The role of multisensory integration and psychological factors in body ownership: experimental approaches

Ph.D. thesis

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Content

1. Abbreviations and glossary

BSC – bodily self-consciousness

FFA – face fusiform area

IHI – invisible hand illusion

LIP – lateral intraparietal area

PMv – ventral premotor cortex

PPC – posterior parietal cortex

PPS – peripersonal space

RHI – rubber hand illusion

rTPJ – right temporo-parietal junction

SC – superior colliculus

SCL-90-R – psychiatric self-report inventory containing nine factors:

 SOM – somatization

 OBS – obsessive-compulsive symptoms

 INS – interpersonal sensitivity

 DEP – depression

 ANX – anxiety

 HOS – hostility

 PHO – phobic anxiety

 PAR – paranoid ideation

 PSY – psychoticism

STS – superior temporal sulcus

TCI-R – psychobiological trait inventory containing seven temperament and character factors

 NS – novelty seeking

 HA – harm avoidance

 RD – reward dependence

 PS – persistence

 SD – self-directedness

 CO – cooperativeness

 ST – self-transcendence

Tpt – temporo-parietal junction

VIP – ventral intraparietal area

Blood-oxygen-level-dependent (BOLD) signal – an index of brain activation based on detecting changes in blood oxygenation with functional MRI (fMRI)

Cross-modal stimuli – stimuli from two or more sensory modalities.

Inverse effectiveness – the degree of the multisensory response to the most effective stimulus component declines as the effectiveness (e.g. salience) of the modality-specific stimulus components increase.

Multisensory enhancement – the response of the multimodal neurons to the cross-modal stimuli is greater than the response to the most effective of it's component stimuli.

Multisensory depression – the response of the multimodal neurons to the cross-modal stimuli is weaker than the response to the most effective of it's component stimuli.

Multisensory integration – the neural processes that are involved in synthesizing information from cross-modal stimuli.

Multimodal neuron (multisensory neuron) – a neuron that responds to stimuli from more than one sensory modality.

Receptive field – the area of sensory space in which presentation of a stimulus leads to the response of the neuron.

Superadditive/additive/subadditive computations – Neural computation in which the multisensory response is larger than/not differ from/smaller than the arithmetic sum of the responses to the component stimuli.

2. General introduction

2.1. Multisensory integration

Incoming signals from different sensory modalities are initially processed in separate ways. Because these signals may arise from a biologically significant event of the external or internal world, integration between them is evolutionarily substantial. *Multisensory integration* refers to the capacity of combining information coming from different sensory modalities to get a more accurate representation of the ambient world and our body. For example, vision and touch help estimate the shapes of the objects, whilst vision and audition are important in speech comprehension.

That is to say, integrating information about our surroundings is one of the most substantial brain functions. This function has powerful driving forces in evolution and have led to the development of an array of multiple specialized brain regions. The obvious advantage of this multimodality is that each of the senses is optimal in different circumstances and together they significantly increase the likelihood of detecting and identifying events.

Multisensory integration can be assessed by considering the effectiveness of a *cross-modal stimulus* combination, in relation to that of its component stimuli, for evoking some type of response from the organism (e.g. the magnitude of a response to an event that has both visual and auditory components is compared with that for the visual and the auditory stimuli alone). In view of this, at the level of a single neuron, multisensory integration is defined as a statistically significant difference between the number of impulses evoked by a cross-modal combination of stimuli and the number evoked by the most effective of these stimuli individually (Stein & Stanford, 2008).

2.1.1. The principles of multisensory integration

The literature of multisensory integration describes three main principles: *spatial principle*, *temporal principle* and the *principle of inverse effectiveness*. Additionally, *experience-based congruence* is considered to be a critical factor in multisensory integration as well, thus I denote it as the fourth principle.

Spatial principle

Each multisensory neuron has multiple excitatory receptive fields (RFs), one for each modality to respond. These RFs usually overlap in space. Two modalities will only be considered as having the same location if they are within the space covered by their overlapping RFs. If one stimulus falls outside the neuron's RF, its response will decrease (Kadunce, Vaughan, Wallace, & Stein, 2001).

Temporal principle

Sensory stimuli also need to be linked in time, if they are to be integrated. The extent of the integrated neural response is sensitive to the temporal congruency of the sensory inputs and is usually maximal when they coincide.

Inverse effectiveness

The "effectiveness" of multisensory integration (multisensory enhancement) is usually inversely related to the effectiveness of the component cues that are being processed individually. Unimodal cues with high salience can be easily detected thus, their combination has a proportionately modest effect on neural activity and behavior. On the other hand, weak cues provoke comparatively weaker neural activity, their combination leads to enhancement of the neural response (Stein & Stanford, 2008). In this case the multisensory response exceeds the arithmetic sum of the individual responses and have positive effect on behavioral performance [(e.g. by increasing the speed (Diederich & Colonius, 2004)].

Experience-based congruence

Here, I define congruence as the relationship between stimuli that are consistent with the experience of the individual or relationships between the senses found in nature (cf. semantic congruence). Functional brain imaging and single neuron studies have only recently begun to investigate this aspect of multisensory integration. In one study, Barraclough et al. (2005) used monkey vocalizations that were either congruent or incongruent with facial movements depicted in video clips of human faces. They found that when response enhancement was obtained in superior temporal sulcus (STS), it was greater for congruent pairings. In another study, Kim, Seitz and Shams, (2008) compared learning efficiency between three groups, one trained with visual stimuli, one with congruent auditory-visual and one

with incongruent auditory-visual stimuli. They found, that facilitation was specific to the congruent condition [for review see Shams & Seitz (2008)].

It is important to note that studies about these principles suggest that multisensory integration is not a unitary phenomenon. Different computational mechanisms may dictate different principles. For example, the principles of space and time are more relevant to the superior colliculus, a structure that is evolved to drive orientation to salient events whilst semantic congruence is more essential to the STS, which plays role in the detection of emotion on human faces.

2.1.2. Temporal and spatial discrepancies

In our everyday life we are largely unaware of these processes. Nonetheless, in some cases small temporal and/or spatial discrepancies disrupt the tight links between cross-modal cues that used to be associated before. This often results in cross-modal illusions. A very popular example of this is the McGurk Effect. Normally, speech perception is executed by integrating the sound and sight (lip movements) of speech. If mismatched cues are paired (the sound for "bows" with the lip movements for "goes"), the resulting synthesis is an entirely different product ("those" or "doze"). Maybe a more well-known type of illusion is the Ventriloquism Effect, in which the performer's lips appear to "capture" a sound and translocate it onto a puppet's lips (Stein & Stanford, 2008). Here must be noted that paradigms (Rubber and Invisible Hand Illusion) used in our experiments are also based on illusionary discrepancies between visual and somatosensory cues (described below).

2.1.3. The magnitude of multisensory integration

Multisensory integration can result in either enhancement or depression of a neuron's response and the direction of the changes is always a measure of the relative physiological salience of an event. Needless to say, if sensory modalities compete for attention (also for access to motor reaction to them), the consequence of multisensory enhancement is an increased likelihood of detecting and initiating a response to the signals. It is understood that the extent of the integration aids the

detection of an event and has a positive effect on the speed with which a response is generated (Diederich & Colonius, 2004; Stein & Stanford, 2008).

The magnitude of multisensory integration can vary for different neurons and even the same neuron can response to different stimuli variably. For multisensory enhancement differences in magnitude reflect different underlying mechanisms: the largest enhancements are due to superadditive combinations of cross-modal influence and the smallest are due to subadditive combinations (Fig. 1).

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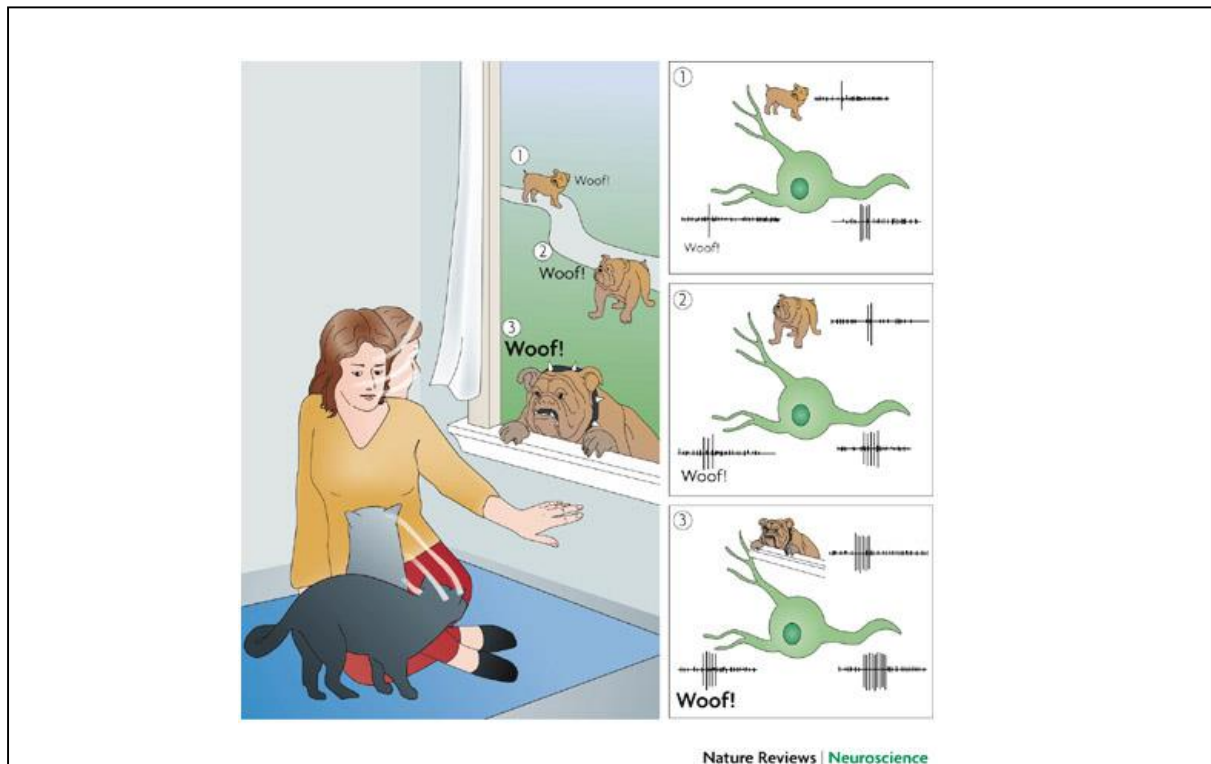
Figure 1. Multisensory integration aids detection and speed response. A cat detects the approach of a dog, based on sight and sound. 1) The cues are weak (the dog is far away). The neural computation is superadditive – proportionately the most significant. 2) The cues are less weak (the dog is closer). The neural computation is additive – proportionately less significant than superadditive. 3) The cues are strong (the dog is close). The neural computation is subadditive – proportionately the least significant. Note, that all enhancements increase the probability of orientation, but the benefits of multisensory integration are proportionately greatest when cross-modal cues are weakest (Stein & Stanford, 2008).

2.1.4. Potential challenges in multisensory integration

The brain needs to solve some computational problems to make multisensory integration successful. Besides the analysis and synthesis of specific sensory modality inputs, the following difficulties can occur (Deneve & Pouget, 2004; Kayser

& Shams, 2015): 1) problem of reliability, 2) problem of encoding, and 3) causal interference problem.

1)   The reliability of sensory modalities varies widely according to the context. For instance, visual cues are more reliable in daylight, however our brain should rely more on auditory cues at night (e.g. to localize an object). This integration problem can be more challenging, when each sense provides a noisy estimate of the respective attribute.

2)   Each modality uses a different format to encode the same properties of the environment. To use an analogy in the linguistic domain: each modality uses its own language and special translation mechanisms are needed to integrate them. For instance, sensory modalities encode the position of a cat in different frames of reference (visual stimuli are represented with RFs on the retina, auditory stimuli with RFs around the head, tactile stimuli with RFs anchored on the skin). To combine these sensory responses, the brain must take into account the posture and the movements of the body in space.

3)   The brain has to decide which sensory inputs originate from the same object and hence provides evidence about this and which inputs originate from distinct objects and hence should be processed separately. One example is at a party, where many faces and voices make it a challenge to know who called our name. Solving the causal inference problem has to rely on several factors including spatial, temporal, and structural congruence, prior knowledge and expectations.

2.1.5. Multisensory areas of the brain

Several cortical areas of higher-order association cortex were considered multisensory.

The superior temporal sulcus (STS)

Large number of studies have demonstrated multisensory convergence in the STS region (for review see Beauchamp, 2005; Ghazanfar & Schroeder, 2006). Hikosaka (1993) revealed that 36-38% of neurons appear to be multimodal in the anterior part and ~12% in the caudal portion of this area. In their interesting study, Barraclough and colleagues (2005) measured single neuron responses on biologically relevant stimuli, including vocalizations and human walking. They found that 23% of neurons

responsive to the sight of motion could be modulated by its corresponding auditory component but only if the auditory signal was congruent with the visual. These finding are consistent with neuroimaging study suggesting that the STS is specialized for integrating visual and auditory speech signals. In this study (G a Calvert, Campbell, & Brammer, 2000) the blood-oxygen-level-dependent (BOLD) signal was enhanced for congruent pairing of audible speech and lip movement suggesting that aforementioned congruence also plays important role in multisensory speech perception.

The intraparietal sulcus and the temporoparietal area (Tpt)
The intraparietal region is composed of subregions that are involved in various aspects of spatial awareness and orchestrating of actions toward spatial goals. Regarding multisensory integration the most prominent among these are the lateral intraparietal (LIP) and ventral intraparietal (VIP) areas. LIP neurons encode visual and auditory stimuli with respect to eye position – a reference frame that is appropriate for computing the vector of a gaze-shift towards a visual, auditory or multimodal goal (Stricanne, Andersen, & Mazzoni, 1996). As they shift with each eye movement, this requires dynamic RFs. VIP is located adjacent to LIP, its neurons respond to visual, auditory, somatosensory and vestibular stimuli.

