al., 2011). The questionnaire can be used with two different instructions, to measure state and trait aspects of affect. The questionnaire is divided into two subscales, positive affect (PA; e.g. enthusiasm), and negative affect (NA; e.g. nervousness); both measured with 10 items. Participants have to rate how intensely they feel the given emotional state on a 5-point Likert scale, from 1 ("*Very slightly or not at all*") to 5 ("*Very much*"). Higher scores refer to higher levels of positive and negative affect, respectively. Cronbach's α values indicated acceptable to high levels of internal consistency in this study (Positive Trait: 0.872, Positive State: 0.922, Negative Trait: 0.854, Negative State: 0.794).

Procedure and statistical analysis

Data was collected in two phases. Participants had to fill out the questionnaires (with the exception of state PANAS) at home in an online form. The order of the questionnaires was: demographic data, trait PANAS, BAQ, Body Competence. Behavioral measures were conducted individually in the laboratory in a randomized order. Before the behavioral tasks, participants had to fill out the state PANAS questionnaire. Statistical analysis was conducted using the Jasp v0.11 software (JASP Team, 2019) using both the frequentist and Bayesian approach. Due to violations of the requirement of normality, associations were estimated using non-parametric correlations, i.e. Spearman’s rho in the frequentist analysis and Kendall’s Tau in the Bayesian analysis. For the Bayesian analysis, values below 0.33 indicated the superiority of the null-hypothesis, and values over 3 indicated the superiority of the alternative hypothesis (Wetzels & Wagenmakers, 2012).

Results

Descriptive statistics of the assessed variables are presented in Table 1.

Table 1. Descriptive statistics of the assessed variables

N = 105	M±SD	Min - max
Cardioceptive accuracy	0.51±0.270	0.0 - 0.963
Cardioceptive confidence	46.80±26.042	1 - 96
Weight discrimination accuracy	15.66±3.622	9 - 29
Weight discrimination confidence	40.74±22.419	0 -94
Joint Position Sense - constant error	6.5±4.652	-11.341 - 21.386
Joint Position Sense - variable error	6.76±2.277	2.287 - 12.352
Joint Position Sense confidence	61.094±22.239	0 - 98
State NA	12.54±3.190 (15.8±-5.9)*	10 - 24
Trait NA	17.22±5.181 (19.5±6.0)*	10 - 36
State PA	31.60±8.247 (29.0±8.0)*	12 - 49
Trait PA	36.429±6.090 (35.7±6.2)*	17 - 50
Interoceptive sensibility - BAQ	80.95±15.449	40 - 122
Body competence	14.45±3.581	4 - 20

Note: Weight discrimination and proprioception of the angle of the elbow joint were conducted with the subdominant hand; NA – negative affect; PA – positive affect; BAQ – Body Awareness Questionnaire *normative data reported by Watson and Clark (1994)

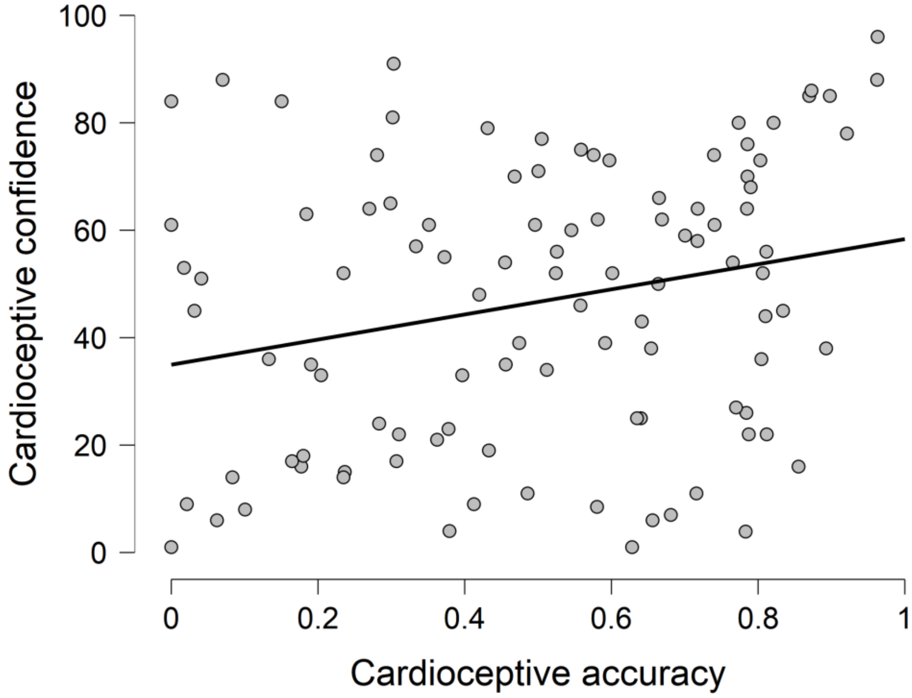
No significant associations but one between accuracy and sensibility (H1) within the included interoceptive modalities were revealed (*Table 2*). For cardioception, accuracy was weakly ($r_s = 0.25$, $p < 0.05$) related to sensibility *(Figure 1)*; this was supported by the Bayesian analysis ($BF_{10} = 5.063$). The null model (i.e. the lack of association) was more probable for all other modalities.

Table 2. Correlations between accuracy and confidence for the three interoceptive modalities

Interoceptive modality	Spearman correlation (p)	Bayesian Kendall's Tau (BF_{10})
Cardioception	0.25* (0.011)	0.182 (5.063)
Weight discrimination	0.05 (0.643)	0.032 (0.144)
Joint Position Sense - constant error	-0.09 (0.433)	-0.058 (0.191)
Joint Position Sense - variable error	-0.05 (0.640)	-0.050 (0.176)

Note: *: $p < 0.05$

Figure 1. Association between cardioceptive accuracy and cardioceptive confidence ratings.



Concerning associations between indicators of accuracy (H2), no significant correlation was found. Only the two joint position sense related indices (i.e. constant and variable error) showed a moderate association ($r_s = 0.41$, $p < 0.001$; $r_\tau = 0.28$, $BF_{10} = 500.816$); Bayesian analysis indicated the superiority of the null hypothesis for all other cases (*Table 3*).

Table 3. Correlations between accuracies for the three interoceptive modalities.

N = 105	Cardioception	Weight discrimination	Joint Position Sense - constant error	Joint Position Sense - variable error
Cardioception	-	0.00 (0.987)	-0.08 (0.455)	-0.09 (0.399)
Weight discrimination	-0.003 (0.127)$^{+}$	-	0.09 (0.395)	-0.01 (0.938)
Joint Position Sense- constant error	-0.058(0.188)$^{+}$	0.059(0.188)$^{+}$	-	0.41(<0.001)***
Joint Position Sense - variable error	-0.051(0.174)$^{+}$	-0.004(0.133)$^{+}$	0.281(500.816)***	-

Note: Upper triangle: frequentist analysis with Spearman's rho coefficients (p-values); Lower triangle: Bayesian analysis with Kendall's Tau coefficients (BF^{10} values); ***: p < 0.001 / BF10 > 100; +: BF10 < 0.33

With respect to confidence ratings, no significant association was found between cardioceptive and weight discrimination related confidence ($r_s = 0.09$, $p = 0.374$; $r_\tau = 0.067$, $BF_{10} = 0.212$), between cardioceptive and joint position sense related confidence ($r_s = 0.14$, $p = 0.198$; $r_\tau = 0.092$, $BF_{10} = 0.314$), and joint position sense and weight discrimination related confidence ($r_s = -0.07$, $p = 0.518$; $r_\tau = -0.037$, $BF_{10} = 0.155$). Again, Bayesian analysis indicated the superiority of the null hypothesis for all cases (*Table 4*).

Table 4. Correlations between confidence ratings for the three interoceptive modalities.

N = 105	Cardioception	Weight discrimination	Joint Position Sense
Cardioception		0.09 (0.374)	0.135 (0.198)
Weight discrimination	0.07 (0.212) +		-0.07(0.518)
Joint Position Sense	0.09 (0.314) +	-0.04 (0.155) +	

Note: Upper triangle: frequentist analysis with Spearman's rho coefficients (p-values); Lower triangle: Bayesian analysis with Kendall's Tau coefficients (BF^{10} values); ***: p < 0.001 / BF10 > 100; +: BF10 < 0.33

Between measures of interoception and questionnaire scores (H3, H4), correlation analysis indicated no significant correlations (*Table 5*).

Bayesian analysis indicated the superiority of the null hypothesis for most of the cases and was inconclusive (i.e in the 0.33 - 3 domain) for the remaining associations (*Table 6*).

Table 5. Associations between indicators of interoceptive accuracy and confidence ratings and questionnaire scores. Frequentist analysis, Spearman's rho coefficients (p values). None of the associations reached the p<0.05 level of significance.

N = 105	State NA	Trait NA	State PA	Trait PA	BAQ	Body competence
Cardioceptive accuracy	0.128 (0.192)	0.065 (0.512)	-0.041 (0.674)	-0.007 (0.947)	0.020 (0.840)	-0.10 (0.331)
Cardioceptive confidence	-0.026 (0.797)	-0.065 (0.519)	0.024 (0.809)	0.132 (0.187)	0.112 (0.262)	0.0 (1)
Weight discrimination - accuracy	0.044 (0.658))	-0.099 (0.316)	-0.021 (0.834)	-0.114 (0.248)	0.043 (0.664)	-0.019 (0.850)
Weight discrimination - confidence	-0.163 (-0.163)	-0.131 (0.189)	0.131 (0.189)	0.041 (0.681)	0.171 (0.084)	0.012 (0.900)
Joint Position Sense - constant error	-0.064 (0.534)	-0.026 (0.802)	-0.152 (0.140)	-0.123 (0.231)	0.117 (0.255)	0.005 (0.963)
Joint Position Sense - variable error	-0.078 (0.448)	0.005 (0.640)	-0.103 (0.317)	-0.075 (0.465)	-0.161 (0.177)	-0.138 (0.179)
Joint Position Sense - confidence	0.048 (0.646)	0.019 (0.854)	0.085 (0.414)	0.027 (0.794)	0.185 (0.073)	0.070 (0.503)

NA – negative affect; PA – positive affect; BAQ – Body Awareness Questionnaire

Table 6. Associations between indicators of interoceptive accuracy and confidence ratings and questionnaire scores.Bayesian analysis, Kendall’s Tau coefficients (BF^{10} values)

N = 105	State NA	Trait NA	State PA	Trait PA	BAQ	Body competence
Cardioceptive accuracy	0.102 (0.412)	0.044 (0.159)[+]	-0.026 (0.318)[+]	-0.006 (0.128)[+]	0.011 (0.129)[+]	-0.07 (0.223)[+]
Cardioceptive confidence	-0.021 (0.136)[+]	-0.045 (0.161)[+]	0.020 (0.135)[+]	0.095 (0.346)	0.079 (0.258)[+]	0.001 (0.129)[+]
Weight discrimination accuracy	0.030 (0.141)[+]	-0.067 (0.211)[+]	-0.014 (0.130)[+]	-0.081 (0.269)[+]	0.033 (0.144)[+]	-0.019 (0.133)[+]
Weight discrimination - confidence	-0.123 (0.680)	-0.088 (0.305)[+]	0.093 (0.337)	0.024 (0.137)[+]	0.107 (0.462)	0.012 (0.131)[+]
Joint Position Sense - variable error	-0.06 (0.195)1[+]	4.507e -4 (0.133)[+]	-0.063 (0.201)[+]	-0.052 (0.176)[+]	-0.106 (0.422)	-0.095 (0.341)
Joint Position Sense - constant error	-0.051 (0.174)[+]	-0.018 (0.137)[+]	-0.107 (0.462)	-0.081 (0.264)[+]	0.085 (0.278)[+]	0.003 (0.133)[+]
Joint Position Sense - confidence	0.034 (0.150)[+]	0.014 (0.137)[+]	0.060 (0.193)[+]	0.014 (0.137)[+]	0.126 (0.677)	0.048 (0.169)[+]

Note: +: BF10 < 0.33; NA – negative affect; PA – positive affect; BAQ – Body Awareness Questionnaire

Discussion

The goal of the present study was to investigate the associations between different modalities (cardioception and two proprioceptive modalities) of interoception and their dimensions (accuracy, confidence ratings and sensibility). Associations with positive and negative affect and perceived body competence were also investigated. Overall, accuracy and confidence were associated with respect to the cardiac modality only; further, no between-modality associations and associations with interoceptive sensibility, affect, and body competence were found.

Interoceptive accuracy and confidence

Contrary to our first hypothesis, accuracy and confidence were found to be independent of each other with respect to the two proprioceptive modalities. In other words, people are not able to sense their actual performance in these tasks. In the cardioceptive modality, however, similar to previous studies (Garfinkel, Seth, et al., 2015), we found a weak positive association between accuracy and confidence. This latter finding is in line with the insight that top-down information substantially impacts performance in the mental tracking task (Ring et al., 2015; Ring & Brener, 2018; Zamariola et al., 2018; Desmedt et al., 2020). Although a strict instruction was applied (i.e. participants were explicitly encouraged not to count if they did not have any sensation to report), which presumably decreases the impact of top-down factors (Ehlers et al., 1995; Desmedt et al., 2018), the involvement of conscious processes in the tracking task is substantial. If one combines knowledge on the usual frequency of his or her heartbeats with the number and timing of actually sensed and counted heartbeats, performance in the task can be estimated (Desmedt et al., 2020). In the case of the proprioceptive modalities, however, no such information is available, thus actual and perceived accuracy show complete dissociation.

In line with our second hypothesis, interoceptive accuracy and the respective confidence ratings proved to be modality-specific. We replicated the findings of Ferentzi and colleagues (2018), namely that cardioceptive accuracy, as assessed with the mental heartbeat tracking task, does not correlate with measures of proprioceptive accuracy (joint position reproduction and weight discrimination tests in this study). Moreover, in accordance with the findings of other studies (Barrack et al., 1984; Grob et al., 2002; Jong et al., 2005; Elangovan et al., 2014; Li et al., 2016; Niespodziński et al., 2018; Yang et al., 2020), no association between accuracies with respect to two proprioceptive modalities was found. This lack of association might reflect the actual independence of the two abilities; however, conceptual differences (i.e. the weight discrimination test does not involve a reproduction element and it was measured with a forced choice paradigm) can also explain this finding.

