

Sense of Agency:
An investigation in typical, atypical
and clinical populations

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Declaration of Authorship

I, Maria Cristina Cioffi, hereby declare that this thesis and the work presented in it is my own. Where I have consulted the work of others, this is always clearly stated.

A handwritten signature in black ink, appearing to read 'Maria Cristina Cioffi'. The signature is written in a cursive style with a large initial 'M'.

, 21st July 2017

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Abstract

The sense of agency (SoA) refers to the feeling of control towards our actions and their effects in the outside world. The aim of this thesis was to study SoA to gain a better understanding of it and how it originated, particularly in light of the cue integration approach to SoA. Additionally, this work aimed to bring greater understanding of agency changes in populations where there has been little or no agency research.

To achieve this, we used paradigms that created agentic uncertainty by modulating external agency cues.

We found that the susceptibility to manipulation of external agency cues predicted schizotypy scores in healthy adults. We also showed that SoA in patients with anosognosia for hemiplegia is overall dominated by their intention to move, while external agency cues are discounted.

When examining changes in SoA throughout adulthood, our results suggested that older adults rely more on internal agency cues and discount external cues; we showed that this is potentially a result of increased reliance on internal agency cues.

For the first time, we investigated changes in SoA in people with Mirror-touch synaesthesia. We found that their experience of agency is more malleable than in non-synaesthetes, perhaps due to an enhanced saliency of external cues in the creation of SoA.

Having tested SoA in these groups, we looked at the neural mechanisms that might be responsible for the observed SoA changes. We used transcranial Direct Current Stimulation to test the contribution of right Temporo Parietal Junction to agency processing, in response to the same tasks used in the previous chapters.

Lastly, we investigated the relationship between sense of agency and sense of ownership, a theme running throughout this thesis.

We suggest that the cue integration approach is a valid framework to understand SoA and discuss future directions.

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CHAPTER ONE

Introduction

Most of our everyday actions feel like they are under our control. We commonly experience a fluent natural flow from our thoughts, to our actions, to the consequences that our actions produce in our environment. When it gets dark, we go and press the light switch and the light turns on. Without even realising it, we are continuously controlling the movements of our body and we feel that we are in charge of those. In other words, we have a 'sense' of our agency. The sense of agency refers to this feeling of control towards our actions and their effects in the outside world.

As with many other aspects of our cognition, we take it for granted until it goes awry. Disturbances in sense of agency can be very dramatic. Patients with schizophrenia may not feel that their actions are under their control, such as for this patient reported by Mellor (1970): "It is my hand and arm which move, and my fingers pick up the pen, but *I don't control them*. What they do is nothing to do with me". Changes in the sense of agency can be much subtler than this, but still have a considerable impact.

In this thesis I examine these changes, whether they are dramatic or subtle. I will present an investigation into sense of agency in different groups, with the aim of understanding more about these groups while increasing our understanding of the sense of agency itself. In this first chapter, I present an overview of the concepts and previous research that is relevant to this thesis and I end by giving a rationale for the following experimental chapters.

Defining sense of agency

The sense of agency (SoA) is defined as the experience of initiating and controlling one's own actions and, through them, influencing the outside world (Haggard, 2017; Moore & Fletcher, 2012). While in other literatures the sense of agency may refer to different and broader concepts (e.g. social psychology, Bandura, 1989), this definition draws the focus onto the experience surrounding a motor act.

The sense of agency around an action can be implicit or explicit. Synofzik and colleagues (Synofzik, Vosgerau, & Newen, 2008) proposed a two-step account of agency that distinguishes between implicit and explicit aspects of agency. The implicit SoA, or 'feeling of agency', is a low-level, pre-reflective feeling of being the agent of an action. That is, for implicit SoA to be formed, it does not require a reflective act of consciousness. The implicit agency is thought to arise from sensorimotor signals, such as motor signals and sensory feedback of an action. On the other hand, the explicit SoA, also known as the 'judgement of agency', is a high-level, reflective process that leads to the explicit attribution of agency to oneself or another. Various factors contribute to explicit SoA such as contextual information, beliefs and desires (Gallagher, 2000; Synofzik et al., 2008).

While these two aspects tap into different processes and certainly can be dissociated from one another (Dewey & Knoblich, 2014; Moore, Middleton, Haggard, & Fletcher, 2012; Saito, Takahata, Murai, & Takahashi, 2015), they are uniquely linked and interdependent (Moore et al., 2012; Synofzik et al., 2008). In most cases, the implicit sense of agency is a necessary condition for the explicit sense of agency. For example, a judgement that I turned the light turned on, is dependent on the lower level experience of pressing the light switch, which in turn causes the light to come on. However, under certain ambiguous conditions this may not be true. For example, if many people act at the same time to produce a single effect, we may attribute agency over an event to ourselves only because we *thought* about making the action, while it was in reality caused by someone else (Wegner, 2003).

Importantly, the circumstances and the context of an action determine the extent to which the implicit and the explicit aspects of agency contribute to the overall sense of agency. In unambiguous circumstances, the implicit SoA towards an action might be so strong that we are not required to form any further conceptual interpretation over it. However, the more the action effects become agent-ambiguous or arbitrary, the more importance is given to the explicit SoA attribution processes. Thus, the overall sense of agency is a 'dialectic combination' of both low-level implicit processes and high-level explicit processes (Synofzik et al., 2008).

Measuring the sense of agency

There are measures for both implicit and explicit aspects of sense of agency. Implicit measures of agency infer participants' SoA over an action without asking them directly about their agentic experience. Until now, the paradigm that has been most commonly used in the investigation of implicit SoA is Intentional Binding (IB) (Haggard, Clark, & Kalogeras, 2002). This is a perceived temporal compression between a voluntary action and its consequences, i.e. the action is perceived to occur later in time, while the sensory effect is perceived as occurring earlier (Figure 1.1). This change in time perception is considered a measure of implicit SoA. IB has been shown to be reliable and robust in studies with both healthy and clinical populations (Moore & Obhi, 2012).

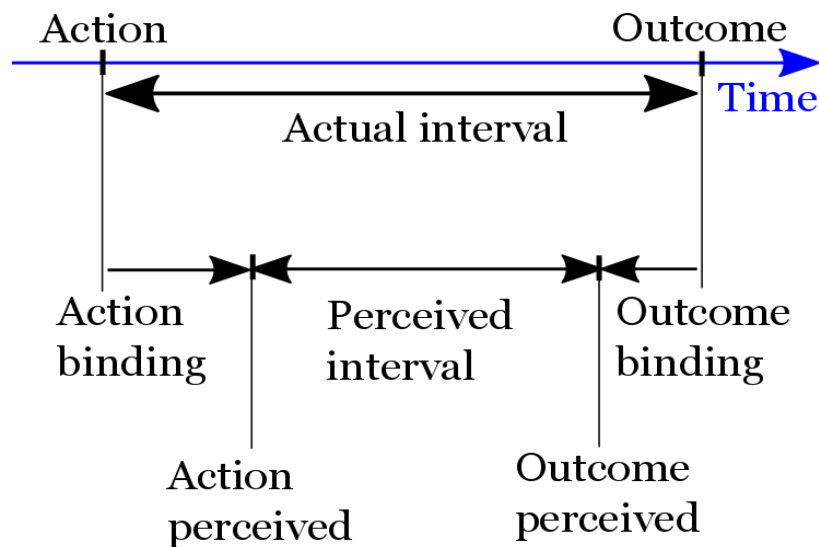


Figure 1.1. Schematic representation of the intentional binding effect. During a voluntary action, the time of action and its effect (i.e. outcome) are perceived as shifted towards one another. The time interval between action and outcome is perceived as shorter than the actual interval.

Another implicit measure of SoA is based on what is called 'sensory attenuation'. Sensory attenuation refers to a reduction in the perceived intensity of sensations caused by voluntary actions compared to externally generated actions (Blakemore, Wolpert, & Frith, 1998), (Figure 1.2). This change in the perceived intensity of an action's sensory effect is used as a measure of implicit sense of agency (e.g. Desantis, Weiss, Schütz-Bosbach, & Waszak, 2012; Dewey & Knoblich, 2014).



Figure 1.2. Representation of the experimental set-up in the study conducted by Blakemore et al. (1998). The horizontal rod could be pressed by either the subject or the experimenter. The pressure of the rod was controlled so that it was the identical in both conditions. Self-produced tactile stimuli corresponded to less activation of the somatosensory cortex, compared to externally generated stimuli. From Blakemore et al. (1998).

Unlike implicit measures of SoA, explicit measures are based on participants' judgements. Participants can be asked about their agentic experience in different ways. For example, they can be asked to rate how much control they felt over an action (e.g. Sato & Yasuda, 2005; Wegner, Sparrow, & Winerman, 2004) or to make action-recognition judgments (e.g. Daprati et al., 1997; Farrer & Frith, 2002; Farrer et al., 2008). Action-recognition tasks require participants to make self-other agency judgments while the authorship of their actions is made ambiguous by the experimental setting. For example, participants perform or control a movement and a temporal or spatial distortion is inserted into the visual feedback of that movement. When the distortion in the feedback goes past a threshold, the participants don't recognise the actions as their own, even when they are. These types of tasks can be used to measure the ways and the degree to which the threshold varies across individuals, as an indication of their SoA.

The debate on whether implicit or explicit agency measures are more accurate in capturing this elusive phenomenon often arises in the field of SoA research. Implicit measures are less vulnerable to demand effects or cognitive biases. However, they fail to directly capture our agentic experiences which play a crucial role in the regulation of our everyday life (Haggard & Tsakiris, 2009). Recent studies have shown how implicit and explicit measures are in fact

weakly correlated (e.g. Dewey & Knoblich, 2014; Moore et al., 2012). Thus, it is plausible that both measures are equally accurate but representative of different aspects of agency, perhaps mapping onto the explicit/implicit distinction described by Synofzik et al (2007; see above).

Before concluding this section it is important to note that, unlike other aspects of our conscious experience such as visual perception, the experience of agency is thin and evasive (Haggard, 2005). That is, while we continuously perform actions, we are rarely aware of our sense of agency. As a result of this, measuring the SoA can be difficult and researchers are pushed to find paradigms that can capture this elusive phenomenon. In this work, I use agency illusions as an informative way to investigate the explicit SoA processing in clinical populations and in healthy populations that do not present clear disturbances of SoA.

Theories of sense of agency

Until recently, there have been two main competing theories of sense of agency. One suggested that sense of agency arises from internal processes within the motor system (Blakemore, Wolpert, & Frith, 2002; Frith, Blakemore, & Wolpert, 2000). This is also known as the ‘Comparator Model’ of SA, and it is based on the computational models of the motor control system (Frith et al., 2000).

The other main theory of SoA deemphasizes the contribution of the motor processes and underlines the importance of external, situational cues (Wegner & Wheatley, 1999; Wegner, 2002). This is the ‘theory of apparent mental causation’, which was developed by Wegner and Wheatley (1999) and Wegner (2002). According to this theory, the SoA does not arise within the motor control system, but instead stems from the perceived relationship between the intention to act and the action.

These two theories were considered mutually exclusive, but a more recent approach reconciles them. The ‘cue integration theory’ proposes that both aspects emphasised by the theories above are equally important for the SoA. According to this theory, the SoA originates with the contribution of both internal motor signals and external situational cues (Moore, Wegner, &

Haggard, 2009; Moore & Fletcher, 2012). Here I outline the main concepts and evidence for all three theories and underline how the cue integration theory seems to be a promising framework for better understanding the cognitive process underpinning SoA.

The comparator model of SoA

According to the comparator model of SoA, the awareness of an action, the SoA, arises from the same motor processes that are responsible for the generation of the action itself (Frith et al., 2000). This theory is based on the computational forward models of motor control (Miall & Wolpert, 1996). The characteristic feature of 'forward' models is that they are based on predictions (Rumelhart, 1992). Figure 1.3 shows the forward model of motor control system reported by Frith et al. 2000. The action starts with an intention or a goal. Based on this, a representation of the desired state of the motor system is created. This representation, combined with the sensory information about the state of the world (i.e. affordances), is used to generate motor commands. A copy (called 'efference copy') of the motor commands is issued at the same time to predict the future state of both the motor system and the sensory consequences of a movement. This representation of the predicted state of the system is compared with the desired state of the system to update the motor commands and prevent errors in the movements. Crucially, the same representation of the predicted state of the system is also compared with the actual state of the system. In this comparison lies the sense of agency: if there is a match then the SoA arises, if there is a mismatch then the SoA is reduced or absent.

A few studies have brought evidence in support of this tight relationship between sensorimotor processes and SoA (e.g. Blakemore et al., 1998; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999). Blakemore et al. (1998) showed that a self-produced tactile stimulus is perceived less ticklish than when the same stimulus is externally induced (i.e. sensory attenuation). In line with the comparator model, for somatosensory sensations to be attenuated to self-produced sensory stimuli, these stimuli need to be predicted accurately. This model has been used to explain various disturbances of agency such as anarchic hand syndrome, anosognosia for hemiplegia or delusions of control

characteristic of schizophrenia (Blakemore et al., 2002; Frith et al., 2000). A patient with delusion of control would produce an action in line with their intention and the action would be successfully performed. However, while being aware that the action matches the intention, there is an experienced mismatch between the predicted and actual sensory consequences of movement. This results in the patient feeling as though his actions are not his own, and instead are being controlled by an external force or agent (Blakemore et al., 2002).



Figure 1.3. Representation of the motor control system proposed by Frith et al. 2000. The sense of agency arises from the comparison between predicted and actual state of the system: if there is a match then the SoA arises, if there is a mismatch then the SoA is reduced or absent. From Frith et al. (2000).

The theory of apparent mental causation

In contrast to the comparator model, the theory of apparent mental causation explains sense of agency in a substantially different way. According to this theory, sensory and motor processes are not consciously accessible and therefore cannot be responsible for the SoA. Figure 1.4, taken from Wegner & Wheatley (1999), represents how the experience of conscious will (i.e. sense of agency) arises. This theory distinguishes between conscious and

unconscious pathways that are formed around a voluntary action. There is an unconscious pathway that takes place in motor control system and is responsible for the action itself (the actual causal path). There is a second unconscious pathway that gives rise to action-relevant, such as intentions. Finally, there is an apparent path (that is conscious) that draws a link between the intention and the action. The relationship between thought and action gives rise to the sense of agency. There are specific conditions that must be met for the SoA to arise: priority, consistency and exclusivity. The intention must happen before the action, the intention and the action must be consistent, and the intention must be the only plausible cause of the action. Importantly, this conscious path responsible of the SoA is only an 'apparent' casual path. That is, the inference that the intention is the cause of the action is fallacious, as the unconscious processes are really responsible for the action.



Figure 1.4. Model of the mental system for the production of the experience of conscious will (i.e. sense of agency). The sense of agency is an illusion that arises from the apparent path between conscious thought and action. From Wegner and Wheatley (1999).

Different studies have supported this theory (Sato, 2009; Wegener & Wheatley, 1999; Wegner et al., 2004). Wegner & Wheatley (1999) induced false SoA over movements that participants had not performed by priming the sensory consequences of the movement (see Figure 1.5). In this study, participants were asked to move the computer cursor on the screen, together with a confederate, presented to them as a participant. Alongside the cursor on the

screen, there were small images of objects displayed (e.g. swan, dog, car...). While moving the cursor, the participant would hear a word read out. They were asked to stop moving the cursor after 30 seconds signalled by the playing of some music. The stop did not need to be abrupt, but when the participant and their co-mover felt they were ready. On some trials, participants were primed with a word, for example 'swan' and the confederate was told through the headphones to move the cursor onto the swan. After each stop, participants were asked how much they intended to make the stop. Results showed that intentionality increased when the primes occurred five or one second before the stop, even when participants were in reality not responsible for the move.



Figure 1.5. Experimental set up of the 'I spy' study conducted by Wegner and Wheatley (1999). Participants were asked to move the computer cursor on the screen, together with another participant, while listening to music and words and that they would stop after 30 seconds. On the screen there were small images displayed (e.g. swan, dog...). The other participant was in reality a confederate. On some trial, participants were primed with a word, for example 'swan' and the confederate was told through the headphones to move the cursor on the swan. Every 30 seconds, participants were asked how much they intended to make the stop. Results showed that intentionality increased when the primes occurred five or one second before the stop, even when participants were in reality not responsible for the move. From Wegner and Wheatley (1999).

Another study by Wegner and colleagues, showed conclusively that the SoA does not have to be tied to motor processes, but instead is largely influenced by external situational agency cues. In a vicarious agency task (Figure 1.6), a participant was asked to remain still and look in a mirror placed in front of them. Another participant placed their hands where the participant's hands would normally be and performed a gesture right after an instruction previewing this gesture had played. Participants felt SoA over movements that they did not

perform just by merely thinking about a movement and seeing the movement performed such as it was theirs.



Figure 1.6. Experimental set up in Wegner et al. 2004. A participant is viewed from the front, as she would see herself in the mirror (left); View from the side where another participant is shown standing behind her with her hands forwards (right). Adapted from Wegner et al. (2004).

These studies demonstrate that the Comparator model fails to fully explain the SoA (see Synofzik et al., 2008 for an extensive discussion of this) and leads us to reconsider the importance of external cues in the creation of SoA.

The cue integration approach

The comparator model of SoA and the theory of apparent mental causation differ substantially on where the primary source of information is for creating SoA. The comparator model puts emphasis on the internal processing within the motor control system, while the theory of apparent mental causation emphasises the role of external information such as environmental, situational cues.

This important conceptual difference has led the two theories to be thought of as incompatible with each other. The ‘cue integration’ approach to SoA challenges this view by advocating that both sources of information, internal motoric signals and external cues, contribute to sense of agency. Specifically, the SoA is in fact the product of various cues. These cues are not additive but interactive and their relative influence is determined by their reliability. That is, various cues are optimally integrated depending on their availability and reliability (Moore et al., 2009; Moore & Fletcher, 2012; Synofzik, Vosgerau, &

Lindner, 2009). For example, in unambiguous circumstances, the motoric signals might be enough for the SoA to arise. The more agent-ambiguous and uncertain the circumstances are, the greater the number of cues that are weighted and integrated.

A few empirical studies have led to this formulation (e.g. Moore et al., 2009; Moore & Fletcher, 2012; Synofzik, Vosgerau, & Lindner, 2009). Moore and colleagues used priming to modulate the SoA for voluntary and involuntary actions. A priming tone (high or low pitched) was presented at the beginning of each trial. After the priming tone had played the participant pressed a key, which caused an effect tone to be played (the effect tones were the same as the primes: either high or low). The participant was then asked to estimate the time interval between action and effect tone, as a measure of implicit SoA. In the involuntary condition, participants were instructed to not press the key. The key was secretly pulled down by the experimenter. The results showed that the primes modulated the perceived intervals for voluntary and involuntary movements, and crucially the modulation was greater for involuntary movements (Figure 1.7). This showed that conscious prior thoughts (induced by primes) influence SoA and that these have a greater influence on involuntary passive movements. In other words, external agency cues exerted a stronger influence on SoA when internal motor signals were weaker (when participant did not actively press the key).



Figure 1.7. Results presented by Moore et al. 2009. Intervals initiated by voluntary movements were perceived as shorter than those following involuntary movements. Congruency between prime and effect led to enhanced SoA for both voluntary and involuntary conditions. Crucially, the effect of prime was greater in involuntary compared to voluntary conditions. From Moore et al. (2009).

Further evidence of the validity of this framework comes from studies with patients with schizophrenia (Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Voss et al., 2010). Synofzik and colleagues showed that the ability to attribute sensory event correctly to their own actions is impaired in patients with schizophrenia. In particular, agency attribution relied more on the visual feedback about an action than on the internal sensorimotor signals. The greater weighting on external cues is predicted by the cue integration framework, as it was shown that patients with schizophrenia have noisier, less reliable, internal signals (Voss et al., 2010).

The cue integration approach provides a unifying framework that promises to be particularly helpful for understanding SoA processing, and SoA changes in different groups. Throughout the work presented in this thesis, I will use this framework to develop and test predictions, to identify agency differences across different groups and bring evidence of its validity across a broader range of cases.

Neural basis of Sense of Agency

Neuroimaging studies as well as patient studies have helped identify some of the brain areas and networks involved in SoA. Here I will give a brief overview of the most significant findings.

Early neuroimaging studies have looked at neural activation in action recognition tasks that require participants to make explicit agency attribution judgements (e.g. Farrer & Frith, 2002; Farrer et al., 2008). As explained above, in these tasks participants perform a movement and a distortion is applied to the visual feedback provided. These studies have consistently highlighted the role of the right inferior parietal cortex (Figure 1.8), and more specifically the right temporo parietal junction (rTPJ). While a more detailed discussion of the role of rTPJ in SoA will be presented later in the thesis, a general observation that arose from these studies is that parietal regions may be more involved in the loss of sense of agency, rather than the positive experience of sense of agency (Moore, Ruge, Wenke, Rothwell, & Haggard, 2010; Sperduti, Delaveau, Fossati, & Nadel, 2011). That is, parietal regions seem to be concerned more with a “this is not my action” feeling. This may be due to the fact that, rather than being associated with the initiation of the action per se, they are responsible of the monitoring and integration of different conflicting signals around the action. This hypothesis is partially explored in two studies presented in this thesis.



Figure 1.8. Activation of the angular gyrus in the rTPJ for perturbed SoA and awareness of action discrepancy during an action recognition task. From Farrer et al. (2008).

One area that has been consistently associated with the positive self-agency is the anterior insula (Farrer & Frith, 2002; Ruby and Decety, 2001), (Figure 1.9). The fundamental role played by the anterior insula in self-awareness is confirmed by patient studies. For example, insular lesions have been associated with anosognosia for hemiplegia (Vocat, Staub, Stroppini, & Vuilleumier, 2010) or somatic hallucination in epileptic patients (Roper, Levesque, Sutherling, & Engel, 1993).



Figure 1.9. Attribution of an action to oneself activates the anterior insula bilaterally during an action recognition task. From Farrer & Frith (2002).

While the aforementioned studies used explicit judgements of agency, studies investigating implicit SoA found that pre-frontal areas are also involved in SoA (Cavazzana, Penolazzi, Begliomini, & Bisiacchi, 2015; Moore, Ruge, Wenke, Rothwell, & Haggard, 2010). Moore and colleagues (2010) used Transcranial Magnetic Stimulation (TMS) to disrupt the activity of pre-supplementary motor area (pre-SMA) during an intentional binding task (see above). They found that disrupting pre-SMA reduced the binding effect, and in particular the binding of outcome towards actions (Figure 1.10). Similarly, a reduction in intentional binding effect was found by Cavazzana and colleagues (2015) by using transcranial direct current stimulation over pre-SMA. Although more work is needed to clarify the exact contribution of pre-SMA in the SoA (Javadi, 2015),

this area seems to play a key role in generating the positive experience of agency (“I did that” type experiences).



Figure 1.10. Figure taken from Moore et al. (2010) showing changes in the perceived time of action and effects following theta-burst brain stimulation (cTBS) in each condition (a) and mean of overall binding between action and effect for each stimulation site (b). Binding effect was reduced following stimulation of pre-SMA. From Moore et al. (2010).

Another prefrontal region that is involved in SoA is the dorsolateral prefrontal cortex (DLPFC). In particular, DLPFC was shown to play a role in selection between action alternatives (Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). In line with this, a more recent meta-analysis of tDCS studies of Intentional Binding concluded that the DLPFC contributes to SoA when participants had to freely select an action (Khalighinejad, Di Costa, & Haggard, 2015).

While these are the principal areas involved in the SoA, it was recently proposed that the key neural correlate of SoA may reside in the *connectivity* between frontal and prefrontal areas responsible of initiating and action and parietal areas that monitor multiple signals relevant to SoA (Haggard, 2017).

Sense of Agency and Sense of Ownership

Sense of agency, as the feeling of generating or controlling an action, is a key aspect of self-awareness. A second fundamental aspect of self-awareness consists of the sense of ownership (SO). The sense of ownership refers to the feeling that I am the one that is moving, regardless of whether the movement is voluntary or not (Gallagher, 2000).

In voluntary actions, SoA and SO usually coincide (e.g. an agent voluntarily moves their limb), however these two components of self-awareness can be experienced separately. For example, in the case of an involuntary action, the

subject has no experience of control (thus no sense of agency), while still experiencing sense of ownership over the part of the body that moved. Conversely, a subject with delusions may report controlling other people's actions, showing sense of agency towards the action itself but not sense of ownership towards the executor of the action.

SoA and SO can also be selectively impaired (De Vignemont, 2007). Patients with the Anarchic hand syndrome show a selective disturbance of SoA, as they experience movements of the hand that are perceived as alien to the patient's volition. Patients with the Alien hand syndrome show a selective disturbance of ownership by reporting a sense of disownership towards their own hand.

Various studies have tried to clarify the nature of the interplay between agency and ownership (e.g. Braun, Thorne, Hildebrandt, & Debener, 2014; Tsakiris, Schütz-Bosbach, & Gallagher, 2007), but this remains unclear (Ma & Hommel, 2015; Tsakiris, Longo, & Haggard, 2010; Tsakiris, Prabhu, & Haggard, 2006). One view suggests that SoA entails body-ownership (additive model), viewing agency as an addition to the somatic experience of ownership. Another view, based on the existence of selective deficits of SO or SoA, along with results from behavioural and neuroimaging studies (e.g. Tsakiris et al., 2010) have suggested that SoA and SO are two independent experiences (independent model).

An extensive investigation of the relationship between agency and ownership is beyond the scope of this thesis. However, there will be an underlying discussion about it, as gaining understanding of one may help with the understanding of the other.

Rationale for experiments within the thesis

In this chapter, I have summarised the concepts that are fundamental to the development of this work.

The aim of this thesis is to study SoA with the principal intention of a) gaining a better understanding of SoA itself and how it originated, particularly in light of the cue integration approach to SoA, and b) improving our understanding of agency changes in populations where there has been little or no agency research. These two objectives bring mutual gains to each other: by investigating agency in groups that deviate from those normally studied (i.e. young neurotypical adults) we gain unique insight into the mechanisms of agency processing. At the same time, improving our understanding of the basic mechanisms involved in sense of agency will help us better understand, and remedy, agency processing problems.

The paradigms used throughout the thesis have been inspired by previous studies investigating explicit sense of agency (Farrer et al., 2008; Wegner et al., 2004). Their characteristic feature is that they aim to create agentic uncertainty. As visual illusions provide a unique window into normal visual processes (Gregory, 2009), authorship illusions give access to aspects of agency processing that would normally be hidden. By modulating external agency cues we were able to test specific predictions about SoA changes in both clinical and healthy populations. Importantly, these predictions were developed on the basis of the cue integration approach framework.

With these aims in mind, I have investigated changes in explicit SoA in relation to schizotypy (chapter 2), in patients with anosognosia for hemiplegia (chapter 3), older adults (chapter 4) and mirror-touch synaesthetes (chapter 5). These groups have been chosen with two principal motivations. Firstly, there were good reasons to expect changes in SoA in these groups (Cioffi, Moore, & Banissy, 2014; Fotopoulou et al., 2008; Metcalfe, Eich, & Castel, 2010; Synofzik et al., 2010) but they have been very little or not at all investigated. Secondly, as SoA is such a fundamental component of our daily lives, acquiring knowledge of how SoA works in these groups can potentially have great impact

on future research that looks into improving the wellbeing of these specific populations.

After having tested SoA in these groups, I looked at the neural mechanisms that might be responsible for the observed SoA changes (chapter 6). Specifically, I used transcranial Direct Current Stimulation to test the contribution of right Temporo Parietal Junction to agency processing in response to the same tasks used in the previous chapters.

Lastly, chapter 7 addresses the underlying discussion about the relationship between SoA and SO. This was investigated directly by testing the interplay between illusory experience of ownership and agency.

This thesis concludes with a general discussion, where I present key findings, limitations and directions for future research.

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CHAPTER TWO

Schizotypy and the vicarious experience of agency

Aberrant experiences of agency in schizophrenia may be characterised by changes in the relative influence of different agency cues, with external cues being more dominant. Here we test this hypothesis in a healthy sample by examining the relationship between schizotypy and performance on a vicarious agency task, where external agency cues are deliberately manipulated.