At the temporo-parietal junction, area Tpt is also reported to contain multimodal representation of space (Leinonen, Hyvärinen, & Sovijärvi, 1980). Area Tpt occupies the border of visual, auditory and somatosensory cortices. It contains trimodal neurons with RFs over the head-neck-shoulder region, leading to the speculation that Tpt is involved in orienting the head in space.

Frontal cortex
The ventral premotor cortex (PMv) is a sensory-motor area located in the frontal lobe just anterior to primary motor cortex. PMv contains neurons with response to visual, auditory and somatosensory inputs. The RFs of these cells tend to be located around the upper body, including face, arm and upper torso, and these neurons usually do not respond to distant visual or auditory stimuli (more than 30 cm from the tactile receptive field). Because a high amount of PMv neurons respond during head or arm movements, the purpose of this area may be to guide movements

toward objects that are relevant around the body (M. S. Graziano, Reiss, & Gross, 1999).

Resent studies have revealed that PMv plays an important role on body ownership as well (Ehrsson, 2005; Petkova et al., 2011).

Multisensory processes in unisensory areas

Growing number of evidences show that multisensory processes are inherent in primary unisensory areas.

Visual and somatosensory processing in auditory cortex. An fMRI study in the anesthetized monkey demonstrated that simultaneously presented auditory and tactile stimuli lead to enhanced activity in a region posterior and lateral to the primary auditory cortex (A1) (Kayser, Petkov, Augath, & Logothetis, 2005). Non-auditory modulation of A1 has been observed as well under conditions in which bar press responses and visual cues were relevant to an auditory sensory task (Brosch, 2005).

Auditory and somatosensory processing in visual cortex. Auditory sensitivity in the visual cortex of cats was reported by quite early studies. Morell reported that ~41% of visual neurons can be driven by auditory stimuli (Morrell, 1972). An fMRI study conducted by von Kriegstein et al. (2005) demonstrated that the face fusiform area (FFA) is activated not only by familiar faces, but also by familiar voices. Haptic object discrimination tasks, in which participants have to identify several types of objects blindly, can activate the lateral occipital complex (LOC) (Pietrini et al., 2004).

Visual and auditory processing in somatosensory cortex. Until now only very few studies have searched somatosensory responses for visual and auditory cues. In one of them Zhou and Fuster (2004) trained monkeys to make visuo-haptic and auditory-haptic associations. In a little while a subset of somatosensory neurons responded both to the auditory or visual and somatosensory stimuli.

Multisensory integration beyond the neocortex

As it was unfolded above multimodal neurons are abundant in the primary sensory and higher-order association cortex. This occurrence begs the question: do subcortical structures also integrate senses? The answer is an apparent "yes".

Careful studies by Stein and his colleagues (e.g. Meredith & Stein, 1986; for review see Stein & Stanford, 2008) in the cat superior colliculus (SC) outlined the main principles of multisensory integration that have served as guidelines for other investigations in other species and brain structures. They have also found that the

enhancement in multisensory integration depends on inputs from neocortex (see also Ghazanfar & Schroeder, 2006).

Many neurons in the primate amygdala respond to visual, auditory and somatosensory stimuli (Nishijo, Ono, & Nishino, 1988). These findings suggest that the multisensory neurons in amygdala are not distributed randomly, rather visually responsive neurons are clustered in the anterior part and neurons responsive to auditory signals are clustered in the posterior portion. An interesting fact about this area is that in contrast to many multisensory areas, where familiar stimuli are needed to drive responses, in the amygdala neurons respond most actively to novel stimuli.

Thalamic structures appear to be multisensory in nature as well. In their study Komura and colleagues (2005) trained rats to perform an auditory spatial discrimination task in which auditory or auditory visual cues were presented. In auditory-visual condition the cues were congruent or conflicting. Almost 15% of auditory thalamic neurons were modulated by visual cues and responses were enhanced only when the visual and auditory stimuli were congruent.

2.1.6. Is our cortex essentially multisensory?

Above described scientific findings identified numerous multisensory regions in all cortical lobules. This conflicts with the classical view of sensory organization, in which multisensory interactions arise from the late-stage convergence of segregated modality-specific cortical streams (Stein & Stanford, 2008). It must be highlighted that multisensory influences on activity in classically defined unisensory regions were also proved by scientific approaches. This necessarily urges us to reconsider the validity of explaining the brain unimodally and suggests a new perspective. Ghazanfar and Schroeder (2006) interpreted these findings provocatively. They claim, that "it is likely that neither the brain nor cognition develops one sensory modality at time, nor do we represent individuals in one modality at time. The world is barrage of sensory inputs, our perception is a unified representation of it, and the neocortex is organized in a manner to make the underlying processes as efficient as possible."

2.2. The concept of body ownership

How do we feel that we own our body? Why do we feel that they are part of our body when we touch or look at our hands? Questions like these have been discussed in philosophy and psychology for centuries (Gallagher, 2000).

As we remember from the textbooks of neurology, people with frontal and parietal lobe damages often fail to recognize their paralyzed body parts. Sometimes they feel as if their hands or legs do not belong to themselves. These conditions are not simply the result of impairments in tactile perception associated with damage to the primary somatosensory cortex. Instead, these neurological observations suggest that the frontal and parietal association cortices are responsible for generating the feeling of owning limbs (Ehrsson, 2012).

Recently, body ownership has become a well-investigated issue in cognitive neuroscience. This development has made possible the manipulation of limb ownership in the controlled laboratory setting: e.g. with the *rubber hand illusion* (RHI)(Botvinick & Cohen, 1998). The RHI, and later versions of it, provide a unique tool for scientists for investigating the multisensory aspects of body ownership (see below).

2.2.1. Scientific evidences

Areas that integrate multisensory information from the body and from the near space surrounding the body are good candidates for the neural substrate of *body ownership*. Populations of neurons in this system could perform the multisensory integration required to bind visual, tactile, proprioceptive, and other multisensory signals to the coherent object that is one's body part as opposed to a visuotactile object that belongs to the external world (Ehrsson, 2012).

The most convincing evidences of the multisensory background of body ownership come from different scientific fields.

Evidence from studies in animals
The multisensory body representation of peripersonal space was first examined by Rizzolatti et al. (1981) in the macaque monkey premotor cortex (area F5). They distinguished between neurons that responded to a visual stimulus only when it was presented close to the monkey (i.e., in the peripersonal space), and neurons that

responded to the same stimulus when it was presented far away from the monkey. Moreover, the population of neurons that responded to visual stimuli within the interpersonal space typically had visual RFs that were spatially related to, and largely overlapping with, the same neurons' tactile RFs. Further studies have revealed a network of brain areas with similar multisensory neurons that show visual and sometimes also auditory RFs with a limited extension into the space surrounding the monkey's body. These brain areas include the VIP, the ventral and dorsal premotor cortex, the putamen , the orbitofrontal cortex, and the parts of somatosensory cortex (Tamar R. Makin, Holmes, & Ehrsson, 2008; Rolls, 2004; C Spence & Driver, 2004).

These studies reported spatial correspondence between the visual, auditory, and tactile RFs of individual cells - that is, selective neuronal responses to visual and auditory stimuli only when they are presented near to the body, typically approaching or receding from the relevant body part.

Evidence from studies in humans

In humans, some of the scientific evidences come from neuropsychological studies with brain damaged patients. People with damage to their frontal or parietal lobes sometimes fail to recognize their paralyzed limbs as belonging to themselves (Arzy, Overney, Landis, & Blanke, 2006). These conditions are not usually accompanied by the inability to perceive somatic stimuli applied to the affected limb (hemianesthesia), indicating that they are not simply the result of impairments in basic tactile perception. In their case study, Làdavas and colleagues (2002) found that acoustic stimuli strongly interfered with the processing of simultaneously presented tactile stimuli in a right brain damaged patient, but only when the sound stimuli were presented near the ear – in the peripersonal space.

Human neuroimaging studies suggest that systems for multisensory integration in peripersonal space also exist in the human brain. fMRI studies have found areas in intraparietal and the premotor cortex that respond to both tactile and visual stimulation in relation to specific body parts (Ehrsson, Spence, & Passingham, 2004; Makin, Holmes, & Zohary, 2007). Lloyd and colleagues (2003) also found the ventral premotor and intraparietal cortex to play important role in body ownership. These areas were active when a real hand was touched in sight of the observer and showed that these activations were modulated by the position of the

arm. Finally, Makin and colleagues (2007) localized brain areas that showed significantly stronger activation when a visual stimulus was approaching the subject's hand, as compared to a similar stimulus moving far from their hands. Those areas within the premotor cortex, the intraparietal sulcus, and in the lateral occipital complex that showed a preference for the near stimulus when it was approaching the hand, did not show a similar preference in a control experiment, in which the hand was retracted away from both stimuli. Since the only difference between the two procedures was the change in hand position, these areas were regarded as representing visual stimuli only when presented in perihand space.

In summary, this system of neural areas that integrate multisensory stimuli from the body end from the space near the body is a good candidate for the neural substrate of body ownership.

2.2.2. Additional constraints of multisensory integration in bodily signals

Although most of the researchers suggest that the integration of multisensory signals including bodily signals –Multisensory integration of Bodily Signals, MIoBS – (i.e. tactile and proprioceptive signals) share similar laws of multisensory integration (spatial and temporal constraints and inverse effectiveness) some experts argue that multisensory integration of bodily signals relies on additional constraints that are absent for exteroceptive events (Blanke, Slater, & Serino, 2015).

1) Proprioceptive constraint: MIoBS is determined by proprioceptive and vestibular inputs signaling the location of body parts and of the whole body in space.

2) Body-related visual information constraint: MIoBS depends on visual information about the shape and the structure of the body or body part.

3) Peripersonal space (PPS) constraint: MIoBS occurs within a limited space surrounding the body, termed PPS.

4) Embodiment constraint. Prolonged multisensory stimulation manipulating the spatio-temporal coherence of bodily signals alters bodily self-consciousness, by reshaping the PPS boundaries and inducing bodily self-consciuosness for non-corporeal objects (e.g. a rubber hand).

2.2.3. Body schema and body image

Humans make sense of their body ownerhip by constructing an internal representation of exteroceptive and interoceptive stimuli, and they also tend to use concepts on the body. Body image, body schema and the conceptual description of the body are the result of a multimodal integration process that receives input from proprioceptive, visual, tactile and other stimuli, that occasionally conflict (Paillard, 2005). Body image contains a set of beliefs, attitudes and concepts about the body and perceptions, dominated by the visual modality. It differs from the body schema, which is a system of the represented motor control, haptic, vestibular and somatosensory stimuli, where proprioception is the dominating modality. The body image is predominantly conscious, while the body schema is primarily unconscious (de Vignemont, 2010; Gallagher & Cole, 1995).

The degree of ownership over the body is the outcome of a successful multimodal integration that fluctuates, depending on task demand and the allocation of attention to the peripersonal or intrapersonal aspects of the body (de Vignemont, 2010). A limited capacity to integrate conflicting information from the peripersonal space and the inadequate perception of hands, legs, head movements and posture is one of the central issues in the aetiology of psychopathological symptoms.

2.3. The Rubber Hand Illusion (RHI)

The RHI is an experimental model invented by Botvinick and Cohen (1998) that allows the controlled manipulation of the experience of body-ownership. In brief, to elicit this illusion, the participant's real hand is kept out of the field of vision (e.g. behind a screen) while a realistic-like rubber hand is placed in front of him or her. The experimenter uses two paintbrushes to synchronously stroke the rubber hand and the participant's real hidden hand (Fig. 2). After a short period (~10-15 sec) the majority of people feels that the rubber hand belongs to them. The RHI is often a vivid illusion, with people making spontaneous verbal comments of surprise and excitement. The majority of the researchers involved in RHI-like manipulations claim that this paradigm is one of the few viable ways of investigating body-ownership scientifically.

2.3.1. Subjective measures of the illusion

The subjective experience of the RHI can be quantified with questionnaire including statements about the key perceptual effects of the illusion, such as "It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand being touched". The experts often use control questions considered to be unrelated to the RHI that is a good tool for identifying response biases (e.g. "It felt as if my hidden hand disappeared").

Figure 2. Induction of the rubber hand illusion.

The most commonly used rating scales are 7, 10 or 11-point Likert scales.

But what is the experience of body-ownership like? Longo and his colleagues (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008) conducted a large sample study investigating the subjective experience during the RHI by asking participants to complete a 27-item questionnaire after synchronous stroking. A Principal Component Analysis revealed that the subjective experience ownership consists of three distinct components: 1) ownership (e.g. rubber hand as part of one's body); 2) location (i.e. the rubber hand and one's own hand were felt in the same place); 3) agency (i.e. being able to move and control the rubber hand). It seems that these aspects are successfully manipulated during RHI.