The confidence-related findings were similar to those for accuracy: there were no associations between cardioceptive and proprioceptive tasks, and between the two proprioceptive tasks. Empirical results concerning interoceptive sensibility across modalities are scarce. Garfinkel, Seth and colleagues (2015) found a strong positive association between confidence ratings of two heartbeat perception tasks (i.e. mental heartbeat tracking task and the discrimination task). In our data, this indicates that the perception of performance is not only more or less independent of actual performance, but also differs between modalities; cardioception-related confidence rating show closer connection than those of proprioceptive sensibility (but again, the lack of association between the two proprioception-related confidence ratings). This also suggests that top-down factors that usually impact perception, such as previous experiences and expectations, may show considerable modality-specific differences.

Interoception and affect

Contrary to our expectation (H3), we did not find any association between state and traitpositive and negative affect and cardioception-related accuracy and confidence In fact, Bayesian analysis supported the lack of association for the majority of the analyses. The same was true for the two proprioceptive modalities. There are several possible explanations for these null-findings. Cardioceptive accuracy showed associations with arousal but not with valence in studies where emotions were experimentally evoked and the two dimensions were assessed independently (Wiens et al., 2000; Barrett et al., 2004; Pollatos, Herbert, Matthias, et al., 2007; Herbert et al., 2007, 2010; Köteles, Teufel, et al., 2020; Pollatos et al., 2005). The approach used in the present study, however, primarily measures affective states that are accompanied with high arousal (Lox et al., 2010) thus cannot separate these components. Further, the actual affective state of participants was measured, which is necessary less intense than experimentally evoked affective states. Under such conditions, the already weak association between cardioception and emotional experience may disappear. Concerning chronic (trait-like) emotional states, previous studies assessed anxiety, an affective state accompanied with marked vegetative changes (i.e. sympathetic activation), particularly for patients with related disorders (e.g. Domschke et al., 2010). For positive and negative affect in healthy participants, however, the intensity of the emotions, including both the experience and the vegetative changes, are much lower. Also, we did not asses other interoceptive channels that might be associated with the emotional experience. This holds particularly true for proprioceptive accuracy, where the investigation of a single joint and task represent only one aspect of the proprioceptive accuracy of the whole body (Han et al., 2013). Secondly, emotions assessed with self-report might not be at the same level of consciousness as accuracy and confidence related decisions (Smith & Lane, 2015).

Proprioception and body-related questionnaires

Finally (H4), we replicated the findings on the independence of proprioceptive accuracy and interoceptive sensibility and body competence (Horváth et al., 2019) and extended them to another proprioceptive modality (weight discrimination) and confidence rating. The lack of association between interoceptive sensibility, a construct that integrates interoceptive experience across multiple channels, and interoceptive confidence ratings is particularly intriguing.

Also, our results indicate that the self-reported acute dimension of interoception is also modality-specific, i.e. cannot be generalized. As both constructs represent perceived abilities and the former is embedded in the latter (at least theoretically), their independence is clearly worthy of further investigation.

Limitations

We investigated a sample of young people without known pathology; in this population, strong emotions were rarely presented. This leads to the decrease of variance in affective ratings which in turn makes the detection of associations difficult. The Schandry task has received considerable criticism recently (Ring et al., 2015; Ring & Brener, 2018; Desmedt et al., 2018, 2020; Zamariola et al., 2018); thus, although we applied a strict instruction which decreases the role of top-down factors, cardioception-related findings of the study might be flawed. Also, the joint reproduction task involves memory processes. Thus, cognitive abilities unrelated to interoception might also influence participants' performance.

Conclusion

Our findings indicate that interoceptive accuracy and confidence ratings are independent from each other in two proprioceptive modalities (joint reproduction with respect to the elbow joint and weight discrimination using the arm flexor muscles) and they are only weakly associated in the cardioceptive modality. There are no associations between accuracy and confidence ratings within the three interoceptive modalities. Finally, proprioceptive and cardioceptive accuracy and confidence ratings are not related to the acute and chronic affective state, interoceptive sensibility/body awareness and perceived body competence.

Acknowledgments

This research was supported by the Hungarian National Scientific Research Fund (KH 130319).

Author Contributions statement

All authors contributed to the conception and design of the study. ÁH and LV contributed to the assessment of data. FK processed the data and performed the statistical analyses. ÁH wrote the first draft of the manuscript, EF and KF wrote sections of the manuscript. All contributing authors read and commented on the last version of the manuscript.

Conflict of Interest Statement

The authors have no competing interest to report.

Contribution to the field statement

Interoceptive information, including proprioception, plays an essential role in the formation of the emotional experience. From both a theoretical and practical point of view, it can be assumed that individual differences in the processing of interoceptive signals may be associated with perceived affective feelings, body awareness and body competence. The processing of interoceptive information includes several major dimensions (1) accuracy, as assessed with behavioral tests, (2) confidence rating with respect to perceived performance in a behavioral test and (3) interoceptive sensibility, i.e., the perceived general ability to sense body changes. These dimensions can be applied to and measured for various modalities of interoception, such as cardioception, joint position sense, and weight discrimination. The goal of the present study was to investigate the between and within-modality associations between these dimensions of interoception, as well as to explore the associations between interception and the affective experience. We found that interoceptive accuracy and the respective confidence rating are only weakly associated for the cardioceptive modality and are independent from each other for joint position sense and weight discrimination. No between-modality associations were found. Finally, no associations between dimensions of interoception and positive and negative affect were found. In conclusion, various aspects of interoceptive processing are not generalized within and across sensory modalities.

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Study 3: Proprioception but not cardiac interoception is related to the rubber hand illusion

Abstract

The rubber hand illusion (RHI) is a widely used tool in the study of multisensory integration. It develops as the interaction of temporally consistent visual and tactile input, which can overwrite proprioceptive information. Theoretically, the accuracy of proprioception may influence the proneness to the RHI but this has received little research attention to date. Concerning the role of cardioceptive information, the available empirical evidence is equivocal. The current study aimed to test the impact of proprioceptive and cardioceptive input on the RHI.

58 undergraduate students (32 females) completed sensory tasks assessing proprioceptive accuracy with respect to the angle of the elbow joint, a heartbeat tracking task assessing cardioceptive accuracy (the Schandry-task) and the RHI.

We found that those with more consistent joint position judgements (i.e. les variable error) in the proprioceptive task were less prone to the illusion, particularly with respect to disembodiment ratings in the asynchronous condition. Systematic error, indicating a systematic distortion in position judgements influenced the illusion in the synchronous condition. Participants with more proprioceptive bias toward the direction of the rubber hand in the proprioceptive test reported a stronger felt embodiment. The results are in accordance with Bayesian causal inference models of multisensory integration. Cardioceptive accuracy, however, was not associated with the strength of the illusion.

We concluded that individual differences in proprioceptive processing impact the RHI, while cardioceptive accuracy is unrelated to it. Theoretical and practical relevance of the findings are discussed.

Keywords: rubber hand illusion, interoception, proprioceptive accuracy, cardioceptive accuracy, multisensory integration

Introduction

The fact that our self is embodied plays a fundamental role in the way we perceive the world (Gallagher, 2005; Allen & Tsakiris, 2018). The actual physiological state of our body forms the basis for emotions and decision making (Schachter & Singer, 1962; Schandry, 1981; Damasio, 1994; Herbert et al., 2007; Dunn et al., 2010; Garfinkel & Critchley, 2013; Quadt et al., 2018). Moreover, we interact with the world via bodily movements, and while doing so, we develop motor abilities that also influence our conscious experience (Gallagher, 2005). Also, bodily self-consciousness, i.e. the pre-reflexive awareness of the body and its functioning plays a vital role in the development of self-consciousness (Gallagher, 2005; Lenggenhager et al., 2007; Tsakiris, 2010; Aspell et al., 2013). It has two major aspects: agency and the feeling of body ownership (Tsakiris et al., 2006). Empirical investigation of these features has gained new momentum recently.

Concerning research on body ownership, one of the most widely used paradigms is the Rubber Hand Illusion (RHI). In this paradigm, one of the participants' hand is covered and visually replaced with a rubber hand. If the latter is synchronously stroked with the unseen real hand, participants will experience a feeling of body ownership (i.e. the feeling that the respective body part is their own hand) towards the fake hand, in addition, a feeling of disownership towards their own hand can also develop. On the behavioral level, when asked to indicate the felt position of their hand, a so-called proprioceptive drift can appear, i.e., the hand will be located between the actual and the rubber hand (Botvinick & Cohen, 1998).

The major factor behind the RHI is the congruency (temporal consistency) of visual and haptic information (Botvinick & Cohen, 1998). A third and incongruent source of information, i.e., the proprioceptive input, is adjusted to the former two by the brain in order to construct a unitary representation of the hand (Ehrsson et al., 2004; Ehrsson, 2011, 2020). As voluntary movements could completely block this process, participants are asked to avoid motor actions during the procedure (Hohwy, 2014). The brain, however, still receives proprioceptive information about the actual position of the hand: mechanoreceptors located in the joints, muscles, as well as in the skin around the joints continuously send input even in resting states (Proske & Gandevia, 2012). As proprioceptive information does not become completely overwritten, the illusion does not work in an all or nothing pattern. The impact of proprioceptive input is also indicated by the observation that increasing the distance between the real and the rubber hand makes the illusion less vivid (Lloyd, 2007; Preston, 2013; Mirams et al., 2017; Kalckert & Ehrsson, 2014).

Beyond exteroceptive and proprioceptive signals, visceroceptive information (i.e. afferent input from the internal organs) might also contribute to the feeling of body ownership. For example, it has been shown that seeing a virtual hand (Suzuki et al., 2013), body (Aspell et al., 2013; Park et al., 2016, 2018), or face (Sel et al., 2017) flashing up in synchrony with participants' heartbeat can increase the feeling of ownership towards it. It was concluded that interoceptive signals play an important role in the maintenance of the stability of bodily self-awareness (Allen & Tsakiris, 2018).

As interoceptive signals impact the feeling of body ownership, and people show individual differences in the perception of interoceptive information, it is reasonable to assume that individual differences in the proneness to the RHI will be associated with individual differences in the perception of interoceptive stimuli. In accordance with this idea, Tsakiris and colleagues (2011) reported a negative association between cardioceptive accuracy (i.e. the accuracy of the perception of heartbeats) and the strength of the RHI. In more detail, participants with high cardioceptive accuracy, as assessed by the mental heartbeat tracking task (Schandry, 1981), experienced less RHI (as assessed by proprioceptive drift) than those with low cardioceptive accuracy when the rubber hand was stroked in synchrony with the real hand. However, this association was not replicated by Crucianelli and colleagues (2018) and there is one study that reports the opposite relationship, namely that higher cardioceptive accuracy is associated with a stronger illusion (Suzuki et al., 2013). Overall, the relationship between cardioceptive accuracy and the RHI is yet to be clarified.

Similar to cardioceptive accuracy, proprioceptive acuity (i.e. the accuracy of perception of the position of the joints), as assessed with joint reproduction tests (Goble, 2010), shows substantial individual differences (Han et al., 2016). For example, acuity with respect to the elbow joint is influenced by handedness (Goble et al., 2006, 2009), age (Goble, 2010), and sport experience (Niespodziński et al., 2018). Considering the role of proprioception in the sensation of body posture (Proske & Gandevia, 2012) and that proprioceptive input is assumed to play a fundamental role in the development and maintenance of the feeling of body ownership (Sacks, 1985; Gallagher, 2005), these individual differences could also impact the RHI. It is also important to note, that interoceptive accuracy can not be generalized across modalities, i.e. there is no significant association between proprioceptive and cardioceptive accuracy (Ferentzi et al., 2018; Horváth et al., n.d.), which indicates that results established with cardioception are not generalizable to the proprioceptive modality.

Proprioceptive acuity with respect to the elbow joint might be especially worthy of investigation, as during the elicitation of RHI the position of the elbow is very probably differs for the real and the rubber hand, further enhancing the incongruency between them. Although this might be an important influencing factor, the position of the two hand is not always exactly specified. In the classical study, the rubber hand was placed "directly in front of the subject" (Botvinick & Cohen, 1998, p. 756), while the two hands were parallel in other studies (e.g. (Tsakiris et al., 2011). In both cases, the actual angle of the respective elbow joint (and perhaps also that of the shoulder) is not the same for the real and the rubber hand which might impact the RHI. Although studies showed that a certain level of congruency is needed between the real and the rubber hand (Pavani et al., 2000; Tsakiris & Haggard, 2005), only one study investigated the role of the individual differences in proprioceptive acuity (Motyka & Litwin, 2019). Motyka and Litwin (2019) reported controversial results: they proposed that precision of proprioceptive information (proprioceptive accuracy) does not play a role in the RHI, and also did not replicate the well-established (Lloyd, 2007; Preston, 2013; Mirams et al., 2017; Kalckert & Ehrsson, 2014) effect of the distance between the real and the rubber hand on the strength of the illusion. The goal of the present study was to test whether individual differences in the processing of cardiac and proprioceptive signals are significantly associated with proneness to the RHI. Based on previous findings and the theoretical considerations presented above, we hypothesized that the accuracy of the perception of (1) the elbow joint position and (2) cardioceptive signals would show a negative association with the proneness to the RHI.

Method

Participants

A priori sample size calculation was conducted using the G*Power v3.1.9.4. software (Faul et al., 2007). Based on the effect size (d = -0.758) derived from the data of Tsakiris and colleagues (Tsakiris et al., 2011) the minimum required sample size for a Student t-test was n = 58 ($\alpha = 0.05$, $1-\beta = 0.8$, two-tailed). Participants, who consumed alcohol and/or took psychoactive drugs within 8 hours before the experiment, and those with severe injury/disability of the arm were excluded. Participants were undergraduate students of the Eötvös Loránd University (N = 60, age = 20.4±1.54 yrs, 53% females, 87% right-handed). The participants took part in the experiment for partial course credit; before participation in the experiment, the completed a number of questionnaires that belong to another study. Questionnaire data belonging to asynchronous stimulation is missing for two cases due to technical issues. Everyone signed an informed consent at the beginning of the experiments. The research was approved by the Research Ethics Committee of the university.

Measurements

Experimental setup

Participants were asked to place their left arm in a box, which made them unable to see the distal part of their arm from the elbow joint to the fingers. Firstly, they were asked to indicate the assumed position of their unseen hand with blinded eyes (see below for details). This served as a baseline measurement for proprioceptive drift. After that, they put on a jacket, which had two left arms down from the elbow joint. The left arm of the participants was placed into the outer arm of the jacket. Next, participants placed their left hand back into the box, and we positioned the rubber hand 40 grades apart (i.e. toward the midline) from the real hand while participants' eyes were covered. When placing the rubber hand, we positioned it to match the length of the forearm and hand of the participants: the end of the middle finger of the rubber hand was placed in the same distance from the elbow joint than the end of the middle finger of the real hand (Figure 1). The next step was the presentation of the synchronous and the asynchronous stimulation block in a random order.