Introduction

Over 100 years after being so named, schizophrenia is still considered one of the least understood and costliest mental disorders (Van Os, Linscott, Delespaul, & Krabbendam, 2009). Around one in 130 individuals are likely to develop schizophrenia in their lifetime (Saha, Chant, Welham, & McGrath, 2005). Symptoms of schizophrenia can be classified into 'positive' and 'negative' symptoms. Positive symptoms are characterised by the presence of perceptions (e.g. visual hallucinations) or delusional beliefs. Negative symptoms consist in the absence, or reduction, of adaptive functions such as emotional understanding, speech or abstract thinking (Kay, Fiszbein, & Opler, 1987). Within the positive symptoms category are included abnormal experiences of agency. Patients with schizophrenia may feel that their actions are not under their own control. Instead they may feel that someone else or an external force is causing them to move. These phenomena are known as passivity symptoms. An example is provided by (Mellor, 1970), with the patient reporting, 'It is my hand and arm that move, and my fingers pick up the pen, but I don't control them. What they do is nothing to do with me.'

Interestingly, while patients with schizophrenia are inclined to experience a lack of agency towards their actions, action-recognition studies in schizophrenia show that patients tend to show an excessive SoA (Daprati et al., 1997; Franck et al., 2001). That is, when patients were asked to distinguish between theirs and someone else's actions, they were consistently more likely to attribute the actions to themselves. For example, Daprati and colleagues asked patients with schizophrenia to perform simple finger and wrist

movements whilst their hand was hidden from view. Instead, the image of their hand or an alien hand was presented on a screen in real time (Figure 2.1). When asked to determine if the hand on the screen was their own or not, patients with schizophrenia were more likely to attribute the alien hand to themselves.



Figure 2.1. Representation of the experimental set up in Daprati et al. (1997) The subject (S) performs simple hand movements without being able to see their hand directly. Instead, with the use of two mirrors (M1 and M2), the participant is presented with a live recording of either their hand or the experimenter's one (E). Patients with schizophrenia were more likely to misattribute the experimenter's hand to themselves. From Daprati et al. (1997).

More recent studies found that these altered experiences of control are associated with specific agency-processing changes (Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Voss et al., 2010). Synofzik and colleagues used an agency attribution paradigm in which participants were required to perform pointing movements in a virtual reality set-up. They were provided with a modified visual feedback of their pointing movements. The results showed that the patients were less able to detect distortions of their pointing in the visual feedback. Importantly, when asked to estimate their pointing direction, they relied more on their visual feedback than on their sensorimotor cues.

Within the cue integration approach to SoA (chapter 1), these studies strongly support the hypothesis that SoA in schizophrenia is characterised by a reduction in the contribution of internal sensorimotor cues, coupled with an increased contribution of external cues (Moore & Fletcher, 2012).

In the experiment presented in this chapter, we provide a direct test of this by examining the relationship between schizotypy and performance in a paradigm testing the influence of external agency cues. The choice to use a healthy population to investigate agency in schizotypy was based on evidence that psychotic experiences lay on a continuum. That is, the same symptoms that are seen in patients with schizophrenia can be measured in non-clinical population (Van Os, Linscott, Delespaul, & Krabbendam, 2009) (Figure 2.2). Preliminary studies have found that people who are highly schizotypal show an abnormal sense of agency (Asai & Tanno, 2007), but the mechanisms behind these changes are still unknown. Using the vicarious agency paradigm, we aim to shed light on these.



Figure 2.2. Representation of how psychosis varies along a continuum. Subclinical psychotic experiences and subclinical psychotic symptoms are associated with a degree of distress and help-seeking behaviour that do not necessarily amount to clinical psychotic disorder. From van Os et al. (2009).

In the vicarious agency illusion set-up, the experimenter's hands are extended on either side of the participant in a body-congruent posture. Participants also wear headphones through which action previews are played. These previews are either congruent or incongruent with subsequent actions of the experimenter. Wegner et al. found that the participant's experience of controlling these movements was increased when the previews were congruent with the experimenter's action.

This paradigm neatly demonstrates the influence of external situational agency cues (action previews and experimenter-made movements) on the sense of agency. These cues can lead people to experience a sense of agency over

movements that are not their own (i.e. in the absence of internal sensorimotor cues). Given the putative link between schizotypy and schizophrenia, we predict that in the vicarious agency task, changes in the experience of control will be predictive of schizotypy. More specifically, the modulation of SoA induced by the illusion should be greater for those scoring higher on our measures of schizotypy, reflecting an increased reliance on external agency cues.

Methods

Participants

A total of 53 participants took part in the experiment (46 females; mean age: 20 years; age range: 17-35 years). All participants had normal or corrected-to-normal vision and no history of mental illness.

Procedure

The description of the vicarious agency task is largely taken from Cioffi et al. (2017), (in appendix).

Vicarious agency task

All participants performed the vicarious agency task first. Participants sat on a chair facing a full-length mirror at a distance of 1m. Participants wore over-ear headphones on which were played the action previews. A blue sheet covered the participants' body from the shoulders downwards and a blue curtain was placed behind their back to block their view of the experimenter (see Figure 2.3).

Participants' arms were placed out of view under the sheet. The experimenter put on another set of headphones to hear the instructions, a blouse that was the same colour as the sheet covering the participant and a pair of white gloves. The experimenter was positioned behind the curtain. The experimenter placed their arm (either left or right) forward through two specific holes in the curtain, so that it appeared where the participant's own arm would have been. Participants were asked to look at the mirror in front of them while the experimenter performed the gestures with either the left or the right hand and to remain still during the experiment.

A tape with a list of 16 unimanual action instructions was played (e.g., “make a waving gesture,” “snap the fingers twice”, “point to the mirror”). The examiner performed an action immediately after each instruction. Each instruction-action stimulus, consisting of one instruction plus action performed by the experimenter, lasted between 8 and 10 seconds with a three second break between stimuli.

There were two within-subject conditions. In the *match condition*, the action corresponded to the instruction; whereas in the *mismatch condition* each instruction was randomly matched with a different action (e.g. after the instruction “make a waving gesture” the examiner snapped their fingers). In this mismatch condition, the gesture was different for every repetition of the same instruction (e.g., on the second repetition, after the instruction “make a waving gesture” the examiner pointed to the mirror). These conditions were completed for both the right and left hand separately. The order of match – mismatch conditions and the order of hand tested were counterbalanced across participants. The list of 16 instruction-action stimuli was repeated from the beginning to the end without interruption 3 times for each of the four conditions (match/mismatch and left/right hand), so as to augment the effects of this manipulation. The list of 16 action instructions was kept identical for the entire experiment, only the actions performed by the experimenter changed accordingly to the condition.

At the end of each condition participants were asked to report their experiences by answering 3 questions on a 7-point scale from 1 - not at all - to 7 - very much (this was done for each hand and the judgements were averaged across hands). In total, each participant was given 12 instruction-action list repetitions (i.e. 3 repetitions for each of the 4 conditions) and provided 4 ratings for each of the questions reported below.

The questions were similar as those included in Wegner et al.'s (2004) study:

- 1) Anticipation: *"To what degree did you feel you could anticipate the movements of the arm?"*

This control question assesses the success of the manipulation and whether the primes were attended to. This was included because a failure to attend to the primes may explain any putative performance differences in the two groups. If primes are attended to then anticipation judgements should be higher in the match than in the mismatch conditions. This question also serves as a control for any response bias (e.g. general tendency of one group to report higher or lower ratings).

- 2) Sense of Agency: *"How much control did you feel you had over the arm's movements?"*

This target question directly assesses the experience of agency.

- 3) Sense of Ownership: *"To what degree did the arm feel like it belonged to you?"*

This question provides an additional measure of the effect of the manipulation, examining the impact on sense of ownership over the body part.

A practice session consisting of 3 match and 3 mismatch trials was performed at the beginning of the experiment.



Figure 2.3. Experimental set-up. Pictured here is the side view (left) and participant view (right). The experimenter sits behind the curtain hidden from the participant's view and places his arm forward in a body congruent position. The participant sits in front of the mirror where she can see the arm as her own. The participant hears instructions through the headphones and observes the action being performed. In the match condition instructions and actions are congruent, while they are incongruent in the mismatch condition. From Cioffi et al. (2017)

Schizotypy scales

After the vicarious agency task, participants completed two schizotypy scales. The Peters Delusion Inventory (PDI), (Peters, Joseph, Day, & Garety, 2004), is a 21-item scale designed to measure delusional ideation in the normal population (e.g. "Do your thoughts ever feel alien to you in some way?"). When an item is endorsed, three five-point scales exploring distress, preoccupation, and conviction are then completed (Figure 2.4). The Cardiff Anomalous Perceptions Scale (CAPS), (Bell, Halligan, & Ellis, 2006), is a 32-item scale designed to measure unusual perceptual experiences in the normal population (e.g. "Do you ever see things that other people cannot?"). When an item is endorsed, three five-point scales exploring distress, intrusiveness, and frequency are then completed (Figure 2.5). The validity and reliability of both measures has been previously demonstrated (Bell et al., 2006; Peters et al., 2004).

According to dimensional perspectives, higher scores on these scales position an individual closer to the psychopathological end of the putative "normal"- "psychopathological" continuum (e.g. Peters et al., 2004).

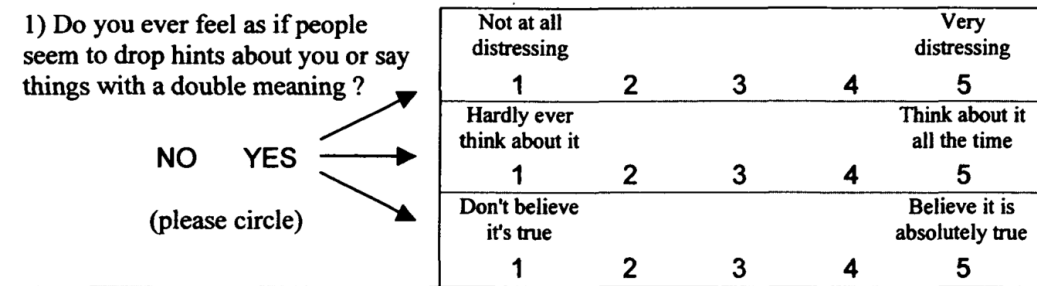


Figure 2.4. Example of an item from the Peters Delusion Inventory (Peters et al., 2004). When an item is endorsed, three five-point scales exploring distress, preoccupation, and conviction are completed.

1) Do you ever notice that sounds are much louder than they normally would be ?

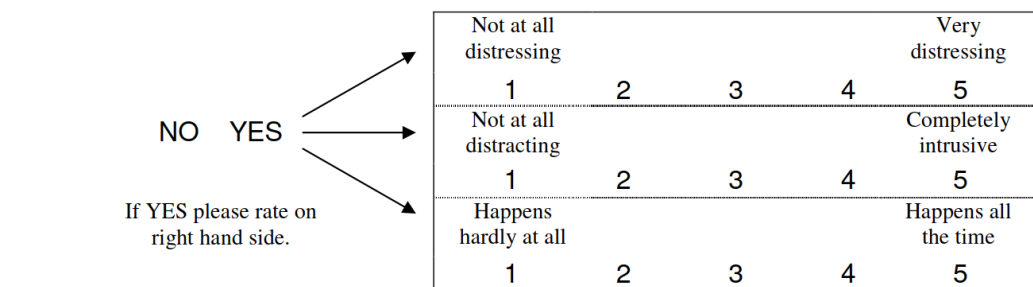


Figure 2.5. Example of an item from the Cardiff Anomalous Perceptions Scale (Bell et al., 2006). When an item is endorsed, three five-point scales exploring distress, intrusiveness, and frequency are then completed.

Results

Vicarious agency task

We replicated the basic vicarious agency effect. There was a main effect of Condition (Match/Mismatch), with mean anticipation, control and ownership judgements higher in the match vs. mismatch conditions ($F(1,52) = 131.99$, $p < .001$, $\eta^2_{\text{partial}} = .72$). There was also a main effect of Question (Anticipation/Agency/Ownership), with overall levels of anticipation higher than control or ownership ($F(2,104) = 39.79$, $p < .01$, $\eta^2_{\text{partial}} = .44$). Finally, there was a significant interaction between Condition and Question ($F(2,104) = 46.16$, $p < .001$, $\eta^2_{\text{partial}} = .47$), with the effect of our manipulation being strongest for anticipation (Figure 2.6).

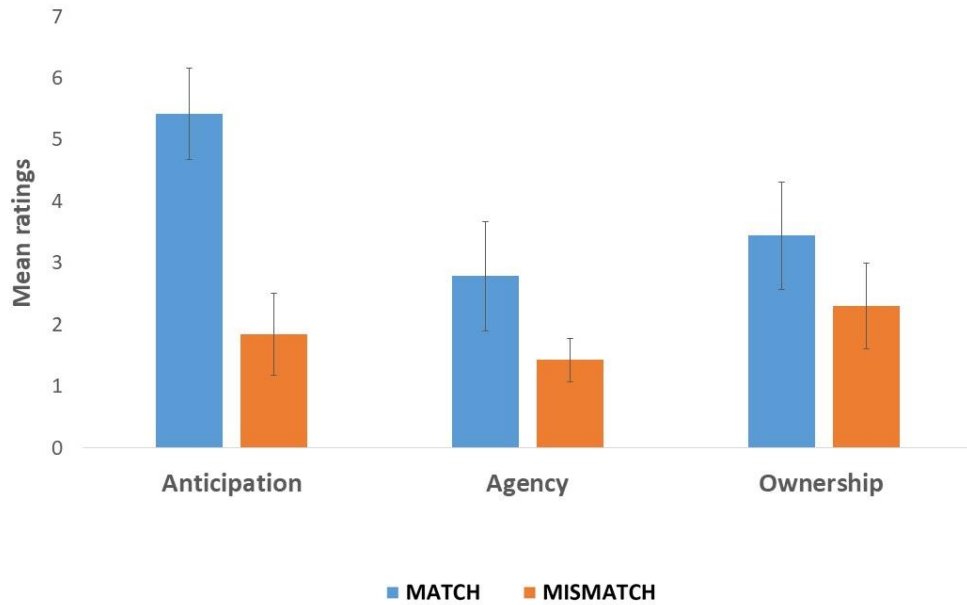


Figure 2.6. Mean ratings for Anticipation Agency and Ownership in Match and Mismatch conditions. Participants showed consistently higher ratings in the match conditions compared to the mismatch conditions.

Schizotypy scales

To calculate the PDI and CAPS total scores for each participant, a 1 was scored for each “yes” response, 0 was for each “no” response, and was summed across all items. Added to this were the scores for the participant’s answers to the three additional 5-point scales for each “yes” response. Summary statistics for total scores and sub-scale scores are presented in Table 2-1.

Table 2-1. Mean scores on the 21 Item Peters Delusion Inventory (PDI) and Cardiff Anomalous Perceptions Scale (CAPS). Standard deviation of the mean in parentheses.

	Mean (SD)	
	PDI	CAPS
Total	53.6 (38.0)	64.4 (48.0)
Distress	16.6 (13.0)	19.0 (15.2)
Preoccupation	16.1 (12.7)	20.1 (15.3)
Conviction	16.9 (12.8)	16.8 (14.3)

Relationship between vicarious agency and schizotypy

In order to examine the relationship between vicarious agency and schizotypy, we ran two separate hierarchical linear regression analyses for the CAPS and PDI respectively. The predictor variables were differences in mean judgements (match – mismatch) for control, anticipation and ownership experiences respectively. Given our initial hypothesis that individual differences in the experience of control would predict schizotypy scores, ‘control’ was entered into the model first followed by the two remaining judgement types (which were entered simultaneously into the linear regression model). The results are presented in Table 2-2. For CAPS, control was a significant predictor of CAPS total scores. This relationship is plotted in Figure 2.7. No other judgement types were predictive of CAPS. For the PDI no judgement types were significant predictors of PDI total scores (Figure 2.7). These results partially support our initial hypothesis – control did predict schizotypy but only for CAPS measure.

Table 2-2. Output for separate hierarchical linear regression analyses assessing the relationship between CAPS and PDI total scores (dependent variables) and mean judgement differences (match – mismatch) for the three judgement types (predictors).

CAPS	<i>Beta</i>	<i>Standard error of beta</i>	<i>Standardised beta</i>
Step 1			
Constant	52.16	8.30	
‘Control’	9.03	3.95	.31*
Step 2			
Constant	46.07	13.75	
‘Control’	11.19	4.96	.38*
‘Anticipation’	2.34	3.38	.10
‘Ownership’	-4.57	4.97	-.16
PDI	<i>Beta</i>	<i>Standard error of beta</i>	<i>Standardised beta</i>
Step 1			
Constant	46.06	6.71	
‘Control’	5.54	3.19	.24
Step 2			
Constant	45.74	11.17	
‘Control’	7.47	4.03	.32
‘Anticipation’	.45	2.74	.02
‘Ownership’	-3.43	4.03	-.15

Note: CAPS: $R^2 = .09$ for Step 1, $\Delta R^2 = .02$ for Step 2 / PDI: $R^2 = .06$ for Step 1, $\Delta R^2 = .01$ for Step 2. * < 0.05

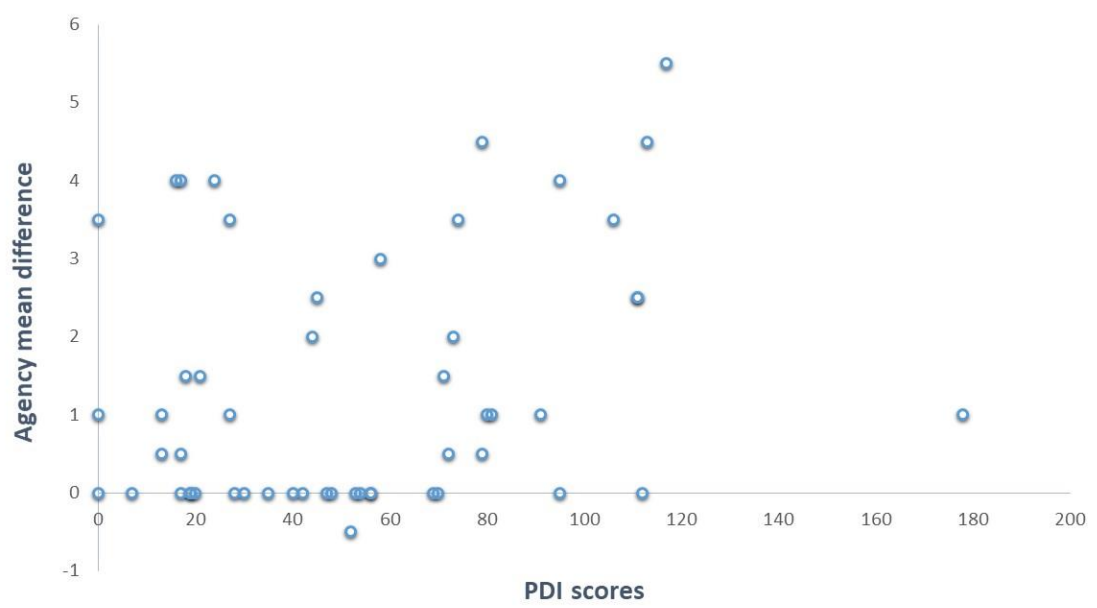
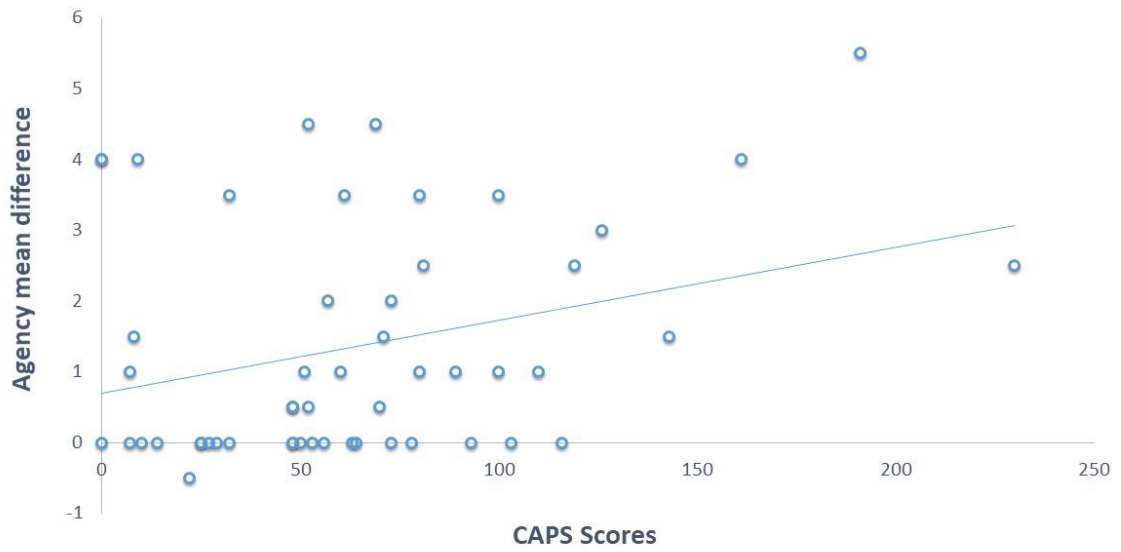


Figure 2.7. Scatterplot depicting the relationship between CAPS total scores and mean agency judgement differences (match – mismatch). The magnitude of the agency illusion is predictive of CAPS total scores. (Above) Scatterplot depicting the relationship between PDI total scores and mean agency judgement differences (match – mismatch). (Below)

Discussion

We explored the relationship between schizotypy and the susceptibility to illusory experience of agency in a group of young adults. Schizotypy was measured with two scales, PDI and CAPS. We showed that the magnitude of illusion of vicarious agency predicted CAPS scores. That is, people with higher schizotypy scores experienced a great effect of agency illusion.

Recent findings suggested that the experience of agency in patients with schizophrenia seems to be dominated by external agency cues, coupled with reduced reliability of internal sensorimotor cues (Synofzik et al., 2010; Voss et al., 2010). Here, we have tested this hypothesis by investigating the relationship between schizotypy and the susceptibility to an agency illusion, which was achieved through the manipulation of external agency cues. Our results showed that a stronger influence of external cues is predictive of higher schizotypy scores in a healthy adult population. These findings are consistent with the hypothesis that agency processing in schizophrenia is characterised by an increased reliance on external cues. However, future studies should extend this investigation to patients with schizophrenia.

Importantly, we have found a relationship between agency illusion and CAPS, but not with PDI. In other words, the malleability of the agency experience seems to be associated with hallucinatory symptoms rather than with delusional beliefs. At first glance, this may look surprising given that abnormal experiences of agency are normally classed as delusions (Nordgaard, Arnfred, Handest, & Parnas, 2008). However, this result may be explained by the largely perceptual nature of the task. The vicarious agency task has a very strong perceptual component: both auditory and perceptual cues have to be processed in order for the vicarious agency illusion to emerge, while internal sensorimotor information is weak as the participant is asked to not move throughout the experiment. Future studies looking at agency in patients with schizophrenia may attempt to further investigate the relationship between agency changes and delusional versus hallucinatory symptoms.

Our results showed that the agency illusion was uniquely predictive of schizotypy, as no relationship was found between schizotypy and the illusion

of ownership. Recent findings have been challenging the idea that schizophrenia presents a selective deficit in the SoA (see Klaver & Dijkerman, 2016 for an extensive discussion). For example, patients with schizophrenia have been consistently found to be more susceptible to illusions of ownership induced by the rubber hand paradigm (e.g. Thakkar, Nichols, McIntosh, & Park, 2011). Importantly, a recent study from Garbarini et al. (2016) showed that when an agentic component is added (i.e. the presence of a hand is combined with the hand moving), the SoA seems to be the aspect of self-awareness that is primarily impaired in schizophrenia. These results combined with the present findings support the view that patients with schizophrenia experience a predominant disorder of agency.

In this chapter, we have shown that the susceptibility to vicarious experience of agency is linked with schizotypy. More specifically, we found that the strength of the influence exerted by the external agency cues is predictive of schizotypy scores, with higher scores corresponding to stronger the influence. These results are informative, increasing our understanding agency abnormalities in schizophrenia while providing further insights in agency processing.

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CHAPTER THREE

Sense of agency and anosognosia for hemiplegia: investigating changes in susceptibility to illusory experiences of control.

Research suggested that patients with anosognosia for hemiplegia may be discounting external feedback around their own movements, while over-relying on their intention to move. Here we investigate anosognosic patients' SoA with a task that manipulates external agency cues. Importantly, for the first time our study will include the healthy limb.

Introduction

Anosognosia is defined as the apparent inability to recognise one's deficits. The term was coined by Babinski (1914) from the Greek "α νοσοζ γνωσιζ", α = without, νοσοζ = disease, γνωσιζ = knowledge, to describe the behaviour of patients with right brain damage who denied their hemiplegia.

Anosognosia for hemiplegia (AHP) is a neuropsychological condition following brain damage (Karnath & Baier, 2010). The reported incidence of anosognosia is extremely varied. For example, Jehkonen and colleagues (2006) reviewed anosognosia studies between 1995 and 2005 and found that its incidence would vary from 8% to 27% of stroke patients. These unprecise estimates are a consequence of many factors, such as the multifaced nature of the phenomenon (see Orfei, Caltagirone, & Spalletta, 2009, for a detailed review of assessment factors) and its change over time (Vocat, Staub, Stroppini, & Vuilleumier, 2010), (Figure 3.1). Furthermore, AHP manifestations can be very different. Some patients may believe that their limbs are completely functional, even when they are faced with opposite evidence. For example, some patients when asked to clap their hands and confronted with the evidence that no sound is produced, they still believe that they were involved in the action. Other patients may instead provide excuses (confabulations) to justify the lack of movement, for example 'my arm is tired', 'I could walk at home, but not here because it is slippery' (Nathanson, Bergman, & Gordon, 1952).



Figure 3.1. Evolution of awareness for the motor deficit over time. Anosognosia was present in almost two thirds of the patients at onset, in around one third after three days and in one fifth a week later. Anosognosia was rarely present after six months. From Vocat et al. (2010)

Early accounts of anosognosia proposed that this is caused by a disconnection between the left (language dominated) hemisphere and the right (sensory) hemisphere (Geschwind, 1965). This would prevent patients from accessing and expressing information about their impaired limbs. Others proposed that AHP is caused by a psychological defence mechanism against negative emotions caused by the injury (Weinstein & Kahn, 1950). More recently it has been argued that AHP may be due to more general cognitive impairments, such as confusion or self-evaluation processes (e.g. Levine, 1990). However, while all these factors may contribute to anosognosia, they do not seem to be able to fully explain it.

More recent accounts of AHP have suggested that this is the result of a malfunctioning motor control system. These approaches draw on computational models of the motor system (Frith, Blakemore, & Wolpert, 2000; Miall & Wolpert, 1996) (e.g. Figure 3.2). As explained in chapter 1, according to these models the action starts with an intention or a goal. Based on this, a representation of the desired state of the motor system is created. This representation, combined with the sensory information about the state of the world (i.e. affordances), is used to generate motor commands. A copy (called 'efference copy') of the motor commands is issued at the same time to predict the future state of both the motor system and the sensory consequences of a

movement. This representation of the predicted state of the system is compared with the desired state of the system to update the motor commands and prevent errors in the movements. Crucially, the same representation of the predicted state of the system is also compared with the actual state of the system. In this comparison lies the sense of agency: if there is a match then the SoA arises, if there is a mismatch then the SoA is reduced or absent.



Figure 3.2. Computational model of the motor system. From Frith et al. (2000)

Various explanations of anosognosia are inspired by this model of motor control and sense of agency. The 'motor intention deficit' theory suggested that anosognosia is due to a lack of intention to move (Heilman, Barrett, & Adair, 1998). If the intention is not present, then the efference copy of the motor system cannot be created. In turn, the comparator is not able to detect any mismatch between predicted and actual state leading to an unawareness of the motor impairment (Figure 3.3).



Figure 3.3. Computational model of the motor system with representation of where the deficit would be if anosognosia was due to lack of motor intention. The patient does not formulate the intention to perform the action. Modified from Frith et al. (2000).

However, subsequent findings provided evidence against the 'motor intention deficit' theory (Berti, Spinazzola, Pia, & Rabuffetti, 2007; Garbarini et al., 2012). Berti et al. (2007) looked at proximal muscles activation using Electromyogram (EMG) measures. It was found that patients with hemiplegia both with and without AHP following right brain damage showed left proximal muscle activation when asked to perform movements, although they were not able to perform them. Based on this new evidence, Berti and colleagues hypothesised that patients with AHP have a preserved intention for movement. They create an appropriate representation of the desired state of their motor system, but they are unable to detect a discrepancy between the desired and the actual state of the system (Figure 3.4).