2.3.2. Objective measures of the illusion

Several objective tests of the strength of the illusion have been developed, but the most widely used is the so-called "proprioceptive drift" – the degree to which people experience their hand to be closer to the rubber hand than it really is. Usually we ask the participants to close their eyes and indicate the perceived position of their hidden hand by drawing their unhidden index finger on a ruler (Fig. 3). During and after stroking people consider their hand to be closer to the rubber hand.
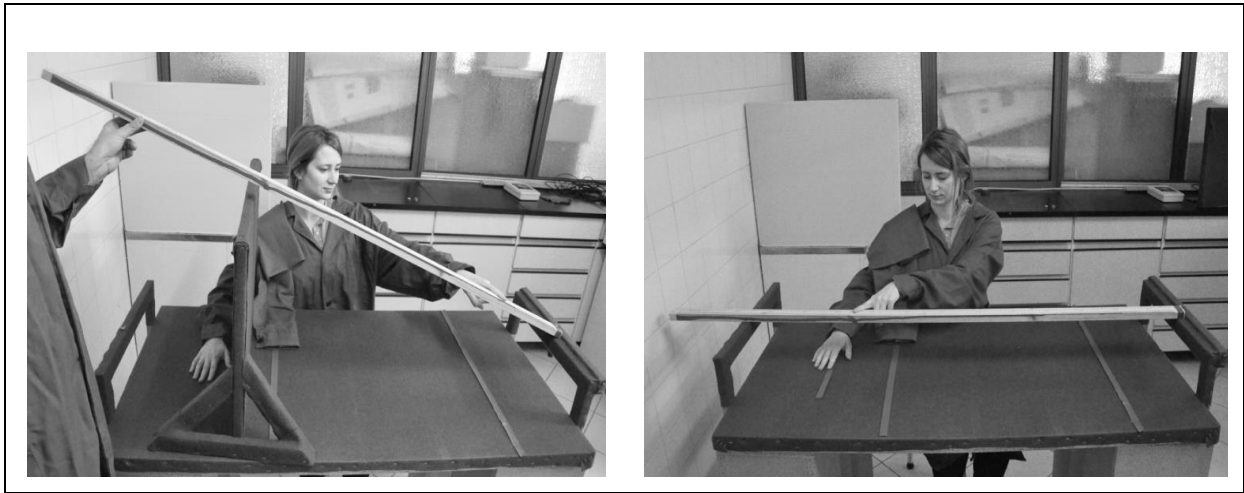
Figure 3. Measurement of proprioceptive drift in the RHI. A ruler is placed in an angular position in front of the participants, who are asked to put their left index finger on an arbitrary point of the initial part of the ruler. Then, after having instructed the participants to close their eyes, the experimenter removes the standing screen and positioned the ruler above the table. The participants are asked to indicate the perceived position of their right index finger by drawing their left index finger on the ruler to the location where they felt it was exactly above the tip of their right index finger.

Armel and Ramachandran (2003) and later Petkova and Ehrsson (2009) simulated injury to the owned rubber hand and recoded emotional responses (sympathetic activation) by registering changes in the conductance of the skin. It is accepted that emotional responses are always associated with enhanced activation of the autonomic nervous system, which produces increased sweating thus increased SCRs (skin conductance response). Another possible autonomic measure of the illusion is to register skin temperature on the real hidden hand. It is suggested that that skin temperature drops by 0.27 Celsius degrees during the illusion (Moseley et al., 2008).

2.3.3. Basic constraints of the RHI

The characterization of the constraints below leads us to important conclusions about the necessary factors for limb ownership (Ehrsson, 2012).

Temporal constraints. The feeling of ownership over a rubber hand depends on the temporal synchrony of multisensory cues, asynchronous stimulation significantly reduces the RHI. The importance of the temporal congruency has two main consequences: 1) asynchronous stroking can be used as a control condition in RHI-based experiments; 2) temporal synchrony bears obvious similarities with the temporal congruency principle in multisensory integration.

Spatial constraints. The RHI is also dependent on the spatial congruence of tactile, proprioceptive and visual information. Armel and Ramachandran (2003) demonstrated that the illusion was significantly weaker when the rubber hand was placed 0.91 meters in front of the adequate position. In his recent study Lloyd et al. (2002) found that the RHI is limited by the distance between the rubber hand and the participant's hidden real hand: by increasing the distance between the two hands she found a significant decrease in the strength of the illusion. It must be noted by the spatial congruence anatomical and postural constraints are also substantial. When the rubber hand is positioned in an anatomical implausible posture (e.g. rotated by 90 degrees), the RHI is abolished (Pavani, Spence, & Driver, 2000). The illusion is also diminished when a left rather a right rubber hand was used in an experiment involving the participant's right hand (Tsakiris & Haggard, 2005).

2.3.4. The bottom-up and top-down accounts of body-ownership

Why is the rubber hand experienced as part of our body? Multisensory integration and the resolution of potential conflicts of sensory modalities are key elements of generating a coherent representation of the world and the body (Tsakiris, 2010). The RHI reflects a three-way interaction between vision, touch and proprioception. Vision of tactile stimulation on the rubber hand captures the tactile sensation on the participant's hand and this visual capture results in a mislocalization of the felt location of one's hand towards the spatial location of the visual percept. Therefore, Botvinick and Cohen (1998) – the inventors – used a bottom-up explanation of the RHI by arguing that intermodal matching between vision and touch is sufficient for self-attribution of the rubber hand. Few years later Armel and Ramachandran (2003)

held a strong version of the Botvinick's and Cohen's view. They suggested that visuo-tactile correlation is both necessary and sufficient condition for the RHI. According to them any object (e.g. a wooden stick) can be experienced as part of one's body if strong correlation is presented between the different sensory modalities.

In contrast, Tsakiris and Haggard (2005) showed conflicting findings. They found that the RHI is not induced when the rubber hand is replaced by a neutral non-corporeal object such a wooden stick. A few years later Haans et al. (2008) used a factorial design where a viewed object could or could not have a hand shape with or without a natural-skin texture. The result showed that hand-shaped natural-skinned object induced stronger illusion as measured with a questionnaire.

These controversial findings are under debate even recently but it seemed obvious that the integration of them will be necessary to set up an adequate model of body-ownership.

2.3.5. The neurocognitive model of body-ownership: interaction between multisensory input and internal models of the body (Tsakiris, 2010)

A neurocognitive model of the RHI consists of several steps.

1) In the first step, the form of the viewed object is compared with a pre-existing body model that contains a description of the visual and anatomical properties of the body as a reference. In this step the right temporo-parietal junction (rTPJ) has been shown to be involved.

2) The second step compares the current state of the body and the postural and anatomical features of the body-part that is experienced as own. The activity in anterior parietal areas underpins this comparison.

3) The third comparison is between the current sensory inputs (between the vision and the felt touch). This comparison is underpinned by the posterior parietal cortex (PPC) by resolving the conflict between visual and tactile information and recalibrating the visual and tactile receptive fields. This recalibration will result in the touch referral, which is underpinned by the premotor cortex.

4) In the final step, the subjective experience of ownership updates the body model. This results in the incorporation of hand and subsequent physiological regulation of the body. A possible candidate for the neural background of ownership updates is the right posterior insula (Tsakiris, 2010).

2.3.6. Integration problems of body schema and body image

The integration of body schema and body image are key elements in psychopathologic syndromes, such as interpersonal over-involvement, schizophrenia and depersonalisation disorders (Graham, Martin-Iverson, Holmes, Jablensky, & Waters, 2014; Sass & Parnas, 2003). Schizophrenic patients with positive symptoms manifest more sensitivity to the RHI than healthy controls (Peled, Ritsner, Hirschmann, Geva, & Modai, 2000), and show elevated depersonalisation (disownership) and diminished agency over their real hand (Graham et al., 2014). However, schizophrenic patients treated with high doses of antipsychotics do not show sensitivity to the RHI (Ferri et al., 2014). On the other hand, schizophrenic patients with higher scores on schizotypy in personality questionnaires show a stronger sensitivity to the RHI (Thakkar, Nichols, McIntosh, & Park, 2011). Similarly, a subgroup of healthy participants with a high score on positive schizotypy and interpersonal reactivity scales, especially empathy scales, could demonstrate the same elevated RHI sensitivity, proprioceptive drift and ownership scores when asked to give a subjective rating of their feelings (Asai, Mao, Sugimori, & Tanno, 2011). Germine and colleagues (2013) found psychosis, such as characteristics involving referential thinking, magical ideation, cognitive distortion and perceptual aberration linked to the RHI. However, in their study, the proprioceptive drift scores remained independent from a positive propensity to psychosis. Eshkevari et al. (2012) detected higher ownership and proprioceptive drift scores in patients with elevated scores on the body dissatisfaction, emotional dysregulation and drive for thinness scales. The examination of patients with autism spectrum disorder resulted in a lower responsiveness to RHI induction, with a less general proprioceptive drift towards the rubber hand (Paton, Hohwy, & Enticott, 2012). The proprioceptive effect to the RHI induction showed a systematic delay, indicating an altered multisensory temporal integration in children with autism (Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012).

2.3.7. The invisible hand illusion (IHI)

Since Botvinick and Cohen (Botvinick & Cohen, 1998) invented the "classical" rubber hand illusion several new variants have occurred in neuroscience and psychology. One of them is the invisible hand illusion (IHI). As it is mentioned above, several models have proposed that a match between the visual information of hand-shaped object and implicit knowledge about the normal visual appearance of the body is an indispensable condition for inducing illusory hand ownership. Guterstam and colleagues (2013) put this assumption into question by showing that it is possible to elicit an illusion of having an invisible hand that "feels" touches applied to it in empty space in direct view of the participants. To induce this, a trained experimenter repetitively and synchronously applied brushstrokes to the participant's hand, which was hidden from view behind a screen (similarly to the RHI), and to a portion of empty space in full view of the participant (Guterstam et al., 2013). During the illusion the people experienced a referral of somatic and ownership sensations to the empty space that was fully visible to them, thereby evoking the experience of having an invisible hand. This effect was supported by complementary questionnaire, behavioral, psychophysiological (fMRI) evidences (Guterstam et al., 2013).

3. Sound induced proprioceptive drift in the IHI

3.1. Introduction

In this study we set up a conditioning protocol to test whether task-irrelevant and spatially and semantically uninformative auditory signals can be used as conditioned stimuli to replace the missing visual cues in the IHI. In an experiment conducted by our research group, and including a classical RHI and an IHI condition, we found the IHI to lead to both lower subjective ratings of the illusion and smaller proprioceptive drifts than the original RHI. Thus, we decided to associate metronome sound (presented diotically over headphones) with the view of an artificial hand through a conditioning process in which the classical RHI would be repeatedly elicited in the presence of metronome beats. We hypothesized that following this conditioning process metronome sound would be able to compensate for the lack of the view of an artificial hand in the IHI, thereby enhancing the illusion as compared with its soundless version. In our first experiment, we tested this hypothesis by predicting that the enhancing effect of metronome sound on the strength of the IHI would be significantly greater in the post-conditioning session than in the pre-conditioning (baseline) session. Since the results did not support our prediction, but unexpectedly revealed a conditioning-independent influence of auditory stimulation on proprioceptive data, we did not set up a more complex protocol to further examine associative learning in the IHI. Instead, a second experiment was conducted in order to check the results when the same experimental design is used as in the first experiment, except that the between-session RHI is elicited without conditioning sound stimuli.

3.2. Methods

3.2.1. Participants

The study was conducted according to the principles of the Declaration of Helsinki and was approved by the Regional Research Ethics Committee. Twenty-six healthy university students participated in both experiments [Experiment 1 (11 females, 15 males, mean age: 19.5 ± 0.8); Experiment 2 (20 females, 6 males, mean age: 20.8

± 1.9)]. Participants had no previous experience with the RHI (or with related illusions), and were blind to the hypothesis of the study.

3.2.2. Experimental setup

Participants wearing headphones sat on a chair with their arms resting comfortably on a table. To prevent subjects from seeing their right hand a standing screen was placed on the table beside the right arm. The experimenter stood opposite the participant. The design of Experiment 1 consisted of three sessions: a pre-conditioning, a conditioning and a post-conditioning session (see Fig. 4).
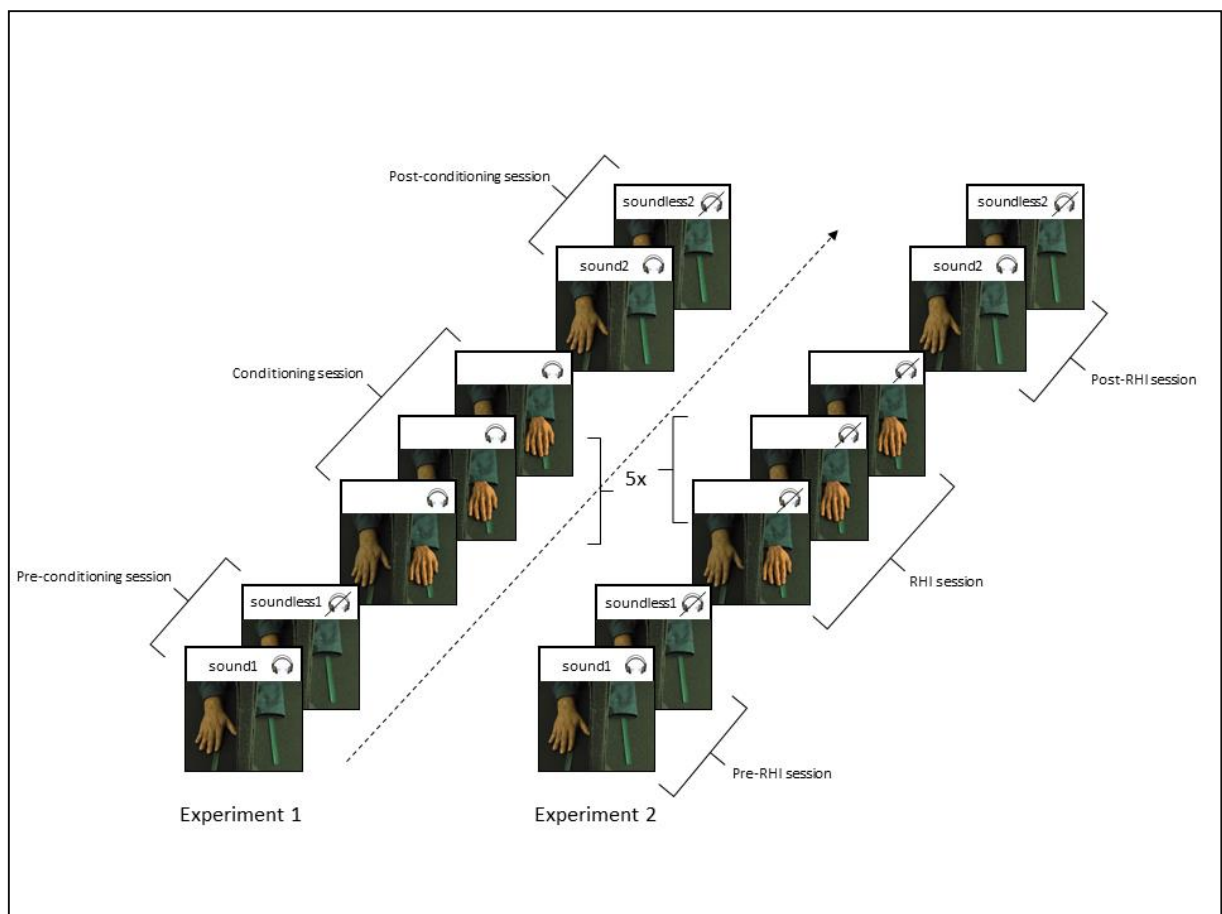
Figure 4. The design in Experiment 1 and Experiment 2. „IHI" refers to the Invisible Hand Illusion and „RHI" refers to the Rubber Hand Illusion. The presence or absence of auditory stimuli is represented by headphone and no headphone icons. The sequence of sound and soundless conditions was counterbalanced across subjects.