In the synchronous condition, the rubber hand and the real hand were stroked in a synchronous and spatially matched manner by the experimenter with a brush. One stroking lasted approximately one half second. We stroked each knuckle on the hand multiple times in a random order. The rhythm of the stroking (one stroke per second) was kept with acoustic help via a head set. The stroking period lasted for 90 seconds. After it, participants were asked to indicate the assumed position of their left hand three times (in the same way as in the baseline measurement) and to fill out the rubber hand questionnaire.

Concerning the asynchronous condition, the rubber hand and the real hand were stroked in an asynchronous manner, i.e., the experimenter stroked the real and the rubber hand in a different place and time. The rhythm and duration of the stroking were comparable to those of the synchronous condition. Following the stimulation, measurement of the perceived position of the left hand was conducted. Finally, the rubber hand questionnaire was filled out.

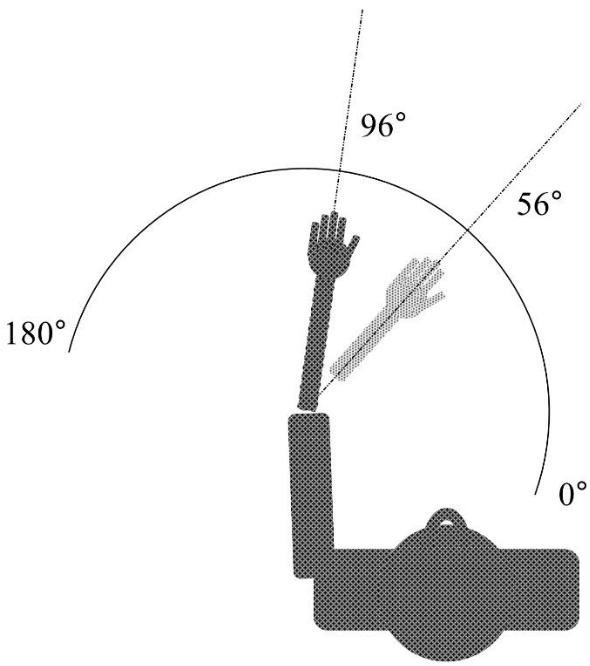

Figure 1. The concept of the experimental setup. The black arm is the real arm of the participant, hidden by a box. The grey arm indicates the rubber hand. The difference between the real and the rubber hand was 40 degrees, and the rubber hand was in the same distance from the elbow joint than the real hand. Measurements on proprioceptive drift were made in grades, using the elbow joint as center.

Proprioceptive drift

To assess proprioceptive drift, participants had to indicate the spatial position of their left hand. The measurement was conducted before any stimulation (baseline measurement), after synchronous stimulation and after asynchronous stimulation. To establish the position, in the first step, the experimenter placed the right index finger of the participant on a rotatable lever, which could move on a circle line. The finger was placed on the lever to be able to reach the same vertical line as the left middle finger (Figure 2). In this way, the end of the left middle finger of the rubber hand and the right index finger of the participant were on the same line, but in a different height. (Figure 2). In the next step, the participant was instructed to push the lever until the tip of the right index finger reached the felt position of the tip of the left middle finger (i.e. it was presumably above the left middle finger). The indicated position was registered in grades (°; see Figure 1). Participants' eye was blinded during the measurements (Figure 2.). Within every measurement (baseline, synchronous, asynchronous), this procedure was repeated three times with different random starting points, and the three judgements were averaged. Internal consistency (Cronbach’s alpha coefficient) of the measures was excellent for the baseline (0.860), synchronous (0.970), and asynchronous (0.976) conditions. Proprioceptive drift in the synchronous and asynchronous conditions was calculated by subtracting the baseline value from the respective post-intervention value. Negative values indicated a bias towards the rubber hand (i.e. towards the medial plane), while positive values showed a lateral bias (if the baseline judgment was bigger than 56° which was always the case).

Figure 2. Measurement of the perceived position of the participants' left hand. Participants had to move the lever until they felt that their right index finger (placed on the lever) was over their left middle finger (placed inside the box). A: rubber hand; B: participant's real hand; C: rotatable level, D: box hiding the real hand

Self-reported aspects of the RHI

To assess the subjective strength of the illusion, participants filled out The Rubber Hand Questionnaire (Hegedüs et al., 2014) after both interventions (synchronous and asynchronous). All but one statements were also included in the psychometric study of Longo and colleagues (2008) The questionnaire consists of 2 scales. One of them measures perceived embodiment towards the rubber hand with 4 items, whereas the other assesses the feeling of disembodiment towards the real hand with 3 items (see the items in Table 1.). Participants rated the statements on 11-point Likert scales (1=strongly disagree ... 11=strongly agree). Embodiment and disembodiment scores were calculated as the average of the respective items. Higher scores referred to higher levels of the RHI for both scales. Both scales in both conditions showed a high level of internal consistency (embodiment synchronous = 0.932, embodiment asynchronous = 0.909, disembodiment synchronous = 0.828, disembodiment asynchronous = 0.890).

Table 1. Items and descriptive statistics of the Rubber Hand Questionnaire

Scale	Question	synchronous M±SD	asynchronous M±SD
embodiment	It seemed like I was feeling the touch of the paintbrush in the location where I saw the rubber hand being touched	8.38±3.157	2.448±2.087
	It seemed like the touch I felt was caused by the paintbrush touching the rubber hand	6.77±3.397	2.757±1.759
	It seemed like the rubber hand was my hand	7.22±3.435	2.76±2.611
	It seemed like the rubber hand belonged to me	6.55±3.301	2.83±2.657
disembodiment	It seemed like I was unable to move my hand	5.017±3.58	3.09±2.952
	It seemed like my hand had disappeared	4.72±3.44	3.24±3.310
	It seemed like my hand was out of control	4.99±3.71	3.48±3.299

Proprioceptive accuracy

Proprioceptive accuracy was assessed via the Joint Position Matching Test in the left elbow joint (Goble, 2010). We used a motorized proprioceptor, which was able to measure the position of the elbow joint with a precision of 0.1 degree and move the hand with a given speed. 180° referred to a fully extended elbow, and 10-15° to a fully flexed elbow. Participants were blindfolded and instructed to hold a stable posture (straight torso, upper arm parallel with the ground, and in a straight line with of the chest), set with the help of an adjustable chair during the measurements. The starting position of the elbow joint was 160° (i.e. a conveniently extended elbow). From there, the device moved the participants' arm to the target positions with a speed of 12°/sec. After staying for 4 seconds in the target position, the arm was moved back to the starting position and stayed there for 1 second. Then the machine started moving again, with a speed of 8 °/sec, and participants had to push the button of the device when they felt that their arm reached back to the target position. After the button press the proprioceptor stopped and a new trial began. Participants executed overall 9 trials, with different target positions (30°, 45°, 60°, 75°, 90°, 105°, 120°, 135°, 150°) presented in a random order.

To evaluate performance, in the first step we calculated the error score for every trial, by taking the difference between the reproduced and the target position. Outliers above and below 2 standard deviations were removed because they may reflect the lack of attention in the given trial . This is especially relevant for this study, as participants' arm was moved by the device, thus they could not execute corrective movements. Missing values were imputed using the fully conditional specification (MCMC) and linear regression model options of SPSS v20 software. To evaluate performance, two scores were used. The systematic error score refers to the mean of the nine error scores; it showed a sufficient level of internal consistency (Cronbach α= 0.745). Variable error was calculated by taking the standard deviation of the error scores. Whereas systematic error score indicates participants' overall systematic bias, the variable error score reflects the consistency of their performance (Stilson et al., 1980; Goble et al., 2012; Boisgontier et al., 2012; Iandolo et al., 2015). Negative values of systematic error score refer to a bias towards the "inside" direction (toward the midline of the body), while positive values mean error towards the "outside" direction. Higher values of variable error score indicate a greater deviation around the systematic error, i.e. less consistency in elbow position judgements.

Cardioceptive accuracy

Cardioceptive accuracy was assessed with the mental heartbeat tracking task (Schandry, 1981). Participants were in a seated position with both feet on the ground and hands on their legs. To avoid estimation that might bias their performance (Ehlers & Breuer, 1996; Desmedt et al., 2018), they were instructed to silently count if they had the slightest heartbeat sensation on any part of their body, but otherwise not to count (i.e. estimation of heartbeats was prohibited). Participants indicated if they were ready to begin the task. Subsequently, the trials started with the experimenter saying "START" and ended with "STOP" instruction. Overall, three test intervals of different length (25,35,50 sec) were presented in a random order after a 15 seconds practice trial. We measured actual heartbeats (ECG) with the NeXus recording system (NeXus Wireless Physiological Monitoring and Feedback: NeXus-10 Mark II, Version 1.02; BioTrace+ Software for NeXus-10 Version: V201581; Mind Media BV, Herten, the Netherlands). For every interval, heartbeat perception scores were calculated as: $1 - |(HB_{recorded} - HB_{counted})/ HB_{recorded}|$. Scores were averaged to determine individual cardioceptive accuracy. Internal consistency of the Schandry task was very high (Cronbach α =0.950).

Procedure

The three assessments - the RHI, proprioceptive accuracy, and cardioceptive accuracy - were presented in a randomized order in one testing session. The entire procedure took approximately 60 minutes.

Statistical analysis

No part of the study procedures and data analyses were preregistered. Raw data is available as supplementary materials. Data was analyzed with the JASP software v0.11 (JASP Team, 2019). Both frequentist and Bayesian statistical analyses were conducted. In the frequentist approach, six repeated-measures analyses of variance (ANOVA) for the two conditions (synchronous vs. asynchronous stimulation) with proprioceptive (systematic error or error variability) and cardioceptive accuracy as covariates were carried out for the three outcome measures of the RHI (drift, embodiment, disembodiment). The centered version of both variables were used

(Schneider et al., 2015). IAc was transformed to better fit normality (demeaned values were divided by the Gaussian membership values of the same demeaned values, and the effect of the demeaning was reset by adding the mean of the original data).

In the Bayesian ANOVA, first strength of the RHI was compared to a null model including subject, then cardioceptive accuracy was compared to a null model including subject and condition (synchronous and asynchronous), finally the measure of proprioceptive accuracy (systematic error or error variability) was compared to a null model including subject, condition and cardioceptive accuracy. Similar to the frequentist analysis, this pattern was repeated for the three RHI related outcome measures, resulting in six analyses overall. Results are uniformly presented as BF_{10} coefficients, i.e., the ratio of the likelihood of the data fitting under the alternative hypothesis to the likelihood of fitting under the null hypothesis. BF_{10} between 0.33 and 1 indicates weak or anecdotal evidence in favor of the null hypothesis; whereas values between 1 and 3 indicate weak or anecdotal evidence in favor of the alternative hypothesis; values above 100 are considered decisive (Jarosz & Wiley, 2014).

Results

Descriptive statistics of the assessed variables are presented in Table 2.

Table 2. Descriptive statistics

	N	M±SD	min-max
Proprioceptive accuracy: Systematic error (º)	60	6.373±4.892	- 11.341 - 15.724
Proprioceptive accuracy: Variable error (º)	60	6.696±2.398	2.344 - 11.612
Cardioceptive accuracy	60	0.474±0.302	0.000 - 0.939
Drift (synchronous) (º)	60	-0.650±6.341	-13.667 - 23.000
Drift (asynchronous) (º)	60	0.117±5.181	-9.333 - 21.333
Embodiment (synchronous)	60	7.229±3.031	1.000 – 11.000
Embodiment (asynchronous)	58	2.621±1.874	1.000 – 8.000
Disembodiment (synchronous)	60	4.906±3.290	1.000 – 11.000
Disembodiment (asynchronous)	58	3.270±2.890	1.000 – 11.000

Associations between indicators of the RHI and measures of interoceptive accuracy are summarized in Table 3.

Table 3. Associations (Spearman rho coefficients; p-values) between measures of the rubber hand illusion and cardioceptive accuracy

	Cardioceptive accuracy	Proprioceptive accuracy: Systematic error	Proprioceptive accuracy: Variable error
Drift (synchronous)	-0.009; 0.947	0.031; 0.812	0.053; 0.686
Drift (asynchronous)	-0.003; 0.985	0.076; 0.562	-0.063; 0.633
Embodiment (synchronous)	0.010; 0.939	-0.137; 0.298	0.141; 0.283
Embodiment (asynchronous)	-0.074; 0.582	-0.031; 0.815	0.326; 0.012*
Disembodiment (synchronous)	-0.102; 0.437	0.056; 0.671	0.050; 0.704
Disembodiment (asynchronous)	0.084; 0.532	0.054; 0.685	0.302; 0.021*

*p<0,05

We found significant correlations in two cases: variable error was associated with embodiment score in the asynchronous condition (r_s=0.326; p=0.012) and disembodiment score the synchronous condition (r_s=0.302; 0.021*) (Figure 3).