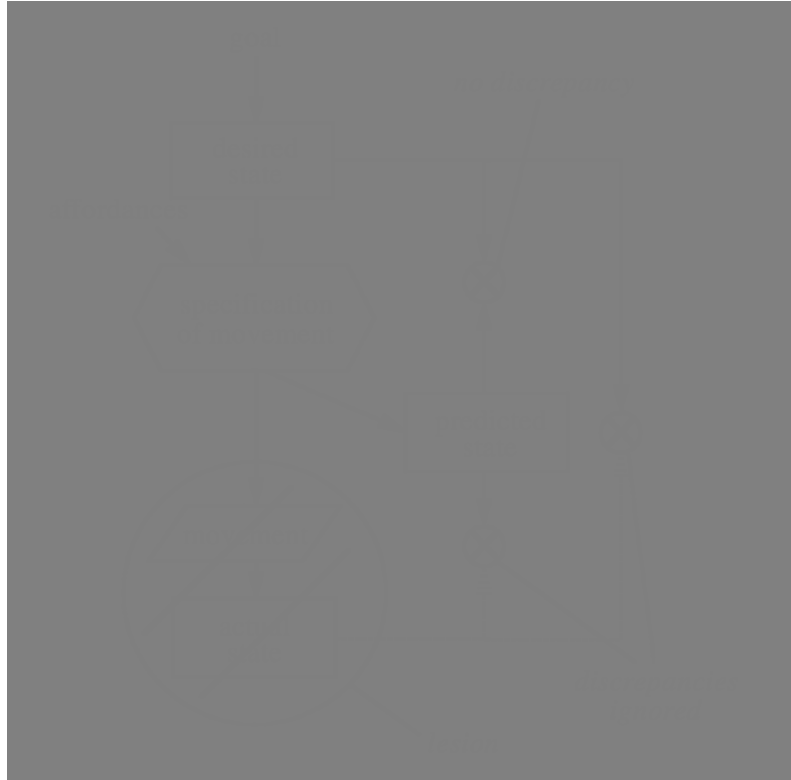


Figure 3.4. Computational model of the motor system with representation of where the deficit would be if anosognosia were caused by a deficit in detecting discrepancy between desired and actual state of the movement. The patient formulates the action needed to fulfil their intention and is aware that the action initiated is appropriate. No information about the actual position of the limb is available to indicate that no action has actually occurred so a discrepancy can't be detected. From Frith et al. (2000)

This hypothesis was supported by findings from Fotopoulou and colleagues (2008). In this study, a group of four hemiplegic patients with AHP were asked to move their paralysed hand or to remain still. They were presented with false visual feedback of their left paralysed arm through the use of a rubber hand. Their ability to visually detect the movement of the hand varied based on whether they were instructed to move it or not. Patients with AHP were more likely to ignore the visual feedback of a hand that did not move (and claim that they had moved it) when they were instructed to move it, compared to when they expected an experimenter to move their hand or when they expected no movement at all. These results suggest that AHP patients' not only have preserved intention to move, but that the intention prevails over any sensory feedback about their movement.

The cue integration approach to SoA (chapter 1) provides a useful framework to understand AHP (Moore et al., 2009; Synofzik et al., 2009). AHP patients' sense of agency seems to be completely influenced by pre-motoric signals

associated with their intention to move, while visual, proprioceptive and external cues are largely discounted. In this chapter we test this hypothesis, by systematically investigating SoA in AHP with a task that is aimed to elicit the patients' intention to move and deliberately manipulates the external visual cues around the movement.

Moreover, for the first time we will investigate AHP patients' SoA by looking at their experience of agency not only around their impaired arm but also around their healthy arm, allowing us to gain an understanding of their SoA for the limb that is seemingly unaffected. By looking at SoA in the healthy arm we aim to provide insights on whether AHP is a disorder specific to the paralyzed limbs or more a general disorder of motor awareness.

Lastly, AHP's severity and its functional impact is influenced by the presence of other body awareness disturbances. The belief of not being paralysed, which is characteristic of AHP, can be associated with a disturbed sense of ownership towards the impaired arm. For example, patients may attribute their limbs to others, such as in the case of somatoparaphrenia (Feinberg et al., 2010), or experience them as not belonging to them, or completely missing, such as in the case of asomatognosia (Loring, 2015). While disturbances of sense of agency and ownership have been found to often coexist in patients with brain damage and hemiplegia (Baier & Karnath, 2008), not all patients with AHP also report disturbance of body ownership (Cutting, 1978). One of the aims of the experiment presented in this chapter is to further investigate the relation between SO and SoA in AHP.

In the following study, hemiplegic patients with and without AHP, and healthy controls completed the so-called vicarious agency task originally developed by Wegner, Sparrow, & Winerman (2004). In this paradigm, the experimental setting is designed such that the participant is led to feel SO over the experimenter's arm and SoA over the experimenter's arm movements. The task requires participants to look in front of them, towards a mirror. Gestures are performed by the experimenter hidden behind the participant in such a way that the gestures look like they are being performed by the participant's hands. The gestures seen in the mirror can be either congruent with the action

instructions heard over a pair of headphones (match condition) or incongruent (mismatch condition). Action instructions are designed to induce the intention to move in the participants, that are asked to remain still. This leads participants to plan the movement without being instructed to do so. Participants are then asked to report their feeling of agency and ownership over the gestures of the hand. If AHP patients discount external visual agency cues, we predict that their sense of agency (and perhaps ownership) would not be modulated by the gestures performed in the mirror.

Methods

Participants

Brain damaged patients

A group of 15 stroke patients (average age = 56.4, sd = 13.01; four females) with unilateral right hemisphere damage took part in this study. All participants were right handed. Demographics are reported in Table 3-1.

Motor and general cognitive assessment

Only patients with contralesional (i.e. left) motor impairment for the upper limb were considered for the study. Motor impairment was assessed with the Motricity Index (Wade, 1992). This test assesses the three core movements of the upper arm: 'pinch grip', 'elbow flexion' and 'shoulder abduction'. For each of these movements the participants' arm was given a score between 0 (no movement) and 33 (normal movement). The total score is therefore calculated by adding the score for each movement plus one, with the total ranging between 1 (severe motor impairment) and 100 (no motor impairment). Extrapersonal neglect was assessed with the Clock Test (Mondini, Mapelli, Vestri, & Bisiacchi, 2003) and their general cognitive state was measured with the Mini Mental State Examination (Folstein, Folstein, & McHugh, 1975). Neuropsychological data is reported in Table 3-1.

Table 3-1. Demographic and neuropsychological data of 15 right brain damaged patients. Note: HP = presence of hemiplegia without anosognosia, AHP = presence of anosognosia for hemiplegia. F/M = female/male. RBD = right brain damage.

PATIENT	GROUP	GENDER	AGE	VATA- UPPER LIMB	MOTRICITY INDEX
P1	HP	M	75	1	83
P2	HP	M	68	1	83
P3	HP	M	33	1	72
P4	HP	M	52	1	0
P5	HP	M	49	1	71
P6	HP	M	64	2	47
P7	AHP	M	72	4	76
P8	AHP	M	61	4	0
P9	AHP	M	65	5	23
P10	AHP	F	72	14	0
P11	AHP	F	49	4	0
P12	AHP	F	41	14	0
P13	AHP	F	50	11	11
P14	AHP	M	68	8	24
P15	AHP	M	63	5	0

Anosognosia assessment

To assess the presence of explicit anosognosia for hemiplegia of the upper limb, all patients were tested with the Visual-Analogue Test for *Anosognosia* for Motor impairment (VATAm) (Della Sala, Cocchini, Beschin, & Cameron, 2009). In this test, patients are required to rate (on a scale from 1 = no problem to 3 = problem) their ability to perform simple motor tasks that require the use of both hands or legs (Figure 3.5). Four questions that elicit obvious answers are also included as 'check questions', for example: 'Do you have any difficulty drinking from a glass?' or 'Do you have any difficulty in juggling five balls in the air?'. These questions are aimed at monitoring poor comprehension, perseveration behaviour or lack of compliance. The scores to these check questions are not considered in the final score. The participants' self-evaluation is compared with ratings of their caregivers who also filled the questionnaire evaluating the patient's motor skills. For the purpose of this study only the eight items testing the performance of the upper limbs were used.

The resulting upper limb score is calculated by subtracting the patient's ratings of the 8 tasks from those of their caregiver (i.e. caregiver - patient discrepancy). The score represents the patient's degree of awareness about their upper limb motor impairment. The score ranges from -24 (negative values indicate that the patient overestimates the motor deficit) to +24 (positive values indicate that the patient underestimates the motor deficit). According to the normative data provided by Della Sala et al.(2009), values falling between 3.8 and 8.0 indicate mild anosognosia, values between 8.1 and 16.0 represent moderate anosognosia and values between 16.1 and 24 are representative of severe anosognosia.

Nine patients showed anosognosia for hemiplegia (AHP) and six patients showed hemiplegia without anosognosia (HP) (Table 3-1).



Figure 3.5. Example of VATAm questions and the visual analogue scale used for ratings. Example of a standard question (a). Example of check questions (b) and (c). Visual - analogue scale (d). From Della Sala et al. (2009).

Control participants

A group of 20 healthy adults matched by age acted as controls. All participants were right-handed, their average age was 60.2 years old (SD = 15.9, age range = 30-77).

Procedure

The task required participants to look in front of them, towards a mirror. Gestures were performed by the experimenter hidden behind the participant in such a way that the gestures look like they were being performed by the participant's hand (Figure 4.4). The gestures seen in the mirror were either congruent with the action instructions heard over a pair of headphones (match condition) or incongruent (mismatch condition). Participants were asked to report their experiences by answering three questions on a 7-point scale with 1 being "not at all" and 7 being "very much".

The questions were similar as those included in Wegner et al.'s (2004) study:

- 1) Anticipation: *"To what degree did you feel you could anticipate the movements of the arm?"*

This control question assesses the success of the manipulation and whether the primes were attended to. This was included because a failure to attend to the primes may explain any putative performance differences in the two groups. If primes are attended to then anticipation judgements should be higher in the match than in the mismatch conditions. This question also serves as a control for any response bias (e.g. general tendency for one group to report higher or lower ratings).

- 2) Sense of Agency: *"How much control did you feel you had over the arm's movements?"*

This target question directly assesses the experience of agency.

- 3) Sense of Ownership: *"To what degree did the arm feel like it belonged to you?"*

This question provides an additional measure of the effect of the manipulation, examining the impact on sense of ownership over the body part.

As the procedure of the vicarious agency task was identical to the one described in chapter 2, further details can be found there.



Figure 3.6. Experimental set-up (based on Wegner et al., 2004). The left picture shows what the participant sees in the mirror placed in front of her. The right picture shows the set up from the side, with the experimenter sitting behind the participant and putting her hand forward so that it appears where the participant's hand would normally be.

Results

Non-parametric statistics were used as data failed the Shapiro-Wilk test of normality ($p < .05$).

The majority of AHP patients failed to show a difference between match and mismatch for the impaired arm in the Anticipation check question (see below preliminary analysis on Anticipation). As this did not allow us to exclude that attentional differences may be responsible for observed changes in SoA and SO, we did not consider the data for the impaired arm. The following analysis and results on SoA and SO refer to the healthy arm data only. For controls, where both arms were healthy, an average between left and right arm ratings was used, as no differences between left and right hand were found.

Anticipation

Anticipation was measured by asking participants 'To what degree did you feel you could anticipate the movements of the arm?'

This question serves as a control, to check that potential changes observed in agency and ownership are not due to differences in attention or any response bias.

A preliminary analysis on anticipation scores was carried out.

We calculated the difference scores between match and mismatch ratings for anticipation for both the impaired and the healthy arm. Seven out of nine AHP patients did not report higher anticipation in match conditions compared to mismatch conditions (i.e. match – mismatch < 1) for the *impaired* arm. As attentional problems for the contralateral arm could not be ruled out, we decided to not run the full analysis on the impaired arm data.

Equally, patients who did not report higher anticipation in match conditions compared to mismatch conditions (i.e. match – mismatch < 1) for the *healthy* arm were removed from the analysis. Two AHP participants (P7-P8) were removed from the sample. Figure 3.7a shows the mean anticipation judgments in the three groups plotted as a function of instruction-action congruence (i.e. match and mismatch conditions). Means and standard deviations are reported in Table 3-2. A Wilcoxon Signed Rank Test showed that the participants of all three groups reported significantly higher anticipation in the match than in the mismatch conditions (Controls Match vs Controls Mismatch: $Z = -3.995$, $p < .001$; HP Match vs HP Mismatch: $Z = -2.232$, $p = .026$; AHP Match vs AHP Mismatch: $Z = -2.555$, $p = .011$). This suggests that all three groups paid attention to instructions and actions.

Kruskall-Wallis tests showed that the three groups did not differ in Anticipation ratings in the match conditions ($p = .109$) but differed in mismatch conditions ($p = .001$). Post-hoc t-tests revealed that AHP patients reported higher anticipation than HP patients ($p = .002$) and Controls ($p < .001$) in the mismatch conditions.

Sense of agency

The SoA was measured by asking participants 'How much control did you feel you had over the arm's movements?'. Figure 3.7b shows mean agency judgments in the three groups plotted as a function of instruction-action congruence (i.e. match and mismatch conditions). Means and standard deviations are reported in Table 3-2. A Wilcoxon Signed Rank Test showed that Controls reported significantly higher agency in the match than in the mismatch conditions (Controls Match vs Controls Mismatch: $Z = -2.944$, $p < .003$). HP patients equally reported higher ratings in match than in mismatch conditions, although this was just above significance (HP Match vs HP Mismatch: $Z = -1.857$, $p = .063$). Equally, AHP patients showed higher agency ratings in the match compared to the mismatch conditions (AHP Match vs AHP Mismatch: $Z = -2.06$, $p = .039$). This replicates Wegner's original findings showing an effect of congruent instructions on the SoA.

Kruskall-Wallis tests revealed that the three groups differed in Agency ratings in match conditions ($p = .030$) and in the mismatch conditions ($p = .003$). Post-hoc t-tests revealed that AHP patients reported higher agency than Controls in the match conditions ($p = .026$) and in the mismatch conditions ($p = .002$). This suggests that AHP patients experienced higher sense of agency in both match and mismatch conditions.

Sense of Ownership

The sense of ownership was measured by asking participants 'To what degree did the arm feel like it belonged to you?'. Figure 3.7c shows mean agency judgments in the three groups plotted as a function of instruction-action congruence (i.e. match and mismatch conditions). Means and standard deviations are reported in Table 3-2. A Wilcoxon Signed Rank Test showed that Controls reported significantly higher ownership in the match than in the mismatch conditions (Controls Match vs Controls Mismatch: $Z = -3.318$, $p = .001$). HP patients and AHP patients did not show any significant differences between match and mismatch conditions (HP Match vs HP Mismatch: $Z = -1.342$, $p = .180$, AHP Match vs AHP Mismatch: $Z = -.816$, $p = .414$).

Kruskall-Wallis tests revealed that the three groups did not differ in Ownership ratings in neither match ($p > .250$) nor mismatch conditions ($p = .197$).

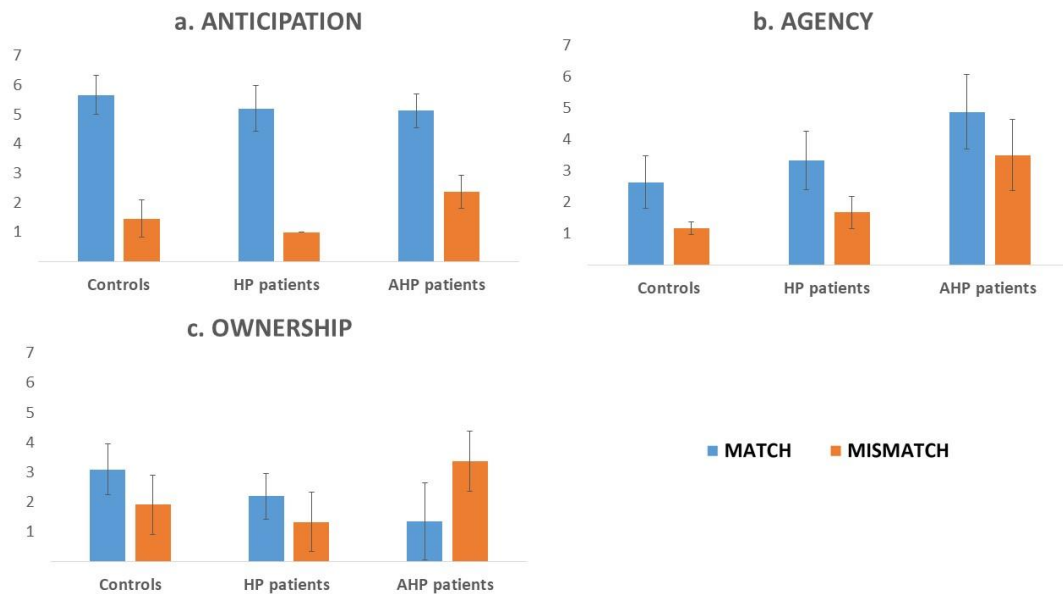


Figure 3.7. Mean ratings for anticipation (a), agency (b) and ownership (c) for Controls, aware patients (HP) and anosognosic patients (AHP). AHP patients show higher sense of agency in both match and mismatch conditions compared to controls. Error bars show standard deviation.

Table 3-2. Average ratings for each question and conditions obtained from Controls, patients without anosognosia for hemiplegia (HP) and with anosognosia for hemiplegia (AHP). Standard deviation in brackets.

Question	Condition	Controls	HP patients	AHP patients
Anticipation	Match	6.13 (1.1)	5.2 (1.2)	4.86 (1.1)
	Mismatch	1.05 (.22)	1 (0)	2.14 (1.21)
Agency	Match	2.33 (1.86)	3.33 (1.877)	4.72 (2.36)
	Mismatch	1.1 (.22)	1.67 (1.04)	3.29 (2.06)
Ownership	Match	2.58 (1.08)	2.2 (1.61)	3.58 (2.94)
	Mismatch	1.45 (.72)	1.33 (.82)	3.14 (2.86)

Discussion

The primary aim of this study was to investigate SoA in anosognosia for hemiplegia by including, for the first time, an investigation on the healthy limb. We did so by testing the susceptibility to the vicarious experience of control in patients with hemiplegia with and without anosognosia, and in a group of healthy participants. The use of the vicarious agency illusion paradigm (based on Wegner et al. 2004) enabled us to directly test the influence of internal and external cues to the SoA in anosognosia. This is particularly relevant in a group such as patients with hemiplegia, where testing the role of sensory feedback can be problematic.

Our results showed that patients with AHP had stronger feeling of agency, in both the match and mismatch conditions. These results are in keeping with previous findings suggesting that motor awareness in patients with AHP is not influenced by external feedback and instead mostly dominated by motor intentions (Fotopoulou et al., 2008). In our experiment, the gesture instructions had the role to generate the intention to move. This was sufficient for AHP patients to feel a strong SoA towards the actions seen in the mirror, regardless of whether these were congruent or incongruent with the instruction. With regards to the models of anosognosia, this finding supports the hypothesis that AHP patients have preserved intention to move and they are unable to detect a discrepancy between their intended movement and the actual state of the movement (Berti et al., 2007; Frith et al., 2000).

In the context of the cue integration approach to SoA, our findings strongly suggest that efferent pre-motor cues predominate in AHP, while external visual agency cues are largely discounted. If AHP patients' SoA was *entirely* dominated by intentions and sensorimotor predictions, we would expect no modulation induced by the congruency of the condition (match or mismatch). Interestingly, patients with AHP still showed a difference between match and mismatch conditions. This could be due to implicit processing taking place (see Cocchini, Beschin, Fotopoulou, & Della Sala (2010) for explicit/implicit AHP double dissociation). Alternatively, this could be attributed to the mild to moderate degree of anosognosia shown by our sample. Patients with severe AHP may not present this match-mismatch modulation, showing a complete

dominance of pre-motor signals associated with their intention to move over external visual feedback.

Our results also speak to the debate on whether unawareness in anosognosia is selective to the impaired arm, or it is a more generalised condition. For the first time, we have shown that the disturbance of SoA, which manifests in the impaired limb, extends to the healthy limbs. While AHP it is not considered a general disorder of unawareness (Jehkonen, Ahonen, Dastidar, Laippala, & Vilkki, 2000), our data suggests that SoA impairment may be generalised.

This result points towards new directions for therapeutic intervention with a more comprehensive focus. In particular, these interventions may involve behaviourally increasing the weighting that patients with AHP give to external visual feedback.

To date, we know of various strategies aimed at better managing AHP but no effective treatment is currently available (see Jenkinson, Preston, & Ellis, 2011, for a review). One of the aims of the experiment presented in this chapter was to contribute to AHP understanding with the intention of laying the groundwork for designing effective treatments. Notably, the impact of unawareness in patients after stroke is significant. AHP can considerably affect motor rehabilitation (Gialanella, Monguzzi, Santoro, & Rocchi, 2005) and it is linked to a poorer prognosis (Appelros, Karlsson, Seiger, & Nydevik, 2002) as well as reduced likelihood of returning to independent living (Pedersen et al., 1996).

With regards to the SO, our data does not highlight any differences between patients with and without AHP, and controls. Some studies support the suggestion that there might be a strong connection between AHP and disturbances of body ownership (e.g. Baier & Karnath, 2008). Others underline the existence of double dissociations between AHP and disturbances of body ownership and support the hypothesis of two independent systems for SoA and SO (e.g. Invernizzi et al., 2013). Our data seems to support the latter view, by showing an alteration of SoA not accompanied by altered SO. Our study is limited to patients with mild or moderate AHP. Further studies should aim to investigate whether the same result is replicated in patients with severe anosognosia.

Furthermore, our study included patients with right brain damage only. Given the evidence that the right hemisphere is heavily involved in SoA and more generally in body self-awareness (e.g. Tsakiris, Costantini, & Haggard, 2008), it is possible that AHP patients with left damage would present a less generalised or even a reduced alteration of SoA than AHP patients with right hemisphere damage. It would be important for future work to compare SoA in anosognosic patients following right vs left brain damage.

In this work, we have tested SoA and SO in patients with AHP. We found a clear change in agency experience in patients with AHP that seems to extend to the healthy limb. We suggest that this is due to an increased weighting of internal agency cues (e.g. motor intention) and a discounting of external sensory feedback (e.g. visual cues).

Significantly, we have argued that knowing how SoA works in anosognosia can not only be informative for the study of SoA, but it also provides new directions for understanding this condition and devising suitable interventions.

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CHAPTER FOUR

An investigation of sense of agency in older adulthood

Research has shown a reduction in the SoA in older adulthood, but the reasons behind this change remain unclear. Here we investigate agency processing differences that may underpin age-related changes in SoA. We do so by manipulating external situational agency cues in younger and older adults. We then investigate the mechanisms that may be responsible for these changes.

Introduction

With an increasingly older population (He, Goodkind, & Kowal, 2016), there has been more interest in understanding the psychological and cognitive changes associated with older adulthood. This is driven by, and is driving, the development of interventions aimed at improving older adults' well-being and promoting successful ageing.

In the last few decades, researchers looking at sense of agency in older adulthood have focussed on the link between ageing and changes in self-reported sense of control over life events (Langer and Rodin, 1976; Heckhausen & Schulz, 1995; Rodin & Langer, 1977, Lachman & Weaver, 1998). Several studies (e.g. Heckhausen & Schulz, 1995; Mirowsky, 1995; Rodin & Langer, 1977) showed a general reduction in feeling of control over life events in older adulthood (Figure 4.1). More recently, Lachman and Firth (Lachman & Firth, 2004) confirmed these findings by examining age differences in sense of control with a large-scale survey of Americans. They found a lower sense of control for those in later life: almost 80% of the young said they are in control of what happens in their life, whereas it was 71% for the middle aged, and only 62% for the older adults.



Figure 4.1. Relationship between age and sense of control in Illinois (left) and U.S. national (right) samples. Average sense of control differs across age groups and decreases progressively with age. From Mirowsky (1995).

Crucially, there is consistent evidence that higher sense of control is associated with successful aging (Baltes & Baltes, 1990; Rowe & Kahn, 1998). Successful aging is defined as 'including three main components: low probability of disease-related disability, high cognitive and physical functional capacity and active engagement with life' (Rowe & Kahn, 1997). Langer and Rodin (1976) conducted a now famous field study set in a nursing home to assess the effects choice and responsibility in older adults. They showed how acquiring sense of control improved quality of life. More specifically, they found that emphasizing personal responsibility and giving the freedom to make choices led to a significant improvement of the resident's alertness, participation and overall well-being. More recent studies have shown that adults that report having a higher sense of control are more likely to have better health (Lachman & Firth, 2004), report fewer memory problems (Lachman, 2005) and are more likely to adopt effective coping strategies (Lachman & Andreoletti, 2006).

Despite this large body of evidence underlining the important psychological and social impact of being an active agent, there is very little experimental research that has focussed on age-related changes in the SoA. To date, only two studies have systematically investigated SoA in older adulthood.

One is a study from Metcalfe and colleagues (2010). In this study, they investigated differences in SA across the lifespan. They tested children, younger adults and older adults on a computer game that required hitting one target and avoiding another (Figure 4.2). In some trials, random spatial distortions ('turbulence') and delays ('lag') were introduced, as well as a 'Magic' condition where participants would be credited for hitting a target even if they had not touched it. These three manipulations were carried out with the aim of decreasing participant's control. After each trial participants had to make a judgment on their agency and their accuracy. The results showed that older adults were less sensitive to these external performance manipulations compared to younger adults. In particular, older adults seemed to not be able to notice when they were left to be more in control compared to when their control was greatly distorted.



Figure 4.2. A screenshot of the task used by Metcalfe et al. (2010). The participant moves the square on the grey bar at the bottom of the screen to catch downward scrolling X's and avoid catching O's. From Metcalfe et al. (2010).

More recently, Wolpe and colleagues (2016) conducted a large population-based study investigating how voluntary movement changes with age. In particular, they looked at a specific component of motor control that is the integration of sensory information with predictions of the consequences of action. They did so by measuring changes in sensorimotor attenuation. As explained in chapter 1, sensory attenuation refers to a reduction in the

perceived intensity of sensations caused by voluntary actions compared to externally generated actions (Blakemore et al., 1998). It is commonly used as a measure of implicit sense of agency (e.g. Desantis, Weiss, Schütz-Bosbach, & Waszak, 2012; Dewey & Knoblich, 2014). In this study they used a Force Matching Task (Shergill, Bays, Frith, & Wolpert, 2003), in which participants were required to reproduce a force applied to their finger (Figure 4.3). It was found that sensorimotor attenuation increased with age, in proportion to reduced sensory sensitivity. In the same study, it was shown that this phenomenon was associated with reduced grey matter volume in the pre-Supplementary Motor Area (SMA) and reduced functional connectivity between pre-SMA and a frontostriatal network. The authors suggested that this reduced functionality and connectivity of the pre-SMA compromises the balance between internal predictive signals and sensory information. That is, ageing seems to increase reliance on sensorimotor predictive internal models, to compensate for a reduced sensory sensitivity.



Figure 4.3. Representation of the task used by Wolpe et al. (2016). Participants were required to match a force applied to their left index finger. In the Direct condition, participants used their right index to apply the force directly on the lever. In the Slider condition, they matched the force by moving a slider. Older adults showed increased sensory attenuation in the Direct condition only. From Wolpe et al. (2016).

The results from both studies imply that there are age-related changes in SoA, but it is still not clear what mechanisms underpin these changes. In the context of the cue integration approach to SoA (chapter 1), these findings suggest that the influence of external agency cues may be reduced in older adults. In the studies presented in this chapter, we directly test this hypothesis by

manipulating external agency cues in groups of younger and older adults. Secondly, we investigate how the reduced influence of external cues in older adults could be due to a relative increase in the reliability of internal cues.

In Experiment 1, younger and older adults completed the so-called vicarious agency task (developed by Wegner et al., 2004). This paradigm is designed such that the participant is led to feel SO and SoA over someone else's arm and arm's movements. In this paradigm, internal sensorimotor signals are absent as the participant remains still throughout the experiment. As such, it can isolate the influence of external situational cues on the SoA. Given the indication that older adults seem less sensitive to external manipulation of agency (Metcalfe et al., 2010), we predicted that the magnitude of the illusory experience of (vicarious) agency in older adults would be reduced.

According to the cue integration approach to SoA, the reduction in the influence of external cues in older adults could be due to a relative increase in the reliability of internal cues. Experiment 2 aimed to explore the relationship between the susceptibility to vicarious experience of agency and the reliability of internal cues in a group of younger adults. We did so by testing young participants with interoceptive and proprioceptive accuracy tasks, as measures of their ability to interpret internal bodily cues. We then tested them with the same vicarious agency illusion paradigm used in Experiment 1 to quantify their susceptibility to illusory experiences of agency induced by external manipulations. We predicted that increased susceptibility to the agency illusion may be linked with worse performance in the interoceptive and proprioceptive tasks.