Within the pre- and post-conditioning sessions the IHI was elicited in two conditions: in a sound and in a soundless condition. In the sound condition metronome beats

were presented to the participants through the headphones in synchrony with visuo-tactile stroking. Metronome beats were short, percussive sounds (stimulus duration: 120 ms; peak sound frequency: 1.2 kHz). In the soundless condition auditory signals were not used. The sequence of the sound and the soundless condition was counterbalanced across subjects both in the pre- and the post-conditioning session. In the conditioning session the classical RHI was repeatedly induced, and metronome beats were presented in synchrony with stroking. The design of the second experiment also consisted of three sessions: a pre-RHI, a RHI and a post-RHI session. The setup was similar to the first experiment except that no metronome beats were presented in the RHI session. The invisible hand illusion paradigm was adopted from Guterstam et al. (2013). The illusion was induced by applying brushstrokes to the participants' hidden right hand and simultaneously moving another paintbrush 2-3 cm above the table as if an invisible hand lying between the participants' right hand and body midline had been stroked. The experimenter tried to move the paintbrush in empty space in exactly the same manner that reflected the movements of the brush touching the real hand. The distance between the index finger of the invisible hand and the index finger of the real hand was 20 cm. The rubber hand illusion paradigm was adopted from Botvinick and Cohen (1998). A realistic-looking prosthetic right hand was placed to the left of the participants' occluded right hand and stroked synchronously with it. The distance between the index finger of the prosthetic hand and the index finger of the real hand was, again, 20 cm.

3.2.3. Procedure

Both the sound and the soundless blocks started with a 90 sec stroking period, during which all fingers (except the thumb) of the invisible and the unseen right hand were at the same time stroked by two brushes synchronously to induce the IHI. After the stroking period the perceived position of the participant's right hand was measured, and then participants reported their perceptual experiences associated with stroking by answering a questionnaire. The sound and the soundless blocks as well as all three sessions of each experiment were separated by a 120 sec rest period containing hand-movement tasks in order to restore the sense of ownership toward the real hand. The conditioning session in Experiment 1 and the RHI session

in Experiment 2 consisted of five RHI blocks, each of which lasted for 60 sec. The RHI blocks were separated by 40 sec rest periods. The predetermined pattern and the frequency (1 Hz) of stroking were the same in all blocks of the study.

3.2.4. Measurements

3.2.4.1. Proprioceptive drift

The perceived position of the participants' right hand was measured by a similar method used by Guterstam et al. (2013, see also Hegedüs et al., 2014). First a ruler was placed in an angular position in front of the participants, who were asked to put their left index finger on an arbitrary point of the initial part of the ruler (see Figure 3). Then, after having instructed the participants to close their eyes, the experimenter removed the standing screen and positioned the ruler 13 cm above the table. Finally, the participants were asked to indicate the perceived position of their right index finger by drawing their left index finger on the ruler to the location where they felt it was exactly above the tip of their right index finger. The subjects were instructed to answer as spontaneously as possible. In accordance with the original study hypothesis, comparative proprioceptive data were collected in Experiment 1, so the zero reference point used for measurements was located at the end of the ruler. In Experiment 2, however, it was important to obtain informative data from each proprioceptive measurement, so the zero point on the ruler corresponded to the fixed position of the participant's right hand. Accordingly, in Experiment 1 values denote distances from the endpoint of the ruler while in Experiment 2 values denote distances from the right index finger. Greater values report drifts toward the invisible hand in both experiments.

3.2.4.1. Questionnaire

To measure the main characteristics of how the participants subjectively experienced the IHI, a questionnaire was administered consisting of 4 statements (see Table 1). We adopted 3 questions from Guterstam et al. (2013) and one from Botvinick and Cohen (1998). Two items were test questions referring to the two main components of the illusion (Q1 was about the mislocalization of tactile stimuli, Q2 was about the ownership over the invisible hand). Two statements (Q3, Q4) were

used as control questions in order to identify any response bias affecting the reported changes in the vividness of the illusion. Item Q3 was taken from Guterstam et al. (2013), while Q4 is a commonly used control question in the RHI literature (see Longo, Schüur, Kammers, Tsakiris, & Haggard, 2008). The subjective component scores were calculated by taking the average of each subject's ratings for Q1-Q2 (average vividness score) and for Q3-Q4 (average control score) questions. Participants answered each question by choosing a number from an 11-point Likert scale ranged from 0 ("strongly disagree") to 10 ("strongly agree"). The questions were presented in a random order.

	Question type	References
Q1. I felt the touch of the brush in empty space in the location where I saw the brush moving.	Test question no. 1	Guterstam et al., 2013
Q2. I felt as if I had an "invisible" hand.	Test question no. 2	
Q3. It felt as if my right hand disappeared.	Control question no. 1	
Q4. It seemed as if I might have two right hands or arms.	Control question no. 2	Botvinick & Cohen, 1998 Longo et al., 2008

Table 1. Questionnaire statements measuring how participants subjectively experienced the invisible hand illusion.

3.2.5. Statistical analysis

Data were analyzed using SPSS statistical software package (version 22.0.0). The level of significance was set at $p < 0.05$. We used the Kolmogorov-Smirnov test to check for the normality of data distribution. The test showed that our data set followed normal distribution.

For within-subject analysis of questionnaire and proprioceptive data repeated-measures ANOVA was used, and the partial eta squared was calculated. To get a clearer picture of the pattern of results, paired samples t-tests with Bonferroni correction were conducted, and Cohen's d_z effect sizes were computed for all post-hoc comparisons (Lakens, 2013). In Experiment 1, the first experimental session was the pre-conditioning session, and the second experimental session was

the post-conditioning session, while in Experiment 2, the pre-RHI and the post-RHI sessions were referred to as the first and second experimental sessions.

3.3. Results

3.3.1. Questionnaire data

We performed a 2 X 2 X 2 analysis of variance (ANOVA) on subjective scores with three within-subjects factors. The factors were 1) Sound (sound vs. soundless), 2) Session (first experimental session vs. second experimental session) and 3) Question type (average vividness score vs. average control score). For post-hoc analysis paired samples t-tests were used, and p values were Bonferroni-corrected by multiplying them by the number of comparisons (n = 8).

3.3.1.1. Experiment 1

Only Question type factor reached significance [$F(1,25) = 64.400$, $p < 0.001$, η^2_p = .729]; the average control scores were lower. Neither Sound factor [$F(1,25) = 1.573$, $p = 0.222$] nor Session factor [$F(1,25) = 3.262$, $p = 0.083$] was significant, and no interactions were found. The post-hoc analysis showed that in each experimental condition, the average vividness score was significantly higher than the average control score ($p < 0.01$). According to these results, neither auditory cueing nor the conditioning process had an influence on the vividness of the illusion.

3.3.1.2. Experiment 2

The repeated measures ANOVA revealed a significant main effect for Question type [$F(1,25) = 33.249$, $p < 0.001$, $\eta^2_p = 0.571$]; the control scores were again significantly lower. Sound [$F(1,25)=1.067$, $p = 0.312$] and Session [$F(1,25) = 3.475$, $p = 0.074$] factors were again not significant. In this experiment, however, the analysis found a significant Sound X Session interaction [$F(1,25) = 5.826$, $p = .023$, $\eta^2_p = 0.189$]. In accordance with this, the subjective vividness of the IHI following soundless stroking was significantly greater after the exposure to the RHI than before [$t(25) = -3.209$, $p = 0.032$, Cohen's $d_z = 0.63$], but no other significant differences were found by the post-hoc comparisons, except that the average vividness scores were again significantly higher than the control scores in all conditions ($p < 0.01$).

Overall, the analysis of questionnaire data indicated that a few minutes exposure to the classical RHI is able to enhance the vividness of the subsequent IHI, an effect which is, however, eliminated or diminished when auditory stimulation is combined either with the IHI or with the RHI.

3.3.2. Proprioceptive drift

A 2 X 2 repeated measures ANOVA was used for the analysis of proprioceptive data. The factors were 1) Sound (sound vs. soundless) and 2) Session (first experimental session vs. second experimental session). For post-hoc analysis paired samples t-tests were conducted, and P values were Bonferroni-corrected by multiplying them by the number of comparisons (n = 4).

3.3.2.1. Experiment 1

The ANOVA revealed a significant main effect for Sound [$F(1,25) = 8.028$, $p = 0.009$, $\eta^2_p = 0.243$], such that the use of auditory cues resulted in that the perceived position of the right hand drifted toward the invisible hand as compared to when only visuo-tactile stimulation was provided. Main effect of Session was also significant [$F(1,25) = 18.107$, $p < 0.001$, $\eta^2_p = 0.420$]; subjects perceived their right hand to be closer to the invisible hand in the post-conditioning session. There was no significant interaction between Sound and Session [$F(1,25) = .698$, $p = 0.411$].

The post-hoc analysis found no significant difference between sound1 and soundless1 conditions [$t(25) = -2.057$, $p = 0.200$, Cohen's $d_z = 0.40$], and neither between sound2 and soundless2 conditions [$t(25) = -1.528$, $p = 0.556$, Cohen's $d_z = 0.30$]. The influence of auditory stimulation on proprioceptive recalibration was, therefore, not significant in the two experimental sessions taking them separately. In contrast, the differences both between sound1 and sound2 [$t(25) = -2.740$, $p = 0.044$, Cohen's $d_z = 0.54$] and between soundless1 and soundless2 [$t(25) = -4.095$, $p = 0.002$, Cohen's $d_z = 0.80$] conditions were found to be significant, showing that the between-session proprioceptive drift was independent of the presence or absence of auditory cues (the results are shown by Figure 5). Overall, this pattern of findings did not support the study hypothesis, thereby suggesting that the observed main effects of Sound and Session were unrelated to the use of the conditioning procedure.
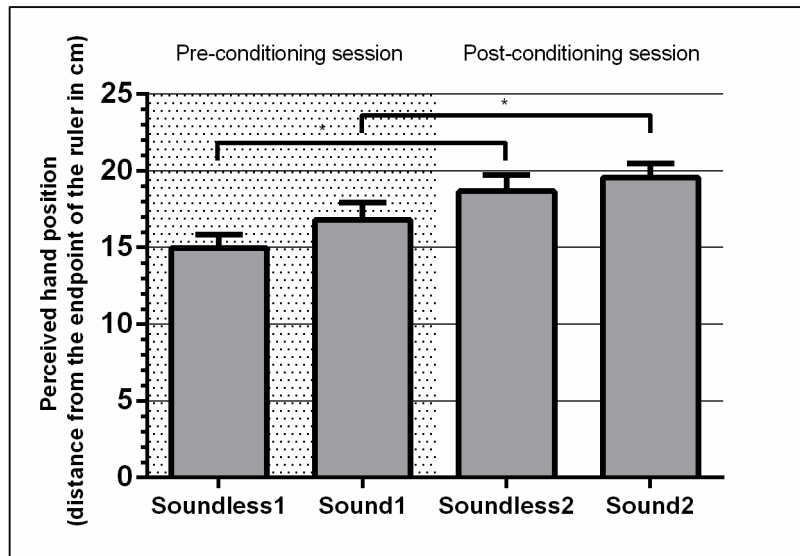
Figure 5. Perceived hand positions across experimental conditions in Experiment 1. Values represent the distance (in cm) between the endpoint of the ruler and the perceived position of the right index finger. Higher values correspond to drifts toward the invisible hand. Asterisk denotes $p < 0.05$, paired t-test with Bonferroni correction. Horizontal bars represent standard error to the mean.

3.3.2.2. Experiment 2

Essentially the same results were obtained in this experiment as in Experiment 1. The ANOVA showed again significant main effects for both Sound [$F(1,25) = 8.277$, $p = 0.008$, $\eta^2_p = 0.249$] and Session [$F(1,25) = 11.587$, $p = 0.002$, $\eta^2_p = 0.317$], while the interaction between Sound and Session was not significant [$F(1,25) = 0.048$, $p = 0.828$]. These findings confirmed the conclusions of Experiment 1 by providing evidence that the conditioning procedure is not necessary for both the sound-induced and the between-session proprioceptive drifts to occur.