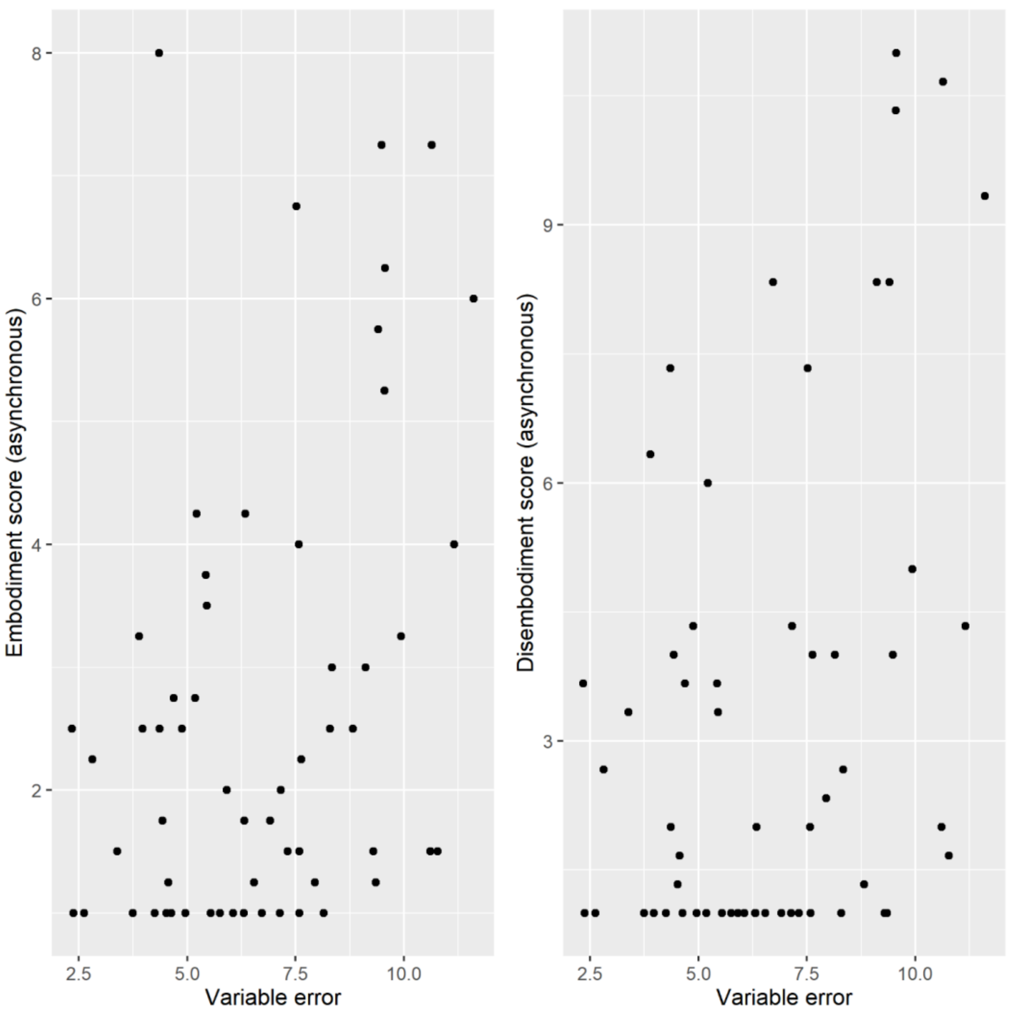

Figure 3. Associations of variable error in proprioceptive judgements ad embodiment score and disembodiment score.

Results of frequentist ANOVAs for the two measures of proprioceptive accuracy are presented in Table 4 and 5, respectively. In summary, no significant effect for proprioceptive drift was found; however, main effects for embodiment and disembodiment were consistently significant. The systematic error measure of proprioceptive accuracy did not significantly impact the outcome of the stimulations, whereas the variable error measure was marginally significant for both embodiment and disembodiment In these cases, higher levels of embodiment and disembodiment indicating higher levels of the RHI, were positively associated with higher variable error. Moreover, the interaction between systematic error and embodiment, and between error variability and disembodiment were also significant. To better understand the origins of these interactions, measures of proprioceptive accuracy were transformed into binary form by median split and visualized (Figure 4 and 5).

Table 4. Results of repeated measures ANOVAs with systematic error as the measure of proprioceptive accuracy

Measure of the RHI	Within-subject main effect (synchronous vs asynchronous condition)	Cardioceptive accuracy	Proprioceptive accuracy	Condition x cardioceptive accuracy interaction	Condition x proprioceptive accuracy interaction
Proprioceptive drift	$F(1,57)=1.980; p=0.165; \eta^2=0.004$	$F(1,57)=6.478e-4; p=0.980; \eta^2<0.001$	$F(1,57)=0.083; p=0.775; \eta^2<0.001$	$F(1,57)=0.005; p=0.944; \eta^2<0.001$	$F(1,57)=0.002; p=0.967; \eta^2<0.001$
Embodiment	$F(1,55)=149,587; p<0.001; \eta^2=0.448$*	$F(1,55)=0.115; p=0.736; \eta^2=0.002$	$F(1,55)=0.486; p=0.488; \eta^2=0.009$	$F(1,55)=0.009; p=0.927; \eta^2=3.667e-5$	$F(1,55)=5.421; p=0.024; \eta 2=0.016$*
Disembodiment	$F(1,55)=17.051; p<0.001; \eta^2=0.0071$*	$F(1,55)=0.127; p=0.722; \eta^2=0.002$	$F(1,55)=1.335; p=0.253; \eta^2=0.024$	$F(1,55)=1.848; p=0.180; \eta^2=0.008$	$F(1,55)=0.061; p=0.806; \eta^2<0.001$

+p<0.10, *p<0.05

Table 5. Results of repeated measures ANOVAs with error variability as the measure of proprioceptive accuracy

Measure of the RHI	Within-subject main effect (synchronous vs asynchronous condition)	Cardioceptive accuracy	Proprioceptive accuracy	Condition x cardioceptive accuracy interaction	Condition x proprioceptive accuracy interaction
Proprioceptive drift	$F(1,57)=17.634; p=0.165; \eta^2=0.004$	$F(1,57)=2.365e-7; p=1.000; \eta^2<0.001$	$F(1,57)=0.178; p=0.674; \eta^2=0.003$	$F(1,57)=0.002; p=0.969; \eta^2<0.001$	$F(1,57)=1.277; p=0.263; \eta^2=0.003$
Embodiment	$F(1,55)=137.770; p<0.001; \eta 2=0.448$*	$F(1,55)=0.002; p=0.961; \eta 2<0.001$	$F(1,55)=3.374; p=0.072; \eta 2=0.058^+$	$F(1,55)=0.116; p=0.735; \eta 2<0.001$	$F(1,55)=0.737; p=0.394; \eta 2=0.002$
Disembodiment	$F(1,55)=18.189; p<0.001; \eta 2=0.070$*	$F(1,55)=0.069; p=0.795; \eta 2=0.001$	$F(1,55)=3.674; p=0.060; \eta 2=0.063^+$	$F(1,55)=2.429; p=0.125; \eta 2=0.009$	$F(1,55)=4.608; p=0.036; \eta 2=0.018$*

+p<0.10, *p<0.05

In the first case (Figure 4), those with lower systematic error score (i.e. more prone to bias the position of the elbow-joint towards the body in Joint Position Reproduction test) reported higher embodiment scores in the synchronous condition than those with higher systematic error.

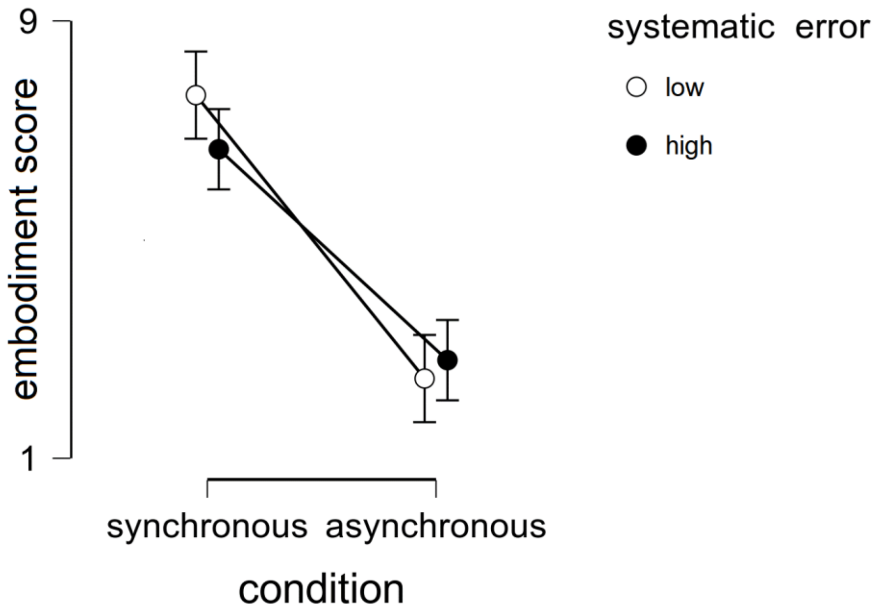

Figure 4. Visualization of the interaction between systematic error (using a binary form) and felt embodiment (error bars indicate 95% confidence intervals)

Concerning the second interaction (Figure 5), lower variable error (i.e. higher consistency) was associated with less felt disembodiment (weaker illusion) in the asynchronous condition.

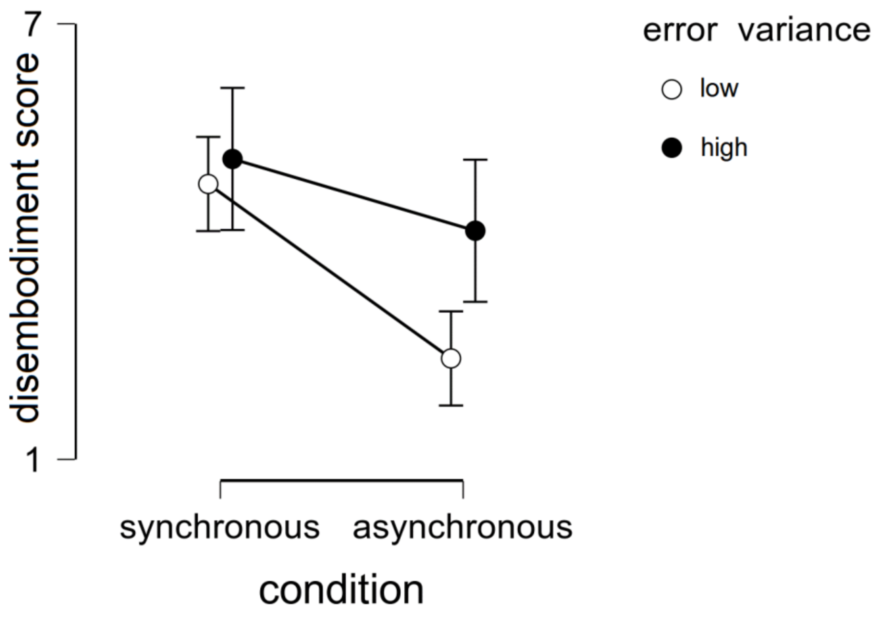

Figure 5. Visualization of the interaction between error variability (using a binary form) and felt disownership (error bars indicate 95% confidence intervals).

In contrast to proprioceptive accuracy, cardioceptive accuracy had no impact on the results whatsoever (i.e. neither significant interactions nor significant main effects were found, see Table 3 and Table 4).

Bayesian analysis supported these conclusions (see Table 6). Evidence on the main effect for embodiment and disembodiment was decisive, whereas weak evidence for the impact of the variable error measure of proprioceptive accuracy was revealed. No BF_{10} was higher than 1 for proprioceptive drift, cardioceptive accuracy, and the systematic error measure of proprioceptive accuracy.

Table 6. Results of Bayesian repeated measures ANOVAs

Measure of the RHI	Within-subject main effect (synchronous/asynchronous condition) *vs.* null model	Cardioceptive accuracy *vs.* null model including condition	Proprioceptive accuracy (systematic error) *vs.* null model including condition and cardioceptive accuracy	Proprioceptive accuracy (variable error) *vs.* null model including condition and cardioceptive accuracy
Proprioceptive drift	BF_{10} = 0.474	BF_{10} = 0.416	BF_{10} = 0.531	BF_{10} = 0.610
Embodiment	BF_{10} = 4.216e+16	BF_{10} = 0.290	BF_{10} = 0.458	BF_{10} = 1.385
Disembodiment	BF_{10} = 182.147	BF_{10} = 0.294	BF_{10} = 0.689	BF_{10} = 1.709

Note: BF_{10}:Probability of the alternative hypothesis compared to the null hypothesis

Post-hoc analysis

In a post-hoc correlation approach, we extended our analysis with another three measures that indicate the strength of the illusion: proprioceptive shift, embodiment index and disembodiment index. These indices were calculated as the differences between the synchronous and asynchronous stimulation (see Supplementary material 1); positive values consistently indicate higher values in the synchronous stimulation. Systematic error was associated negatively with the embodiment index (r=-0.247, p=0.037), indicating that systematic distortion in hand position judgements towards the rubber hand predicts stronger illusion. Variable error was negatively associated with disembodiment index (r=-0.289, p=0.028), i.e. less reliable joint position sense predicts a stronger illusion. No other significant relationships were revealed (for details, see Supplementary material 1)

Further, to shed more light on the factors behind the associations, we subdivided the two self-report scales used in this study: the embodiment scale was subdivided into "referral of touch" and "ownership" subscales. The disembodiment scale was subdivided into "loss of agency" and "loss of hand position" subscales. The ownership subscale in the asynchronous condition correlated with variable error (r=0.287, p=0.029), and loss of agency subscale in the asynchronous condition also correlated with variable error (r=0.276, p=0.036). No other significant relationships were observed. For calculation and results, see Supplementary material 2.

Moreover, we replicated previous findings (Ferentzi et al., 2018; Horváth et al., n.d.) on the independence of cardioceptive and proprioceptive accuracy (Supplementary material 3).

Discussion

Somatosensory illusions such as the RHI represent intriguing phenomena and scientifically useful opportunities to better understand how the brain constructs the conscious representation of our body in terms of bodily self-consciousness. The primary aim of this study was to test whether cardioceptive and proprioceptive accuracy are significantly associated with the strength of the RHI. In an experiment with the participation of 60 young individuals, no difference between synchronous and asynchronous skin stimulation with respect to proprioceptive drift was measured, whereas changes in felt embodiment of the rubber hand and disembodiment of the real hand were observed. Individual differences in the variance of position judgements (proprioceptive variable error) with respect to the elbow joint showed a weak positive association with felt embodiment and disembodiment, whereas no association for the systematic error measure of proprioceptive accuracy was revealed. Moreover, those with lower proprioceptive systematic error score reported higher embodiment scores in the synchronous condition than those with higher systematic error. Lower variance of the proprioceptive error score was associated with less felt disembodiment in the asynchronous condition. After subdividing the embodiment and disembodiment scales to referral of touch, ownership, loss of agency and loss of hand subscales, we found that only ownership and loss of agency subscales in the asynchronous condition correlated with variable error. These results suggest that probably these are the two key aspects of the RHI that are influenced by the reliability of proprioceptive signals. In a post-hoc analysis, we also found that embodiment index (the difference between embodiment scores the synchronous and the asynchronous stimulation) was associated with systematic error, and embodiment index (the difference between disembodiment scores the synchronous and asynchronous stimulation) was associated with variable error. These results show that the conclusion of our study (i.e. proprioceptive accuracy is associated with the RHI) still holds true if the RHI is conceptualized differently. Finally, cardioceptive accuracy, as assessed by the mental heartbeat tracking paradigm by Schandry (1981), was not associated with any indicator of the strength of the illusion (embodiment, disembodiment or proprioceptive drift).