In Experiment 3 we aimed to test the hypothesis that age-related changes in SoA observed in Experiment 1, are due to increased reliability on internal cues in older adults. We therefore tested younger and older adults with the interoceptive and proprioceptive tasks, and with the vicarious agency illusion paradigm. Along with replicating the findings of Experiment 1, we predicted that older adults would perform better in the interoceptive and proprioceptive accuracy tasks, relative to younger adults.

Experiment 1: Age-related changes in the experience of vicarious agency

A group of younger adults and a group of older adults were tested on a modified version of a vicarious agency paradigm created by Wegner and colleagues (Wegner, Sparrow, & Winerman, 2004). The task requires participants to look in front of them, towards a mirror. Gestures are performed by the experimenter hidden behind the participant in such a way that the gestures look like they are being performed by the participant's hands. The gestures seen in the mirror and the action instructions heard over a pair of headphones can either be congruent (match condition) or incongruent (mismatch condition). Participants are asked to report their feeling of agency and ownership over the gestures and the hand.

The following method and results sections are partially taken from Cioffi, Cocchini, Banissy and Moore, 2017 (in appendix).

Method

Participants

Two groups of participants were recruited. The 'Younger Adult' group consisted of 14 participants (6 females; average age = 23.0 years, sd = 4.7, range= 17-34). The 'Older Adult' group consisted of 14 participants (6 females; average age= 64.2 years, sd = 6.2, range = 54-72).

Procedure

The task required participants to look in front of them, towards a mirror. Gestures were performed by the experimenter hidden behind the participant in such a way that the gestures look like they were being performed by the participant's hand (Figure 4.4). The gestures seen in the mirror were either congruent with the action instructions heard over a pair of headphones (match condition) or incongruent (mismatch condition). Participants were asked to report their experiences by answering three questions on a 7-point scale with 1 being "not at all" and 7 being "very much".

The questions were:

- 1) Anticipation: *“To what degree did you feel you could anticipate the movements of the arm?”*
- 2) Agency: *“How much control did you feel you had over the arm’s movements?”*
- 3) Ownership: *“To what degree did the arm feel like it belonged to you?”*

As the procedure of the vicarious agency task was identical to the one described in chapter 2, further details can be found there.



Figure 4.4. Experimental set-up (based on Wegner et al., 2004). The left picture shows what the participant sees in the mirror placed in front of her. The right picture shows the set up from the side, with the experimenter sitting behind the participant and putting her hand forward so that it appears where the participant’s hand would normally be. From Cioffi et al. (2017)

Results

Anticipation

Anticipation was measured by asking participants ‘To what degree did you feel you could anticipate the movements of the arm?’. Figure 4.5a shows mean anticipation judgements in the ‘Younger Adult’ and ‘Older Adult’ groups plotted as a function of instruction-action congruence. A 2x2 mixed-design ANOVA was performed on the mean anticipation judgements (between-subjects factor: ‘Age’ young/old, within-subjects factor: ‘Condition’ match/mismatch). We found a significant main effect of Condition ($F(1, 26) = 85.56, p < .001, \eta^2_{\text{partial}} = .77$). Participants reported greater anticipation in the match condition, where the gesture corresponded to the listened instruction, than in the mismatch condition. Crucially, there was no main effect of ‘Age’ ($F(1, 26) = .05, p > .250$,

$\eta^2_{\text{partial}} = .01$) and no significant interaction between Age and Condition ($F(1,26) = .78, p > .250, \eta^2_{\text{partial}} = .03$). Overall, these results show that the primes and actions were equally well attended to in each group.

Sense of Agency

The SoA was measured by asking participants 'How much control did you feel you had over the arm's movements?'. Figure 4.5b shows mean agency judgements in the 'Younger Adult' and 'Older Adult' groups plotted as a function of prime-action congruence. A 2x2 mixed-design ANOVA was performed on the mean agency judgements (between-subjects factor: 'Age' young/old, within-subjects factor: 'Condition' match/mismatch). We found a significant main effect of Condition ($F(1, 26) = 18.02, p < .001, \eta^2_{\text{partial}} = .41$). Participants reported having a stronger experience of control over the experimenter's arm movements in the match condition than in the mismatch condition. There was also a significant main effect of 'Age' ($F(1, 26) = 9.81, p = .004, \eta^2_{\text{partial}} = .27$), showing that the overall SoA was significantly weaker in the older adults. Crucially, there was a significant interaction between 'Age' and 'Condition', ($F(1, 26) = 4.26, p = .049, \eta^2_{\text{partial}} = .14$). Inspection of Figure 4.5b suggests that the effect of the experimental manipulation was weaker in older adults. Two post-hoc t-tests were carried out to examine this interaction (Bonferroni correction: $p < .025$). Although there was a significant effect of congruence in both age groups, this effect was weaker in older adults ('Younger Adults', Match vs. Mismatch, match: $M = 3.36$, mismatch: $M = 1.39$, mean difference = 1.97, 95%, CI = [0.72, 3.21], $t(13) = 3.41, p = .005, d = 1.28$; 'Older Adults', Match vs. Mismatch, match: $M = 1.71$, mismatch: $M = 1.04$, mean difference = 0.67, 95%, CI = [0.16, 1.19], $t(13) = 2.85, p = .014, d = 1.03$). These findings suggest that the vicarious agency illusion was attenuated in older adults.

Sense of Ownership

The sense of ownership was measured by asking participants 'To what degree did the arm feel like it belonged to you?'. Figure 4.5c shows mean ownership judgements in the 'Younger Adult' and 'Older Adult' groups plotted as a function of prime-action congruence. A 2x2 mixed-design ANOVA was performed on the mean ownership judgements (between-subjects factor: 'Age' young/old, within-subjects factor: 'Condition' match/mismatch). We found a significant

main effect of Condition ($F(1, 26) = 22.16, p < .001, \eta^2_{\text{partial}} = .46$). Participants reported a stronger experience of ownership in the match condition than in the mismatch condition. There was also a significant main effect of 'Age' ($F(1, 26) = 5.88, p = .023, \eta^2_{\text{partial}} = .18$) suggesting that the overall experience of ownership was weaker in the older adults. Moreover, there was a significant interaction between 'Age' and 'Condition' ($F(1, 26) = 4.89, p = .036, \eta^2_{\text{partial}} = .16$). Inspection of Figure 5c suggests that the effect of the experimental manipulation was weaker in older adults. Two post-hoc t-tests were carried out to examine this interaction (Bonferroni correction: $p < .025$). These tests show that there was only a significant effect of congruence on ownership in the younger adults ('Younger Adults', Match vs. Mismatch, match: $M = 4.11$, mismatch: $M = 1.93$, mean difference = 2.18, 95%, CI = [1.01, 3.35], $t(13) = 4.03, p = .001, d = 1.36$; 'Older Adults', Match vs. Mismatch, match: $M = 2.39$, mismatch: $M = 1.61$, mean difference = .78, 95%, CI = [0.09, 1.48], $t(13) = 2.44; p = .030, d = 0.78$). These findings mirror the agency effects reported above and confirm that the older adults were less sensitive to the vicarious agency illusion.

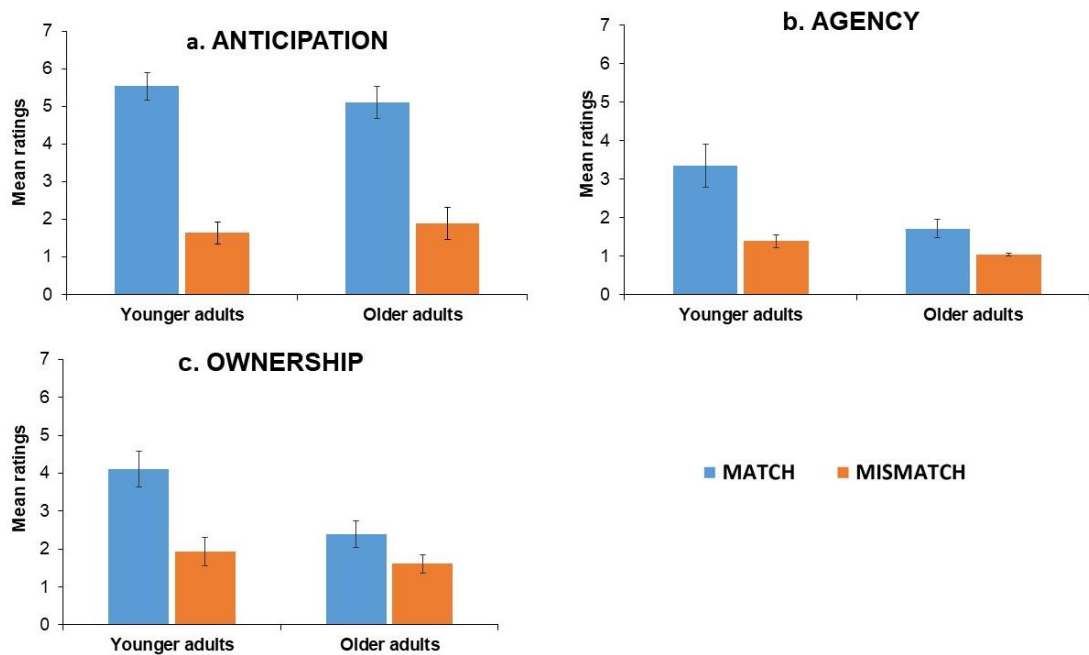


Figure 4.5. Mean ratings for anticipation (a), agency (b) and ownership (c) in match and mismatch conditions. The error bars show standard deviation across participants. Older adults show a weaker effect of agency and ownership illusion. Modified from Cioffi et al. (2017)

Discussion

The aim of this study was to investigate the modulation of SoA by external agency cues in younger and older adults. First, we replicated the vicarious agency effect found by Wegner et al. (2004). Both younger and older adults showed increased feeling of agency and ownership in the match conditions, compared to the mismatch conditions. Second, we found that the vicarious experience of agency and ownership was less pronounced in older adults. Importantly, as no differences were found between groups in the check question (i.e. anticipation question), we can conclude that the effects in SO and SoA are not due to differences in attention, or any response bias.

In line with our predictions, our findings show that the influence of external agency cues seems to be reduced in older adults. Increased reliability of internal sensorimotor cues in older adults can explain this reduction. That is, older adults may rely more on their internal sensorimotor cues, that leads them to discount external cues, and consequently, show a reduced susceptibility to the vicarious agency illusion. This hypothesis is tested in the experiments that follow.

Experiment 2: Individual differences in susceptibility to the vicarious experience of agency: an investigation in young adults.

The aim of this experiment is to explore the relationship between susceptibility to illusory experience of control and individual differences in awareness of internal bodily signals, in young healthy participants. Afferent information arising from within the body is defined as interoception (Ádám, 1998). This is typically assessed with an 'interoceptive accuracy' task, which consists of a heartbeat perception measure (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Previous work has shown that interoceptive accuracy predicts malleability of ownership experience, that is, people with lower interoceptive accuracy experienced a stronger illusion of ownership measured with the Rubber Hand Illusion (Tsakiris, Tajadura-Jiménez, & Costantini, 2011). However, nothing is known about interoceptive accuracy and malleability of agency experience. Here we tested a group of younger adults with an

interoceptive accuracy task and the vicarious agency paradigm presented in Experiment 1. We predict that worse performance at interoceptive accuracy corresponds to increased experience of vicarious agency and ownership.

Participants were also tested with a proprioceptive accuracy task. Proprioception refers to the ability to sense stimuli arising within the body regarding its position in the space (Sherrington, 1948). It was measured here with a modified version of a well-established contralateral concurrent matching task (Goble, Coxon, Wenderoth, Van Impe, & Swinnen, 2009) that required participants to place their arms in specific positions, without the help of vision. Similarly to our predictions about interoception, we expected that a worse performance in proprioceptive accuracy would correspond to an increased illusion of agency and ownership.

Method

The following method section is partially taken from Cioffi, Cocchini, Banissy and Moore, 2017 (in appendix).

Participants

Thirty participants were recruited. The average age was 23.87 years (sd = 7.1; age range 18-41; 16 females). All participants gave informed consent prior to taking part in the study. The study was approved by the Goldsmiths Ethical Committee.

Procedure

Vicarious agency illusion

The procedure was identical to the one described in Experiment 1.

Interoceptive accuracy

As a measure of interoceptive accuracy, a heartbeat monitoring task was used (Knoll & Hodapp, 1992; Tsakiris et al., 2011). Participants were asked to sit comfortably, keep their legs uncrossed and close their eyes. Their heartbeat was monitored by a pulse transducer (Xpod, model 3017LP, Nonin Medical Inc., MN, USA) attached to the participant's non-dominant index finger. They were instructed to silently count their own heartbeats during an interval of time that started and finished with an audio cue. At the end of each interval, each participant was asked to report the number of heartbeats counted. The six

intervals presented in a randomised order were 20, 20, 30, 30, 40 and 40 seconds. The interoceptive accuracy was measured by calculating the proportional discrepancy between the perceived and the actual number of heartbeats: $|\text{counted heartbeats} - \text{recorded heartbeats}| / \text{recorded heartbeats}$. This was averaged across intervals to provide an accuracy error index, with 0 indicating no discrepancy between perceived and actual numbers of heartbeats, and larger discrepancies indicated by larger values.

Proprioceptive accuracy

Proprioceptive accuracy was measured using a task inspired by well-established contralateral concurrent matching tasks (Goble et al. 2010). Participants were asked to sit in front of a desk and to familiarise themselves with a plain sheet of A3 paper. They were then asked to close their eyes and keep them closed until they were explicitly required to open them. While the experimenter verbally explained this, an A3 sheet was placed in front of them, centred on the participant's body. The experimenter took the participant's right index finger and placed it on a pre-printed dot. The participant was asked to place their left index finger such that it was mirroring their right index finger across the centre of the A3 sheet. The procedure was repeated for a total of six dots, three for each hand (Figure 4.6). The participant was asked to open their eyes only at the end of the six trials. The proprioceptive accuracy measure was calculated as the average of the discrepancy (in cm) between each actual mirrored position and the one indicated by the participant (0 = no discrepancy).

The tasks were presented in counterbalanced order.

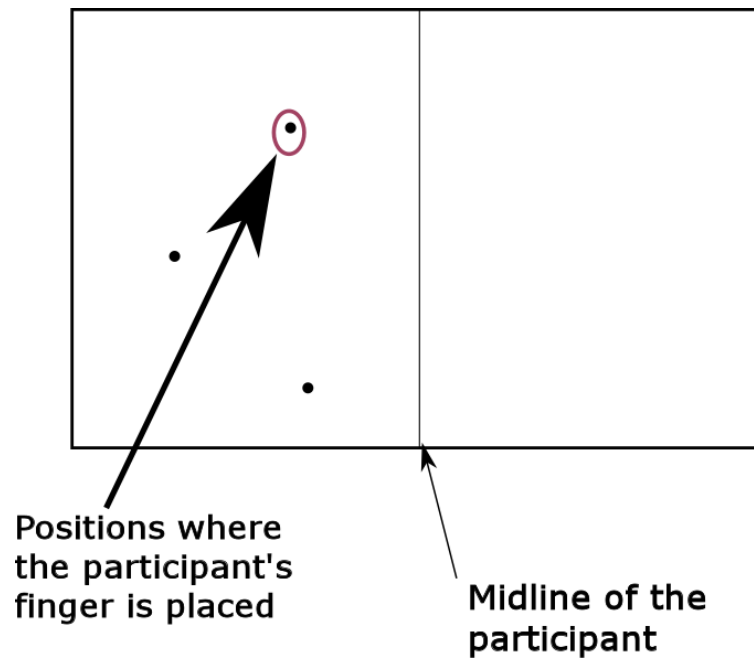


Figure 4.6. Schematic representation of the proprioceptive accuracy task. The participant has their eyes closed. Their left index finger is placed by experimenter on one of the dots on the left half of the paper. The participant has to place their right index finger such that it is mirroring their left index finger across the centre. The procedure is repeated for all positions and for each hand.

Results

Non-parametric tests were used as the variables did not meet normality criteria (Shapiro-Wilk test, $p > .05$).

Vicarious Agency illusion

Anticipation

The overall effect Condition (Match vs Mismatch) was examined using a Wilcoxon signed ranks test on the mean of Anticipation match ratings compared to Anticipation mismatch ratings. Participants reported significantly higher anticipation in the match compared to the mismatch conditions ($z = -4.66$, $p < .001$), (Figure 4.7). This shows that differences in attention to the actions or instructions, or any response bias, are unlikely to explain agency or ownership effects.

Sense of Agency

The overall effect Condition (Match vs Mismatch) was examined using a Wilcoxon signed ranks test on the mean of agency match ratings compared to agency mismatch ratings. Participants reported significantly higher sense of agency in the match compared to the mismatch conditions ($z = -3.42$, $p = .001$), (Figure 4.7)

Sense of Ownership

The overall effect Condition (Match vs Mismatch) was examined using a Wilcoxon signed ranks test on the mean of ownership match ratings compared to the ownership mismatch ratings. Participants reported significantly higher sense of ownership in the match compared to the mismatch conditions ($z = -3.51, p < .001$), (Figure 4.7).

These results show the significant effects of the manipulation on agency and ownership.

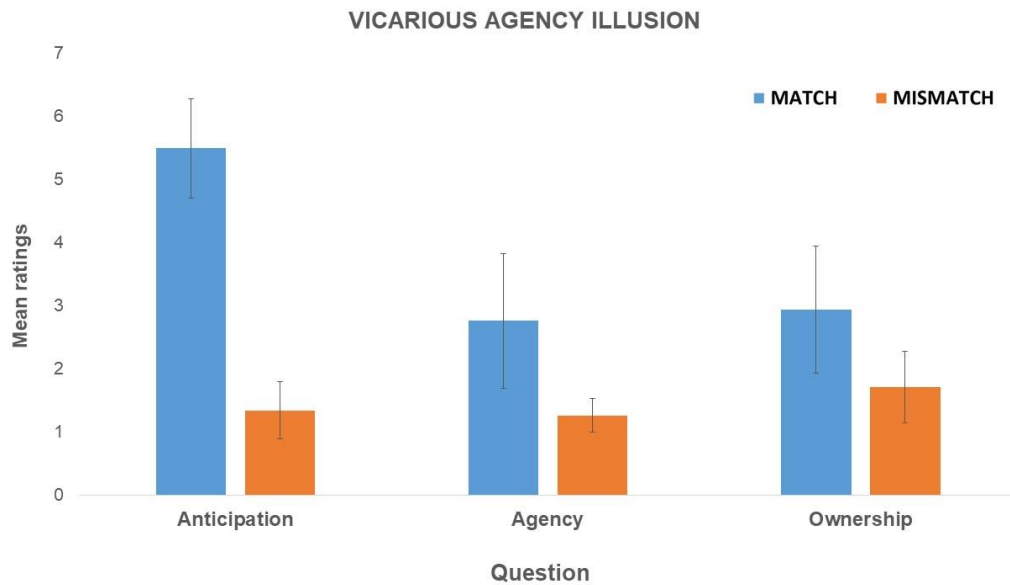


Figure 4.7. Mean ratings for Anticipation, Agency and Ownership in both Match and Mismatch conditions. Error bars show standard deviation across participants.

Interoceptive and proprioceptive accuracy

To investigate how interoception and proprioception influence the SoA and SO, we ran correlation analyses between individual differences in performance on tests of interoceptive and proprioceptive accuracy and individual differences in the vicarious agency illusion. These were calculated as the difference between match and mismatch trials for the agency question (Agency effect) and the difference between match and mismatch trials for the ownership question (Ownership effect).

Interoceptive and proprioceptive accuracy on SoA

We found that the strength of the agency illusion was correlated with interoceptive accuracy error ($r = .45, p < .001$) and with proprioceptive accuracy error ($r = .53, p < .001$). These results suggest that people that

performed worse on the interoception and proprioception tasks were more susceptible to the illusion of agency (Figure 4.8).

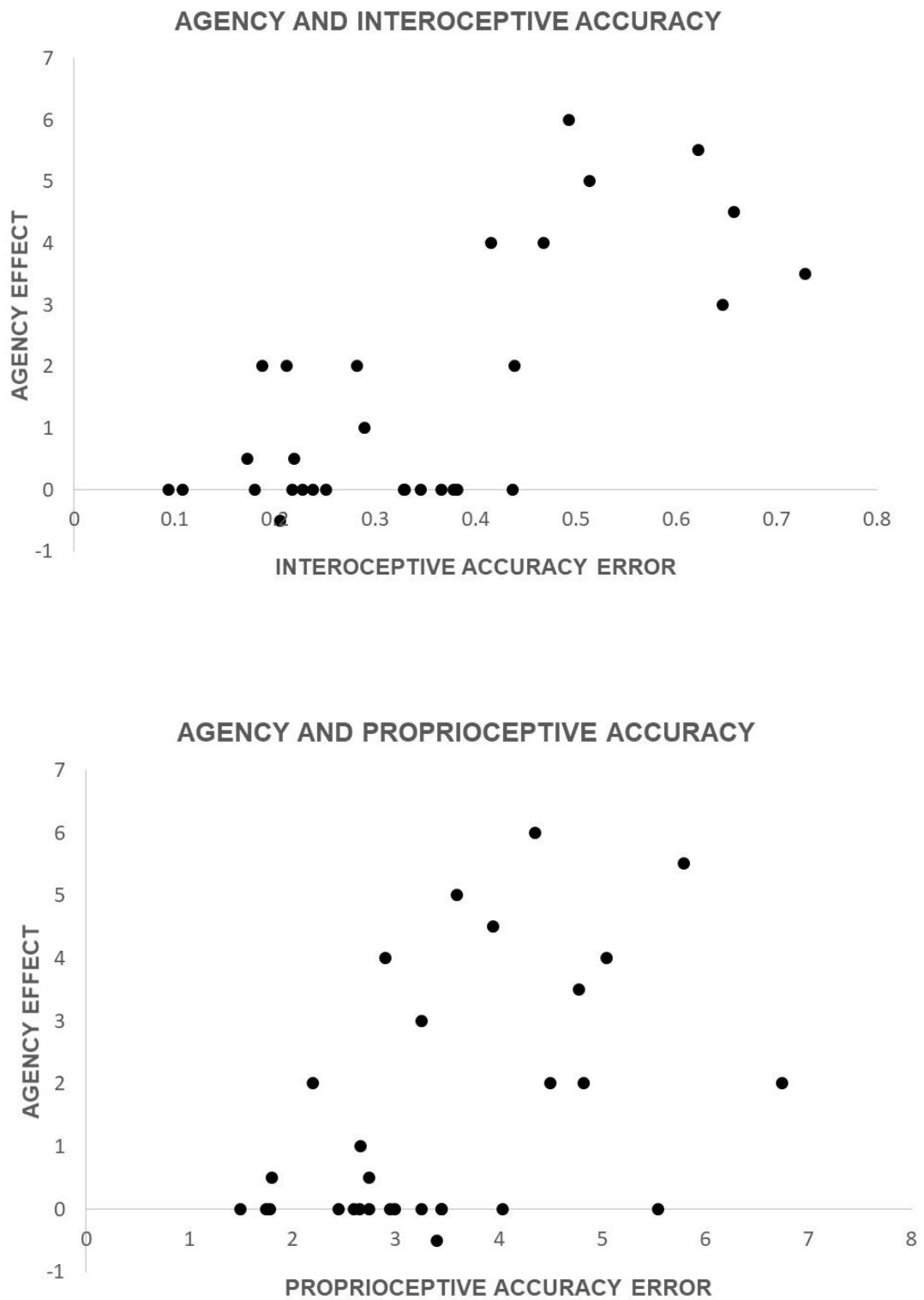


Figure 4.8. Scatterplot depicting the relationship between Agency effect (calculated as match-mismatch) and interoceptive (above) and proprioceptive (below) accuracy error

Interoceptive and proprioceptive accuracy on SO

We found that the strength of the ownership illusion was correlated with interoceptive accuracy error ($r = .55, p < .001$) and with proprioceptive accuracy error ($r = .76, p < .001$). These results suggest that people who performed worse on the interoception and proprioception tasks were more susceptible to the illusion of ownership (Figure 4.9).

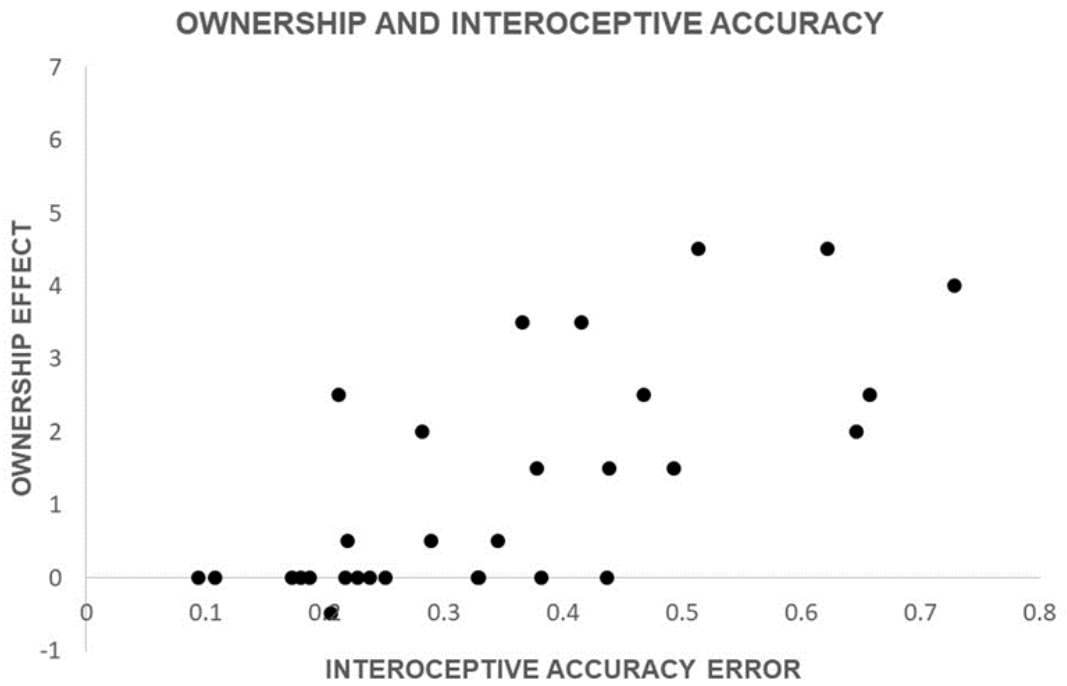
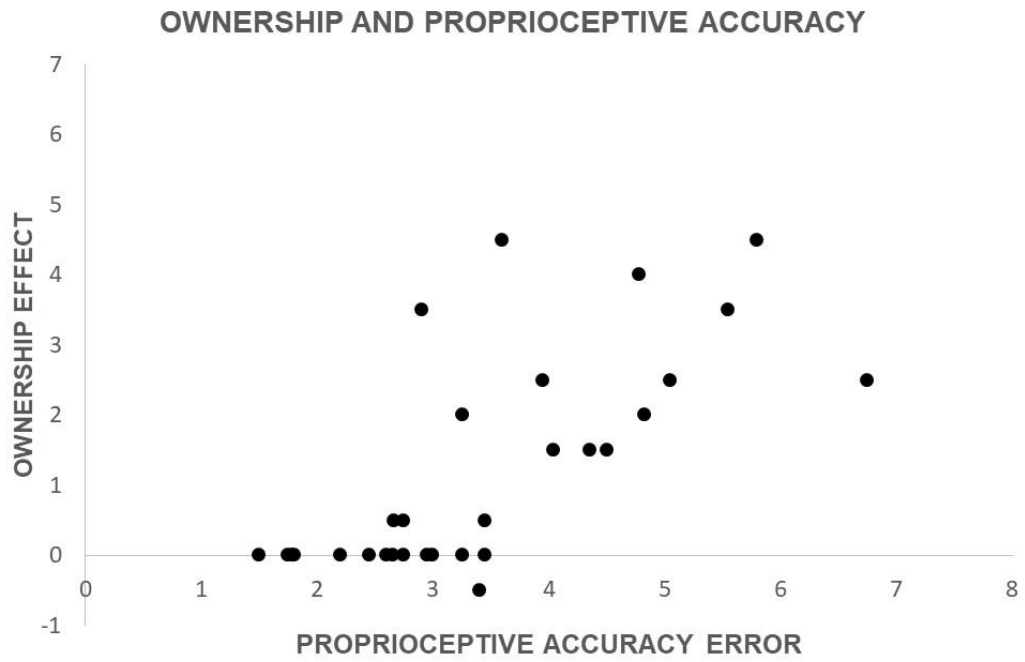


Figure 4.9. Scatterplot depicting the relationship between Ownership effect (calculated as match-mismatch) and interoceptive (above) and proprioceptive (below) accuracy error.