The post-hoc analysis also revealed similar results to those found in Experiment1 (see Figure 6). According to the Bonferroni-corrected paired samples t-tests, the differences neither between sound1 and soundless1 conditions [$t(25) = -1.598$, $p = 0.492$, Cohen's $d_z = 0.31$] nor between sound2 and soundless2 conditions [$t(25) = -2.596$, $p = 0.064$, Cohen's $d_z = 0.51$] were significant. The between-session differences were, however, again significant both when the sound1 and sound2 conditions were compared [$t(25) = -2.796$, $p = 0.040$, Cohen's $d_z = 0.55$] and when the soundless1 and soundless2 conditions were compared [$t(25) = -3.305$, $p = 0.012$, Cohen's $d_z = 0.65$].
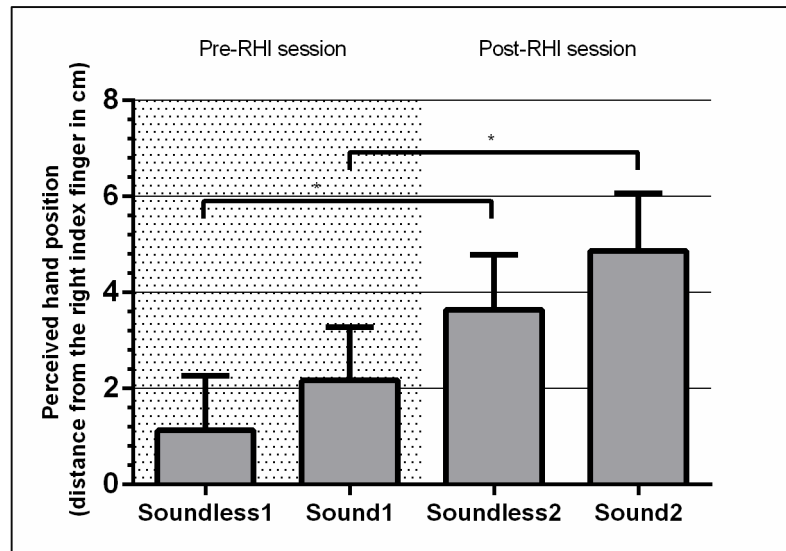
Figure 6. Perceived hand positions across experimental conditions in Experiment 2. Values represent the distance (in cm) between the real and the perceived position of the index finger. Higher values correspond to drifts toward the invisible hand. Asterisk denotes $p < 0.05$, paired t-test with Bonferroni correction. Horizontal bars represent standard error to the mean.

3.3.2.3. Combined analysis

The analysis of variance found a main effect of Sound in both Experiment 1 and Experiment 2, but post-hoc comparisons did not show significant differences between the sound and the soundless conditions in any of the experimental sessions taking them separately. Since exactly the same pattern of proprioceptive results was observed in both experiments, we decided to perform a combined analysis of the two data sets, thereby using proprioceptive data of all the 52 participants (double sample size) for statistical analysis. To accomplish this, the standardization of variables was first required due to the difference in the data recording method between the two experiments. The data transformation was performed by the method of subtracting the mean; in each of the two data sets taking them separately, the mean of all proprioceptive scores was subtracted from each data point, so that the scores were no longer influenced by where the zero point had been located on the ruler. After this standardization of variables, the two data sets were merged and analyzed according as described above.

The 2 X 2 ANOVA showed significant main effect for Sound [$F(1,51) = 16.399$; $p < 0.001$, $\eta^2_p = 0.243$] and Session [$F(1,51) = 29.690$; $p < 0.001$, $\eta^2_p =$

0.368]. No significant interaction was found. According to the Bonferroni corrected paired sample t-tests, all post-hoc comparisons were significant (see Table 2), including the difference between sound1 and soundless1conditions [t(51) = -2.616; p = 0.048], and between sound2 and soundless2 conditions [t(51) = -2.850; p = 0.024]. The degree of sound-induced proprioceptive drift was found to correspond to 5-7 percent of the distance between the invisible and real hand. The combined analysis of the two experiments, therefore, unambiguously clarified that the use of auditory cues during the induction of the IHI affects the proprioceptive aspect of the illusion.

Conditions		t (df)	Mean diff. (SD) in cm	p	Cohen's d_z
sound1	soundless1	2.616 (51)	1.444 (3.981)	.048*	.36
sound2	soundless2	2.850 (51)	1.050 (2.657)	.024*	.40
sound1	sound2	-3.952 (51)	-2.719 (4.962)	<.001***	.55
soundless1	soundless2	-5.260 (51)	-3.113 (4.268)	<.001***	.73

Table 2. t-test results of proprioceptive data comparing experimental conditions in the combined analysis of the two experiments. One asterisk denotes p < 0.05, three asterisks denote p < 0.001, paired t-test with Bonferroni correction.

3.4. Discussion

The classical rubber hand illusion is partly caused by a trisensory interaction in which the integration of visual and tactile information leads to the recalibration of hand proprioception (Botvinick & Cohen, 1998; Rohde, Di Luca, & Ernst, 2011). As the IHI paradigm shows, this trisensory interaction takes place even in the absence of a rubber hand, i.e. when only the brush strokes are seen by the subjects (Guterstam et al., 2013). Though we failed to demonstrate the effect of associative learning on the IHI, the presented results provide relevant contributions to the study of the multimodal processes underlying the IHI. Most importantly, our data reveal that the IHI paradigm can be extended by combining auditory cues with visuo-tactile stimulation, since we found the synchronous use of metronome sound and visuo-tactile stroking to lead to a change in the perceived hand position as compared to when only visuo-tactile stimulation was used. The resulting sound-induced proprioceptive drift toward the invisible hand was observed irrespective of whether

or not sound stimuli was associated with the RHI in between the experimental sessions, showing that the auditory contribution to the IHI was independent of conditioning.

When we designed our study we considered the metronome sound to be a neutral signal that could be used as a conditioned stimulus during the investigation of how conditioning can influence body perception. The rationale behind this was that metronome sound presented diotically through headphones is both semantically and functionally unrelated to the IHI, and conveys no information about the spatial location of the hand. In the literature on multisensory interactions there is a growing body of evidence that task-irrelevant and uninformative auditory signals can enhance visual perception and visual detection task performance merely through the temporal correspondence between the auditory and visual events (see eg. Noesselt, Bergmann, Hake, Heinze, & Fendrich, 2008; Van der Burg, Olivers, Bronkhorst, & Theeuwes, 2008; Vroomen & Gelder, 2000; Zou, Müller, & Shi, 2012). Furthermore, some experiments have demonstrated that tactile perception can also be influenced by the temporal properties of spatially, functionally and semantically irrelevant sounds (see e.g. Bresciani et al., 2005; Ro, Hsu, Yasar, Elmore, & Beauchamp, 2009). To our best knowledge, however, our results are the first to show that irrelevant auditory cues presented in synchrony with rhythmic visuo-tactile stimuli can enhance the effect of visuo-tactile integration on bodily self-perception.

The sound-induced proprioceptive drift we observed could not be predicted on the basis of the existing theoretical accounts of the RHI-like illusions. Nevertheless, a possible explanation for these results is provided by the Bayesian causal inference model of multisensory perception, which takes into account that the integration of information from different modalities is beneficial only if the different sensory cues have a common origin, and therefore optimal integration must depend on the probability distribution the brain associates with the possible causal structures of sensory events (Körding et al., 2007; Shams & Beierholm, 2010; and see for a review, Shams, 2012). A recent study has shown that this computational model is well applicable to the RHI, and explains why the perceived temporal relation between the visual and tactile stroking strongly influences whether and how visual, tactile and proprioceptive stimuli are integrated during the induction of the RHI (Samad, Chung, & Shams, 2015). Our sound-induced proprioceptive findings also fit well with this model when considering that in the IHI the visible brush moves

in the air without touching a rubber hand, so the capture of visuo-tactile synchrony may be uncertain enough that auditory cues signaling when a portion of empty space is 'touched' could effectively increase the precision of estimates regarding the temporal proximity between the seen and felt strokes. If the presentation of sound stimuli is able to reduce uncertainty associated with the perception of visuo-tactile synchrony, thereby increasing the probability that the seen and felt strokes have a common cause, then, according to the Bayesian causal inference model of the RHI-like illusions, it must lead to stronger proprioceptive responses in the sound conditions. This speculation is consistent with the findings of many previous studies showing that audition often dominates the temporal perception of events in other modalities (see eg. the "temporal ventriloquism" effect, Bertelson & Aschersleben, 2003; Morein-Zamir, Soto-Faraco, & Kingstone, 2003; Recanzone, 2003; Spence & Squire, 2003; J Vroomen & Gelder, 2004).

Nonetheless, the role of attentional modulation in the sound-related proprioceptive change cannot be excluded either, especially when considering the Dynamic Attending Theory, which assumes that in the presence of rhythmic sensory cues, attentional oscillations become synchronized to the rhythm of stimulation, and perceptual events in phase with the peaks of attention are more expected and better processed (Jones & Boltz, 1989.; Large & Jones, 1999; see for further details, Brochard, Tassin, & Zagar, 2013). Accordingly, it is reasonable to suppose that the presence of metronome beats in the sound conditions may have increased the oscillatory attention effect of rhythmic visuo-tactile stroking, which resulted in an enhanced processing of the on-beat visuo-tactile inputs.

The discovery that audition can influence the proprioceptive aspect of the IHI is consistent with the literature findings on the neural processes associated with the illusion. Neuroimaging studies have identified the activation in the premotor and intraparietal cortices as neural correlates of the RHI-like illusions, and an increased effective connectivity between these areas has been found to be related to the IHI (Ehrsson et al., 2004; Guterstam, Björnsdotter, Gentile, & Ehrsson, 2015; Guterstam et al., 2013). The neurophysiological properties of neurons located in these brain regions were thoroughly examined by studies on nonhuman primates, and the resulting data also suggest that the neural activity in the human premotor-parietal circuits must play an essential role in how multisensory processes underlie such illusions like the IHI (see for a review, Blanke et al., 2015). With respect to the

proprioceptive drift, one of the most remarkable observations was that the intraparietal cortex of the macaque contains neurons that respond to both proprioceptive and visual signals in order to monitor the static arm position, and synchronous visuo-tactile stimulation of a visible fake hand and the monkey's unseen real hand is able to alter the sensitivity of these neurons to visual inputs, thereby affecting how the brain encodes the spatial location of the arms (Graziano, Cooke, & Taylor, 2000). Other studies have also shown that several populations of neurons in the premotor and parietal areas have the capacity to integrate proprioceptive, tactile and visual inputs representing the hand and the space around the hand (see for reviews, Graziano & Cooke, 2006; Guterstam et al., 2013, and see also the Perihand Space Model of the RHI-like illusions, Makin et al., 2008).

Of particular significance to the present report is the discovery that a high percentage of neurons in the intraparietal areas respond also to auditory signals, and that both the premotor and the intraperital cortex contains somatosensory-visual-auditory trimodal neurons in monkeys (Graziano et al., 1999; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005, and see for a review, Ghazanfar & Schroeder, 2006). It has been observed that the auditory as well as the visual receptive field of premotor trimodal neurons matches their tactile receptive field; these neurons selectively or preferentially respond both to the tactile stimulation of the head, and to the sound sources (or visual events) near the head, within approx. 30 cm (Graziano et al., 1999). The existence of such body-part-centered coding of auditory stimuli in humans has also been confirmed by neuropsychological and behavioral studies examining audio-tactile interactions in which the auditory modulation of tactile perception has been found to be stronger when the sound source is sufficiently close to the body part (trunk/head/ hand) to which the tactile stimulation is applied (see eg. Canzoneri, Magosso, & Serino, 2012; Farnè & Làdavas, 2002; Serino, Canzoneri, Marzolla, di Pellegrino, & Magosso, 2015). Additionally, TMS and tDCS studies have provided evidence for the critical role of human premotor-parietal networks in the representation of auditory peripersonal space (Avenanti, Annela, & Serino, 2012; Serino, Canzoneri, & Avenanti, 2011). Since complex sound was used in our experiments, it is important to note here that in the audio-tactile interactions mentioned above, complex sounds have been demonstrated to have a stronger and more space-sensitive effect on the detection or localization of touch sensations than pure tones

(Farnè & Làdavas, 2002; Kitagawa, Zampini, & Spence, 2005; Occelli, O'Brien, Spence, & Zampini, 2010). Moreover, evidences suggest that for some audio-tactile interactions limited to the peripersonal space, sound stimuli presented within the space surrounding the head have an overall higher degree of saliency than those resulting from a source far away from the head even when the affected tactile stimuli are delivered to the hand (Occelli et al., 2010; Teramoto, Nozoe, & Sekiyama, 2013). Taking these findings together, it seems likely that an interplay between the neuronal populations of premotor-parietal areas is sufficient to provide mechanisms through which complex sound stimuli presented within the perihead space can modulate the processing and integration of visual and tactile signals so that it leads to an enhanced recalibration of the felt hand position in the IHI.