Our results suggest that individual differences in proprioceptive information processing do impact the subjective strength of the illusion. This result is in contrast with that of Motyka and Litwin (2019), who found that proprioceptive accuracy is not associated with the strength of the RHI. One possible explanation for the inconsistency may be the difference in the measurement of proprioceptive accuracy: Motyka and Litwin (2019) used an active version of the Joint Position Reproduction task (i.e. participants had to move their arm), while we used a passive version (i.e. the arm was moved by the device). Accuracy measured with passive and active versions may underlie different aspects of proprioception (Elangovan et al., 2014), and it is likely that the passive version is the more relevant in this case, as participants can not conduct movements during the induction of the RHI. Another possible explanation is that their setting to measure RHI was also different from ours, as they applied a subliminal and displacement procedure.

Different indicators of proprioceptive accuracy (systematic error and error variability) showed different relationship with the RHI. Error variability, indicating the unreliability of elbow joint position judgements (Boisgontier et al., 2012; Goble et al., 2012), had a weak main effect on felt embodiment and disembodiment. Thus, those who process proprioceptive information in a less reliable way appear more likely to experience a more vivid RHI, independently of the stimulation (synchronous or asynchronous). One possible explanation for this finding is based on the nature of multisensory integration. Probabilistic models of multisensory integration propose that when information from different sources becomes integrated, various modalities are considered with different weight in the calculation. For optimal integration, the weight the given modality gets is based on its relative reliability (Ernst & Banks, 2002). When judging hand-position, the central nervous system can combine visual and proprioceptive information very efficiently by taking their direction-dependent precision into account (van Beers et al., 1999, 2002). Feeling of body ownership relies on multisensory integration and Bayesian causal inference (Kilteni et al., 2015). In relation to the RHI, Samad and colleagues (2015) presented a computational account for the RHI, and proposed that it is based on two factors: the spatial consistency of proprioceptive and visual information, and the temporal consistency of visual and haptic information. Fang and colleagues (2019) showed electrophysiological evidence in macaques, while Chancel and Ehrsson (2020) showed behavioral data in human participants, which supports the Bayesian causal interference model of body ownership. With respect to proprioceptive information, there are two important predictions of the aforementioned models: the less precise proprioceptive signals are, and the closer the rubber hand to the real hand is, the higher the probability of the occurrence of the illusion or its strength should be (Motyka & Litwin, 2019). Assuming that variable error in the Joint Position Reproduction test signals the precision of proprioceptive information, the prediction is in accordance with our findings: for those individuals, who process proprioceptive information in a less reliable way (i.e. show a higher level of variable error), proprioceptive information (indicating that the real hand belongs to the person) gets relatively less weight compared to other stimuli (suggesting that the rubber hand belongs to them). In consequence, the illusion will be stronger. Assuming that the direction and magnitude of the systematic error in position judgements are signaling the central nervous system's tendency to make a distortion in a similar magnitude and direction while encoding hand position, the prediction is in accordance with our findings: for those individuals, whose central nervous system encodes the position of their hand closer to the rubber hand will experience a stronger illusion.

The above discussed multisensory explanation for the main effect of error variance is further supported by the significant interaction between proprioceptive error variance and the disembodiment scores. The analysis of the interaction revealed that lower levels of variability in proprioceptive accuracy was found to be associated with lower levels of disembodiment of own hand during asynchronous stimulation, whereas no such association was observed in the synchronous stroking condition. (Figure 5.). This finding is consistent with the Bayesian causal inference (BCI) model of body representation (Samad et al., 2015; Fang et al., 2019), which takes into account that multisensory integration is beneficial only if the different sensory cues have a common origin, therefore it assumes that the statistical-computational features of cue combination depends on the inferred probability of that the sensory stimuli originate from the same source. Evidence of how neural processes implement causal inference during the RHI was recently shown by Fang and colleagues (2019) who collected both behavioral and electrophysiological data from experiments in monkeys. As their analysis suggests, the probability that visual and proprioceptive stimuli share a common source influences two characteristic features of cue combination: (1) the extent to which sensory signals are fused corresponding to the computational rules of optimal integration, and (2) the extent to which sensory signals are segregated resulting in the separate unisensory processing of stimuli (see also: Ehrsson & Chancel, 2019). It follows that when the likelihood of the common cause is low, the segregation of visual and proprioceptive information dominates the statistical characteristics of cue combination, and not optimal integration (or forced fusion, as it was termed by Fang and colleagues, 2019) - consequently, the representation of own hand is determined dominantly by proprioceptive information. The BCI model elaborated by Fang and colleague predicts that sensory uncertainty modulates the dynamics between the fusion and the segregation of signals (see also: Ehrsson & Chancel, 2019). Another important prediction of the model is that when the estimated probability of the common source is low, proprioception gets more weight in the dynamics mentioned above than vison, in contrast to when the integration of proprioceptive and visual information dominates the neural processes underlying the sense of hand ownership. The interaction between proprioceptive error variance and disembodiment confirms these predictions by showing that proprioceptive uncertainty had a greater impact on the RHI in the asynchronous condition (when the inferred likelihood of common cause is lower) than during synchronous stroking. Even though the interaction was significant only with respect to disembodiment ratings, it is important to emphasize that the correlational analysis of our data revealed the very same pattern of associations between embodiment and proprioceptive error variability scores as was discussed above in relation to disembodiment scores, when comparing synchronous and asynchronous conditions (see Table 2. and Figure 4.).

Systematic error, indicating systematic distortion (towards the center of the body) in elbow joint position judgements (Boisgontier et al., 2012; Goble et al., 2012) had no main effect on embodiment and disembodiment ratings. However, based on the interaction between condition and systematic error, we can conclude that those whose perception of the hand is more biased towards their body experienced a comparatively stronger embodiment in the synchronous condition (Figure 4.). Since the rubber hand was positioned toward the center of the body relative to the real hand in our experimental setting, systematic distortion towards the body in fact meant a bias towards the rubber hand. In this sense, this result is in accordance with studies showing that the closer the real and the rubber hands are, the stronger the illusion is (Lloyd, 2007; Preston, 2013; Kalckert & Ehrsson, 2014; Mirams et al., 2017).In our case not the real, but the felt position was closer to the rubber hand. However, we detected this effect only for the embodiment score in synchronous condition.

In this study, contrary to our hypothesis, we did not find a significant association between cardioceptive accuracy and the strength of the RHI. In fact, Bayesian analysis revealed positive evidence in favor of the null hypothesis (i.e. the lack of association). There is no agreement in the literature about the role of cardioceptive accuracy in the development of the RHI. Our results do not support the conclusions of previous studies that reported positive (Suzuki et al., 2013) or negative (Tsakiris et al., 2011) relationships between cardioceptive accuracy and the strength of the illusion. Our finding is rather in accordance with that of Crucianelli and colleagues (2018) namely, that cardioceptive accuracy is not associated with the vividness of the rubber hand illusion. Cardioceptive accuracy is often considered generalizable to other interoceptive modalities and used as a measure of general interoceptive ability, however empirical findings do not support this approach (Ferentzi et al., 2017, 2018; Garfinkel et al., 2017). Thus, it seems more plausible that more localized interoceptive modalities, such as thermosensation and proprioception with respect to the hand, are primarily involved in the RHI. The present findings support this idea. It is also important to note that whereas the ,Crucianelli and colleagues (2018) study and the present study used the mental heartbeat tracking task, a forced-choice task was applied by Suzuki and colleagues (2013).

Limitations

One limitation of our study is that we did not find significant difference in proprioceptive drift between asynchronous and synchronous position. Other studies are quite consistent that participants feel the position of their stimulated hand more closely to the rubber hand in the synchronous condition than in the asynchronous (e.g. (Botvinick & Cohen, 1998; Tsakiris et al., 2011). One possible explanation for the lack of proprioceptive drift is that we used a rather unusual experimental setting. In most of the studies, the rubber hand is parallel with the real hand which was not the case in our setting (e.g. (Botvinick & Cohen, 1998; Tsakiris et al., 2011). The sharp difference in the subjective judgements between the two conditions showed that the illusion was evoked. Abdulkarim and Ehrsson (2016) also showed that proprioceptive drift is not a necessary factor in the development of the subjective changes in body ownership in the RHI

In our experimental arrangement, the only difference in the position of the real and the rubber hand was in the angle of the elbow joint. This means that every other joint angle (most importantly the position of the shoulder), was consistent with the position of both the real and the rubber hand. Since proprioceptive accuracy scores measured in different joints are not necessarily related (Han et al., 2013), our findings are limited to the elbow joint only. Another notable point should be made concerning the measurement of cardioceptive accuracy. There are scholars who use the Whitehead-paradigm (Whitehead et al., 1977) along with the RHI, arguing that it involves the comparison of interoceptive and exteroceptive information, so it requires multisensory integration (Suzuki et al., 2013). Processes of multisensory integration, however, occur at a non-conscious level in the case of RHI, while the Whitehead-paradigm requires conscious multitasking. The Schandry task does not have this limitation. On the other hand, the validity of the Schandry task was questioned recently based on the argument that it is influenced by factors that are not inherent part of interoception (Desmedt et al., 2018; Ring & Brener, 2018; Zamariola et al., 2018; Corneille et al., 2020; Zimprich et al., 2020).

Future directions

These findings are of relevance not only for basic research on the phenomenon of the RHI but also for better understanding clinical phenomena that have been associated with disturbances in interoception and body representation such as chronic somatic symptom distress which has been found to be associated with alterations in the RHI (Miles et al., 2011). In this regard, a lower strength of the RHI as found in people with higher levels of chronic somatic symptoms and somatoform dissociation (Miles et al., 2011) may suggest an overreliance on proprioceptive information processing as part of chronic symptom perceptions. In accordance with the aforementioned study, a clinical group of somatoform patients also reported a less strong illusion than healthy control (Perepelkina et al., 2019). The cause of the lower level illusion is attributed to a decreased reliance on the current sensory input in these studies (Miles et al., 2011; Perepelkina et al., 2019). But our study's conclusion, namely that better proprioceptive accuracy is associated with a less strong illusion, and the results of Scholtz and colleagues (2001), who found that somatoform patients showed better proprioceptive acuity, together may suggest an overreliance on proprioceptive information processing as part of chronic symptom perceptions. Further studies preferably in patients suffering from relevant clinical conditions are needed to directly test this hypothesis.

Conclusion

In this empirical study, we investigated the association between the RHI and cardioceptive accuracy and proprioceptive, respectively. We revealed that less consistent judgement and the degree of distortion towards the rubber hand in proprioception increased subjective aspects of the illusion. However, cardioceptive accuracy was not associated with it. These findings have important theoretical relevance for different models of multisensory integration and body ownership, and may have important consequences for clinical practice too.

Acknowledgements

This research was supported by the Research Fund of the National Research, Development and Innovation Office (KH 124132).

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Study 4: The measurement of proprioceptive accuracy: A systematic literature review

Highlights

- Proprioceptive accuracy is an important aspect in the evaluation of sensorimotor functioning.
- No standard, widely accepted assessment exists.
- In this review, we found that different aspects of proprioception (i.e., the perception of joint position, movement and movement extent, trajectory, velocity and the sense of force, muscle tension, weight, and size) can be measured with different paradigms.
- As different tests do not necessarily measure the same construct, the appropriate aspect should be measured.

Abstract

Proprioceptive accuracy refers to the individual's ability to perceive proprioceptive information, i.e., the information referring to the actual state of the locomotor system, which originates from mechanoreceptors located in various parts of the locomotor system and from tactile receptors located in the skin. Proprioceptive accuracy appears to be an important aspect in the evaluation of sensorimotor functioning; however, no widely accepted standard assessment exists. In this systematic review, our goal was to identify and categorize different methods that are used to assess different aspects of proprioceptive accuracy. A literature search was conducted in 5 different databases (PubMed, SPORTDiscus, PsycINFO, ScienceDirect, and SpringerLink). Overall, 1139 scientific papers reporting 1346 methods were included in this review. The methods assess 8 different aspects of proprioception: (a) the perception of joint position, (b) movement and movement extent, (c) trajectory, (d) velocity, and the sense of (e) force, (f) muscle tension, (g) weight, and (h) size. They apply various paradigms of psychophysics (i.e., the method of adjustment, constant stimuli, and limits). As the outcomes of different tasks with respect to various body parts show no associations (because proprioceptive accuracy is characterized by site-specificity and method-specificity), the appropriate measurement

method for the task needs to be chosen based on theoretical considerations and/or ecological validity.

Keywords: Assessment; Kinaesthesia; Motor control; Proprioception; Proprioceptive accuracy

Introduction

Optimal motor control requires proprioceptive information, which originates from mechanoreceptors located within the locomotor system (Riemann & Lephart, 2002). To experience proprioception, the brain processes input from proprioceptors (i.e., muscle spindles, which are located in the muscle belly and process information about the length and rate of stretch, and Golgi tendon organs, which pass on information about tension and, consequently, the force of contraction) and mechanoreceptors (i.e., Pacinian, Ruffini, Merkel, and Meissner corpuscle end-organs) located in the skin and ligaments as well as in joint capsules (Proske & Gandevia, 2012). Moreover, not only afferent but efferent signals (i.e., efference copy of the motor command, sense of effort) contribute to the sensation (Proske & Gandevia, 2012). Normally developed humans are able to automatically process, integrate, and consciously perceive force, effort, weight and their body position, movement, and muscle tension based on this type of (proprioceptive) information (Stillman, 2002) and use it for goal-oriented motor behavior (Sarlegna & Sainburg, 2009).

Proprioceptive accuracy refers to the individual’s ability to perceive proprioceptive information (Goble, 2010; Han et al., 2016). This ability is associated with important aspects of motor control and performance. For example, proprioceptive accuracy is positively associated with sport achievement in elite athletes (Han et al., 2015). Moreover, better proprioceptive accuracy in the elbow joint was found to be related to better throwing performance in basketball (Sevrez & Bourdin, 2015), darts (Feng et al., 2019) and water-polo (Hams et al., 2019). Concerning the negative aspects, worse proprioceptive accuracy predicts a higher chance of getting injured (Cameron et al., 2003); also, as proprioceptive accuracy deteriorates with aging (Goble, 2010) it may contribute to an increased risk of falls (Wingert et al., 2014). It has also been shown that physically active individuals are characterized by better proprioceptive accuracy, and physical activity can compensate for the negative impact of aging on proprioceptive accuracy (Ribeiro & Oliveira, 2007). Proprioceptive training (i.e., "an intervention that targets the improvement of proprioceptive function," (Aman et al., 2015, p. 2) often including proprioceptive accuracy) is an efficient method to prevent injuries and improve motor performance (Aman et al., 2015).