Discussion

We explored the relationship between interoceptive and proprioceptive accuracy and the susceptibility to illusory experience of agency in a group of younger adults. The results show that interoceptive and proprioceptive accuracy predict the magnitude of illusion of vicarious agency and ownership, with lower interoception and proprioception corresponding to greater illusion.

Previous research has shown that lower interoception is associated with various aspects of cognition, for example with reduced sensitivity to emotion of others (Terasawa, Moriguchi, Tochizawa, & Umeda, 2014), or higher levels of alexithymia in typical adults (Herbert, Herbert, & Pollatos, 2011). Importantly, reduced interoception has been linked to increased malleability of body representation measured with body ownership illusion (Tajadura-jiménez & Tsakiris, 2014; Tsakiris et al., 2011). Here we confirm these previous findings on body ownership and show that a similar link is present with regards to the sense of agency. Crucially, within the cue integration approach framework, our findings seem to suggest that a reduction in the influence of external agency cues is due to a relative increase in the reliability of internal signals. In light of this, if the age-related differences in SoA found in Experiment 1 are due to increased reliability on internal cues in older adults, we should expect elderly participants to perform better in interoceptive and proprioceptive accuracy tasks. This hypothesis is tested in Experiment 3.

Experiment 3: Age-related differences in the experience of vicarious agency: a closer investigation into the underlying mechanisms.

The aim of this experiment is to further investigate the possible mechanisms responsible for age-related changes in SoA and SO. The results of Experiment 1 suggest that the influence of external cues on agency and ownership processing is attenuated in older adults. In experiment 2 it was found that, in younger adults, a stronger illusion of agency and ownership is linked with reduced interoceptive and proprioceptive accuracy. This strongly supports the hypothesis that increased susceptibility to external manipulation of external agency cues is related to reduced reliability of internal cues.

In this experiment, we examine the possibility that age-related differences in SoA are explained by increased reliance on internal cues in older adulthood. A group of older adults and a group of younger adults were tested with the vicarious agency paradigm and with the interoceptive and proprioceptive tasks. If our findings in older adults are due to increased relative reliability of internal cues, older adults should show improvements in interoceptive and proprioceptive accuracy relative to younger adults.

Method

Vicarious agency illusion

The procedure was identical to that used in Experiment 1 and Experiment 2.

Interoceptive and proprioceptive accuracy

The procedure was identical to the one used in Experiment 2.

Results

The following results section is partially taken from Cioffi et al. 2017 (in appendix).

Vicarious agency task

The vicarious agency task was analysed with separate 2x2 mixed-design ANOVAs on the mean judgments for each question, with 'Congruence' the within-subjects factor and 'Age' (young/old) the between-subjects factor.

Anticipation

The results presented in Figure 4.10a directly replicate those from Experiment 1. A main effect of Congruence was found ($F(1, 33) = 489.96, p < .001, \eta^2_{\text{partial}} = .94$), showing that participants reported a greater feeling of anticipation in the match conditions compared to the mismatch conditions. Importantly, there was no main effect of Age ($F(1,33) = .15, p > .250., \eta^2_{\text{partial}} < .01$) and no interaction between Congruence and Agency ($F(1,33) = 2.00, p = .166, \eta^2_{\text{partial}} = .06$). These results showed that the prime-action relationship was equally well attended to by both groups. Therefore, differences in attention are unlikely to explain differences in agency and ownership on this task.

Sense of Agency

The results presented in Figure 4.10b directly replicate those from Experiment 1. A main effect of Congruence was found ($F(1, 33) = 37.57, p < .001, \eta^2_{\text{partial}} = .53$), showing that participants felt a stronger sense of agency over the experimenter's arm in the match compared to the mismatch conditions. A main effect of Age was also found ($F(1, 33) = 7.91, p = .008, \eta^2_{\text{partial}} = .19$), showing that the overall sense of agency was lower in older adults. Crucially, a significant interaction between Age and Congruence was also found, ($F(1, 33) = 7.84, p = .008, \eta^2_{\text{partial}} = .19$). Two post-hoc t-tests were carried out to examine this interaction (Bonferroni correction: $p < .025$). Although there was a significant effect of congruence in both age groups, this effect was weaker in older adults ('Younger Adults', Match vs. Mismatch, match: $M = 3.22$, mismatch: $M = 1.25$, mean difference = 1.97, 95%, CI = [1.19, 2.75], $t(17) = 5.34, p < .001, d = 1.43$; 'Older Adults', Match vs. Mismatch, match: $M = 1.76$, mismatch: $M = 1.03$, mean difference = 0.73, 95%, CI = [0.24, 1.23], $t(16) = 3.18, p = .006, d = 1.08$). These results replicate those of Experiment 1, showing that the experience of agency in older adults was not as strongly modulated by the experimental manipulation.

Sense of Ownership

The results directly replicate those from Experiment 1. A main effect of Congruence was found ($F(1, 33) = 38.16, p < .001, \eta^2_{\text{partial}} = .54$), showing that participants felt a stronger sense of ownership over the experimenter's arm in the match compared to mismatch conditions. A main effect of Age was also found ($F(1, 33) = 8.15, p = .007, \eta^2_{\text{partial}} = .20$), showing that the overall sense of ownership was lower in older adults. Crucially, a significant interaction between Age and Congruence was also found, ($F(1, 33) = 4.54, p = .041, \eta^2_{\text{partial}} = .121$). Inspection of Figure 4.10c suggests that the effect of the experimental manipulation was weaker in older adults. Two post-hoc t-tests were carried out to examine this interaction (Bonferroni correction: $p < .025$). Although there was a significant effect of congruence in both age groups, this effect was weaker in older adults ('Younger Adults', Match vs. Mismatch, match: $M = 3.50$, mismatch: $M = 2.11$, mean difference = 1.39, 95%, CI = [0.79, 1.98], $t(17) = 4.93, p < .001, d = 0.88$; 'Older Adults', Match vs. Mismatch, match: $M = 2$, mismatch: $M = 1.32$, mean difference = 0.68, 95%,

CI = [0.31, 1.04], $t(16) = 3.95$, $p = .001$, $d = 0.79$). These results directly replicate those of Experiment 1, showing that the experience of ownership in older adults was not as strongly modulated by the experimental manipulation.

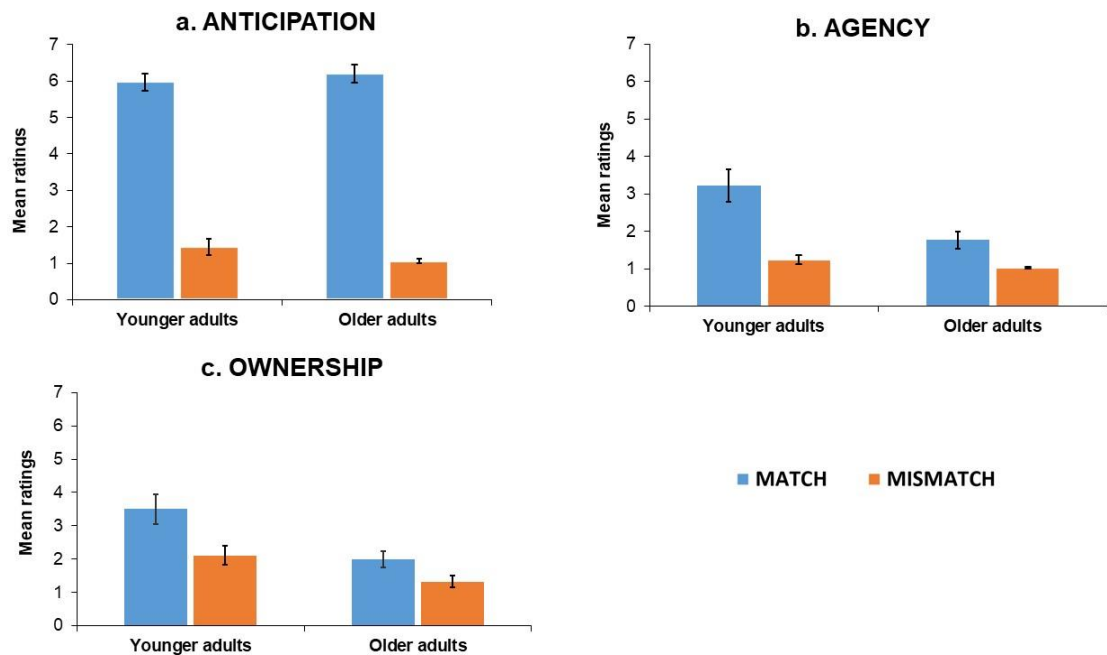


Figure 4.10. Mean ratings for anticipation (a), agency (b) and ownership (c) for younger and older adults, in match and mismatch conditions. Error bars show standard deviation across participants. Older adults show a weaker illusion of agency and ownership, compared to younger adults.

Interoceptive and proprioceptive accuracy

We compared the performance of the two age groups on the proprioceptive and interoceptive tasks (Figure 4.11). We found that older adults performed significantly better than younger adults on both tasks ('Interoceptive Error', Younger Adults vs Older Adults, younger adults: $M = 0.47$, older adults: $M = 0.33$, mean difference = 0.14, 95%, CI = [0.02, 0.26], $t(33) = 2.21$, $p = .034$, $d = 0.80$; 'Proprioceptive Error', Younger Adults vs Older Adults, younger adults: $M = 4.28$, older adults: $M = 3.16$, mean difference = 1.12, 95%, CI = [0.31, 1.94], $t(33) = 2.80$, $p = .009$, $d = 0.95$). This result suggests that older adults monitor internal bodily signals more successfully than younger adults.

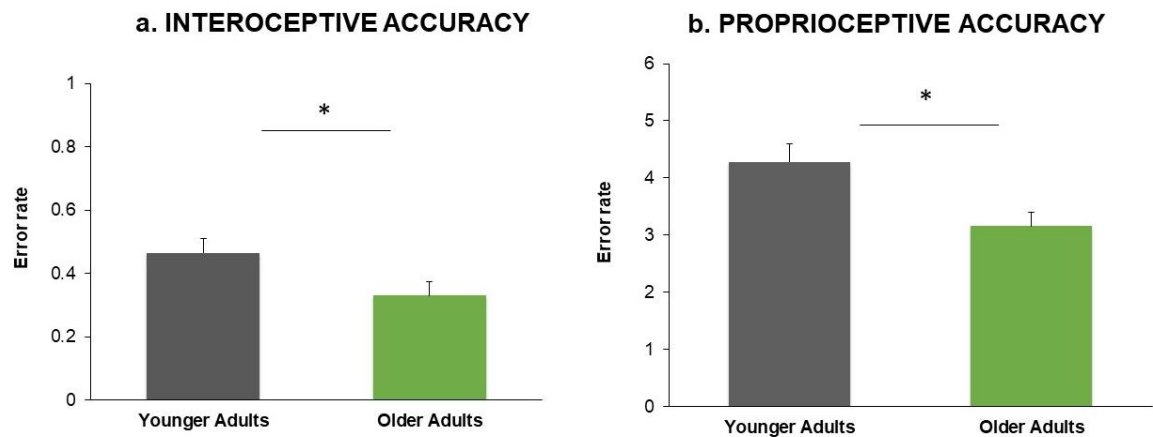


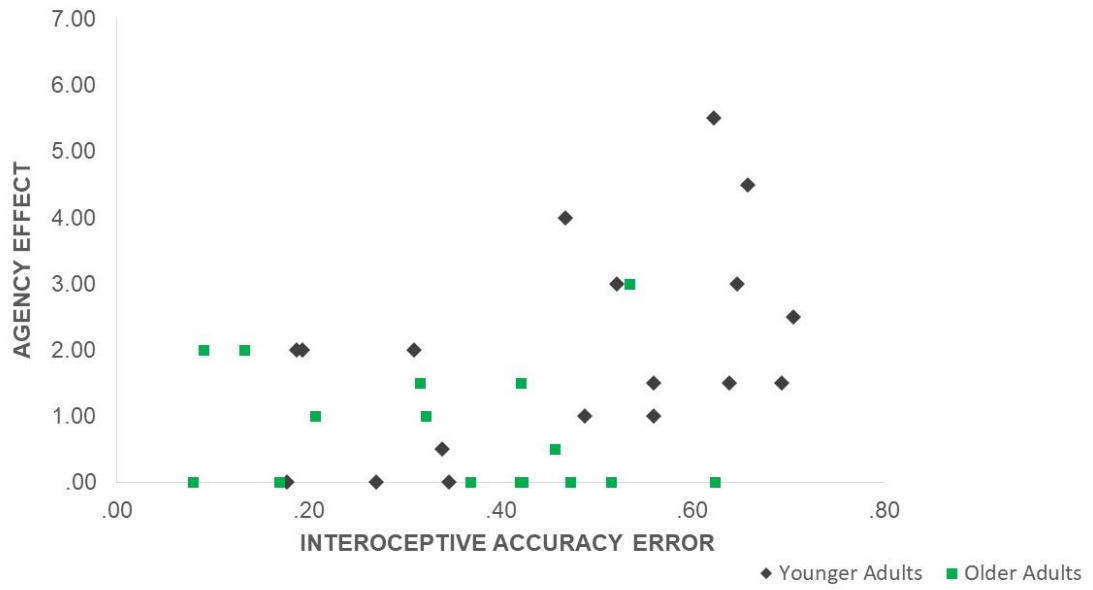
Figure 4.11. (a) Error rate of interoceptive accuracy, with 0 indicating no discrepancy between actual and estimated number of heartbeats. (b) Error rate of proprioceptive accuracy with 0 indicating no discrepancy between actual and estimated position. The error bars show standard deviation across participants. Older adults perform better in both interoceptive and proprioceptive accuracy.

Agency, interoceptive and proprioceptive accuracy

We wanted to investigate further the relationship between susceptibility to the illusion of agency, and interoceptive and proprioceptive accuracy. To do so, we looked at individual differences in performance on tests of interoceptive and proprioceptive accuracy, and the overall correlations between individual differences in the vicarious agency illusion. The latter of which was calculated as the difference for the agency question between match and mismatch trials. A reduction in the strength of the illusion was correlated with improved interoceptive and proprioceptive accuracy (interoceptive: $r = .40$, $p = .019$; proprioceptive: $r = .38$, $p = .026$), see Figure 4.12. These findings confirm our initial prediction that better performance on the interoceptive and proprioceptive measures would be correlated with a reduction in the strength of the illusion.

We then looked at correlations *for each age group separately*. In younger adults, there was a significant correlation between interoceptive accuracy and the agency effect ($r = .49$, $p = .038$). Although there was no significant correlation with proprioception, this finding is consistent with the overall correlation analyses reported above. In the older adults, there were no significant correlations between the agency effect and proprioception or interoception.

AGENCY AND INTEROCEPTIVE ACCURACY



AGENCY AND PROPRIOCEPTIVE ACCURACY

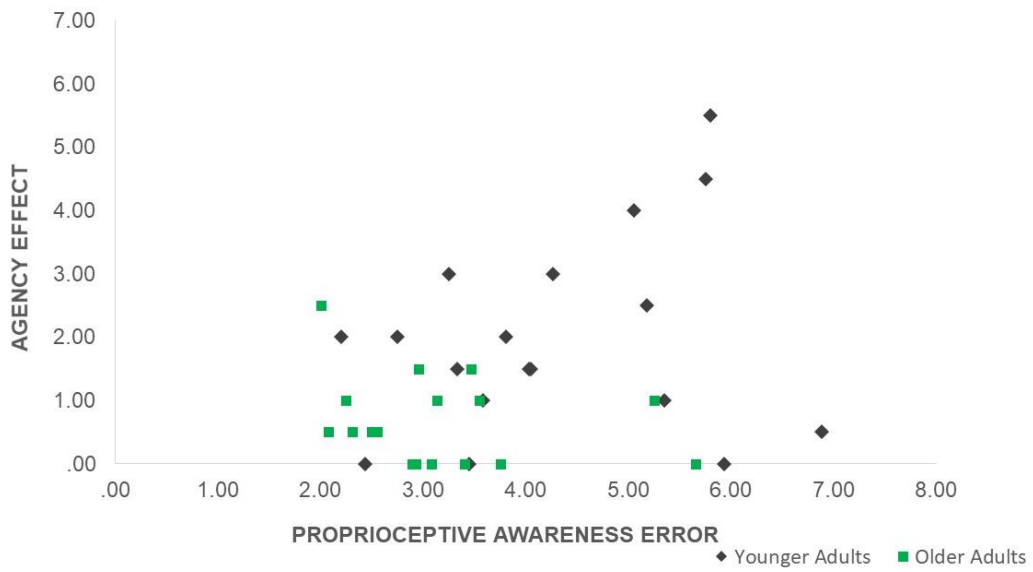


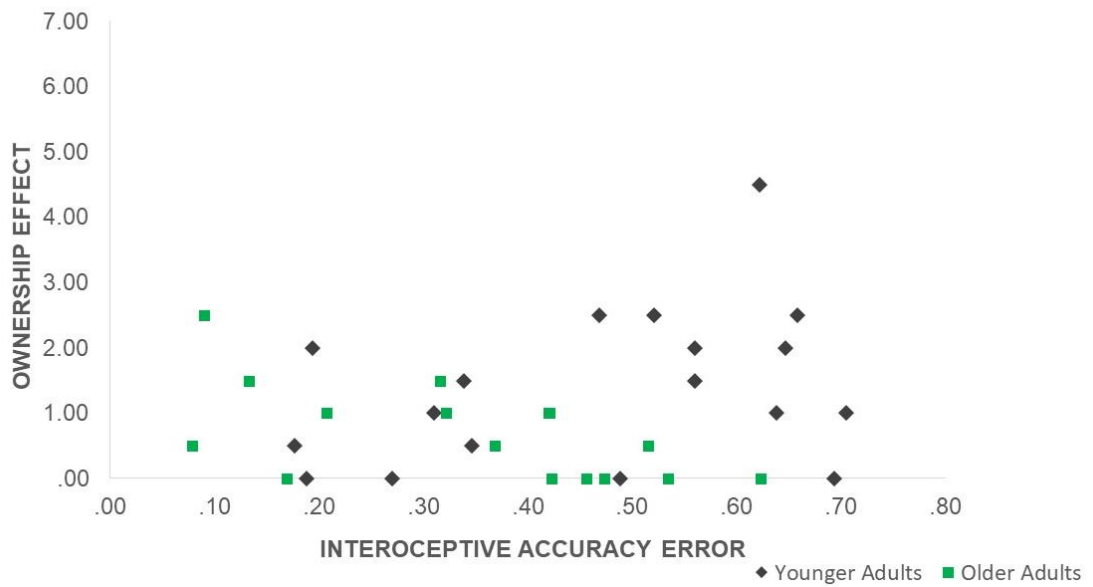
Figure 4.12. Scatterplot depicting the distribution of interoceptive accuracy (above) and proprioceptive accuracy (below) error individual scores, in relation to the agency effect (calculated as the difference between match and mismatch).

Ownership, interoceptive and proprioceptive accuracy

To further investigate the relationship between susceptibility to the illusion of ownership and interoceptive and proprioceptive accuracy, we looked at overall correlations between individual differences in the illusion of ownership and individual differences in performance on tests of interoceptive and proprioceptive accuracy. There was no significant correlation between the ownership effect and the interoceptive accuracy task ($r = -.17$, $p > .250$). We found instead that a reduction in the strength of the illusion was correlated with improved proprioceptive accuracy ($r = .38$, $p = .022$), (Figure 4.13).

We then looked at correlations *for each age group separately*. In younger adults, we found that the strength of the illusion was correlated with proprioceptive accuracy ($r = .50$, $p = .035$) but not with interoceptive accuracy ($r = -.35$, $p = .147$). In the older adults, there was no significant correlation between the ownership effect and proprioceptive accuracy ($r = -.24$, $p > .336$) but there was a significant correlation between the ownership effect and interoceptive accuracy ($r = -.51$, $p = .034$). This suggests that a reduction in the strength of the ownership illusion was correlated with a worse performance in the interoceptive accuracy task in older adults. This is in contrast with our previous findings.

OWNERSHIP AND INTEROCEPTIVE ACCURACY



OWNERSHIP AND PROPRIOCEPTIVE ACCURACY



Figure 4.13. Scatterplot depicting the distribution of interoceptive accuracy (above) and proprioceptive accuracy (below) error individual scores, in relation to the ownership effect (calculated as the difference between match and mismatch).

Discussion

The aim of this experiment was to explore the possibility that age-related differences in SoA are explained by increased reliance on internal cues in older adulthood. We tested a group of younger adults and a group of older adults with the vicarious agency paradigm as well as the interoceptive and proprioceptive accuracy tasks. The results from the vicarious agency task replicated those of Experiment 1, showing that external cues have less influence on agency (and ownership) in older adults. Importantly, we found that older adults were better on the proprioceptive and interoceptive tasks. This may help explain, in line with the cue integration approach to SoA, why the older adults are less sensitive to the illusion.

We also found that, across both age groups, performance on interoceptive and proprioceptive tasks is correlated with a reduction in the vicarious agency illusion. This is consistent with the findings of Experiment 2, and with the cue integration framework: the external manipulation was less effective in those that were better in monitoring internal bodily signals.

However, when looking at each age group separately, the results of our investigations were less clear-cut. When correlating performance on interoceptive and proprioceptive tasks with the illusion of agency for each age group, we failed to find a significant relationship in older adults. Results were similar with regards to the illusion of ownership. We did not find any significant relationship between SO and proprioceptive awareness in older adults. Furthermore, we found a relationship between interoceptive accuracy and SO which was going in the opposite direction to our predictions: i.e. older adults that showed better interoceptive accuracy were more susceptible to the illusion of ownership. These correlations might have to be interpreted carefully as the stability of correlations can be influenced by sample size in smaller samples.

So, although it remains a strong possibility that differences in the weighting of internal cues can explain agency processing differences in older adults, our data are not definite on this matter and future work should address this.

General discussion

The studies presented in this chapter sought primarily to investigate a) agency changes in older adulthood b) cue integration in agency processing.

In Experiment 1, we investigated age-related changes in SoA by testing younger and older adults with a vicarious agency illusion. We found that older adults are less sensitive to external manipulation of agency cues compared to younger adults.

In Experiment 2, we investigated the relationship between susceptibility to manipulation of external cues and reliability of internal bodily signals. We did so by testing a group of younger adults with a vicarious agency illusion and interoceptive and proprioceptive tasks. We found that in younger adults reduced sensitivity to external cues is linked with reduced reliability of internal sensory signals.

In Experiment 3, we tested the hypothesis that age-related changes in SoA are due to increased reliability on internal cues in older adults. We tested both younger and older adults with the interoceptive and proprioceptive tasks, along with the vicarious agency illusion paradigm. We replicated the results of Experiment 1 and found that older adults performed better in interoceptive and proprioceptive tasks. While our data were not unequivocal on this, we suggested that age-related differences in SoA may be due to increased reliability of internal cues in older adults.

These results are in line with previous work on SoA in older adults (Metcalf et al., 2010; Wolpe et al., 2016) and give considerable insights into the mechanisms underpinning age-related changes in SoA.

Our experiments strongly suggest that older adults rely more on internal agency cues and discount external ones. This enhanced weighting of internal cues could be the result of increased reliability of internal information (as shown by our results) combined with a decreased reliability of external information. When viewed within the context of the *optimal* cue integration framework, this pattern of agency processing may be disadvantageous. The fact that the experience of agency in older adults is less sensitive to compelling

external cues suggests that they may be discounting potentially useful sources of information. This sub-optimal integration might be linked to the overall reduction in SoA associated with older adulthood. That is, by not optimally integrating different sources of information, older adults may be less likely to recognize their own agency and feel less in control of their own life. Although this is entirely speculative, it could be extremely informative for future research aimed at furthering the understanding of successful ageing and developing interventions that promote older adults' well-being.

In the narrower context of agency research, it would be informative if future work extended our investigation to the implicit aspects of agency, as nothing is currently known about implicit SoA in older adulthood.

In this chapter, we have uncovered agency changes in older adulthood, and started to understand their underlying mechanisms. In turn, this has been informative in the study of SoA.

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CHAPTER FIVE

An investigation of explicit sense of agency in mirror-touch synaesthesia

Recent accounts postulate that mirror-touch synaesthesia is linked with atypical self-other representations. Here we examine whether or not putative self-other processing abnormalities in mirror-touch synaesthesia extend to sense of agency.

Introduction

For most of us, observing another person being touched activates neural regions in the somatosensory cortex that are also involved in experiencing touch (e.g., Keysers, Kaas, & Gazzola, 2010; Schaefer, Heinze, & Rotte, 2012). However, this activation does not lead to overt sensations of the observed event. In other words, we typically do not feel any tactile sensation when observing the tactile experience of others. People with mirror-touch synaesthesia (MTS) do: they feel a tactile sensation on their body when simply seeing someone else being touched (Blakemore, Bristow, Bird, Frith, & Ward, 2005). Mirror-touch synaesthesia occurs when there is a conscious experience of a tactile sensation that occurs automatically following the observation of touch applied to another person (Banissy, Kadosh, Maus, Walsh, & Ward, 2009). This experience of touch can be felt exactly in the same place as the touch seen on the other person (anatomical correspondence) or in a mirrored position - hence the name - (specular correspondence) (Banissy & Ward, 2007) (Figure 5.1).



Figure 5.1. Illustration of the specular and anatomical correspondences. Modified from Banissy and Ward (2007).

The first case of MTS was reported in 2005 by Blakemore and colleagues (Blakemore et al., 2005). MTS is currently thought to affect 1.6% of the population (Banissy et al., 2009).

A behavioural protocol to test the authenticity of the condition was developed in 2007 by Ward and Banissy. This is a Visuo-Tactile Stroop task, where participants are required to report the location of the actual touch applied on their own cheeks (left, right or both cheeks) whilst looking at a video of a face being touched either on the left or the right cheek (Figure 5.2). Since participants with MTS are confused by the synaesthetic touch (i.e. touch induced by vision), they make a significantly higher number of errors and their reaction times are significantly slower in incongruent conditions. An example of an incongruent trial is when a participant receives a touch on the right cheek, so they should answer 'right', while they see a touch applied on the opposite cheek. In such a trial, a mirror-touch error consists of reporting 'both'. All participants considered as MT synaesthetes in this work, have been tested with the Visuo-Tactile Stroop.



Figure 5.2. Illustration of the Visuo-Tactile Stroop used to confirm potential cases of mirror touch synaesthesia. Participants are required to report the site on which they received the actual touch (that is, left cheek, right cheek, both cheeks or no touch) while ignoring the touch observed on the screen (and the synesthetic touch induced by it). From Banissy and Ward (2007).

Accounts of MTS have pointed out how MTS is linked with empathy (Banissy & Ward, 2007). In particular, Banissy and Ward (2007) reported that MT synaesthetes score significantly higher on the emotional reactivity subscale of the EQ (Empathy Quotient) compared to controls. More recently, studies have focused on how mirror-touch synaesthetes may have atypical self-other representations. More specifically, MTS may be linked to an impairment in the ability to *control* self-other representations, leading to a difficulty in inhibiting the experiences of others (Banissy & Ward, 2013; Heyes & Catmur, 2015; Santiesteban, Bird, Tew, Cioffi, & Banissy, 2015; Ward & Banissy, 2015). This suggestion is based on neuroimaging data that shows that MT synaesthetes have reduced grey matter in the right temporo-parietal junction (rTPJ) compared to non synaesthetes (Holle, Banissy, & Ward, 2013). In fact, rTPJ has been shown to be involved in controlling self-other representations: Santiesteban and colleagues (2012) used transcranial direct current stimulation (tDCS) to show how modulating the cortical excitability of rTPJ has an impact in controlling self-other representations. Interestingly, rTPJ is commonly associated with the sense of agency (Decety & Lamm, 2007; Farrer, Franck, Paillard, & Jeannerod, 2003). In the context of SoA, it might be that rTPJ is executing the same 'controller' role, influencing self-other agency judgments. While this hypothesis is tested directly in the studies presented in

chapter 6, investigating SoA behaviourally in MTS offers an opportunity to explore how the control of self-other representations influences SoA.