In our experiments, the sound-induced proprioceptive drift was not followed by changes in how participants subjectively experienced the IHI. This observation confirms the results of previous studies showing that there is no direct causal connection between proprioceptive recalibration and the feeling of ownership over a fake hand (Dempsey-Jones & Kritikos, 2014; Holle, McLatchie, Maurer, & Ward, 2011; Holmes, Snijders, & Spence, 2006; Rohde et al., 2011). It also reveals that the dissociation between subjective and proprioceptive measures is a common feature of the RHI and the IHI. A possible explanation for why multisensory processes leading to the sound-induced proprioceptive drift could not enhance the experience of the illusion can be given by taking into account that the features of auditory stimuli presented during the induction of the IHI did not correspond to the participants' pre-existing knowledge about what kind of sound should be heard when one's hand is stroked by a brush. Appropriate acoustic signals occurring in synchrony with unseen tactile stimuli can modulate hand representation, thereby producing such illusions like the parchment-skin or the marble hand illusion (Jousmäki & Hari, 1998; Senna, Maravita, Bolognini, & Parise, 2014). An opposite, inhibitory effect, however, can also be expected when, on the basis of the subjects' prior experiences and knowledge, there is a conflict between the auditory and viso-tactile cues used for manipulating the perception of the hand. Moreover, in our Experiment 2, a between-session increase in the ratings of the illusion was observed, but only in the soundless conditions, which suggests that the presence of metronome beats prevented the between-session enhancement of the illusory experience. Thus, the 'peculiarity'of metronome sound associated with brush

stroking may explain the divergence between sound-related proprioceptive and questionnaire data under the assumption that the neurocognitive mechanisms which underlie the referral of touch sensations to, and the feeling of ownership over a portion of empty space are more complex, and more influenced by top-down regulatory processes than those resulting in proprioceptive recalibration. It is important to note, that the latter assumption is supported by RHI experiments in which higher-order cognitive factors together with conflicting visuo-proprioceptive cues abolished the illusion without eliminating proprioceptive drift (Dempsey-Jones & Kritikos, 2014; Holle et al., 2011; and see also the Neurocognitive Model of Body Ownership, Tsakiris, 2010).

There are several limitations to this study. The most important one is that asynchronously presented sound stimuli were not used in our experiments, due to the explorative nature of the study. Thus, on the basis of the presented results, there remains some uncertainty about whether the synchrony between the metronome beats and the visou-tactile stroking is a necessary condition for the sound-induced proprioceptive drift to occur in the IHI. An additional limitation is that the absence of asynchronous stroking control makes it difficult to unambiguously interpret between-session effects.

4. Temperament and syndromes specific susceptibility for RHI

4.1. Introduction

The aim of the study is to explore individual capacity for self-integration, susceptibility to the RHI and the role of temperamentum factors in the emergence of body schema and body image dissociation. The RHI is considered to be a body boundary provoking experimental situation, used with patients and healthy persons alike. Psychopathological vulnerability, especially to schizophrenia, delusional experiences, anxiety, and interpersonal sensitivity in participants with a vivid RHI response were detected in both healthy persons and patients (Germine et al., 2013; Graham et al., 2014; Peled et al., 2000; Thakkar et al., 2011).

Considering the association among the embodiment scores and schizotypy, magical ideation and interpersonal sensitivity related emphatic diffusion we predict elevated ownership scores in participants with enhanced vulnerability to those symptoms that are related to a weakened ability to differentiate between the self and others. Following other studies (Eshkevari et al., 2012; IJsselsteijn, de Kort, & Haans, 2006; Kammers et al., 2009; Longo et al., 2008; Preston & Ehrsson, 2014), the association between psychopathologic vulnerability traits and the RHI will be based on ownership, disownership and proprioceptive drift scores.

4.2. Methods

4.2.1. Participants

Forty-eight healthy volunteers, including 20 males (mean age 21.8, SD = 2.72) and 28 females (mean age 20.9, SD = 2.01) were recruited from a pool of students at the University of Pécs. No participants had any previous psychiatric illness or experience with the RHI, and they were blind to the hypothesis tested by the study. Participants received a small fee for taking part in the study, which was conducted according to the principles of the Declaration of Helsinki and approved by the Regional Research Ethics Committee.

4.2.1. Experimental setup and procedure

Participants sat on a chair with their arms resting on a table with the palm facing down. Three experimental conditions were used in our study: pre-test condition (no-stroking) when a baseline proprioceptive drift was measured, illusion induction condition (synchronous stroking), and no illusion induction control condition (asynchronous stroking) (see Fig. 7). In the synchronous and the asynchronous conditions, a realistic-looking prosthetic left hand was placed to the right of the participant's real left hand. A standing screen was placed between the artificial and the real hand, in order to prevent participants from seeing their own left hand.
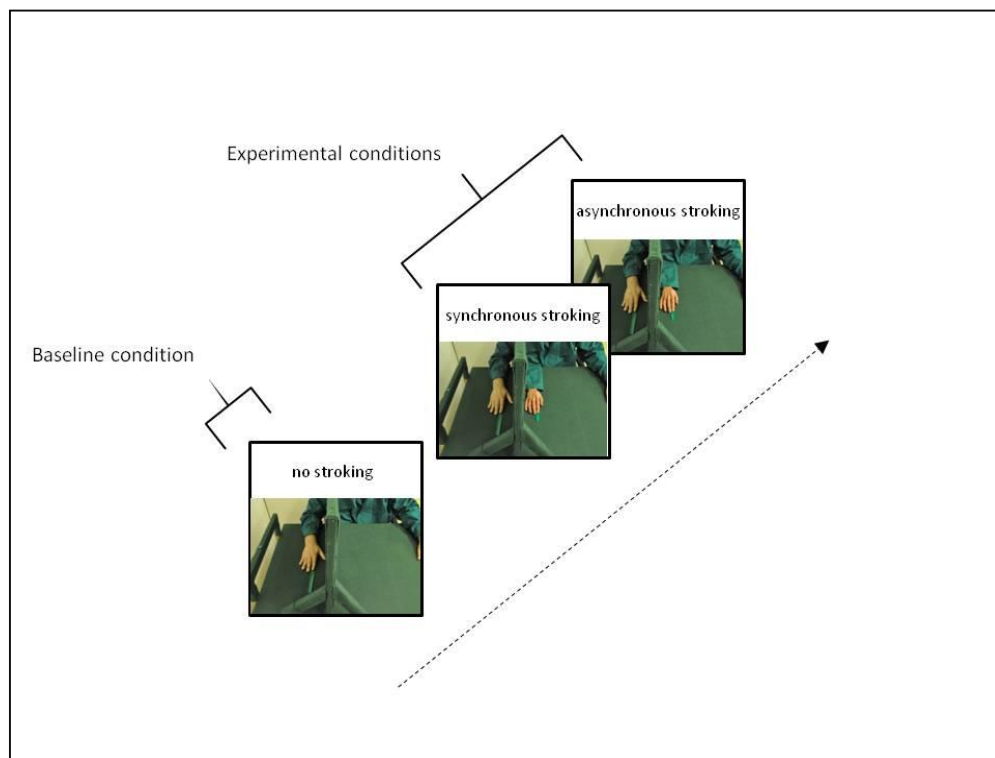
Figure 7. The experimental design. The study consisted of three conditions involving a baseline proprioceptive drift measurement and two experimental conditions. The sequence of synchronous and asynchronous conditions was counterbalanced across subjects.

The examination consisted of three conditions involving a baseline proprioceptive drift measurement and two blocks corresponding to the two experimental conditions, synchronous and asynchronous stimulation on their own hand and on the rubber hand. Before starting the synchronous stroking and asynchronous stroking, participants went through a pre-test (no-stroking) condition.

They were asked to point to the location of their real hand with closed eyes to define the baseline point to assess the extent of the proprioceptive drift. After this two blocks, synchronous and asynchronous stroking were applied in random order. Both the synchronous and the asynchronous block consisted of two-minutes stroking period. The pattern and the frequency (1 Hz) of stroking were predetermined in both conditions by the use of a metronome that guided the experimenter over an earphone. There were five-minute rest periods between the experimental blocks. After the 'stroking period', the proprioceptive drift was assessed. After this, the participants were asked to fill in a questionnaire that consisted of test items concerning ownership and disownership statements.

4.2.1. Measurements

4.2.1.1. Proprioceptive drift

The change in the perceived position of the participant's left hand was assessed by a procedure known from our previous experiments (Hegedüs et al., 2014). First, a ruler was placed in an angular position in front of the participants, who were asked to put their right index finger somewhere on the front part of the ruler. After instructing the participants to close their eyes, the experimenter removed the standing screen and positioned the ruler 13 cm up the table. Finally, participants were asked to indicate the perceived position of their left index finger by drawing their right index finger on the ruler to the location where they felt it was exactly above the tip of their left index finger. The extent of the proprioceptive drift was defined by the distance between the participant's pre-test and post-test (synchronous or asynchronous) report of location. A higher score indicates a higher pointing error, that is, the participant perceived the real arm's location closer to the rubber hand.

4.2.1.2. Questionnaire

A questionnaire consisting of eight statements was administered to assess how the participants subjectively experienced the rubber hand-related ownership and real hand–related disownership experiences in synchronous and asynchronous conditions. The eight questions were adopted from Longo et al. (2008), referring to the two main components of the participant experience. The summation of questions

1 to 4 concerned the embodiment (ownership score) of the rubber hand, and the summation of questions 5 to 7 concerned the relative loss of their own hand feelings (disownership score), and question 8 was a control item for test response bias (see Table 3). Participants answered each statement by choosing a number from an 11

Ownership, disownership and control statements	Synchronous stimulation	Asynchronous stimulation	Wilcoxon rank scores, and its significance level
	mean (SD)	mean (SD)	Z–score
Ownership statements			
Q1. It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched.	6.02(3.3)	2.43(2.5)	−5.31**
Q2. It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.	5.07(3.5)	2.14(2.3)	−4.94**
Q3. It felt as if the rubber hand were my hand.	5.60(3.4)	2.60(2.9)	−4.69**
Q4. It seemed like the rubber hand belonged to me.	5.68(3.3)	2.56(2.7)	−4.83**
Disownership statements			
Q5. It seemed like I was unable to move my hand.	4.00(3.4)	2.39(2.8)	−3.73**
Q6. It seemed like I couldn't really tell where my hand was.	4.02(3.2)	2.43(2.8)	−4.05**
Q7. It seemed like my hand had disappeared.	3.83(3.1)	2.29(2.7)	−3.18**
Control item			
Q8. It seemed as if I might have more than left hand or arm.	.89(2.29)	.66(1.9)	−.66 n.s.

Table 3. Rubber hand questionnaire statements and control item for assess ownership and disownership feeling after synchronous or asynchronous haptic stimulation. Wilcoxon rank test scores and *p*-values. **$p < .001$.

point rating scale, ranging from zero ('strongly disagree') to 10 ('strongly agree'). Data from synchronous and asynchronous conditions were treated separately, as suggested by Longo et al. (2008), Marieke Rohde et al. (2011) and Preston and Ehrsson (2014).

4.2.1.3. Personality and psychopathological predispositions

The SCL-90-R is a psychiatric self-report inventory, containing 90 items scored on a five point rating scale, ordered in nine different subscales, indicating the rate of occurrence of the symptom during the time reference (Bandura, Barbaranelli, Caprara, & Pastorelli, 2010). The SCL-90-R has been widely used as a predisposition or outcome measure to assess mental status, symptom-specific psychological distress, and as a screening inventory (Holi, Sammallahti, & Aalberg, 1998). The SCL-90-R contains the following factors: Somatization (SOM); Obsessive-compulsive (OBS); Interpersonal sensitivity (INS); Depression (DEP); Anxiety (ANX); Hostility (HOS); Phobic anxiety (PHO); Paranoid ideation (PAR), and Psychoticism (PSY). The Hungarian standard T-scores for age and gender were defined by (Unoka et al., 2004)

The psychobiological trait predisposition to RHI sensitivity, primarily Novelty Seeking, was analysed in the frame of the Seven Factor Model of Personality, and assessed by the TCI-R questionnaire (Cloninger & Svrakic, 1997), adapted to the Hungarian context (Rózsa, Kállai, Osváth, & Bánki, 2005), which contains temperament and character factors to assess psychological predispositions. The rating scale based inventory involves four temperament factors: Novelty seeking (NS); Harm avoidance (HA); Reward dependence (RD), and Persistence (PS). It also contains three character factors: Self-directedness (SD), Cooperativeness (CO), and Self-transcendence (ST). The temperament dimensions were assumed to be independently heritable, related to different neurotransmitter system activation (NS = dopaminergic, HA = serotoninergic, RD = noradrenergic), and a function of the uncontrolled procedural learning system. The character factors are determined by rule-following, conscious behaviour control and modulation during social development, and are related to the propositional learning system. The TCI-R selectively measures the personality related to top-down and bottom-up cognitive processes; it is a biologically well-grounded and usable method, both for patients

and healthy participants, mainly to assess predispositions to different personality disorders (Cloninger & Svrakic, 1997). The standard Hungarian T-scores for different ages and genders were defined by (Rózsa et al., 2005).

4.2.2. Statistical analysis

In both synchronous and asynchronous conditions, each item of the RHI questionnaire was tested for normal distribution. The Kolmogorov-Smirnov test yielded significant deviations from normality for many of the items. Therefore, the non-parametric Wilcoxon rank test was performed separately for each item, to analyse the difference between the synchronous and asynchronous conditions. In contrast with the individual items, the distribution was found to be normal for the ownership and disownership scores. As the assumption of normal distribution was violated only for one scale, bivariate correlations were calculated using parametric Pearson's correlation coefficients to examine how the outcome measures of the RHI are associated with personality and psychopathology factors. The correlation between the RHI and non-normal anxiety data were computed by parametric correlation analysis. Alpha level was set at .05 in all cases.