Based on the aforementioned associations, proprioceptive accuracy appears to be an important characteristic in the evaluation of sensorimotor functioning, for example, for sport selection (Han et al., 2015) or for assessing the risk of injury and falls (Cameron et al., 2003; Hoang et al., 2016; Lord et al., 1994; Witchalls et al., 2012). Also, measuring the change in proprioceptive accuracy is often used to evaluate the effectiveness of different interventions, e.g., various surgical outcomes (Isaac et al., 2007) rehabilitation (Edmonds et al., 2003) and warming-up (Subasi et al., 2008) techniques.

There is a wide variety of methods that have been developed to measure various aspects of proprioceptive accuracy. Hillier and colleagues (2015) identified three clusters of methods: joint position detection, passive motion detection, and passive motion direction discrimination. Starting from a different point of view, Han and colleagues (2016) described three paradigms based on the classical methods developed for psychophysical experiments (Gescheider, 1997): (a) joint position reproduction test, based on the method of adjustment, i.e., participants have to adjust the level of a stimulus to a reference; (b) active movement extent discrimination assessment, based on the method of constant stimuli, i.e., the stimuli are presented in pairings, and participants have to compare them; and (c) threshold to detection of passive motion, based on the method of limits, i.e., participants have to indicate when they perceive the appearance or disappearance of a stimulus (Gescheider, 1997; Han et al., 2016). An important limitation of these reviews is their relatively narrow definition of proprioception. Han and colleagues (2016) defined proprioceptive accuracy as "an individual's ability to integrate the sensory signals from mechanoreceptors to thereby determine body segment positions and movements in space" (Han et al., 2016, p. 81). This account does not take into consideration certain important aspects of proprioception, such as the perception of heaviness, force, and muscle tension (Proske & Gandevia, 2012). Similarly, the review of Hillier and colleagues (2015) also included only a narrow range of methods, namely: joint position detection, passive motion detection threshold, and passive motion direction detection. Our recent review applies a more inclusive approach to proprioception than the previous papers (Han et al., 2016;

Hillier et al., 2015). A new review is also reasonable because of the growing literature on proprioception and the need to cover new tests developed since the publication of previous reviews.

The primary goal of the present systematic review was to identify and categorize the methods developed and used to measure proprioceptive accuracy in a comprehensive way by taking into consideration all important aspects of proprioception (i.e., sense of joint position, movement and movement extent, force, and heaviness). In doing this, this paper will help practitioners and researchers to find the method that best suits their needs for the assessment of proprioceptive accuracy.

Methods

The study was registered at PROSPERO (CRD42020209136). While conducting this review, we followed the recommendations of the PRISMA (Preferred Reporting Items for Systematic Reviews and Metal-Analysis) statement (Liberati et al., 2009). Search strategy characteristics and study inclusion/exclusion criteria are reported in Table 1. The abstracts and titles of the articles were searched in 5 different databases (PubMed, SPORTDiscus, PsycINFO, ScienceDirect, and SpringerLink), including every available article (i.e., not only free text articles), without a restriction to publication date. The search was conducted on November 11, 2020. Proprioceptive accuracy was defined as the acuity of perception of proprioceptive information, i.e., the information referring to the actual state of the locomotor system. It includes the processing of input from proprioceptors located in various parts of the locomotor system and from tactile receptors on the skin. It does not include visual and vestibular information. To decide on inclusion, 2 independent readers (KS and ÁH) read the titles and abstracts of the papers as a first step. An article was excluded in this step only if both authors deemed it ineligible. In the next step, ÁH read the full text articles and made the final decision on inclusion. In case of any ambiguity, FK and EF decided on the inclusion of the article.

Table 1. Characteristics of the literature search.

Keywords for literature search	("propriocept*") AND ("accuracy" OR "acuity" OR "ability" OR "abilities" OR "awareness" OR "sensibility" OR "sensitivity" OR "weight discrimination" OR "movement discrimination" OR "movement detection" OR "joint position sense" OR "force sense" OR "movement sense" OR "movement perception" OR "force perception")
Databases	PubMed, SPORTDiscus, PsycINFO, ScienceDirect, and SpringerLink
Language	English only
Document type	Peer-reviewed empirical article
Inclusion criteria	Population: any human Intervention: not necessary Comparison: not necessary Outcome: objective measure of proprioceptive accuracy
Exclusion criteria	dissertations, theoretical papers, conference materials, non-English articles

Results

Included studies

Overall, 6378 articles were identified in the database research. After removing the duplicates, 4293 remained. After reading the titles/abstracts, a further 2332 articles were excluded because they did not meet the inclusion criteria. Based on the full texts of the remaining 1961 articles, a further 822 studies were excluded. In total, 1139 studies were included in the review. Following this, 1346 proprioceptive accuracy measurements were identified in a total of 1139 papers (Fig. 1); in a number of papers, multiple methods for the assessment of proprioceptive accuracy were used in the same sample. After that, measurement techniques were clustered based on their approach to measurement (Table 2). We used 2 main criteria to categorize the methods: (a) what aspect of proprioceptive accuracy was assessed, and (b) what psychophysical approach was applied, which could be: (a) the method of adjustment, where participants have to adjust the level of a stimulus to a reference; (b) the constant methods, which include both the method of constant stimuli, where participants have to judge standard and comparison stimuli presented in pairings, and the method of single stimuli, where participants judge a single stimulus presented alone; or (c) the method of limits, where participants have to indicate the appearance or disappearance of a stimulus. The full list of included articles is available at: https://osf.io/8f2zn/.

Fig. 1. Selection process of the articles, based on Moher and colleagues.(2009)

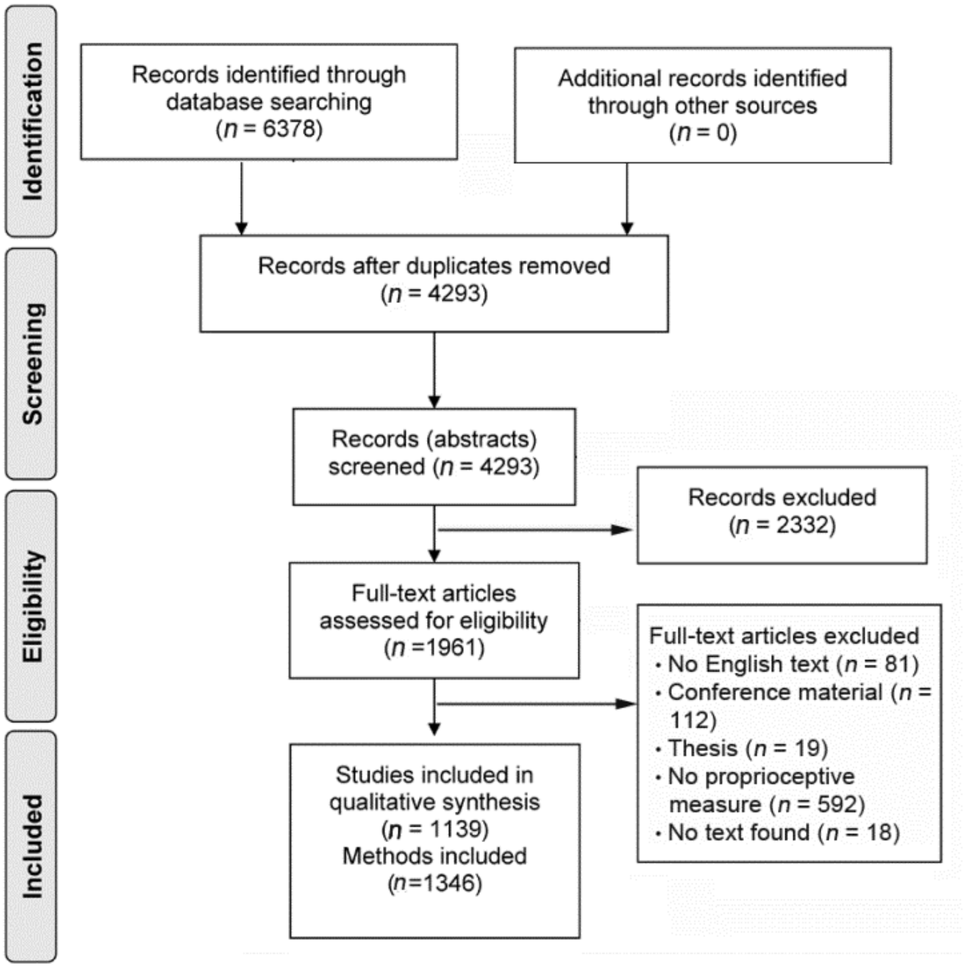

Table 2. Summary table of the proprioceptive accuracy measurement techniques.

<table>
<tr><th>Aspect of proprioception</th><th>Method of adjustment</th><th>Method of constant stimuli</th><th>Method of limits</th></tr>
<tr><td>Joint position sense</td><td>Joint Position Reproduction, Pointing to Proprioceptive target</td><td>Joint Position Discrimination</td><td rowspan="4">Threshold to Detection of Passive Motion</td></tr>
<tr><td>Movement sense</td><td>Movement Reproduction</td><td>Movement Discrimination</td></tr>
<tr><td>Trajectory sense</td><td>Trajectory Reproduction</td><td>N/A</td></tr>
<tr><td>Velocity sense</td><td>Velocity Reproduction</td><td>Velocity Discrimination</td></tr>
<tr><td>Force sense</td><td>Force Reproduction, Keep Force Level</td><td>Force Discrimination</td><td>N/A</td></tr>
<tr><td>Muscle tension sense</td><td>Muscle Tension Reproduction</td><td>N/A</td><td>N/A</td></tr>
<tr><td>Weight sense</td><td>N/A</td><td>Weight Discrimination</td><td>N/A</td></tr>
<tr><td>Size sense</td><td>N/A</td><td>Size Discrimination</td><td>N/A</td></tr>
</table>

Abbreviation: N/A = no method is available.

Proprioceptive accuracy measurement techniques

Method of adjustment

Eight different types of proprioceptive accuracy measurements using the method of adjustment were identified.

Joint Position Reproduction (*n* = 836): Participants have one or more joints of their body moved to a target position. Then they are asked to reproduce the position of the joint(s) as accurately as possible. In different versions of this task, movement can be active or passive, and the reproduction may happen with the same or with the contralateral joint (see also the discussion).

Pointing to Proprioceptive Target (*n* = 42): One of the body parts is set to a target position. One has to point or reach to the position of the body part as accurately as possible.

Movement Reproduction (*n* = 21): One of the body parts is moved through a given trajectory, with a given velocity, to a given endpoint. Participants are required to reproduce the trajectory, the speed, and the endpoint of the movement as accurately as possible.

Trajectory Reproduction (*n* = 2): A body part is moved along a given trajectory. Participants have to reproduce the trajectory of the movement. This can happen with the same or with the contralateral joint.

Velocity Reproduction (*n* = 9): A body part is set to move with a given velocity. The task of the participant is to reproduce the speed with the same or with the contralateral body part.

Force Reproduction (*n* = 76): The participant is guided to produce a certain level of force with a muscle or muscle group. After production, they have to reproduce the same force with the same or with the contralateral muscle.

Keep Force Level (*n* = 6): Participants have to produce a given amount of (submaximal) force and keep it on the same level.

Muscle Tension Reproduction (*n* = 1): The participant is asked to produce a given level of muscle tension with a muscle or muscle group. After the production, one has to reproduce the same level of muscle tension as accurately as possible.

Method of constant stimuli

Six different proprioceptive accuracy measurement types were identified that were based on the method of constant stimuli.

Joint Position Discrimination (*n* = 81): Participants have to compare 2 joint positions and decide whether these were the same or different (note: The Active Movement Extent Discrimination Apparatus,(Han et al., 2016) which presented a single stimuli for judgement in each trial, was also categorized as a Joint Position Discrimination test).

Movement Discrimination (*n* = 6): Participants have to compare 2 movements (with a given trajectory, velocity, and endpoint) and decide if these were the same or different.

Velocity Discrimination (*n* = 8): Participants have to perform 2 movement velocities and decide if these were the same or different.

Force Discrimination (*n* = 5): Participants have to produce a given level of force twice and decide if these were the same or different level of forces.

Weight Discrimination (*n* = 19): Participants are presented with 2 objects and have to decide if these were of the same or different weight.

Size Discrimination (*n* = 3): Participants are presented with 2 objects and have to decide if these were of the same or different size.

Method of limits

One widely used proprioceptive accuracy measurement technique using the method of limits was identified.

Threshold to Detection of Passive Motion (*n* = 231): One body part of the participant is moved passively. The task is to give a signal as soon as the displacement is perceived. This paradigm is based on the ascending method of limits (i.e., the level of stimuli gradually increases until perceived), whereas we did not find any example of the descending method (i.e., level of stimulus gradually decreases until perceived) used to assess proprioceptive accuracy.

Discussion

In this review, we identified and categorized the existing methods used for the assessment of proprioceptive accuracy. Also, we identified 8 different aspects or "senses" of proprioception (Table 2): the ability to perceive (a) joint position, (b) movement and movement extent (c) trajectory and (d) velocity, and the level of (e) force and (f) muscle tension, and (g) weight and (h) size of different objects based on proprioceptive information. These aspects can be measured with the classical methods of psychophysics, i.e., the method of adjustment, the method of constant stimuli, and the method of limits.

Proprioceptive accuracy assessment can be operationalized by taking different approaches and different paradigms. A common misconception in the literature is that results obtained with the use of one particular method with respect to one particular body part (e.g., joint, muscle) can be generalized. In other words, it is (often implicitly) assumed that a generalizable proprioceptive accuracy exists and that each test measures this general ability. If this would be the case, a strong association between results obtained with different tests for different body parts should exist. In other words, the best performers in one particular test (e.g., Joint Position Reproduction) with respect to one particular body part (e.g., elbow) would probably be the best performers in another test (e.g., Threshold to Detection of Passive Motion) assessing another body part (e.g., knee). Empirical findings, however, do not support the existence of such a strong relationship. In fact, proprioceptive accuracy is characterized by both site-specificity and method-specificity. Table 3 summarizes the studies investigating the relationship between different tests; none of them reported a significant correlation.

Table 3. Summary table of studies investigating the association between different tests of proprioceptive accuracy. None of the studies found a significant association.