Behavioural studies have shown that a disturbance in the ability to inhibit representations of others and an augmented malleability of self-other boundaries are core features of MTS (Maister, Banissy, & Tsakiris, 2013; Santiesteban et al., 2015). In particular, Maister and colleagues (2013) ran an 'enfacement illusion' study with mirror-touch synaesthetes, where the touch component was removed (Figure 2). In the traditional 'enfacement illusion', participants are shown images of faces that are morphed between their own and that of another person. They are asked to say to what extent the images look like themselves or the other. The participant is then touched on their face while watching a video of the other person being simultaneously and congruently touched on their face. After experiencing a synchrony between the observed and felt touch, the images that participants had initially perceived as containing equal quantities of self and other became more likely to be recognized as the self (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008; Sforza, Bufalari, Haggard, & Aglioti, 2010; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Tajadura-Jiménez, Grehl, & Tsakiris, 2012). In the adaptation of Maister et al. (2013), individuals observed a touch to other person, but synchronous touch was not physically applied to the face. MT synaesthetes experienced the same effect of 'enfacement illusion' in the absence of a touch applied to their face. Simply viewing the touch on others evokes changes in self-other representations in MTS.



Figure 5.3 A representation of the enfacement illusion paradigm used by Maister et al (2013). The 'touch condition' is presented above and the 'no touch condition' below. In the traditional version of the enfacement illusion only the 'touch condition' is present. During both conditions, participants are required to perform a self-recognition task before and after viewing a video. From Maister et al. (2007).

This evidence that MT synaesthetes seem to have blurred boundaries between self and other, along with more malleable body representations (Banissy & Ward, 2013; Maister et al., 2013) is very relevant when talking about the two main components of self-awareness, the sense of ownership and the sense of agency.

Aimola Davies and White (2013) looked at the sense of ownership using the paradigm of the rubber hand illusion (RHI) (Botvinick & Cohen, 1998). The results of their studies showed how mirror-touch synaesthetes experienced the rubber hand illusion in a 'no-touch condition', where participants were just looking at the prosthetic hand with no-touch delivered to their real hand (Figure 5.3). This study shows that this self-other discrimination disturbance is extended to the SO.



Figure 5.4 Rubber hand paradigm. 'touch condition' (left): the experimenter (E) strokes both the rubber hand and the participant's hand; 'no-touch condition' (right): the experimenter strokes the rubber hand only. Figure adapted from Aimola Davies and White (2013).

Although nothing is known about SoA in MTS, this disturbance in the SO is likely to have consequences on the SoA. Theoretical accounts of agency propose that the experience of agency over a movement is predicated on the feeling that body part that moves is one's own (Gallagher, 2000). Changes in the sense of agency in MTS could be the result of a fundamental ownership deficit. Despite this being the most likely scenario, the opposite can also be true: as the sense of agency itself can play a role in structuring the sense of ownership (Ma & Hommel, 2015; Tsakiris, Longo, & Haggard, 2010), it could be that the SO disturbances that characterise MTS may be a result of SoA abnormalities. In the experiments presented in this chapter, we test both agency and ownership in MT synaesthetes, taking the opportunity to shed light on how these two crucial components of self-awareness interact.

This work on MTS may be especially informative with regards to models of agency. In the context of the cue integration approach, where agency is created by optimally integrating external and internal cue, it can be hypothesised that a MT synaesthetes' agency is more heavily influenced by external cues. In fact, external stimuli seem to dominate the creation of self-representations in MTS, with SO being driven almost exclusively by visual stimuli (Aimola Davies & White, 2013; Maister et al., 2013). This is not surprising when taken in the context of the condition itself: MTS happens precisely in the presence of a visual component, by definition 'MT synaesthetes feel a tactile sensation on their body when simply *seeing* someone else being touched'.

In this chapter, I present two experiments that tested the influence of external agency cues on MTS's agency processing. In the two paradigms used, a situation of agentic uncertainty is artificially created, and the biasing effects of external agency cues are then assessed.

In Experiment 1, participants completed the so-called vicarious agency task (developed by Wegner et al., 2004). In this paradigm, the experimental setting is designed such that the participant is led to feel SO over the experimenter's arm and SoA over the experimenter's arm movements. Owing to the purported blurring of self-other boundaries in MTS, it is expected that these individuals

would be more vulnerable to this illusion, showing stronger experiences of vicarious agency and ownership.

In Experiment 2, participants completed an action recognition task (based on the paradigm developed by Farrer et al., 2008). Here they were asked to judge whether a video that they are watching showed their own finger movements or those of the experimenter. In reality, the video always showed the participants' movement with a temporal delay. Farrer et al. showed that this set up created a bi-stable impression of sense of agency, with agency reports flipping spontaneously between "self" and "other". It can be predicted that participants with MTS may be prone to shift more often between self and other actions as a consequence of their more malleable self-other representations.

Experiment 1: An illusion of agency and ownership in Mirror-touch synaesthesia

The aim of this study is to investigate SoA and SO in MTS, and how these two components of self-awareness interact. A group of participants with MTS and non-synaesthete controls were tested on a modified version of a vicarious agency paradigm created by Daniel Wegner and colleagues (Wegner, Sparrow, & Winerman, 2004). The task requires participants to look in front of them, towards a mirror. Gestures are performed by the experimenter hidden behind the participant in such a way that the gestures look like they are being performed by the participant's hands. The gestures seen in the mirror can be either congruent with the action instructions heard over a pair of headphones (match condition) or incongruent (mismatch condition). Participants are asked to report their feeling of agency and ownership over the gestures and the hand.

The following Method and Results sections are largely taken from Cioffi, Banissy, & Moore, (2016) (in appendix)

Method

Participants

A group of eight adult mirror-touch synaesthetes (age range = 19-60, average age = 36.3, SD = 16.8, one male) and a group of eight non-synaesthetes controls (age range = 19-38, average age = 26.5, SD = 8.33, four males) were recruited. All participants were right-handed. All mirror-touch synaesthetes were confirmed as individuals with MTS using the Visuo-Tactile Stroop task, designed to detect the authenticity of the condition (Banissy et al., 2009; Banissy & Ward, 2007). All MTS participants differed significantly on a single subject basis (using Crawford's modified t-test; Crawford & Howell, 1998) to previous published control data on this task (Banissy et al., 2009; Banissy & Ward, 2007). All controls were interviewed with a synaesthesia questionnaire (including a question on MTS; adapted from Banissy et al., 2009) and did not report any synaesthetic experiences. Three of the mirror-touch synaesthetes self-reported other types of synaesthesia. All participants gave consent to participate in the study and were paid £10/hour to take part in the experiment. The study was approved by the local ethical committee.

Procedure

The task required participants to look in front of them, towards a mirror. Gestures were performed by the experimenter hidden behind the participant in such a way that the gestures look like they were being performed by the participant's hand (Figure 5.5). The gestures seen in the mirror were either congruent with the action instructions heard over a pair of headphones (match condition) or incongruent (mismatch condition). Participants were asked to report their experiences by answering three questions on a 7-point scale with 1 being "not at all" and 7 being "very much".

The questions were:

- 1) Anticipation: *"To what degree did you feel you could anticipate the movements of the arm?"*
- 2) Agency: *"How much control did you feel you had over the arm's movements?"*
- 3) Ownership: *"To what degree did the arm feel like it belonged to you?"*

As the procedure of the vicarious agency task was identical to the one described in chapter 2, further details can be found there.



Figure 5.5 Experimental set-up. Pictured side view (left) and participant view (right). The experimenter sits behind the curtain hidden from the participant's view. Here, the experimenter places his arm forward, where the participant's arm would normally appear. The participant sits in front of the mirror where she can see the arm as her own. The participant hears instructions through the headphones and observes the action being performed by the arm. In the match condition instructions and actions are congruent, while they are incongruent in the mismatch condition. From Cioffi et al. (2016)

Results

A preliminary analysis on left and right hands were carried out for each condition using a paired sample test to see if their results could be distinguished. As no significant differences emerged, the mean judgements for left and right hands were collapsed into a single score (for example: (Anticipation match condition Left hand + Anticipation match condition Right hand)/2). These were entered into mixed design ANOVAs. Any interactions were explored using planned paired comparisons or where relevant post-hoc tests (corrected for multiple comparisons using a Bonferroni correction). In any cases where individual variables did not meet assumptions of normality non-parametric paired comparisons were used.

The mean ratings were entered into a 3 (Question) X 2 (Condition) X 2 (Group) mixed measure analysis of the variance with 'Question' (Anticipation/ Agency/ Ownership) and 'Condition' (Match/Mismatch) as within-subjects factors and 'Group' (MTS/Controls) as a between-subjects factor. The ANOVA showed main effects of Question ($F(2, 28) = 11.2, p < .001, \eta^2_{\text{partial}} = .445$), Condition

($F(1, 14) = 87.3, p < .001, \eta^2_{\text{partial}} = .862$) due to higher ratings overall in the match condition and Group ($F(1, 14) = 41.3, p = .009, \eta^2_{\text{partial}} = .392$), this was due higher ratings showed by the MTS group compared to controls (figure 5a). The interaction between Question and Group was significant ($F(2, 28) = 10.32, p < .001, \eta^2_{\text{partial}} = .424$) as well as the interaction Question by Condition ($F(2, 28) = 24.855, p < .001, \eta^2_{\text{partial}} = .640$). A three-way interaction between Question, Condition and Group was also significant ($F(1, 14) = 4.35, p < .023, \eta^2_{\text{partial}} = .237$). The three-way interaction was explored by running separate 2 (Condition) X 2 (Group) mixed measures analysis of the variance for each question (Anticipation/Agency/Ownership). Further analyses exploring this interaction can be found in the supplementary results.

Anticipation

The analysis of the mean ratings for Anticipation showed a significant main effect of Condition ($F(1, 14) = 295.7, p < .001, \eta^2_{\text{partial}} = .955$). Participants reported significantly greater anticipation in the match condition, where the gesture corresponded to the voiced instruction, than in the mismatch condition. There was no significant interaction ($p > .250$) and no main effect of Group ($p > .250$), (Figure 5b). This shows that both groups attended equally well to the prime-action relationship.

Sense of Agency

The analysis of the mean ratings for Agency also showed a main effect of the Condition ($F(1, 14) = 37.03, p < .001, \eta^2_{\text{partial}} = .726$). Participants reported significantly greater SA in the match condition, than in the mismatch condition. A significant main effect of Group ($F(1, 14) = 8.09, p = .013, \eta^2_{\text{partial}} = .366$) was found showing that, overall, the SA was stronger in the MTS Group. A significant Group by Condition interaction was also found ($F(1, 14) = 4.64, p = .049, \eta^2_{\text{partial}} = .249$), indicating that the effect of the manipulation was different for the two groups. In order to further explore this interaction, we performed planned comparisons on the mean ratings for each group: the Agency ratings were significantly different in the match condition ($t(14) = 2.60, p = .021$), (Figure 5c).

Sense of Ownership

The analysis of the mean ratings for Ownership showed a main effect of Condition $F(1, 14) = 15.37, p < .001, \eta^2_{\text{partial}} = .523$. Participants reported significantly greater SO in the match condition, than in the mismatch condition. A significant main effect of Group ($F(1, 14) = 12.008, p = .004, \eta^2_{\text{partial}} = .462$) was found: as predicted people with MTS reported an overall greater SO during the task (Figure 2a). Interesting, there was no significant interaction between Condition and Group ($p > .250$) suggesting that the differences in the SO between mirror-touch synaesthetes and controls were similar across the match and mismatch conditions. In line with this, planned comparisons on ownership ratings revealed that mirror-touch synaesthetes reported a higher SO compared with controls in the match conditions ($t(14) = 2.56, p = .046$) and a higher SO in the mismatch condition ($U = 34.00, p = .03$). Overall, these results suggest a heightened SO on this task in the MTS group (Figure 5d).

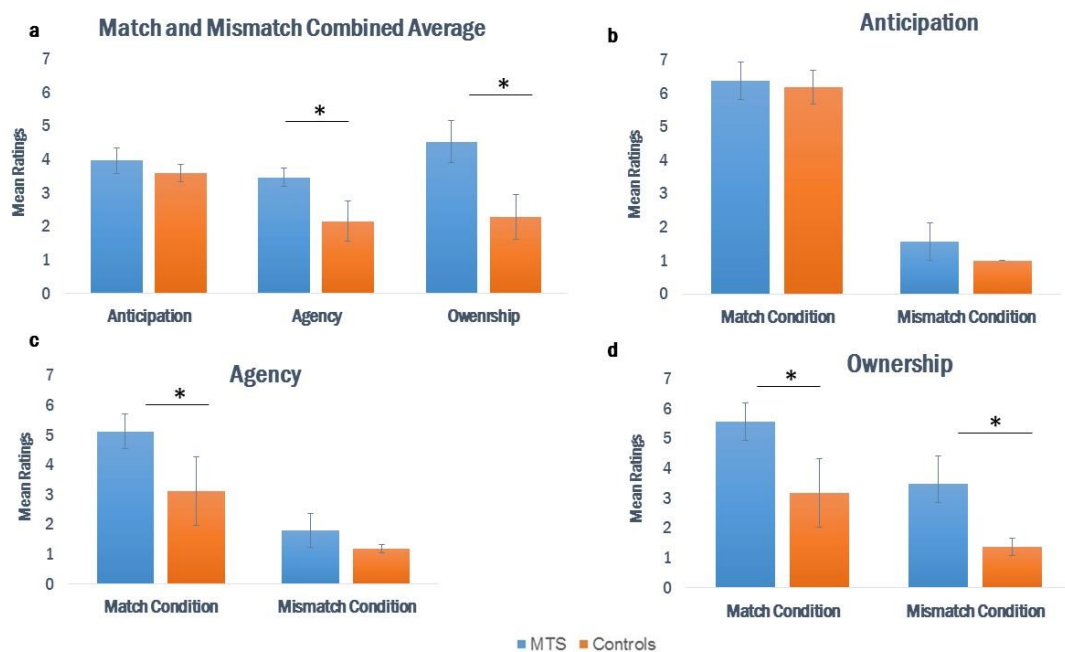


Figure 5.6 Overall mean ratings of match and mismatch conditions for each of the three questions (a); mean ratings plotted as a function of condition ('Match', 'Mismatch') and group ('Mirror-touch synaesthetes – MTS', 'Controls'), for Anticipation (b), Agency (c) and Ownership (d). The error bars show Standard Deviation across participants. * = $p < .05$. The results show that mirror-touch synaesthetes reported overall higher ratings in both match and mismatch conditions for Agency and Ownership but not for Anticipation (a). Mirror-touch synaesthetes (MTS) reported greater sense of agency compared to controls in match conditions (c) and greater sense of ownership in both match and mismatch conditions (d). No differences between MTS group and controls were found in the ratings of anticipation. Modified from Cioffi et al. (2016)

Discussion

We used a modified version of a well-established paradigm developed by Wegner et al (2004) to investigate changes in self-awareness associated with mirror-touch synaesthesia. Our results showed that people with MTS experienced higher SoA over the movements when in the match condition. This shows for the first time that previously reported alterations of self-awareness in MTS extend to the SoA.

In the context of the cue integration approach to SoA, the exaggerated SoA shown by MT synaesthetes could be due to a stronger weighting placed on external cues than on internal signals. That is, external visual stimuli may exert a stronger influence on agency-processing in MT synaesthetes compared to non synaesthetes. The greater weight attributed to external agency cues is compatible with the finding that MTS is characterised by a specific difficulty in inhibiting 'the other' (Santiesteban et al. 2015).

With respect to SO, synaesthetes showed a stronger feeling of ownership compared to controls, in *both* the match and mismatch conditions. This is in keeping with previous findings, which showed changes in SO in MTS (Aimola Davies 2013), and suggests that SO may be the primary aspect of self-awareness altered in MTS, with changes in SoA being a *consequence* of this.

As this is the first investigation of SoA in MTS, further studies looking at both SoA and SO are needed in order to gain a better understanding of how these aspects interact in MTS. The relationship between SoA and SO in MTS is further investigated in Experiment 2.

Experiment 1 demonstrated that MTS is associated with changes in sense of agency. In Experiment 2 we looked at one of the possible consequences of these changes, namely whether or not they impact on the *stability* of sense of agency in MTS.

Experiment 2: Explicit agency in mirror touch synaesthesia: an action recognition task

The aim of this study is to further investigate SoA and SO in MTS by using an action recognition task. This type of task requires participants to make self-other agency judgments while the authorship of their actions is made ambiguous by the experimental setting. This is achieved by creating a mismatch between the prediction of the movement and the sensory feedback: participants perform a movement and a temporal or spatial distortion is inserted into the visual feedback of that movement. When the distortion in the feedback goes past a threshold, the participants do not recognise the actions as their own, even when they are (Daprati et al., 1997; Farrer et al., 2008). These tasks can be used as an indication of agency-processing changes in different groups. Here we compare the performance of a group of MT synaesthetes and a group of non-synaesthete controls in an action recognition task.

Method

Participants

A group of six mirror-touch synaesthetes (age range = 19-48, average age = 28.6, SD = 11.36, one male) and a group of twelve non-synaesthetes controls (age range = 19-43, average age = 25.17, SD = 8.86, one male) were recruited. All participants were right-handed. All the mirror-touch synaesthetes were confirmed as individuals with MTS using the Visuo-Tactile Stroop task, designed to detect the authenticity of the condition (Banissy et al., 2009; Banissy & Ward, 2007). All the MTS participants significantly differed on a single subject basis (using Crawford's modified t-test; Crawford & Howell, 1998) to previous published control data on this task (Banissy et al., 2009; Banissy & Ward, 2007). All controls were interviewed with a synaesthesia questionnaire (including a question on MTS; adapted from Banissy et al., 2009) and did not report any synaesthetic experiences. One of the mirror-touch synaesthetes self-reported other types of synaesthesia. All participants gave consent to participate in the study. The study was approved by the Goldsmiths Psychology Department ethical committee.

Procedure

The action recognition task consisted of a modified version of the paradigm developed by Farrer et al. (2008). Participants sat in front of a computer display (See experimental set-up in Figure 5.7). This display was covered using black fabric so that only a small region of the display was visible. Participants were told to make simple tapping movements, alternating the index and middle fingers. These movements could not be seen directly, as the participants' hand was to be hidden behind the computer monitor. Instead, a camera attached to the top of the computer monitor would provide video feedback of their movements on the visible region of the display. Tapping speed was kept at a constant tempo. The participants were previously trained with a metronome to perform the movement at a constant speed throughout the experiment: 60 Beats Per Minute (BPM). Participants were told that the experimenter would be making the same simple tapping movements, and that the video feedback on the computer monitor would undetectably switch from their own to the experimenter's actions randomly. In fact, the experimental setting was arranged so that the experimenter had a display and a camera recording their movements exactly as the participants had. In reality, the footage was always of the participant, but a 800ms delay was introduced. According to Farrer et al. (2008) this delay produces in the participant a bi-stable impression of agency, with participants spontaneously switching between "self" and "other" judgements throughout the task.

Both the participant and the experimenter wore a rubber glove and a black cloth was used to cover their arm and part of their hand, with two holes in the cloth where the index and middle fingers were passed through. There were no distinguishable features the participant could identify to judge whether it was the experimenter's actions or the participant's actions being displayed on the screen.

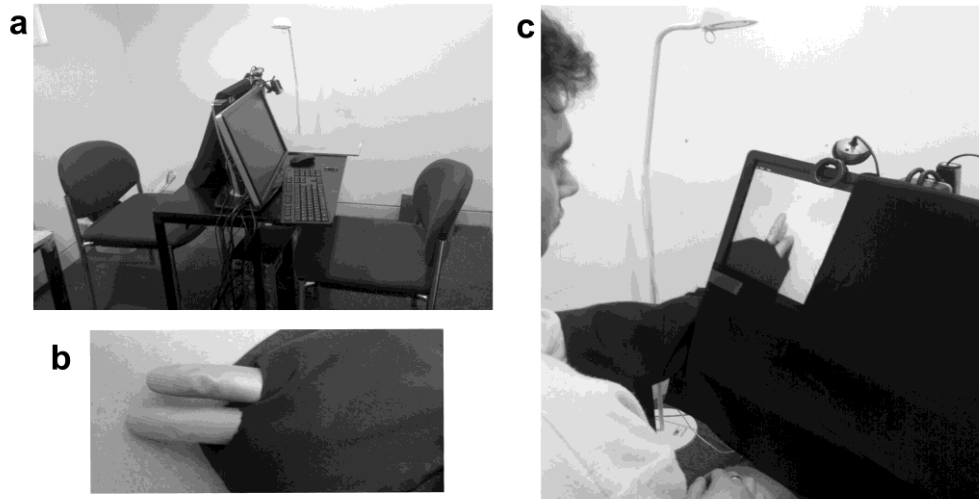


Figure 5.7 Action-recognition set-up. Participant and experimenter sit in front of each other. The participant is shown how the setting works with one camera placed such that it records the experimenter's movements and one the participant's movements (a); Both participant and experimenter put on a pair of gloves and a cloth covering everything except their index and middle finger (b); The participant looks at the screen where his finger movements are shown while his hand is hidden from view behind the screen (c).

To indicate whether they were viewing their own actions or the experimenter's actions, participants gave a verbal report – either “self” for their own movements, or “other” for the experimenter's. The response was recorded by audio recording software. Each trial lasted for a period of exactly 150 seconds. There were three 150 seconds trials, with 30 seconds rest between the trails. During the rest period participants did not move and the screen did not display anything.

In addition to recording the time spent in self and other judgment, we recorded the number of self-other switches as a measure of the stability of SoA throughout the experiment.

Farrer et al. (2008) showed that under conditions of uncertainty created by the task, participants tended to attribute agency more to themselves compared to others. As uncertainty is an important factor in agency attribution (Desantis, Roussel, & Waszak, 2011; Farrer et al., 2008; Moore & Fletcher, 2012), we decided to measure the degree of certainty around the experience of agency reported by participants to investigate whether this changed across trials.

After each trial, participants were asked to rate their certainty regarding the agency judgements they made on a Likert scale from 1 being 'not at all certain' to 7 being 'almost certain'.

At the end of the final trial, participants were asked to give overall ratings of their sense of ownership and agency felt during the entire duration of the experiment. In particular, they were asked how much they felt that the hand "belonged to them" (Q1), how much they felt the hand was "part of their body" (Q2), and how much they experienced the hand "in their control" (Q3) or "out of their control" (Q4). These questions were answered using a Likert scale from 1 to 7, with 1 being 'not at all' and 7 being 'very much'.

Results

Three 2 x 3 mixed Analyses of Variance (ANOVA) were run with Group (MTS/Controls) as a between-subjects factor and Trial (Trial 1/ Trial 2/ Trial 3) as a within-subjects factor. The dependent variables considered were: 'number of self-other switches', 'time spent in self-judgment' and 'certainty' scores.

Certainty scores and post session ownership and agency ratings had not been collected with two subjects.

Self-other switches

The ANOVA investigating the effect of Group (MTS/Controls) and Trial (Trial 1/ Trial 2/ Trial 3) on 'number of self-other switches' showed no main effect of Group ($p > .250$) and no main effect of Trial ($p > .250$), as well as no interaction between Group and Trial ($p > .250$). These results suggest that MTS and controls did not differ in the stability of their sense of authorship over their own actions in this task. This stability also remained the same over the course of the experiment (Figure 5.8a).

Time spent in self-judgement

The ANOVA investigating the effect of Group (MTS/Controls) and Trial (Trial 1/ Trial 2/ Trial 3) on 'time spent in self-judgement' showed no main effect of Group ($p > .250$) with MTS and controls showing no significant difference on the time spent in self. There was no main effect of Trial ($p > .250$) showing no changes across trials and no interaction between Group and Trial ($p > .250$). These results suggest that MTS and control did not show any differences in

the feeling of authorship over their own actions in this task and that this did not significantly change across trials (Figure 5.8b).

While no differences between groups were found, we also performed a one-sample t-test on the whole data looking at the time spent in self-judgment. Results showed that participants perceived the observed movements significantly more as their own versus those of the experimenter ($t(17) = 2.835$, $p = .011$). This result replicates the one reported by Farrer and colleagues (2008).

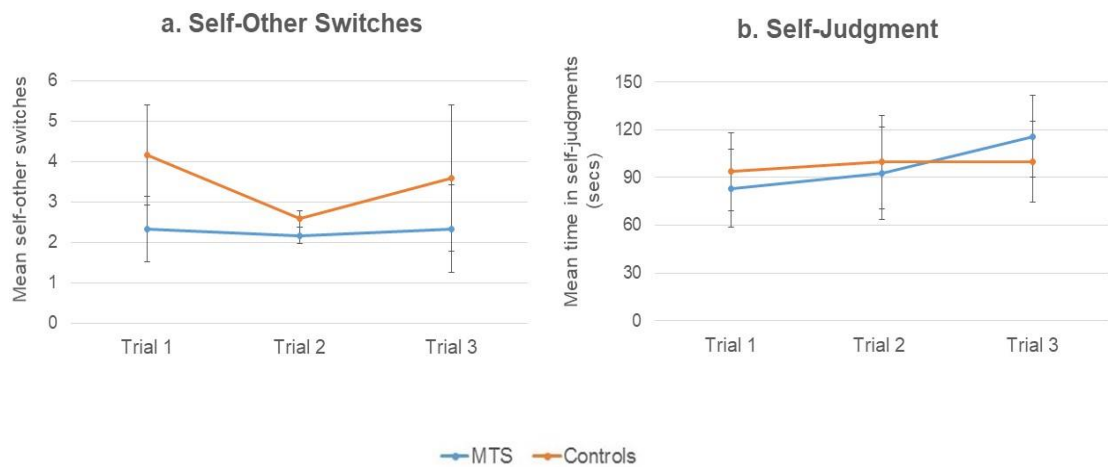


Figure 5.8. Average number of self-other switches in MT synaesthetes and Controls, for each Trial. No significant differences between groups were found (a); Average time (in seconds) spent in self-other judgment in MT synaesthetes and Controls, for each Trial (b). No significant differences between groups were found. Overall, both groups spent more time in 'self-judgment' than in 'other-judgment'

Certainty

The ANOVA investigating the effect of Group (MTS/Controls) and Trial (Trial 1/ Trial 2/ Trial 3) on 'certainty' showed no main effect of Group ($p > .241$) and no main effect of Trial ($p > .250$), as well as no interaction between Group and Trial ($p > .250$). These results suggest that both MTS and Controls felt the same degree of certainty over their self-other judgements and this degree did not change across trials.

Post session agency and ownership judgments

Two independent samples t-test were carried out to examine the effect of Group on post-session ownership (Q1+Q2) and agency (Q3+Q4) ratings. While no significant difference in the agency ratings between MTS and Control was found (MTS: $av = 4.75$, $sd = .65$; Controls: $av = 3.71$, $sd = 1.23$; $t(14) = -1.592$, $p = .134$), we found a significant difference in the ownership

ratings, with MTS reporting higher feeling of ownership towards the moving hand compared to controls (MTS: $av = 5.87$, $sd = 1.44$; Controls: $av = 4.5$, $sd = .95$; $t(14) = -2.21$, $p = .044$), (Figure 5.9).

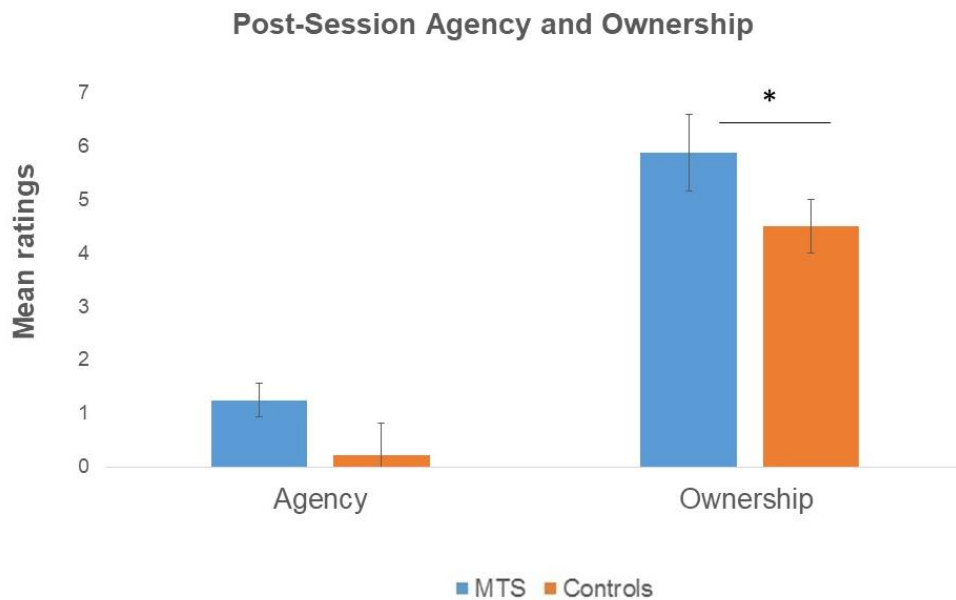


Figure 5.9. Post-session average ratings for agency and ownership, for MT synaesthetes and Controls. MT synaesthetes reported higher sense of ownership over the hand compared to Controls.