4.3. Results

An analysis was conducted to reveal differences in the vividness of ownership and disownership experiences to understand the nature of within-subject changes between the synchronous and asynchronous conditions. The Wilcoxon rank test revealed that each ownership and disownership item (questions 1 to 7, Z = −531, p < .001, Z = −4.94, p < .001, Z = −4.69, p < .001, Z = −4.83, p < .001, Z = −3.73, p < .001, Z = −4.05, p < .001, Z = −3.18, p < .001) differed significantly in the synchronous and asynchronous conditions. The scores for all items amplified in the synchronous and declined in the asynchronous haptic stimulation condition. The detected lack of difference between the synchronous and asynchronous response bias control items (question 8, Z = −.66, ns.) suggested that participants used the rating scale considerably (see in Table 3). In the next phase, the three outcome RHI scores were used to check the validity of the synchronous stimulation for the RHI. The Paired Samples Test showed a significant contrast between the synchronous and asynchronous conditions in the scores for proprioceptive drift (t =

3.1, p < .01), ownership (t = 7.9, p < .001), and disownership (t = 5.5, p < .001) (Table 4). Therefore, the results indicate that synchronous tactile stimulation enhances the rate of the proprioceptive drift when compared to asynchronous stimulation, and elevates the vividness of ownership and disownership experiences. To examine the relationship between the outcome variable of the RHI and personality traits and the psychopathological symptoms list, in the next step we conducted a correlation analysis (see descriptive statistical values in Table 5 and correlation matrix and values in Table 6).

RHI components in different conditions	Mean(SD)	Max–Min.	t(df)	Sign
Propriocptive drift				
synchronous	3.7 (5.2)	22–(−6.5)	3.1(47)	.01
asynchronous	1.6 (4.1)	21–(−10)		
Ownership				
synchronous	22.4 (12.7)	0–40	7.9(47)	.001
asynchronous	9.8 (9.2)	0–30		
Disownership				
synchronous	11.8 (8.8)	0–30	5.5(47)	.001
asynchronous	7.1 (7.5)	0–30		

Table 4. Descriptive statistics for rubber hand illusion outcome values, and paired t–test results between synchronous and asynchronous conditions.

The results indicated that the synchronous proprioceptive drift correlated with temperament factors of the TCI-R, especially for participants with a high score on synchronous proprioceptive drift also showed a high score in Novelty seeking (r = .48, p < .001) and a low score in Harm avoidance factors (r = −.39, p < .01). No similar correlations have found in the asynchronous condition (NS: r = .18, ns., HA: r = −.14, ns.) and other factors in TCI-R (see in Table 6). Furthermore, participants with high score on synchronous ownership showed a high score in NS (r = .40, p < .01) and low score in HA (r = −.31, p < .05), but no similar correlation have found in the asynchronous condition (NS: r = −.26, ns., HA: r = −.10, ns.) and in other temperament and character factors of TCI-R (Fig. 8). Further, participants with high score on synchronous disownership showed a high score in NS (r = .37, p < .01)

	TCI-R			SCL-90-R	
	Mean(SD)	Min-Max		Mean(SD)	Min–Max
NS	49.8(9.2)	24–68	SOM	50.6(9.5)	39–77
HA	47.7(8.9)	20–61	OBS	54.4(9.6)	40–76
RD	48.6(8.9)	24–65	INS	53.1(10.2)	40–82
PS	55.8(8.6)	34–74	DEP	52.3(9.2)	40–80
SD	51.5(8.1)	26–68	ANX	53(10.6)	40–86
CO	50.3(12.2)	17–74	HOS	50.5(8.7)	40–74
ST	50.8(10.3)	33–75	PHO	47.6(6.8)	40 -70
			PAR	52.2(9.8)	40–86
			PSY	53.2(10.6)	41–81

Table 5. Descriptive statistics of Cloninger Temperament and Character Inventory (TCI-R): Novelty seeking (NS), Harm avoidance (HA), Reward dependency (RD), Persistence (PS), Self-directedness (SD), Cooperativeness (CO), Self-transcendence (ST); and symptom checklist 90-R (SCL-90), Somatization (SOM), Obsessive-compulsive (OC), Interpersonal sensitivity (INS), Depression (DEP), Anxiety (ANX), Hostility (HOS), Phobic anxiety (PHO), Paranoid ideation (PAR), Psychoticism (PSY).

and low score in HA (r = −.34, p < .05), but no similar correlation have found in the asynchronous condition (NS: r = .19, ns., HA: r = −.15, ns.). On the other hand, the proprioceptive drift was not associated with any psychopathological symptom list (SCL-90-R) factors, either in the synchronous or in the asynchronous conditions (see Fig. 9).

Examining the relationship between the ownership and disownership outcome variable of the RHI and the SCL-90-R symptom list scores, we found associations between ownership and factor scores for Interpersonal ensitivity (r = .32, p < .05), Paranoid ideation (r = .39, p < .05), and Psychoticism (r = .50, p < .001). Furthermore, an association between disownership and Psychoticism scores (r = .36, p < .05) was also detected. No similar associations were found in the asynchronous conditions. Other RHI outcome score associations were no found with SCL-90-R factors (see in Table 4 and Fig. 9).

Personality and psychopatology factors	Prorioceptive drif		Ownership		Disownership	
	sync	async	sync	async	sync	async
TCI-R						
Novelty seeking	.480***	.175	.401**	−.256	.370**	.186
Harm avoidance	−.385**	−.137	−.310*	−.096	−.338*	−.152
Reward dependency	−.066	.075	.097	.245	.241	.254
Persistence	.095	.164	−.057	.066	−.068	.053
Self−directedness	.021	−.016	−.211	−.062	−.116	−.013
Cooperativity	−.125	.058	−.139	.071	.033	.162
Transcendency	−.156	.046	−.138	.150	−.057	.100
SCL-90 -R						
Somatization	−.221	−.047	−.122	−.067	−.107	−.012
Obsession-compulsion	−.007	.052	.110	−.087	.035	−.011
Interpersonal sensitivity	.007	−.032	.324*	.115	.244	.113
Depression	−.025	.112	.185	.088	.201	.277
Anxiety	−.012	.003	.150	.104	.124	.198
Hostility	−.083	−.074	.101	.093	.085	.148
Phobia	−.098	−.016	.030	.197	.100	.256
Paranoid ideations	.120	.107	.389*	.206	.190	.125
Psychotocism	.163	.178	.499***	.096	.358*	.198

Table 6. Pearson correlations between Rubber Hand Illusion outcome measures and Cloninger Temperament and Character (TCI-R) and Symptom Checklist 90 (SCL-90) psychopathology predispositions factors for synchronous (sync) and asynchronous (async) conditions. *$p < .05$, **$p < .01$, ***$p < .001$.

4.4. Discussion

The aim of this study was to explore temperament, character and psychopathology vulnerability factors, which may play a role in the multisensory integration of body image and body schema, and the instability of self–experiences provoked by the induction of the RHI. The results demonstrated that synchronous proprioceptive

drift, synchronous ownership and synchronous disownership are elevated after the RHI induction.

Our results suggest that some of the outcome values of the RHI and personality predisposition (TCI-R) and psychiatric symptom factors (SCL-90-R) show close association. The conducted correlation analysis revealed that the proprioceptive drift in the synchronous conditions predict higher scores in Novelty seeking and lower values in Harm avoidance. On the other hand, ownership in the synchronous condition predicted higher scores in the Interpersonal sensitivity, Paranoid ideation, and Psychoticism symptom-specific scales. The correlation analysis showed an association between synchronous disownership scores and Psychoticism, Novelty seeking and Harm avoidance scales. Furthermore, the synchronous ownership showed an association with Novelty seeking and Harm avoidance. Other symptom-specific factors and temperament factors proved to be non-reactive to the RHI.

Most of the studies focus on three main indicators for the RHI. In certain cases, these are treated separately but interpreted in a common frame. A study, where ownership and proprioceptive drift were treated as an overall score (Asai et al., 2011), suggested that Schizotypy symptoms and Interpersonal sensitivity are essential personality traits for RHI sensitivity. Our data showed similar associations: ownership scores predicted the values in Interpersonal sensitivity, Paranoid ideation and Psychoticism traits, but no similar prediction was found in the case of proprioceptive drift. Psychotypy, as assessed by the SCL-90-R questionnaire, was considered as a dimension of human experiences, representing a continuum from mild depersonalisation to dramatic evidence of psychosis involving withdrawal, isolation and schizoid lifestyle, and first-rank schizophrenia symptoms such as hallucinations and thought-broadcasting, splitting and coherence lost among thoughts, body image, and body schema dissociation. Furthermore, schizotypal traits, in part covered by psychotypy with psychotic disorders, certainly predispose an individual to mental illness, but they may also lead to positive outcomes such as creativity or spiritual experience (Claridge, 1997). Another significant factor that plays a role in the vividness of the RHI is Interpersonal sensitivity, which involves feelings of personal adequacy and inadequacy in comparison with others, and discomfort during interpersonal interactions.
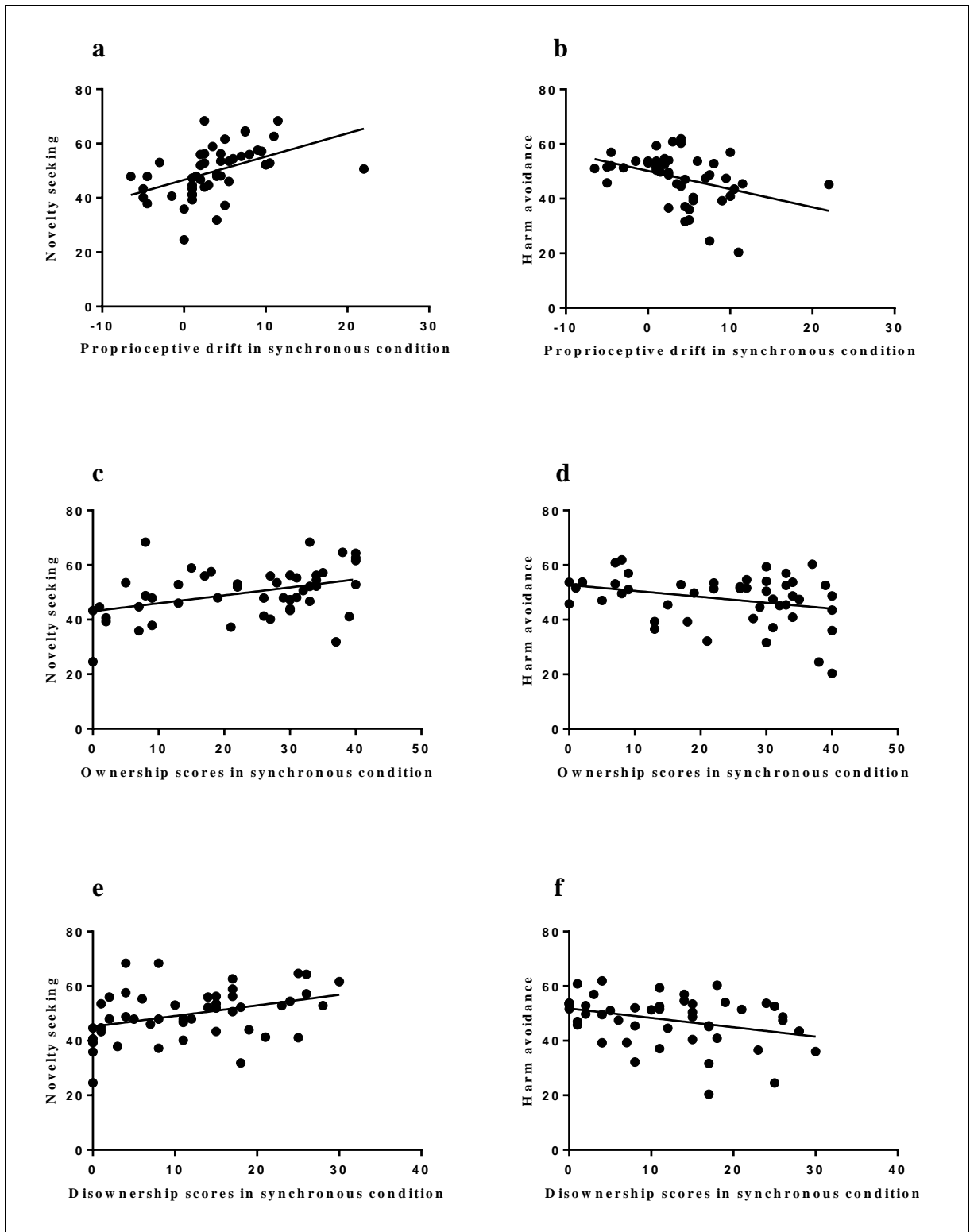
Figure 8. Scatterplots representing the significant relationships between RHI outcome measures and temperament (TCI-R) factors. The synchronous proprioceptive drift, ownership and disownership scores predict high values on Novelty seeking and low values on Harm avoidance.
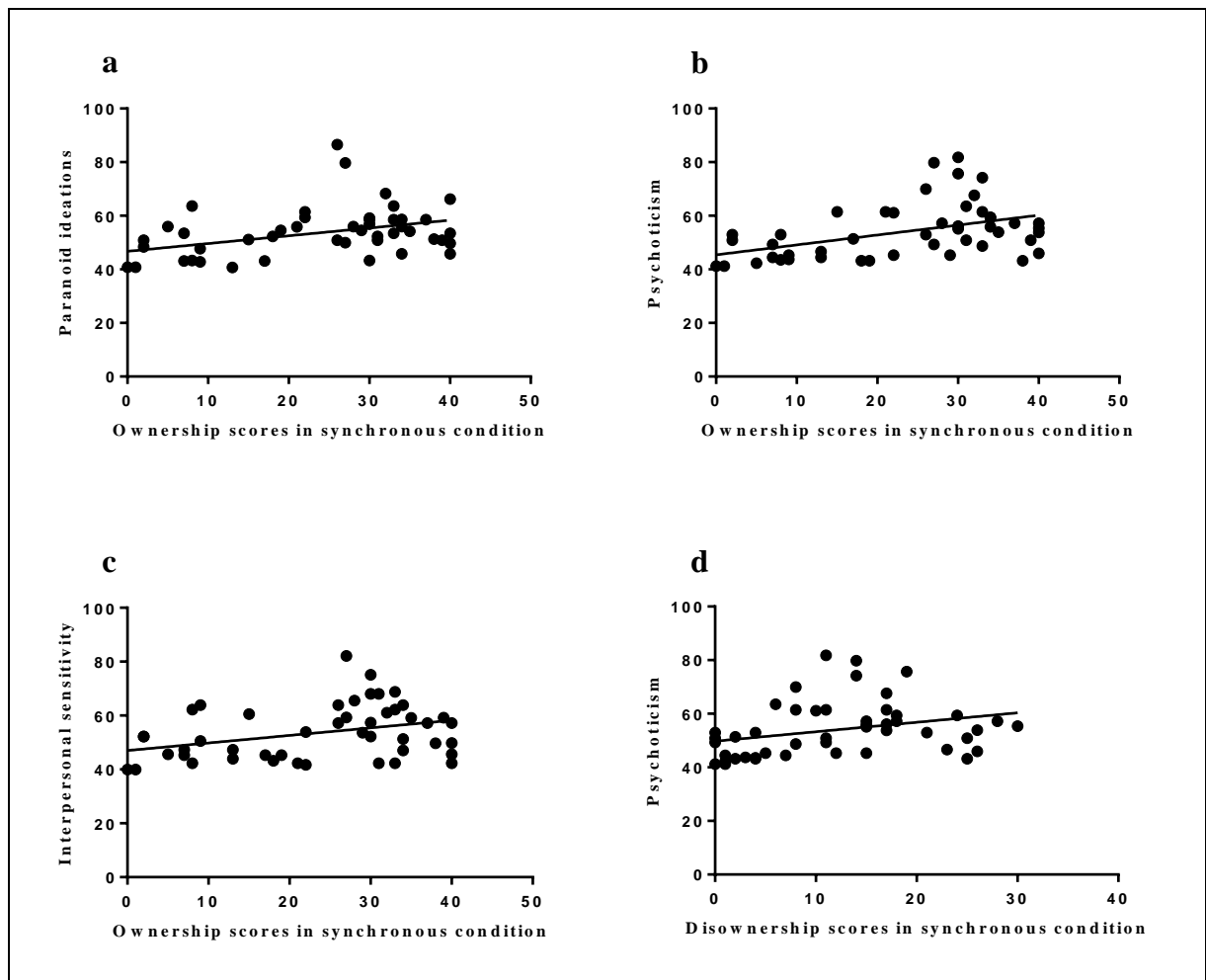
Figure 9. Scatterplots representing the significant relationships between RHI outcome measures and psychopathological symptom list (SCL-90-R) factors. The synchronous ownership scores predict high values on Paranoid ideations, psychoticism and Interpersonal sensitivity factors, while high disownership scores are associated with high values on Psychoticism.