First author, year	Tests
Grob et al., 2002	Joint Position Reproduction, Threshold to Detection of Passive Motion
Janwantanakul et al., 2003	Joint Position Reproduction, Threshold to Detection of Passive Motion
de Jong et al., 2005	Joint Position Discrimination, Threshold to Detection of Passive Motion
Elangovan et al., 2014	Joint Position Discrimination, Joint Position Reproduction
Li et al., 2016	Joint Position Reproduction, Threshold to Detection of Passive Motion, Force Reproduction
Nagai et al., 2016	Joint Position Reproduction, Velocity Reproduction, Threshold to Detection of Passive Motion, Force Reproduction
Niespodziński et al., 2018	Joint Position Reproduction, Force Reproduction
Yang et al., 2020	Movement Discrimination, Joint Position Reproduction
Horváth et al., 2021	Joint Position Reproduction, Weight Discrimination

The existence of such a discordance is further supported by studies revealing test-specific differences in certain proprioceptive abilities. For example, Barrack and colleagues (1983) found that dancers perform worse than controls in Joint Position Reproduction test but are better at Threshold to Detection of Passive Motion with respect to the proprioceptive accuracy of the knee joint. It was also reported that Force Reproduction test, but not Joint Position Reproduction test is related to ankle instability index (Docherty et al., 2006) and ankle stiffness (Docherty et al., 2004). Another example is that deficits in motor functioning, such as walking disability, sensory disturbance, and central motor conduction time, were only associated with proprioceptive accuracy assessed with the Joint Position Reproduction test and not with that measured with the Threshold to Detection of Passive Motion test in compressive neuropathy (Okuda et al., 2006). Finally, experimentally-induced pain influenced the outcome of the Threshold to Detection of Passive Motion test, but did not affect participants' performance in the Joint Position Reproduction test (Sole et al., 2015).

Also, evidence shows that results with respect to one body part may not be generalized to others. With respect to the Joint Position Discrimination (AMEDA) test, there is a strong correlation between the same joints on the 2 body sides, but no association between different joints (Han, Anson, et al., 2013; Waddington & Adams, 1999). Moreover, lack of association can be observed in many cases within the same test and joint too. For example, no association was found between detection threshold when the limb is moved with different speeds (de Jong et al., 2005). Finally, results may be joint-position specific; for example, people with functional ankle instability showed position-specific deficits in a Joint Position Reproduction task (Yokoyama et al., 2008).

Another consideration is related to the question of how performance in the tests should be scored. Most of the methods allow the use of many performance scores. For example, for the method of adjustment, absolute error refers to the mean absolute difference between the reference and the reproduced stimuli, constant error refers to the signed difference (indicating systematic bias in judgements), and variable error refers to the standard deviation of the error score (indicating dispersion around the constant error) (Boisgontier et al., 2012; Goble et al., 2012; Schutz & Roy, 1973). In a similar vein, the method of constant stimuli allows the use of the sensitivity (proportion of correct judgements when the 2 stimuli differ) and specificity (proportion of correct judgements when the 2 stimuli are the same) indices, and the Just Noticeable Difference (the lowest level of difference that one can detect, for example, at least 50 percent of the time). There is no clear agreement in the literature how these tests should be scored; even the correlation between the various indices is rarely reported. From a more practical point of view, the use of multiple indices often makes the comparison of findings of various studies impossible.

Altogether, these issues (i.e., test- and site-specificity and the lack of agreement on how tests should be scored) imply that when using the term proprioceptive accuracy, the test used, the score used to evaluate the test, and the joint measured always need to be specified. As proprioceptive accuracy is not a general ability, it cannot be assessed with the use of a single test (de Jong et al., 2005) and so one should always choose a method that best suits the research or practical question at hand (Nagai et al., 2016). For researchers, an important task for the future is to find the best method to measure proprioceptive accuracy. One important consideration is ecological validity, for example, how well different tests reflect the effects of injury and expertise (Laboute et al., 2019; Steinberg et al., 2019).

Moreover, there are other important factors that should be taken into consideration when choosing the appropriate test. Some tests inherently require active effort from the participants (e.g., force reproduction and discrimination, muscle tension reproduction, weight discrimination), but in other cases (e.g., joint position reproduction) the test can be based on passive movement only. For certain patient groups with movement disorders, only the passive movement versions are applicable. Because of the tight interaction between the input and output aspects of motor control (Cullen, 2004; Miall & Wolpert, 1996), active motion involves the processing of both afferent (e.g., the feedback from muscle spindles) and efferent (i.e., the efference copy of motor command) signals. Therefore, people tend to be more accurate when active muscle activity increases, for example, by allowing active motion (Lönn et al., 2001) or by increasing shoulder elevation angle (Suprak et al., 2006) and weight bearing (Stillman & McMeeken, 2001). Weight bearing can also compensate for the negative effect of experimentally induced joint effusion (Cho et al., 2011) From the viewpoint of external (ecological) validity, tests that involve active motion should be preferred, as they better reflect the individual’s performance under everyday circumstances. Important for the choice of an appropriate test is that some patients with movement disorders may not be able to move the limb or joint up to a specific position even though it may have been possible passively (e.g., the affected upper or lower limb in patients with unilateral stroke), which will affect the results of the proprioceptive accuracy test dramatically. As such, it has to be considered whether the reproduction/comparison happens with the ipsilateral or with the contralateral joint. The ipsilateral version requires memory while the contralateral version requires interhemispheric transfer (Goble, 2010), so in patients with significant memory impairment, the ipsilateral version is not preferred. In other words, additional abilities and features beyond the processing of proprioceptive signal(s) can substantially impact performance. Another important factor that can influence the outcome of the assessment is the measured body side, as there might be differences between the dominant and subdominant limb in the processing of proprioceptive information (Goble et al., 2009; Goble & Brown, 2007, 2008; Han, Anson, et al., 2013; Han, Waddington, et al., 2013).

The approach to proprioception and proprioceptive accuracy used in this systematic review paper is broader than that of previous literature reviews (Han et al., 2016; Hillier et al., 2015). This enabled us to explore methods not included in those reviews. It is worth noting that our definition excluded signals that do not originate in the locomotor system or the skin (and related efferent signals) but that might play an important role in the perception of our body, most importantly the visual modality. Also, because of the definition used, only methods of assessment that require the subject to consciously be aware of proprioceptive information were included. These factors may limit the ecological validity of proprioceptive accuracy tests. To reach cognitive perception of proprioceptive accuracy, proprioceptive and related somatosensory signals are processed through the conscious relay pathways (i.e., dorsal column/medial lemniscus system) (Lundy-Ekman, 2013). However, in activities of daily life, movement regulation is a dominantly non-conscious (automatic) process that does not require conscious perception of proprioceptive signals (Gallagher, 2005). Proprioceptive information that does not reach conscious awareness is forwarded through the spinal reflex pathway or the spinocerebellar tract to contribute to automatic postural adjustments and balance control (MacKinnon, 2018). As indicated by previous neuro-imaging research, central processing of ankle proprioception can predict balance performance in younger and older adults (Goble et al., 2011). In other words, ankle proprioception will provide important non-conscious feedback regarding body sway, which is crucial for restoring or maintaining a state of balance. Hence, some researchers incorporate "sense of balance" in the definition of proprioception (Stillman, 2002). Following this logic, a balance task can be used as an alternative method to (indirectly) assess the functional ability to use non-conscious proprioception (to keep a state of balance), especially in situations where visual information is eliminated (i.e., where participants are blindfolded) (Shumway-Cook & Horak, 1986). In this way, some researchers attribute increased postural sway (e.g., Romberg test) to loss of proprioceptive sensation (Khasnis & Gokula, 2003). However, it is important to note that balance control is a complex process depending on multiple sensorimotor mechanisms (Shumway-Cook & Woollacott, 2007). So, in this way, it can be stated that an increment in postural sway cannot be attributed exclusively to a reduction in proprioceptive information as other sensory feedback systems can play an important role as well (e.g., the vestibular system and other somatosensory senses, such as plantar cutaneous foot sensation), not to speak of the required motor functions.

This review is not without shortcomings. A single author made the decision about the final inclusion of the articles at the full-text stage, which could lead to biased selection. Also, articles reporting methods that contain the search terms may be overrepresented.

To choose the appropriate method to measure proprioceptive accuracy, the first step is to decide which aspect of proprioception one wants to assess: the sense of joint position, trajectory, speed, movement and movement extent, force, muscle tension, weight, or size. For researchers, theoretical consideration may guide this decision, while for practitioners, ecological validity may be the most important factor. It is important to consider whether a passive test, where participants do not have to conduct active movement or effort, or an active test is more appropriate. In the former case, afferent sensory signals play a more dominant role, while in the latter case, efferent signals also contribute to perception. However, it is also important to note that these systems (afferent and efferent) may not be completely separable (Cullen, 2004; Miall & Wolpert, 1996). In specific patient populations, researchers and practitioners should take into account the motor capacity, range of motion, and muscle strength of the limb or joint of interest and adapt the test to the needs of the patient. Additionally, in patients with severe memory impairment, a contralateral version is recommended. Different aspects can be measured with the method of adjustment, method of constant stimuli, or with the method of limits (Gescheider, 1997; Han et al., 2016). Besides the decision regarding the measurement method, the relevant joint and body side should be measured with an appropriate stimulus intensity (i.e., joint position, speed, trajectory, force, contraction level, weight, or size.). Importantly, one should be aware that proprioceptive accuracy is body site- and test-specific, meaning that results obtained with a given test are not generalizable for other tests nor for other joints. Accuracy might also be specific to the target stimuli (e.g., speed of motion, target joint position). Better understanding of the benefits and shortcomings of different paradigms can also be helpful in the development of novel tests meant to assess new aspects of proprioception. For example, the loss of proprioceptive accuracy over long-duration spaceflights to Mars (Macaulay et al., 2021) suggests that astronauts with good initial proprioceptive acuity should be selected for the journey. An important practical question is, however, how their proprioceptive accuracy should be measured.

Acknowledgments

Áron Horváth was supported by the ÚNKP-20-3 New National Excellence Program of the Ministry for Innovation and Technology from the source of the National Research, Development and Innovation Fund (ÚNKP-20-3-II-ELTE-163). Nina Jacobs was supported by the FWO Research Foundation Flanders (11M2622N) and the Special Research Fund (BOF) of Hasselt University (BOF19KP08).

Author contributions

Áron Horváth: took part in designing the study, in selection process, and wrote the first draft of the manuscript. Eszter Ferentzi took part in designing the study. Kristóf Schwartz took part in the selection process. Nina Jacobs wrote sections of the manuscript. Pieter Meyns wrote sections of the manuscript. Ferenc Köteles took part in designing the study and wrote sections of manuscript

All authors have read and approved the final version of the manuscript, and agree with the order of presentation of the authors.

Competing interests

All authors declare that they have no competing interests.

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General Discussion

Discussion and integration of the findings

Discussion of the findings

First, I will discuss the findings of the four study, and highlight the most important details for integrating the findings.

The first study of the dissertation investigated the relationship between proprioceptive accuracy and Perceived Body Competence, Body Awareness, and Affect. We assessed the proprioceptive accuracy of 67 university students with the Joint Position Reproduction Test. Participants were passively guided to five different elbow joint positions and had to reproduce the positions as accurately as possible. This procedure was used for the left and right elbows, and we applied both the ipsilateral and the contralateral versions of the test, and the absolute value of the constant error was used to evaluate the performance. None of the proprioceptive accuracy indices showed a significant correlation with Perceived Body Competence, Body-Awareness and Affect.

The second study aimed to replicate and to extend these findings. The sample consisted of 105 University students, whose proprioceptive accuracy was assessed with two different tests at the non-dominant hand: Joint Position Reproduction test at the elbow joint, with passive setting and passive reproduction, using constant and variable error. Weight Discrimination test at the non-dominant hand, with 200 g reference weight and 215 g comparison weight. In this study, in addition to proprioceptive accuracy, cardioceptive accuracy was measured with the Schandry task. Also, not only accuracy (objective performance), but confidence (perceived performance) was assessed. Again, we found a lack of correlation with the questionnaires (Perceived Body Competence, Body-Awareness and Affect). More surprisingly, confidence and accuracy were independent of each other, meaning that objective and perceived performance did not overlap in case of the Joint Position Reproduction and Weight Discrimination tasks, and only weakly overlapped for the Shandry task. Also, accuracy measured in the Joint Reproduction Test and Weight Discrimination test did not show association.

Given the important role of proprioceptive accuracy in the feeling of body ownership, in the third study, the association between the Rubber Hand Illusion and proprioceptive accuracy was studied. The Joint Position Reproduction task at the subdominant elbow joint was used, with passive setting and passive reproduction. We also assessed cardioceptive accuracy with the Shandry task. The dissociation between cardioceptive and proprioceptive accuracy was replicated again. We also found that the Rubber Hand Illusion is not associated with cardioceptive accuracy. However, it was associated with proprioceptive accuracy, but only in the asynchronous condition of the illusion.

In the fourth study of the dissertation, we attempted to identify methods that are used to assess proprioceptive accuracy. We found as much as 15 testing methods for this purpose. Looking over the abstracts of more than 4000 papers, and the full text of almost 2000 articles, gave us a good opportunity to evaluate the studies, where the association was investigated between different methods. The results consistently show that accuracy measured with different methods are uncorrelated, suggesting that every test measures a different construct.

Integration of the findings

The conclusion of the fourth study of this dissertation implies that proprioceptive accuracy can be only used as an umbrella term, and for a deeper and accurate understanding, one needs to specify the method used and the body site measured. This assumption is very relevant when interpreting the findings of the first three studies of the dissertation. In this light, it is important to highlight that the conclusions of our studies are only valid for the used proprioceptive measurement technique. We can conclude that perceived body competence, body awareness and affect is not associated with the Joint Position Reproduction test at the elbow joint (with passive setting and passive/active reproduction), Weight Discrimination ability regarding the tension of arm flexor muscles, but we cannot be sure if it applies to other tests and other body sites too. Also, we can conclude that the strength of the Rubber Hand Illusion is associated with the Joint Position Reproduction Test, with passive setting and passive reproduction, in case of the left hand. But again, we cannot be sure if it applies to other tests. To illustrate that point, one may analyze the difference between the third study of this dissertation, and the study of Motyka and Litwin (2019), who conducted a similar study, with the same research question: to test if proprioceptive accuracy is associated with the rubber hand illusion. In contrast to our study, they did not find a significant relationship. They applied the Joint Position Reproduction test, however, not at the elbow, but at the shoulder joint. Also, the testing consisted of an active reproduction phase, while we used a passive setting with passive reproduction paradigm. We argue that using a passive test is more adequate to test the relationship with the Rubber Hand Illusion, because the hand of the participant is in a passive state (i.e. no movements can be conducted while the illusion is evoked). An active proprioceptive test protocol might be more suitable, if one would like to investigate for example the relationship between proprioceptive accuracy and the Virtual Hand Illusion, that is elicited because of a virtual hand is set to move in the same direction and with the same speed as the real hand (Sanchez-Vives et al., 2010).