Discussion

In this action recognition paradigm, the visual feedback of the participant's tapping movement had been deliberately distorted, making the authorships of their movement ambiguous. Under these conditions, a group of mirror-touch synaesthetes and a group of non-synaesthetes were asked to make self-other agency judgments. We found that both MTS and controls did not differ in their stability of agency experience (i.e. number of self-other switches), nor in the content of their agency experience (i.e. predominance of self or other judgments).

In Experiment 1 we found augmented agency in participants with MTS and we attributed this to an increased reliance on external cues in MTS. We might have expected MT synaesthetes to report a more predominant experience of self-judgments in this action-recognition paradigm, compared to controls. That is, just seeing a movement on the screen automatically triggers authorship of that movement in people with MTS, even when the visual feedback is distorted

to deliberately induce ambiguity. However, in this action recognition paradigm, participants are not just seeing the fingers moving but they themselves are performing the same finger movements. This fundamentally changes the strength of the internal cues: in this action-recognition paradigm the internal sensorimotor signals are stronger compared to the vicarious agency illusion paradigm. As internal and external cues *interact* to form SoA, it may be that under those conditions the weight of internal motor cues dampened the increased reliance on external cues in MTS, resulting in a SoA that did not differ from the ones of controls. This hypothesis could be addressed in the future by modifying this paradigm so that the weight of internal cues is reduced, such as by passively moving the fingers of the participants. It has been already shown that neurotypical individual have reduced SoA over passive movements compared to active movements (Engbert, Wohlschläger, & Haggard, 2008; Moore, Wegner, & Haggard, 2009), this may not occur in participants with MTS.

Alternatively, the fact that this task did not detect changes in SoA in MTS may be also attributed to the task itself not being intrinsically suitable to uncover those changes. Perhaps to elicit these changes it is necessary to provide more striking external evidence about the origin of the action being in another agent, as for the case of the vicarious agency task in Experiment 1.

Lastly, we also found that MTS reported a higher feeling of ownership towards the hand compared to non-synaesthetes. This is in line with previous findings on ownership in MTS and with the results of Experiment 1. It suggests that ownership, compared to agency, may be the principal component of self-awareness that is affected by mirror touch synaesthesia.

General Discussion

The studies presented in this chapter sought to primarily investigate a) possible agency changes in MTS, b) cue integration in agency processing, and c) how SO and SoA interact. Experiment 1 investigated sense of agency and sense of ownership in MTS with the use of a vicarious agency illusion. It was found that both sense of agency and sense of ownership are augmented in MTS. However, these aspects of self-awareness were found to be affected

differently, with the sense of ownership being more profoundly altered compared to SoA. Experiment 2 investigated the sense of agency and ownership in MTS further by using an action recognition task. No difference was found in the type and stability of self-other agency judgments between controls and participants with MTS. When looking at post-session ratings of agency and ownership, MT synaesthetes reported a higher sense of ownership over the moving hand compared to controls.

From the results of these studies, the experience of agency in MTs seems to be more malleable than in non synaesthetes. Experiment 1 clearly shows how MT synaesthetes are likely to experience a higher sense of agency over someone else's movements in an ambiguous situation. It is proposed that this may be due to an enhanced saliency of external cues in the creation of the SoA, possibly the result of a general deficit in inhibiting 'the other' that characterises MTS (Santesteban et al., 2015; Ward & Banissy, 2015).

In addition to providing insight on self-other processes in MTS and in agency processing, these findings may help shed light on the relationship between SA and SO. Our results show that SO is more dramatically disrupted than SoA in MTS. In Experiment 1, the augmented SO was present not only in the match but also in the mismatch conditions. This suggests that for MT Synaesthetes, seeing a body part that looks like their own is enough to elicit a sense of ownership over the body part, regardless of whether SoA is felt over its movements (i.e. like controls, MT synaesthetes did not show high SoA in the mismatch conditions). This hypothesis is confirmed by the overall higher SO reported by MT synaesthetes in Experiment 2. Based on these findings, it is speculated here that SO is the primary aspect of self-awareness to be disturbed in MTS. This primary disturbance of SO in turn leads to the alterations in the SoA we have observed. This is consistent with the theoretical accounts of agency processing, which argue that the experience of agency is predicated on the feeling that the body part is one's own (Gallagher, 2000).

However, whilst our findings demonstrate a clear change in explicit agency and ownership experiences in MTS, nothing is known yet about implicit agency in MTS. Future research should address this, by testing whether the changes in

explicit agency correspond to similar changes at the implicit level. This would allow both the examination of whether self-other control disturbance in MTS extend to the implicit aspect of sense of agency and provide an opportunity to test the not yet fully understood relationship between explicit and implicit agency.

In this chapter, we have shown how investigating MTS can be particularly informative in the study of SoA. Significantly, the gain is reciprocal, knowing how SoA works in MTS provides new directions for understanding this condition.

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CHAPTER SIX

The role of right Temporo Parietal Junction in agency attribution

After testing sense of agency in different groups, we now look at the neural mechanisms that might be responsible for the observed SoA changes. Specifically, we use transcranial Direct Current Stimulation to test the contribution of right Temporo Parietal Junction to agency processing in response to the same tasks used in the previous chapters.

Introduction

The areas that are involved with sense of agency processing have been identified with the help of neuroimaging, non-invasive brain stimulation studies and lesion analyses (chapter 1). Consistently, these studies have pointed out the fundamental role of the parietal cortex and, in particular, the role of the right Temporo Parietal Junction (rTPJ). The rTPJ is a supramodal association area located between the right temporal and parietal lobes (Figure 6.1).



Figure 6.1. Schematic representation of right Temporo Parietal Junction's location.

It is sometimes referred to as posterior inferior parietal lobule, angular gyrus or Brodmann area 39 (Bzdok et al., 2013; Decety & Lamm, 2007). This area has been linked with many heterogeneous cognitive functions. These include

low-level attentional processes (e.g. Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Downar, Crawley, Mikulis, & Davis, 2000), various aspects of social cognition (e.g. Santiesteban, Banissy, Catmur, & Bird, 2012; Uddin, Molnar-Szakacs, Zaidel, & Iacoboni, 2006), as well as the integration of sensory (bottom up) stimuli and contextual (top down) information in sensorimotor control (Bzdok et al., 2013), (Figure 6.2).



Figure 6.2. A seed region combining rTPJ's functional diversity. Modified from Bzdok et al. (2013)

As mentioned in chapter 1, a great wealth of work has looked specifically at the role that rTPJ plays in sense of agency processing. Early neuroimaging studies identified strong activation of the rTPJ in situations in which participants were required to distinguish between self-produced actions and those generated by others (Farrer and Frith 2002; Ruby and Decety 2001). Interestingly, it was then found that this activation increased in proportion to the difficulty in distinguishing between self or other's actions (Farrer, Franck, Paillard, & Jeannerod, 2003). In this study, Farrer and her colleagues used a device that allowed them to change the degree of control participants had over the movements of a virtual hand presented on a screen. They found that the activity of the rTPJ was modulated by the degree of discrepancy between the movement executed and the movement seen on the screen. That is, the mismatch between normally congruent sets of action related cues (e.g. external visual cues and internal motor commands) is likely to result in an

increased activation of this area. This suggests that rTPJ plays a crucial role in *integrating* different agency cues.

Studies investigating the role of the rTPJ on susceptibility to body illusions have shown that this is the case with the sense of ownership. Papeo and colleagues (Papeo, Longo, Feurra and Haggard, 2010) found that disrupting rTPJ with single-pulse Transcranial Magnetic Stimulation (TMS) impaired the ability to detect conflict between different cues in the mirror-illusion paradigm devised by Ramachandran et al. (1995). In this paradigm, participants place their hands on either side of a mirror in such a way as to hide their left hand and reflect their right hand, thereby creating the illusion that they are looking directly at their left hand. The experimenter simultaneously strokes either the same fingers in both hands (congruent condition) or different fingers for each hand (incongruent condition). Papeo et al. found that following TMS stimulation of rTPJ, participants were less accurate at localising the touch delivered on the hidden hand, particularly in the incongruent condition. This suggests that rTPJ is responsible for the ability to identify mismatches between external visual information and internal proprioceptive feedback. In light of findings like this, it might be that the rTPJ plays a fundamental role in maintaining a coherent and stable sense of ownership over one's own body and sense of agency over one's own actions (Farrer et al., 2008; Tsakiris, Costantini, & Haggard, 2008).

Studies have shown how disruption of the neural processing in rTPJ can lead to dramatic disruptions of SO and SoA. Daprati et al. (2000) described the case of a patient (PA) with somatoparaphrenia who had right TPJ lesions. Somatoparaphrenia is a neuropsychological condition characterised by unawareness of ownership of one's limb associated with delusional misidentification and confabulation (Feinberg et al., 2010). Patient PA was tested with an action-recognition task where he was required to identify his own actions, the same actions produced by the experimenter or different actions produced by the experimenter. In all three conditions patient PA denied that the actions were his own. Similarly, Bundick and Spinella (2000), reported the case of patient with infarct of the rTPJ and low density in part of the right frontal white and grey matter. This patient showed involuntary movements and would express 'perplexity and estrangement' from those movements, clearly

manifesting symptoms of alien hand syndrome (Della Sala, Marchetti, & Spinnler, 1991).

Additionally, the rTPJ has also been shown to be involved in non-clinical conditions, such as Mirror-Touch Synaesthesia (discussed in chapter 5) (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Holle, Banissy, & Ward, 2013). Neuroimaging data showed that MT synaesthetes have reduced grey matter in the right temporo-parietal junction (rTPJ) compared to non synaesthetes (Holle et al., 2013). Recent accounts of MTS propose that rTPJ may be responsible of a specific impairment in the ability to *control* self-other representation in MTS (Banissy & Ward, 2013; Ward & Banissy, 2015). In support of this hypothesis, Santiesteban and colleagues (2012) used transcranial direct current stimulation (tDCS) to show that an increase in the cortical excitability of rTPJ leads to improved self-other distinction. In the context of SoA, these results strongly support the hypothesis that rTPJ may be executing the same 'controller' role, regulating self-other agency judgments.

In the studies presented in this chapter we test this hypothesis and investigate the causal role of the rTPJ in agency attribution in healthy adults. Specifically, while previous research has shown the crucial role played by rTPJ in integrating different ownership cues (e.g. Papeo et al., 2010), less is known about the role of the rTPJ in integrating different *agency* cues. Here we use anodal tDCS to enhance the activity of the rTPJ and test participants in two tasks where external agency cues are deliberately manipulated in order to create a situation of agentic uncertainty.

Transcranial Direct Current Stimulation is a non-invasive brain stimulation method that delivers low intensity current (between 1 and 2 mA) over a cortical area through the use of electrodes placed on the scalp. By doing so, it modulates the excitability of the cortex within its physiologic range (Nitsche et al., 2008). The current runs from the anode to the cathode electrode: the anode electrode induces facilitation of the neural firing and cathode induces inhibition. The tDCS has been used extensively as a safe method to investigate brain – behaviour relationship in clinical and healthy populations (Costa, Lapenta, Boggio, & Ventura, 2015).

In Experiment 1, participants received anodal tDCS on rTPJ (experimental condition) or anodal tDCS on the occipital cortex (V1) (control condition) before completing the so-called vicarious agency paradigm developed by Wegner et al. 2004 and used in previous chapters. The task is designed to blur self-other boundaries as the participant is led to feel SO over the experimenter's arm and SoA over the experimenter's arm movements. In light of the evidence that rTPJ plays a role in resolving discrepancies in a situation of agentic ambiguity (Farrer, Franck, Georgieff, et al., 2003), and that hyperactivation of rTPJ led to enhanced control of self-other representations (Santiesteban et al., 2012), we expect that hyperactivation of rTPJ would lead to a reduced susceptibility to the illusion of agency.

Similarly, as rTPJ has been shown to play a role in maintaining a coherent SO (e.g. Tsakiris et al., 2008), it is expected that participants who received excitatory anodal stimulation on rTPJ would present a reduced illusion of SO compared to the control group

In Experiment 2, participants received anodal tDCS stimulation on rTPJ or sham stimulation before completing an action recognition task (based on the paradigm developed by Farrer et al., 2008 and used in chapter 5). Here participants were asked to judge whether a video that they were watching showed their finger movements or those of the experimenter. In reality, the video always showed the participants' movements with a temporal delay. Farrer et al., showed that this set up created a bi-stable impression of sense of agency, with agency reports flipping spontaneously between "self" and "other". Using this task, Farrer and colleagues found that participants were more likely to perceive observed movement as their own rather than those of another. Moreover, they found that activation of rTPJ was greater when subjects experienced a perturbed SoA. The authors suggested that the rTPJ activation may have reflected the process of integration of conflicting signals.

Here we investigated whether inducing hyperactivation of rTPJ influences agency attribution. Crucially, this task not only allows us to test whether hyperactivation of rTPJ affects participants' SoA but whether it has an impact on the *stability* of their agency experience.

It is predicted that participants who received anodal stimulation rTPJ would show increased tendency to attribute authorship of the movements to themselves, as well as a generally more stable experience of agency (i.e. fewer alterations between self and other during the task).

Experiment 1: The role of the right Temporo Parietal Junction in the vicarious experience of agency

The aim of this experiment is to investigate the role of right Temporo Parietal Junction in the susceptibility to a vicarious agency illusion. A group of participants received anodal transcranial current stimulation on rTPJ, and a control group received anodal rTPJ on the primary visual cortex (V1). Participants were then tested on a modified version of a vicarious agency paradigm (Wegner et al., 2004). In this paradigm, gestures are performed by the experimenter hidden behind the participant in such a way that the gestures look like they are being performed by the participant's hands. The gestures seen in the mirror can be either congruent with the action instructions heard over a pair of headphones (match condition), or incongruent (mismatch condition). Participants are asked to report their feeling of agency and ownership over the gestures and the hand.

Method

Participants

A group of 30 adults took part in the study (age range 20-49, average age = 26.6, SD = 6.9; 12 females). They were randomly assigned to two groups: the anodal stimulation on rTPJ (n = 15) or the anodal stimulation on the occipital cortex (V1), (n = 15). Two participants were left handed. All participants met criteria for participation and read an information sheet containing description of non-invasive brain stimulation. The study was approved by Goldsmiths Ethical Committee.

Procedure

tDCS Protocol

Transcranial direct current stimulation was administered through a battery-driven current stimulator (NeuroConn GmbH, Germany). The stimulation was delivered through a two 5x7cm sponge electrodes, that had been previously soaked in a saline solution.

In the experimental condition (rTPJ stimulation), the anodal electrode was placed on CP6 according to the international 10-20 EEG system (Herwig, Satrapi, & Schönfeldt-Lecuona, 2003). This location has been used in previous studies investigating rTPJ (e.g. Hogeveen et al., 2015; Santiesteban et al., 2012). The reference electrode was placed on the vertex (CZ) (Figure 6.3).

In the control condition (V1 stimulation), the anodal electrode was placed on the primary visual cortex, OZ according to the international 10-20 EEG system. This brain region was chosen as control site because it has never been identified for its involvement in agency processing. In both groups, the stimulation (1mA) was delivered for 20 minutes. The fade in and fade out time were both set at 15s each. The stimulation was delivered offline (i.e. before performing the task).

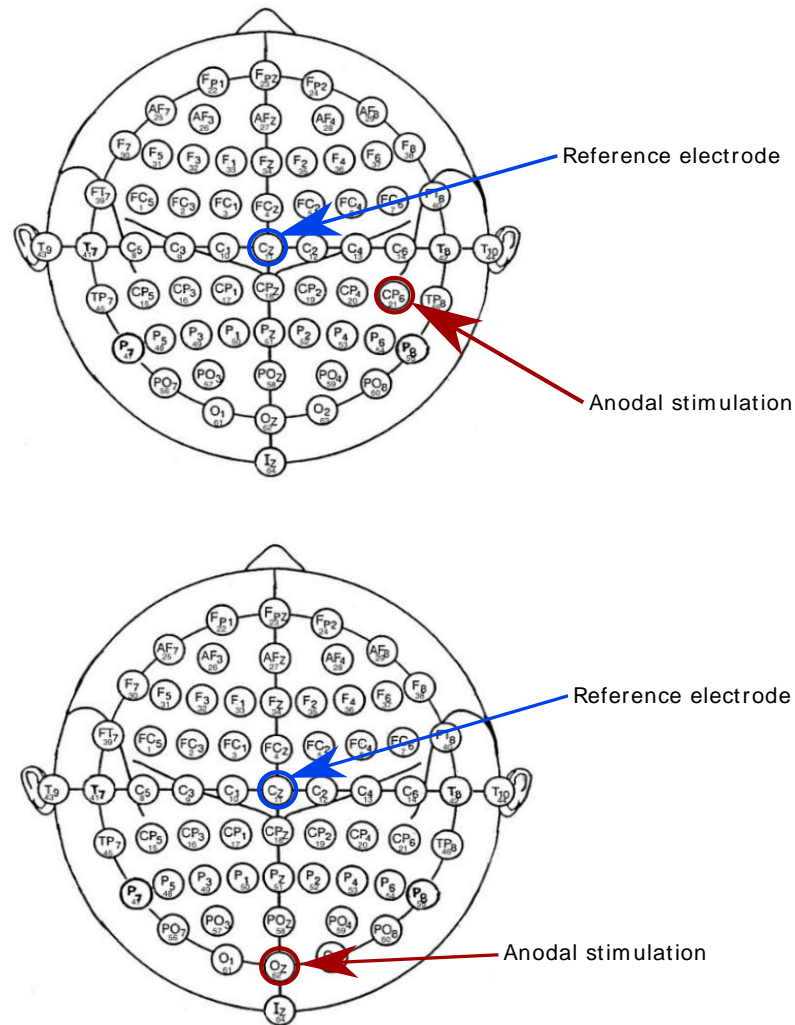


Figure 6.3. Depiction of the electrodes set-up. In the experimental condition (above) anodal stimulation was placed on rTPJ (CP6) and the reference electrode on the vertex (CZ). In the control condition (below) anodal stimulation was placed on the occipital cortex (OZ) and the reference electrode on the vertex (CZ).

Vicarious agency task

The task required participants to look in front of them, towards a mirror. Gestures were performed by the experimenter hidden behind the participant in such a way that the gestures look like they were being performed by the participant's hand (Figure 6.4). The gestures seen in the mirror were either congruent with the action instructions heard over a pair of headphones (match condition) or incongruent (mismatch condition). Participants were asked to report their experiences by answering three questions on a 7-point scale with 1 being "not at all" and 7 being "very much".

The questions were:

- 1) Anticipation: *“To what degree did you feel you could anticipate the movements of the arm?”*
- 2) Agency: *“How much control did you feel you had over the arm’s movements?”*
- 3) Ownership: *“To what degree did the arm feel like it belonged to you?”*

As the procedure of the vicarious agency task was identical to the one described in chapter 2, further details can be found there.



Figure 6.4 Experimental set-up (based on Wegner et al., 2004). The left picture shows what the participant sees in the mirror placed in front of her. The right picture shows the set up from the side, with the experimenter sitting behind the participant and putting her hand forward so that it appears where the participant’s hand would normally be.

Results

Preliminary analyses on left and right hands were carried out for each condition using a paired sample test to see if their results could be distinguished. As no significant differences emerged, the mean judgements for left and right hands were collapsed into a single score (for example: (Anticipation match condition Left hand + Anticipation match condition Right hand) / 2). These were entered into 2 X 2 mixed design ANOVAs for each Question (Anticipation/Agency/Ownership), with ‘Condition’ (Match/Mismatch) as within-subjects factors and ‘Condition’ (rTPJ stimulation/Control stimulation) as a between-subjects factor.

Anticipation

The analysis of the mean ratings for Anticipation showed a significant main effect of Condition ($F(1, 28) = 232.7, p < .001, \eta^2_{\text{partial}} = .892$). Participants reported significantly greater anticipation in the match condition, where the gesture corresponded to the voiced instruction, than in the mismatch condition. There was no significant interaction ($p > .250$) and no main effect of Group ($p > .250$), (Figure 6.5a). This shows that both groups attended equally well to the prime-action relationship.

Sense of Agency

The analysis of the mean ratings for Agency also showed a main effect of the Condition ($F(1, 28) = 57.79, p < .001, \eta^2_{\text{partial}} = .674$). Participants reported significantly greater SoA in the match condition, than in the mismatch condition. There was no significant interaction ($p > .250$) and no main effect of Group ($p > .250$), (Figure 6.5b).

Sense of Ownership

The analysis of the mean ratings for Ownership showed a main effect of Condition ($F(1, 28) = 44.35, p < .001, \eta^2_{\text{partial}} = .613$). Participants reported significantly greater SO in the match condition, than in the mismatch condition. There was no significant interaction ($p = .136$) and no main effect of Group ($p > .250$), (Figure 6.5c).

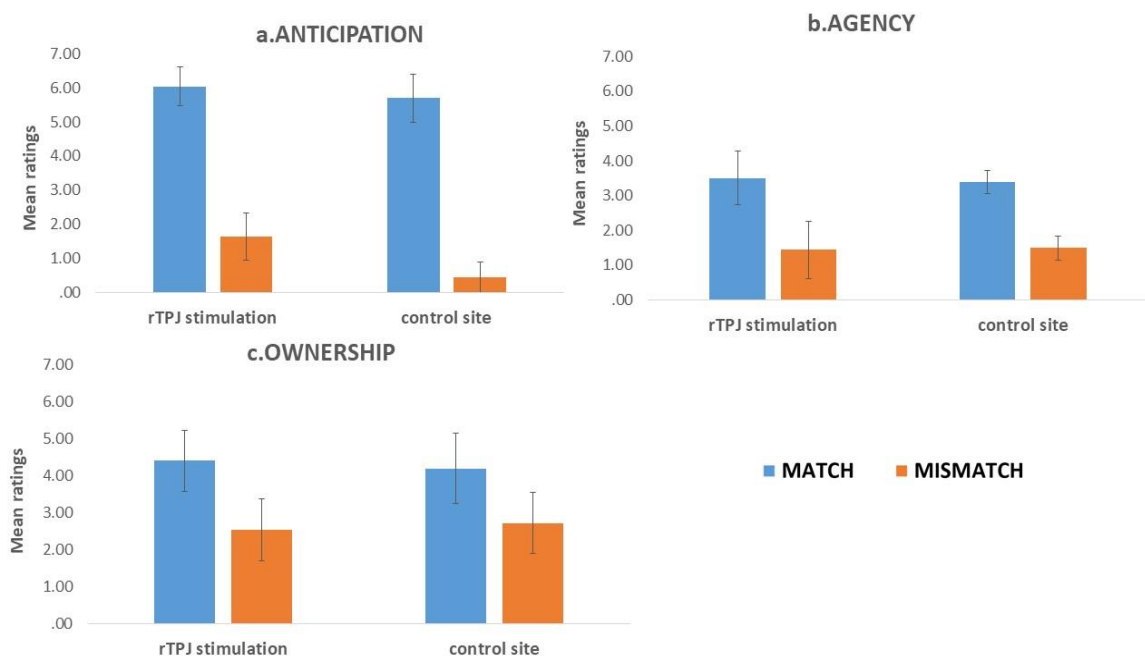


Figure 6.5. Mean ratings for anticipation (a), agency (b) and ownership (c) in match and mismatch conditions. The error bars show standard deviation across participants. No differences between the rTPJ stimulation group and the control (occipital stimulation) group were found.

Discussion

We investigated the causal role of the rTPJ in the susceptibility to a vicarious agency illusion. Participants received either anodal stimulation on rTPJ or on the occipital cortex prior to taking part in the so-called vicarious agency paradigm. The results show that participants who received anodal stimulation on rTPJ and participants who received anodal stimulation on V1 did not show any difference in the illusion of vicarious agency and ownership. Previous studies showed the importance of the rTPJ in integrating different bodily cues (Leube et al., 2003; Papeo, Longo, Feurra and Haggard, 2010), and maintaining a coherent sense of self (Tsakiris et al., 2008). Furthermore, hyperactivation of rTPJ was shown to boost self-other control (Santiesteban et al., 2012). In light of this, we would have expected that anodal stimulation of the rTPJ reduced the susceptibility to vicarious sense of agency and ownership elicited by this paradigm. The reasons why we found that hyperactivation of rTPJ did not influence the susceptibility to the vicarious agency illusion may reside in the characteristics of the task.

This task is characterised by strong agency visual cues and very weak sensorimotor cues. If rTPJ plays a role in integrating conflicting agency cues (Farrer & Frith, 2002; Farrer et al., 2008), it is possible that stimulation of the rTPJ was not sufficient to elicit agency changes because the relative strength of internal and external cues was polarised. That is, the combination of weak sensorimotor cues and strong external visual cues might not have been the ideal scenario for testing the role that rTPJ plays in resolving cue discrepancy.

It is also possible that hyperactivating rTPJ may not directly affect agency attribution per se, but may affect the *stability* of agency experience over time. Experiment 2 addresses these points. We combine anodal rTPJ stimulation with a task that captures the stability of self/other agency experiences over time.

Experiment 2: The role of the right Temporo Parietal Junction in self-other agency attribution.

The aim of this experiment is to investigate the causal role of the rTPJ in self-other agency attribution, as well as in its stability over time. Participants received either anodal stimulation on rTPJ or sham stimulation before completing an action recognition task. This type of task requires participants to make self-other agency judgments while the authorship of their actions is made ambiguous by the experimental setting. This is achieved by creating a mismatch between the prediction of the movement and the sensory feedback: participants perform a movement and a temporal distortion is inserted into the visual feedback of that movement. When the distortion in the feedback goes past a threshold, the participants do not recognise the actions as their own, even when they are (Daprati et al., 1997; Farrer et al., 2008).

Here we predict that participants who received anodal stimulation on rTPJ would show increased tendency to attribute authorship of the movements to themselves, as well as a generally more stable experience of agency.

Method

Participants

Twenty-six participants took part in this experiment (age range 19-27, average age 21.5, SD = 1.61, 14 females). All participants were right-handed. They were randomly assigned to two groups: anodal stimulation of the rTPJ (n = 13) or sham stimulation (n = 13). All participants met the criteria for participation and read an information sheet containing a description of non-invasive brain stimulation. The study was approved by Goldsmiths Ethical Committee.

tDCS protocol

Transcranial direct current stimulation was administered through a battery-driven current stimulator (NeuroConn GmbH, Germany). The stimulation was delivered through a two 5x7cm sponge electrodes, that had previously been soaked in a saline solution.

In the experimental condition (rTPJ stimulation), the anodal electrode was placed on CP6 according to the international 10-20 EEG system (Herwig et al., 2003). This location has been used in previous studies investigating rTPJ

(Hogeveen et al., 2015; Santiesteban et al., 2012). The reference electrode was placed on the vertex (CZ) (Figure 6.6). The stimulation (1mA) was delivered for 20 minutes. The fade in and fade out time were both set at 15s each.

In the control condition (sham stimulation), the set up was identical to the experimental condition, with participants being led to believe that they were receiving stimulation for 20 minutes while it only lasted 15 seconds. In both conditions the stimulation was delivered offline (i.e. before performing the task).

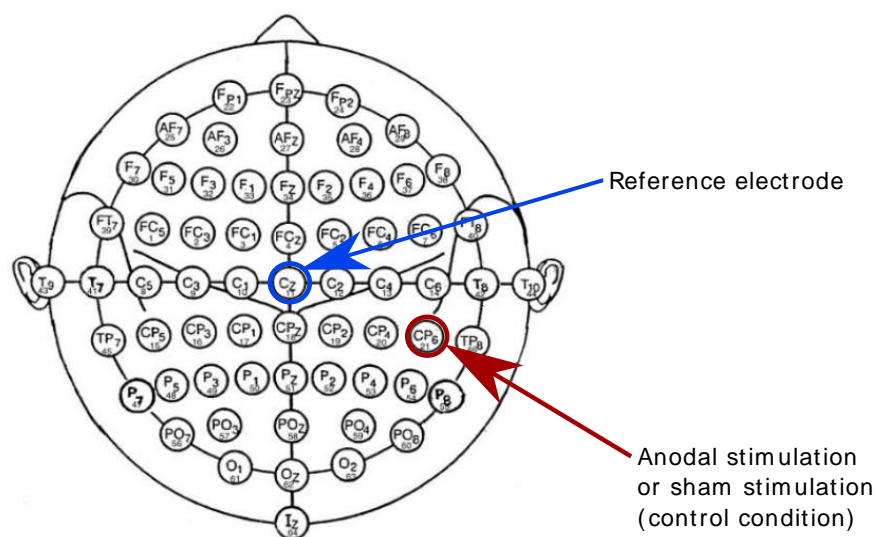


Figure 6.6. Depiction of the electrodes set-up. In the experimental condition anodal stimulation was placed on rTPJ (CP6) and the reference electrode on the vertex (CZ). In the control condition, anodal stimulation was substituted with sham stimulation.