Interpersonal sensitivity is a basis from which to compare and interpret feelings as 'mine' and 'not mine', and to incorporate and separate them (Mast, Preuss, Hartmann, & Grabherr, 2014). The separation and assimilation of the observer's inner emotional state is accompanied by ownership and disownership feelings at the same time, fluctuating in their intensity (Baron-Cohen & Wheelwright, 2004; de Vignemont & Singer, 2006; Rognini et al., 2013). Based on these issues in the openness and closeness toward the perception of experiences from one's own body or others' body requires more than two superficially opposite processes, that has been suggested by Pineda (2008) and Asai et al. (2011). The first component is the interpersonal sensitivity and emotional empathy that assimilates the self and other

50

feelings and the second one is an ownership-involved agency component that defines external objects, people or images. In this context, schizotypy functions as a coping mechanism for the detected fusion between 'me' and 'other objects' or 'other people', making a split or generating a fusion, depending on the current state of the multimodal integration of the body representation. On the other hand, considering our results, the RHI generated synchronous proprioceptive drift can be counted as a third additional component for the opponent process model. The synchronous proprioceptive drift predicts a sensation seeking cognitive bias involving continuous openness to novel and alien experiences. Novelty seeking is in inverse relation to the Harm avoidance factor, is positively associated with the five factors model trait, and positively related to impulsive sensation seeking and Psychoticism (De Fruyt, Van De Wiele, & Van Heeringen, 2000). The acceptance of novel and strange, or alien experiences is a basic bottom-up component in the formation of body sensations. Especially in the case of low Novelty seeking associated with high Harm avoidance, the body boundaries are protected, but when the Novelty seeking is high and Harm avoidance is low, the body accepts the body-related strange and alien experiences. Previous findings confirm that proprioceptive drift plays a significant role in the generation of the RHI, but involves a different process to ownership and disownership (Haans, Kaiser, Bouwhuis, & IJsselsteijn, 2012; Rohde et al., 2011). The drift of the real hand towards the artificial hand is a behavioural indicator of an acute body schema distortion or weakness, indicating that the boundary of the represented body is weak and relatively malleable.

Our results for proprioceptive drift and its association with ownership experiences confirm our suggestion. Proprioceptive drift is in connection with most of the temperament factors, but it is relatively independent from the propositionally based character functions. Temperament, unlike character, manifests early in personality development and influences a person's affective and cognitive reactions throughout life, both in form and intensity. Most of the temperament factors are associated with monoaminergic neurotransmitter activity. Novelty seeking is associated with dopaminergic, whereas Harm avoidance is associated with serotonergic activity (Stallings, Hewitt, Cloninger, Heath, & Eaves, 1996). The temperament dimensions are determined by procedural learning mechanisms that control responses to novelty, danger, and sensitivity to reward and punishment, as

well as maintaining motivation towards intended goals, thus providing a stable motivational basis for persistent behaviour (Cloninger & Svrakic, 1997).

Considering our data on the RHI scores related to personality traits, psychopathological symptoms predictions and the association with behavioural and embodiment scores, we support the validity of the two superficial-opposite processes model for the RHI as suggested by Asai et al. (2011). However, parallel with this model, we need to consider the third component that would be able to articulate the dual opposite process in the genesis of the RHI. We pointed to a third mechanism that plays a role in evoking the illusory ownership of an artificial object. This is a temperament-based, procedural function, which is closely related to the multisensory integration processes as embodied in proprioceptive drift. The Novelty seeking and the related low rate of Harm avoidance serves as a key component to opening a perceptual gate for novel and strange incongruent visuotactile experiences that presented simultaneously in the participants' peripersonal space. In contrast, the two superficial opposite processes model is based on propositional categories that differentiate between one's own body and others' body experiences, separating the self-relevant and self-irrelevant events.

Nevertheless, certain limitations of this study need to be mentioned. The method of the RHI is well operationalised, but the interpretation of outcome scores is multicoloured. Recently, the control condition of the RHI has been articulated (Brozzoli, Gentile, & Ehrsson, 2012; Holmes, 2012; Longo et al., 2008; Morgan et al., 2011; Tsakiris, 2010), since ownership seems to be a general personality trait that evokes independently from the induction of the RHI and occurs in the asynchronous conditions as well. This means that RHI induction, generated by synchronous haptic stimulation, does not evoke, but rather amplifies the body schema changes and elevation of body image awareness in a visually controlled peripersonal space, where a body part-like object is located.

5. Final conclusions

1) In our first study we failed to demonstrate that the IHI can be modified by conditioning, our major findings, which might even mask the effect of associative learning, provide relevant contributions to the investigation of multisensory integration and bodily self-consciousness. Most importantly, the results reveal that irrelevant auditory cues presented in synchrony with rhythmic visuo-tactile stimuli can enhance the effect of visuo-tactile integration on proprioceptive updating. Further studies are needed to better understand this kind of complex multimodal interaction.

2) Secondly, the findings confirm that proprioceptive recalibration gradually increases over time in the RHI-like illusions, and that a longer exposure to such an illusion produces a considerable after-effect on proprioception.

3) Our data indicate that a few minutes exposure to the classical RHI is able to enhance the subjective vividness of the subsequent IHI.

4) Our second study into this area could be fruitful for a deeper insight into the dual nature of self–identity, and the genesis of the role of the controlled and uncontrolled process in agency and psychopathological states. These associations provide an opportunity for conducting effective studies to gain important insights into the dynamics of body boundary spectrum disorders in healthy participants and patients, respectively.

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Publications related to the thesis

Kállai, J., Hegedüs, G., Feldmann, Á., Rózsa, S., Darnai, G., Herold, R., … Szolcsányi, T. (2015). Temperament and psychopathological syndromes specific susceptibility for rubber hand illusion. *Psychiatry Research*, 229(1-2), 410–419. http://doi.org/10.1016/j.psychres.2015.05.109 **IF: 2.467**

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Publications unrelated to the thesis

Altbäcker, A., Plózer, E., Darnai, G., Perlaki, G., Horváth, R., Orsi, G., … Janszky, J. (2015). Problematic internet use is associated with structural alterations in the brain reward system in females. *Brain Imaging and Behavior*. http://doi.org/10.1007/s11682-015-9454-9 **IF: 4.598**

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Plózer, E., Altbäcker, A., Darnai, G., Perlaki, G., Orsi, G., Nagy, S. A., … Janszky, J. (2014). Intracranial volume inversely correlates with serum 25(OH)D level in healthy young women. *Nutritional Neuroscience*, *18*(1), 37–40. http://doi.org/10.1179/1476830514Y.0000000109 **IF: 2.114**

Lectures and Posters related to the thesis

First author

20. Neuroimaging Workshop, Pécs, Hungary 19-20 April 2013
A gumikéz illúzió és kérgi aktivitás

Magyar Pszichológiai Társaság XXII. Országos Tudományos Nagygyűlése, Budapest, Hungary 5-7 June 2013
A gumikéz illúzió indukciója során aktív ideghálózatok: fMRI vizsgálat

Magyar Pszichológiai Társaság XXIII. Országos Tudományos Nagygyűlése, Marosvásárhely, Romania 15-17 May 2014

Fantom kéz és műkéz kondicionálása: a testi integritás és a gumikéz illúzió egy újabb példája

11th Alps-Adria Psychology Conference, Pécs, Hungary 18-20 September 2014

Sound-induced proprioceptive changes in the invisible hand illusion

Co-author

First World Congress on Personality, Stellenbosch, South Africa 19-23 March 2013

Role of personality factors in the induction of Rubber Hand Illusion

Magyar Pszichológiai Társaság XXII. Országos Tudományos Nagygyűlése, Budapest, Hungary 5-7 June 2013

A Gumikéz Illúzió: teória és eljárási mód

Magyar Pszichológiai Társaság XXIII. Országos Tudományos Nagygyűlése, Marosvásárhely, Romania 15-17 May 2014

A gumikéz illúzióra való érzékenységgel összefüggő temperamentum sajátosságok és pszichopatológiai szindrómák

19th ESCOP, Paphos, Cyprus 17-20 September 2015

Can bodily self-perception be modified by auditory signals? Sound-induced proprioceptive drift in the invisible hand illusion

Lectures and Posters unrelated to the thesis

First author

10th Magatartástudományi Napok, Pécs, Hungary 25-26 May 2010

Időészlelésünk változatossága: az impulzív viselkedés hatásai

19th MAKOG, Kaposvár, Hungary 27-29 January 2011

Az időészlelésünk változatossága: az impulzivitás hatása az időészlelésre

30th OTDK, Kecskemét, Hungary 7-9 April 2011

Az időészlelésünk változatossága: az impulzivitás hatása az időészlelésre

Kerényi 18: A Kerényi Károly Szakkollégium szakmai hete, Pécs, Hungary 27th April 2011

Az impulzív idő: az időészlelés és az impulzivitás kapcsolata

11th Magatartástudományi Napok, Gödöllő, Hungary 28-29 June 2011

Mentális fáradtság és a megosztott figyelem

Magyar Ideg- és Elmeorvosok Társaságának XXXV. Vándorgyűlése, Debrecen
22-24 November 2012

D-vitamin hatása a kognitív funkciókra

5th European Congress of the International Neuropsychiatric Association, Athens, Greece 30th October 2014 – 2nd November 2014

Iron deposition in subcortical nuclei and Intelligence in young adults

9th Word Congress on Controversies in Neurology (CONy), Budapest, Hungary 26-28 March 2015

Iron deposition in subcortical nuclei inversely correlates with visual memory in healthy young adults (Karger award winner poster)

Co-author

12th Magatartástudományi Napok, Szeged, Hungary 14-15 June 2012

A testkép módosításának hatása a fájdalomérzetre

12th Magatartástudományi Napok, Szeged, Hungary 14-15 June 2012

Mentális forgatási képesség és agytérfogat összefüggésének nemi összehasonlító vizsgálata

12th Magatartástudományi Napok, Szeged, Hungary 14-15 June 2012

Az időészlelés neuropszichológiája

10th Alps Adria Psychology Conference, Lignano, Italy 27-29 September 2012

The impact of the modification of body image on pain perception

Magyar Ideg- és Elmeorvosok Társaságának XXXV. Vándorgyűlése, Debrecen, Hungary 22-24 November 2012

Az alexitímia és D-vitamin kapcsolata

Magyar Ideg- és Elmeorvosok Társaságának XXXV. Vándorgyűlése, Debrecen, Hungary 22-24 November 2012

D-vitamin és az egészséges agyszerkezet – kvantitatív MR vizsgálatok

20. Neuroimaging Workshop, Pécs, Hungary 19-20 April 2013

Strukturális agyi elváltozások internetfüggőségben (előtanulmány)

20. Neuroimaging Workshop, Pécs, Hungary 19-20 April 2013

Az intrakraniális térfogat és a 25(OH)D szint közötti összefüggés vizsgálata fiatal nőkben

20. Neuroimaging Workshop, Pécs, Hungary 19-20 April 2013

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Magyar Pszichológiai Társaság XXII. Országos Tudományos Nagygyűlése,

Budapest, Hungary 5-7 June 2013

A gumikéz illúzió hatása a fájdalom-észlelésre