Wider perspective and future research directions

Association between proprioceptive accuracy measurements

To put the findings into a wider perspective, it is important to note, that proprioception is a sub-modality of interception. Interoception refers to the processing of information originating from within the body. It can be divided into two main categories, where one is visceroception, that refers to the information originating from the internal organs (e.g. the heart, stomach, intestinal tract), and the other category is proprioception (Cameron, 2002). There are a lot of studies about the role of visceroception, especially cardioceptive accuracy in psychological functioning (Ferentzi et al., 2021; Herbert et al., 2010). In many studies, authors used one test, for example the Schandry task to assess interoceptive accuracy, and generalized the results to other modalities. Hovewer, this practice turned out to be false, as accuracy measured in one modality cannot be generalized to other modalities (Ferentzi et al., 2018). This problem turned out to be very relevant besides proprioception too, based on the literature cited in the fourth study of this dissertation.

From a methodological point of view, a comprehensive investigation of the association between different methods and joints would be desirable. Most of the studies, that investigate the relationship between different proprioceptive accuracy assessment paradigms, only consider a few paradigms (typically two to four), and most of the times the sample size is too small to serve as strong evidence for the lack of association. A study, where more joints of the body are tested, with many different paradigms, using a high sample size, and applying Bayesian statistics could give more satisfactory evidence about the test and joint specific nature of proprioceptive accuracy.

Because of the very high number of tests, such a study would require approximately one full day test one individual only.

Investigating causal relationships via modifying proprioceptive accuracy

Most of the studies in this dissertation utilized a cross-sectional, correlational design, meaning that causal relationships could not be established (it was however possible to reject the existence these effects, because of the lack of correlation, supported by the Bayesian statistical analysis). For future research, improving proprioceptive accuracy might be a valuable tool to investigate causal relationships. Proprioceptive training is “an intervention that targets the improvement of proprioceptive function, focusing on the use of somatosensory signals such as proprioceptive or tactile afferents in the absence of information from other modalities such as vision. Its ultimate goal is to improve or restore sensory and/or sensorimotor function.” (Aman et al., 2015, p. 2). Given that proprioceptive training is very popular in many fields, for example in rehabilitation to restore healthy functioning (Lee et al., 2015), or in sports to prevent injuries and improve performance (Federici et al., 2020), a lot of training programs were developed, that could be also used for future research purposes. It would be interesting to investigate how improving proprioceptive accuracy would affect the Rubber Hand Illusion. Based on the third study of this dissertation, improving proprioceptive accuracy in the passive version of the Joint Position Reproduction test at the elbow joint should reduce the strength of the Rubber Hand Illusion.

Given the role of proprioceptive information in movement control, it would be a valuable question to investigate if improving proprioceptive accuracy could make the learning of new motor skills more efficient. Proprioceptive accuracy was shown to be associated with throwing performance in many sports, including darts (Feng et al., 2019), water-polo (Hams et al., 2019) and basketball (Sevrez & Bourdin, 2015). Also, a positive correlation with muscle strength in hip osteoarthritis (Shakoor et al., 2014), and a positive correlation with balancing ability in anterior cruciate ligament reconstructed individuals were revealed (Armitano-Lago et al., 2020). The beneficial effect of providing proprioceptive information in learning of new motor skills is demonstrated by the study of Wong and colleagues (2012), where proprioceptive presentation of a movement trajectory (i.e. moving the passive arm of the participant) made learning more efficient, compared to when participants could only rely on visual presentation. It was also shown, that after the procedure, proprioceptive accuracy (assessed with passive joint position discrimination task) increases (Wong et al., 2011). Also, improvement of proprioceptive accuracy due to motor learning improves dart-throwing performance (Chiyohara et al., 2020). Interestingly, we do not know about any study that would investigate how individual differences in proprioceptive accuracy affect the acquisition of new motor skills.

Another important question, related to motor performance and proprioceptive training is the transfer effect. It was shown that long-term proprioceptive training of the dominant knee can improve the performance of the non-dominant knee too (El-Gohary et al., 2016). We do not know about any study that would investigate the transfer to other tests and body sites. If there is no transfer effect, that could further support the test-specific and joint-specific nature of proprioceptive accuracy.

One might find it too resource-demanding to train individuals for months to achieve a long-term improvement. To solve this problem, it would be possible to use different techniques that improve/reduce proprioceptive accuracy immediately, and the effect lasts only for short-term. Acutely improving proprioceptive accuracy is thought to be beneficial for motor control, so numerous techniques were tested that target this possibility. Different warming-up (Bartlett & Warren, 2002) and stretching techniques (Walsh, 2017) were found to be effective, and also taping, especially for people with below average ability (Callaghan et al., 2002; Halseth et al., 2004). Also, there are procedures that were shown to decrease this ability, that makes it possible to investigate the effect of reducing proprioceptive accuracy, that would be obviously unethical to do in a chronic way. Cryotherapy and fatiguing the muscle with weight exercises are such procedures (Ribeiro & Oliveira, 2011). However, it is suspected that these techniques only partially rely on physiological changes: conscious expectation (i.e. the placebo response) might also play an important role in their mechanism. For example in relation to maximal strength, it was shown that kinesio taping improves maximal grip strength only for those, who are users, but not for those individuals who are new to the technique (Mak et al., 2019). Also, if participants do not know that taping is applied, an increment in maximal strength does not occur (Poon et al., 2015). As many aspects of motor performance, for example maximal strength and endurance were shown to be modifiable via placebo and nocebo effects (Bérdi et al., 2011; Horváth et al., 2021; Hurst et al., 2019), it is possible that proprioceptive accuracy is susceptible to these influences too. However, the direct effect of placebo and nocebo instruction on proprioceptive accuracy was not investigated to date. This could be done for example by applying a sham-treatment, that is claimed to improve or reduce accuracy. For example, a cream that contains no active substance, or a sham-sub-threshold electric stimulation. If proprioceptive accuracy can be modified via placebo and/or nocebo response, we should see an increase and/or decrease in accuracy after the application of the sham-treatment.

Effect of psychological processes on proprioception

In this dissertation, the focus was on the possible role of proprioceptive accuracy in psychological functioning. However, the question of how different emotions and mental processes may influence accuracy is also relevant. For example, Şenol and colleagues (2018) showed that proprioceptive accuracy, assessed by active reproduction ability of the ankle joint is reduced because of stress. They also showed that this decrease is specific to the processing of proprioceptive signals, as stress did not affect the same task when participants could use visual feedback of their ankle. The study of Şenol and colleagues (2018) applied a quasi-experimental design, as they did not evoke stress, but compared the performance of the subjects in a relatively stressful (exam period for university student) and non-stressful period. Replication of this finding and using an experimental manipulation of stress (for example via a demanding mental task) and measuring the accuracy in other body sites and with different tests would help our understanding of this topic. It was also shown that proprioceptive accuracy can be modified by inducing different emotional states. Ackerley and colleagues (2017) found that sad music can increase muscle spindle dynamic response (as opposed to happy and neutral music, that did not have an effect). In another study, it was revealed that proprioceptive accuracy, as assessed with a threshold to detection of passive motion paradigm at the ankle joint of the left foot, was decreased as participants were listening to sad music, but not when listening to happy or neutral music (Samain-Aupic et al., 2019). According to the explanation of the authors, these changes are a sign that the emotion prepares the organism for the appropriate behavioral response. It would give a lot to our understanding to investigate the modification of proprioceptive accuracy in a more detailed way. For example, by using the Joint Position Reproduction test, that enables to evaluate separately the systematic distortion in the perception of joint position (i.e. systematic error), and the variability of the position judgements (i.e. variable error).

Working memory and proprioception

As mentioned in the Introduction part of this dissertation, cognitive factors, such as attentional load can also influence proprioceptive accuracy (Goble et al., 2011; Yasuda et al., 2014). One other important factor is working memory capacity. The working memory's function is to store and manipulate information from different sources in the short term. Storage capacity is limited and varies considerably between individuals. There were originally two modality-specific subsystems of working memory, the phonological loop, and the spatial sketchpad. While the former is responsible for retaining verbal information, the latter is responsible for retaining spatial-visual information (Baddeley, 1992; Baddeley & Logie, 1999). Later, it was discovered that a motor subsystem also exists, than can store movement-related information (Smyth et al., 1988; Smyth & Pendleton, 1990), and that visual and spatial short-term memory are independent (Della Sala et al., 1999). So overall the existence of four modality-specific subsystems is accepted, these can retain information in verbal, spatial, visual, or motor form. To explore the effect of spatial working memory in storing proprioceptive information, Goble and colleagues (2012) studied patients with cerebral palsy. The Joint Position Reproduction test was used with passive setting and active reproduction. Elbow joint positions were presented for a shorter (2 sec) or a longer (12 sec) time. Cerebral palsy patients could improve their performance due to the long presentation time. Also, the higher spatial working memory span one had, the greater the improvement in accuracy was. From these results, the authors concluded that spatial working memory has an essential role in storing proprioceptive information. We also conducted two studies to test this assumption. To further investigate the question of how proprioceptive information is stored in short-term memory, we developed a procedure, where it is possible to measure the individual’s ability to store proprioceptive information in working memory. That is a modified version of the Joint Position Reproduction task, where the maximal number of joint positions are measured that one can retain (Horváth et al., 2020). We presented the participant with two to eight joint positions to remember and recorded the mean absolute error in every sequence. After that, we established a break point in the performance (i.e. the number of position after which the magnitude of the errors starts to disproportionately increase) with the help of a step function. That break point was the proprioceptive span of the participant. We used the Corsi-black tapping task to assess the capacity of spatial short-term memory, and the Digit span task to assess the capacity of verbal short-term memory. Overall, we tested 39 university students. Based on the study of Goble and colleagues (2012), it was hypothesized that proprioceptive span will show an at least medium level, positive association with spatial span, and no association with verbal span. In contrast, the Bayesian analysis showed that there is a lack of correlation between proprioceptive span and spatial span. Verbal span was also found to be independent of proprioceptive span (Horváth et al., 2020). In another study, the goal was to further investigate this question with interference paradigm (Horváth et al., 2022). We also tested the role of motor and visual short-term memory, not only the role of verbal and spatial memory. The sample consisted of 35 university students. Here we modified our previous paradigm to assess proprioceptive span, to make it more comparable to other short-term memory span measures (e.g. Corsi Block Span Test, Digit Span Test). Participants were presented firstly sequences containing three elbow joint positions. If they could correctly reproduce two sequence of a given length out of a maximal three attempts, the number of presented positions increased by one in the next sequence. If sequences of a given length were reproduced twice incorrectly, the task ended, and one got the capacity score as the number of positions in the longest, at least two times correctly reproduced sequence. A given sequence was correct if the movement pattern was correct, and there was no bigger than 30 degrees deviation from the target position in any case. Firstly, this task was done without any competing task. After that, proprioceptive span was measured in four conditions: motor suppression (repeatedly touching body parts in a given order), spatial suppression (repeatedly touching spatial positions in a given order), visual suppression (watching abstract pictures on the computer screen), verbal suppression (repeatedly counting from one to four). The conditions were randomly presented after each other. It was revealed that the execution of spatial and verbal competing tasks decreased proprioceptive span, while no effect of motor and visual interference was found. Overall, the three studies investigating the modality-specific storage of proprioceptive accuracy (Goble et al., 2012; Horváth et al., 2020, 2022) have come to different conclusions. One important difference was the investigated populations: cerebral palsy patient with severe movement disorder, university students with more sport expertise, and university students with less sport expertise (Horváth et al., 2022). As it was shown that motor expertise might influence the storage processes in working memory (Moreau, 2013), this might explain the differences, meaning that people with more sport expertise might encode proprioceptive stimuli in a motor form in short term memory, while people with movement disorder or less sport expertise may use other, such as verbal and spatial strategies. To test this hypothesis, it would be possible to assess proprioceptive memory task with verbal, spatial, visual and motor interference (Horváth et al., 2022), with samples from different populations. For example, professional athletes, physically inactive individuals and individuals with movement disorder (e.g. cerebral palsy). Also, until this time, proprioceptive memory was tested only with Joint Position Reproduction test at the elbow joint. It would be interesting to test other joints and use other tests (e.g. Force Reproduction) to see if the findings are generalizable across tests and joints.

Role of proprioceptive information

The assessment of proprioceptive accuracy gives us information about how people perform when they can fully attend to one joint or muscle. However, in everyday circumstances, even the execution of basic motor skills (such as reaching for a cup of tea), requires controlling a high number of muscles and joints. Some parts and aspects of the movement may become conscious but because of the limited capacity of consciousness, the most part of the movement pattern will run in an automatic way (Gallagher, 2005). That is why it is important to investigate how proprioceptive information can affect psychological functioning, an vice versa, in situations when people do not necessary fully attend proprioceptive information. For example, the study of Cacioppo and colleagues (1993), where contraction of arm flexor muscles caused a positive evaluative bias in judging neutral stimuli, and contraction of arm extensor muscles caused a negative bias, is worth further investigation. The finding was replicated (Neumann & Strack, 2000) and can manifest itself in real life situations: it was shown that when buyers grab a vertical shopping cart handle, instead of a horizontal one, money spending increases because the vertical handle activates the flexor muscles of the arm (Estes & Streicher, 2021). However, the theory (Cacioppo et al., 1993) has not been tested with an actual arm movement towards or outside the body. A proprioceptor, that can precisely move and/or measure the position of a given joint (for example the elbow), would be perfect for this task. It is also a question if passively moving the arm cold elicit this effect, or active effort to move the arm (and consequently efferent copy of the motor command) is required. The difference between active and passive motion is demonstrated by the study of Kilteni and colleagues (2020), where they found that active movement is required to attenuate self-generated touch. If the touching arm is moved passively, the touch feels as strong as external touch (Kilteni et al., 2020).

Conclusion

Overall, the aim of this dissertation was to investigate the role of proprioceptive accuracy in psychological functioning. It was revealed that proprioceptive accuracy, measured with the Joint Position Reproduction test at the elbow joint is with passively guiding the arm to the target position and with actively/passive reproduction is not associated with Perceived Body Competence, Body Awareness and Affect, but the passive-to-passive test is associated with the strength of the Rubber Hand Illusion. It also turned out, that there are several different methods to measure proprioceptive accuracy, that assess different aspects of the ability, and results can be easily body site- and test-specific. The role of proprioceptive accuracy and proprioceptive information in psychological functioning is worth of further investigation.

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