Action recognition task

The action recognition task consisted of a modified version of the paradigm developed by Farrer and colleagues in 2008 (Farrer et al., 2008).

Participants sat in front of a computer display (See experimental set-up in Figure 6.7). This display was covered using black fabric so that only a small region of the display was visible. Participants were told to make simple tapping movements, alternating the index and middle fingers. These movements could not be seen directly, as the participants' hand was hidden behind the computer monitor. A camera attached to the top of the computer monitor provided video feedback of their movements on the visible region of the display. The experimental setting was arranged so that the experimenter had a display and

a camera recording their movements in exactly the same way. Tapping speed was kept at a constant tempo. The participants were previously trained with a metronome to perform the movement at a constant speed throughout the experiment (60 Beats Per Minute, BPM). Participants were told that the experimenter would be making the same simple tapping movements, and that the video feedback on the computer monitor would undetectably switch from their own to the experimenter's actions randomly. In reality, the footage was always of the participant, but a 800ms delay was introduced. According to Farrer et al. (2008) this delay produces in the participant a bi-stable impression of agency, with the participant spontaneously switching between "self" and "other" judgements throughout the task.

Both the participant and the experimenter wore a rubber glove and a black cloth was used to cover their arm and part of their hand, with two holes in the cloth where the index and middle fingers were passed through. There were no distinguishable features the participant could identify to judge whether it was the experimenter's actions or the participant's actions being displayed on the screen.

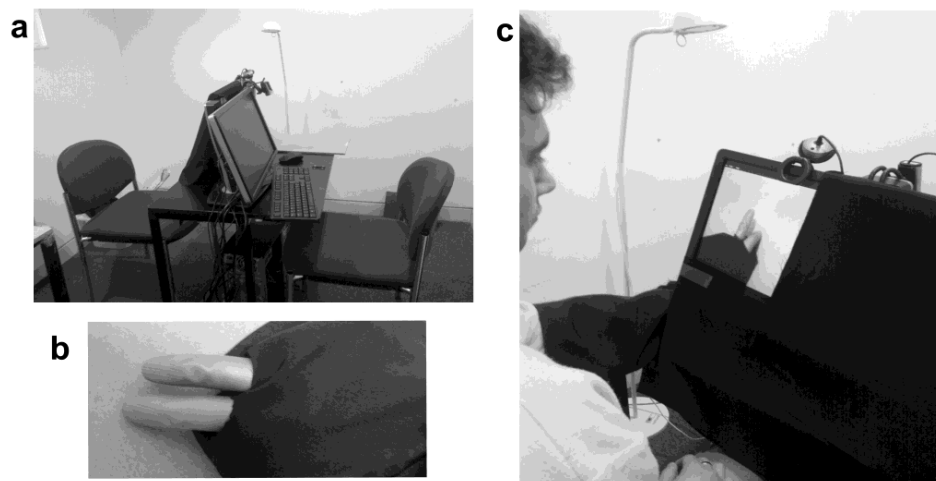


Figure 6.7 Action-recognition set-up. (a) Participant and experimenter sit in front of each other. The participant is shown how the setting works with one camera placed such that it records the experimenter's movements and one the participant's movements; (b) Both the participant and experimenter put on a pair of gloves and a cloth covering everything except their index and middle finger; (c) The participant looks at the screen where his finger movements are shown while his hand is hidden from view behind the screen.

To indicate whether they were viewing their own actions or the experimenter's actions, participants gave a verbal report – either “self” for their own movements, or “other” for the experimenter's. The response was recorded by audio recording software. Each trial lasted for a period of exactly 150 seconds. There were three 150 second long trials, with 30 seconds rest between the trials. During the rest period participants did not move and the screen did not display anything.

In addition to recording the time spent in self and other judgment, we recorded the number of self-other switches as a measure of the stability of SoA throughout the experiment. Farrer et al. (2008) showed that under conditions of uncertainty created by the task, participants tended to attribute agency more to themselves compared to others. As uncertainty is an important factor in agency attribution (Desantis, Roussel, & Waszak, 2011; Farrer et al., 2008; Moore & Fletcher, 2012), we decided to measure the degree of certainty around the experience of agency reported by participants to investigate whether this changed with rTPJ stimulation or across trials. After each trial, participants were asked to rate their certainty regarding the agency judgements they made on a Likert scale, with 1 being ‘not at all certain’ to 7 being ‘almost certain’. At the end of the final trial, participants were asked to give overall ratings of their feelings of sense of ownership and agency during the entire duration of the experiment.

In particular, they were asked how much they felt that the hand “belonged to them” (Q1), how much they felt the hand was “part of their body” (Q2), and how much they experienced the hand “in their control” (Q3) or “out of their control” (Q4). These questions were answered using a Likert scale from 1 to 7, with 1 being ‘not at all’ and 7 being ‘very much’.

Results

Three 2 x 3 mixed Analyses of Variance (ANOVA) were run with Condition (rTPJ/sham) as a between-subjects factor and Trial (Trial 1/Trial 2/Trial 3) as a within-subjects factor. The dependent variables considered were: 'number of self-other switches', 'time spent in self-judgment' and 'certainty' scores.

Self-other switches

The ANOVA investigating the effect of Condition (rTPJ/Sham) and Trial (Trial 1/ Trial 2/ Trial 3) on 'number of self-other switches' showed no main effect of Condition ($p = .091$) and no main effect of Trial ($p = .053$), as well as no interaction between Condition and Trial ($p > .250$). These results suggest that the stimulation did not have an effect on the stability of their sense of authorship over their own actions in this task. This stability also remained the same over the course of the experiment (Figure 6.8a).

Time spent in self-judgement

The ANOVA investigating the effect of Condition (rTPJ /Sham) and Trial (Trial 1/ Trial 2/ Trial 3) on 'time spent in self-judgement' showed no main effect of Condition ($p > .250$) nor interaction between Condition and Trial ($p = .206$). There was a main effect of Trial ($F_{1(24)} = 6.982$, $p = .014$, $\eta^2_{\text{partial}} = .225$). Pairwise comparisons revealed that Time of Self-judgment in Trial 3 was significantly greater (av = 80.24, sd = 41.33) than in Trial 1 (av = 63.33, sd = 33.26), ($t(25) = -1.649$, $p = .015$), (Figure 6.8b). While no differences in Condition (rTPJ vs sham) were found, we performed a one-sample t-test on the whole data looking at the time spent in self-judgment. Results showed that participants perceived the observed movements significantly more as their own versus those of the experimenter ($t(25) = 11.62$, $p = < .001$) (Time of Self Judgement for one trial: av = 71.95, sd = 31.51; Time of Other judgment: av = 63.96, sd = 31.22). This result replicates that reported by Farrer and colleagues (2008).

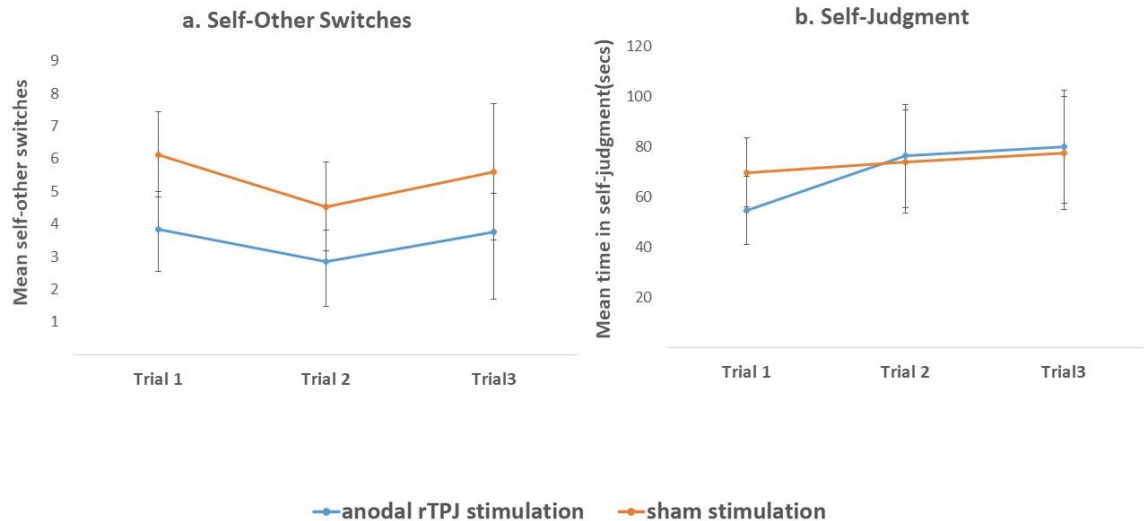


Figure 6.8. (a) Average number of self-other switches in the anodal rTPJ stimulation and sham stimulation conditions, for each Trial. No significant differences between conditions were found. (b) Average time (in seconds) spent in self-other judgment in the anodal rTPJ stimulation and sham stimulation conditions, for each Trial. No significant differences between conditions were found. Overall, both groups spent more time in 'self-judgment' than in 'other-judgment'

Certainty

Data on certainty ratings was missing for one participant. The ANOVA investigating the effect of Condition (rTPJ /Sham) and Trial (Trial 1/ Trial 2/ Trial 3) on 'certainty' showed no main effect of Condition ($p = .248$) and no main effect of Trial ($p = .175$). There was also no significant interaction between Condition and Trial ($F(2, 22) = 3.238, p = .059$). These results suggest that the stimulation did not influence the degree of certainty over participants' self-other judgements and this did not change across trials.

Post session agency and ownership judgments

Questionnaire data was missing for one participant. Four independent samples t-test were carried out to examine the effect of Condition on post-session ownership (Q1 and Q2) and agency (Q3 and Q4) ratings. No differences were found between conditions in Question 1 ($p > .250$), Question 3 nor Question 4 ($p > .250$). However, there was a significant effect of Condition on Question 2 (i.e. how much did you feel your hand as part of your body?). Greater sense of ownership towards the hand was shown by participants that received rTPJ stimulation (av = 4.24, sd = 1.48) compared to participants in the Sham condition (av = 2.92, sd = 1.25), $t(23) = 2.41, p = .024$, (Figure 6.9).

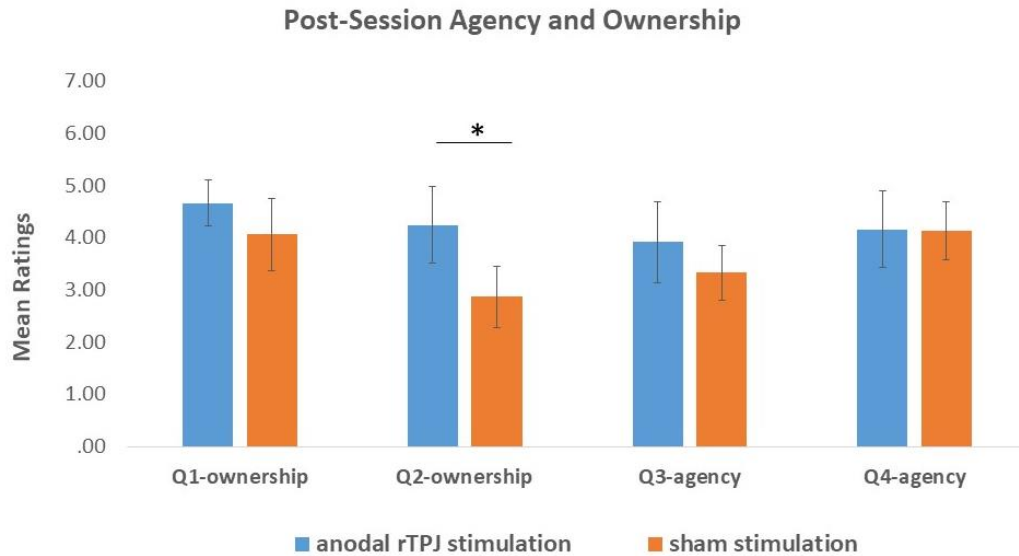


Figure 6.9. Post-session average ratings for agency and ownership, for the rTPJ stimulation and the sham stimulation groups. Participants who received anodal rTPJ stimulation showed greater sense of ownership towards the hand (Q2: How much did the hand feel like it was part of your body?).

Discussion

Participants received anodal rTPJ stimulation or sham stimulation before completing an action recognition task. In this action recognition paradigm, the visual feedback of the participant's tapping movement had been deliberately distorted, making the authorship of their movement ambiguous. Under these conditions, participants were asked to make self-other agency judgments. We found that the two groups of participants did not differ in their stability of agency experience (i.e. number of self-other switches), nor in the content of their agency experience (i.e. predominance of self or other judgments). Results also showed that participants spent significantly more time in self-judgment compared to other judgment. This result is a replication of the effect found by Farrer and colleagues (2008). Interestingly, the time spent in self-judgment increased across trials suggesting that the experience of self-agency was enhanced as trials went on.

rTPJ stimulation did not have a significant effect on time spent in self-judgment nor in the stability of the agency experience. However, a trend in the number of self-other switches suggests that increasing the statistical power of the study may unveil an effect of rTPJ on the stability of the agency experience. That is, hyperactivation of rTPJ would lead to a more stable experience of agency.

While the stimulation did not seem to influence the sense of agency, participants who received anodal stimulation on rTPJ, reported an overall higher sense of ownership over the hand compared to participants who received sham stimulation. This finding is in line with previous work showing the crucial role of the rTPJ in embodiment (e.g. Arzy, Thut, Mohr, Michel, & Blanke, 2006; Blanke, 2005). In light of findings showing that hyperactivating rTPJ leads to improved self-other distinction (Santiesteban et al., 2012), this result may be the effect of an enhanced self-representation. That is, hyperactivating rTPJ reduced the malleability of the boundaries between self and other, leading participants to feel greater SO towards their own hand.

The fact that rTPJ stimulation did not elicit changes in the SoA could be attributed to the nature of the task. Humans show an automatic tendency to imitate movements of others (Heyes, 2011), in particular when they are similar to those they are executing (Heyes, Bird, Johnson, & Haggard, 2005). It could be hypothesised that, under the conditions created by the present task, participants were led to synchronise with the movements seen on the video and therefore not have kept the rhythm constant as instructed. This could have affected the validity of the study and may have covered putative changes in the SoA. Future studies may address this aspect by recording participants' finger movements in order to check whether there is a tendency to synchronise with the visual feedback.

General discussion

The studies presented in this chapter sought to investigate the role of the rTPJ in the rise of one's own SoA under conditions of agentic uncertainty. In particular, we used tDCS to look at the effects of anodal rTPJ stimulation on a) vicarious experience of agency and b) self-other agency attribution.

Our results showed that enhancing the activity of the rTPJ did not have any effects on the experience of SoA reported by the participants. The absence of significant results could be due to the complex nature of SoA. The SoA is a multifactorial, multi-layered and dynamic phenomenon (David, 2012; Gallagher, 2013; Synofzik, Vosgerau, & Newen, 2008). Consequently, while rTPJ has been consistently shown to be involved in the sense of agency, other

brain areas have also been shown to play a role in its creation (e.g. Khalighinejad, Di Costa, & Haggard, 2015; Moore, Ruge, Wenke, Rothwell, & Haggard, 2010).

Similarly, we hypothesised that rTPJ could be the area where different cues integrate to give rise to the SoA. By enhancing its activity during tasks where external cues were manipulated, we sought to uncover its role. One possible explanation for our lack of significant effects may be that integrating different cues does not reside in a single brain structure, but in the connectivity between the various areas that contribute to SoA (Haggard, 2017).

Alternatively, the absence of changes in SoA following stimulation may be attributed to the inefficacy of tDCS stimulation. A recent quantitative review on cognitive effects of single session tDCS have shown that one tDCS session does not have a reliable effect on cognition in healthy adults (Horvath, Forte, & Carter, 2015). Future studies could address this point by enhancing the activity of the rTPJ with a different type of brain stimulation, for example the relatively novel transcranial Alternating Current Stimulation (tACS) (Antal & Paulus, 2013).

In this chapter, we have tested the contribution of the rTPJ to agency attribution. We did so by enhancing its activity through anodal transcranial Direct Current Stimulation. Although our results failed to find significant effects of rTPJ stimulation on sense of agency we do feel that this approach is worth persevering with. However, such research should perhaps consider alternative stimulation modes and agency paradigms, and be mindful of power issues associated with this approach.

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CHAPTER SEVEN

Agency and Ownership: Rubber Hand and Vicarious Agency illusions combined.

Throughout the studies presented there has been an underlying discussion about the relationship between SoA and SO. Here we aim to test this directly, by combining the rubber hand illusion with the vicarious agency task.

Introduction

As discussed in chapter 1, the relationship between the sense of agency (SoA) and the sense of ownership (SO) has long been investigated. However, it still remains unclear (Ma & Hommel, 2015; Tsakiris, Longo, & Haggard, 2010; Tsakiris, Prabhu, & Haggard, 2006).

Some studies have argued that SoA and SO are two separate components of self-awareness (e.g. Tsakiris, Schütz-Bosbach, & Gallagher, 2007), while others have shown that these two components interact (e.g. Caspar, Cleeremans, & Haggard, 2015; Dummer, Picot-Annand, Neal, & Moore, 2009).

This interplay between SoA and SO has often been investigated using ownership illusions and, in particular, with paradigms inspired by the traditional Rubber Hand Illusion (Botvinick & Cohen, 1998) with the addition of a movement component. In the traditional RHI illusion, an artificial hand is placed in a body congruent position in front of the participant whose hand is hidden from view. By synchronously stroking the artificial and the real hand, visual and tactile information are combined and the perceived location of the real hand is shifted towards the artificial hand. This is known as proprioceptive drift. Explicit measures (i.e. questionnaires) also reveal that participants report experiencing sense of ownership towards the artificial hand.

With the aim of investigating the interplay between SoA and SO, recent studies have created paradigms that would allow the implementation of voluntary or involuntary motor control over the artificial hand. This has been achieved with different technologies, such as with the use of robotic hands or Virtual Reality (VR) (e.g. Caspar et al., 2015; Kokkinara & Slater, 2014; Ma & Hommel, 2015).

Findings from these studies are not consistent. For example, Caspar et al. (2015) investigated both SoA and SO with the use of a robotic hand (Figure 7.1). They reported a significant positive correlation between SoA and SO ratings, that is, an increase in illusory SO would correspond to an increase in illusory SoA (

Figure 7.2). Along these lines, a VR study by Kokkinara et al. (2014) (Figure 7.3), showed that SO towards a virtual leg would increase with active movement compared to visuotactile stimulation only. On the other hand, Dummer et al. (2009) found the opposite pattern: the SO illusion towards a prosthetic rubber hand was stronger in the visuotactile condition, compared to conditions where SoA was induced with active or passive movements.



Figure 7.1. Pictures of the robotic hand and experimental set-up used by Caspar et al. (2015). Participants put their hand under the table while the robotic hand was placed above the table. The robotic hand was programmed to execute exactly the same movements performed by the participant. From Caspar et al. (2015).



Figure 7.2. Correlation between agency and ownership scores reported by Caspar et al. (2015). From Caspar et al. (2015)



Figure 7.3. Virtual reality set up used by Kokkinara et al. (2014). Real movement made by the participant (left) and virtual movement (right). From Kokkinara et al. (2014)

Ma and Hommel (2015) suggest that one reason behind these contradictory findings may be the confusion between objective and subjective sense of agency, where 'objective' refers to the question of whether the subject was actually performing a movement and 'subjective' refers to whether this subject was perceiving to have control over the movement. While the two aspects are undoubtedly linked, the authors suggest it is crucial to distinguish them, as they rely on different sources of information.

The majority of the studies that looked at the interplay between SO and SoA, have used objective agency (i.e. the participants actually moving the artificial limb) to investigate the nature of the relationship between subjective ownership (i.e. feeling of belonging towards the limb) and subjective agency (i.e. feeling of control towards the limb). The conflicting findings may be an effect of this confusion, which is exacerbated by the types of methods used to investigate both SoA and SO. For example, in studies with virtual reality, the induction of objective agency (i.e. actually moving the hand) can be much stronger than when the hand is completely static (such as in the traditional rubber hand) or when its movements are very limited (e.g. Dummer et al. 2009). The different degree of sensorimotor cues available may have a different impact on the subjective agency and ownership experienced by the participant.

In the work presented in this chapter, we try to overcome this confusion by testing participants with a standard RHI (Botvinick & Cohen, 1998), followed by the vicarious agency task (originally developed by Wegner, Sparrow, & Winerman, 2004). In this task, participants are not actually moving but they are induced to feel agency towards the moving hand. Therefore, we will induce

subjective agency to investigate the relationship between subjective sense of ownership and subjective sense of agency. Sensorimotor signals are kept constant throughout the experiment allowing us to test the influence of subjective ownership on subjective agency, while keeping at the minimum the influence of objective agency.

Participants were tested on two separate occasions with the RHI paradigm, followed by the vicarious agency illusion. In one testing session, they received synchronous RH stimulation followed by the vicarious agency task and, in another testing session, they received asynchronous RH stimulation followed by the same vicarious agency task. Importantly, the experimental setting was designed to establish a connection between the hands used in the RHI and the moving hands in the vicarious agency task. If the SO exerts an influence over the SoA, we would expect participants to experience higher vicarious agency after the synchronous RH stimulation, compared to asynchronous stimulation.

Method

Participants

Thirty participants (18 males) took part in the study. Their average age was 22.1 years (age range = 19-26). All participants signed a consent form prior taking part to the experiment. The study was approved by Goldsmiths Ethical Committee.

Procedure

All participants took part in two testing sessions which were scheduled a week apart from each other. One testing session consisted of the rubber hand illusion synchronous condition, followed by the vicarious agency illusion. The other testing session consisted of the rubber hand illusion asynchronous condition, followed by the vicarious agency illusion. The order of synchronous/asynchronous conditions was counterbalanced across participants.

Rubber Hand Illusion

Participants were seated at a table facing the experimenter. A box with open sides was placed on the table. Participants were asked to place their hand inside the box, where it was hidden from view. The participant's hand was placed 40 cm away from their midline and the rubber hand, located inside the box, was half way between the participant's hand and their midline. This spatial arrangement is known to elicit a reliable illusion (Holle, Mclatchie, Maurer, & Ward, 2011). The participant could see the rubber hand from a hole the top of the box, while their real hand was always kept hidden from view. Before each trial began, the hole was covered in order to keep the rubber hand concealed and a tape measure was placed on top of the box.

At the start of each trial the participant was asked to indicate where they thought their index finger was located, by reporting a number on the tape measure. For each judgement, the tape measure was placed with a different offset in order to prevent memory effects. The tape measure was then removed along with the covering cloth to make the rubber hand visible. The experimenter stroked both the real and the rubber hand with identical paintbrushes. Each stroke went from the major knuckle to the fingertip and lasted between half a second and one second. In the synchronous condition, both real and rubber hands were stroked simultaneously. In the asynchronous condition, the rubber hand was stroked before the real hand with the asynchrony randomly varied between half a second and one second. Participants were asked to look at the rubber hand throughout the stimulation period, which lasted 120 seconds. After the stimulation had finished, the covering cloth and the ruler were placed back on top of the box. The participant was once again asked to indicate the position of their index finger. The proprioceptive drift elicited by the stimulation was calculated by subtracting the pre-stimulation position from the post-stimulation position.

The same procedure was repeated for both the right and the left hand. The order of the stimulation of the hand was counterbalanced across participants. After both hands had been stimulated, participants were asked to verbally answer a questionnaire. Eight questions from the short rubber hand questionnaire from Longo et al (2008) were used. Four items investigated the

SO felt by the participant and four items acted as check questions to control for task compliance or any response bias.

In order to create a stronger association between the participant's hands, the rubber hands and the experimenter's hands used in the vicarious agency task (see below), both the participant and the experimenter wore a pair of red gloves. The rubber hand was also covered with red gloves.

Vicarious agency task

The task required participants to look in front of them, towards a mirror. Gestures were performed by the experimenter hidden behind the participant in such a way that the gestures look like they were being performed by the participant's hand. The gestures seen in the mirror were either congruent with the action instructions heard over a pair of headphones (match condition) or incongruent (mismatch condition). Participants were asked to report their experiences by answering three questions on a 7-point scale with 1 being "not at all" and 7 being "very much".

The questions were:

- 1) Anticipation: *"To what degree did you feel you could anticipate the movements of the arms?"*
- 2) Agency: *"How much control did you feel you had over the arms' movements?"*
- 3) Ownership: *"To what degree did the arms feel like they belonged to you?"*

The procedure of the vicarious agency task was identical to the one described in chapter 2, except for the two arms being tested simultaneously instead of separately.

Results

Non-parametric tests were used as variables did not meet normality criteria (Shapiro-Wilk test, $p > .05$).

We first analysed the RHI and the vicarious agency task separately, to establish whether they elicited the classical illusory effects. We then investigated the effects that the RHI had on the vicarious agency illusion.

Rubber hand illusion

The effect of Stimulation (Synchronous vs Asynchronous) on Ownership questionnaire ratings was examined by conducting Wilcoxon signed ranks tests on the mean ratings for ownership in synchronous compared to asynchronous trials. Participants reported significantly higher ownership ($z = -4.79$, $p < .001$) in the synchronous condition ($av = 4.95$, $sd = .79$) compared to the asynchronous condition ($av = 1.29$, $sd = .29$) (Figure 7.4).

A Wilcoxon signed rank test on the mean proprioceptive drift revealed that participants showed significantly greater proprioceptive drift after the synchronous ($av = 2$, $sd = 1.07$) compared to the asynchronous condition ($av = .62$, $sd = .79$), ($z = -4.16$, $p < .001$), (Figure 7.5). These results show that participants displayed the classical RHI effects for both ownership questionnaire and proprioceptive drift.

We used a Wilcoxon signed rank test to compare the Ownership ratings to the Check question ratings. As expected, participants reported higher ratings in the Ownership questions compared to the Check questions in both the Synchronous ($z = -4.79$, $p < .001$) and in the Asynchronous condition ($z = -2.06$, $p = .039$).

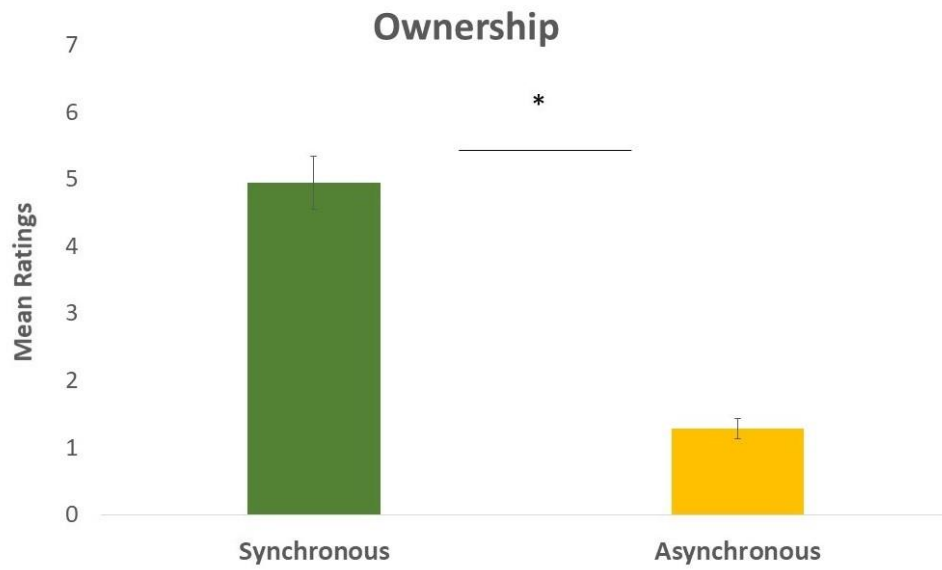


Figure 7.4. Mean Ownership ratings reported by the participants following synchronous and asynchronous stimulations. Participants reported significantly higher ownership after synchronous stimulation. Error bars represent standard deviation.

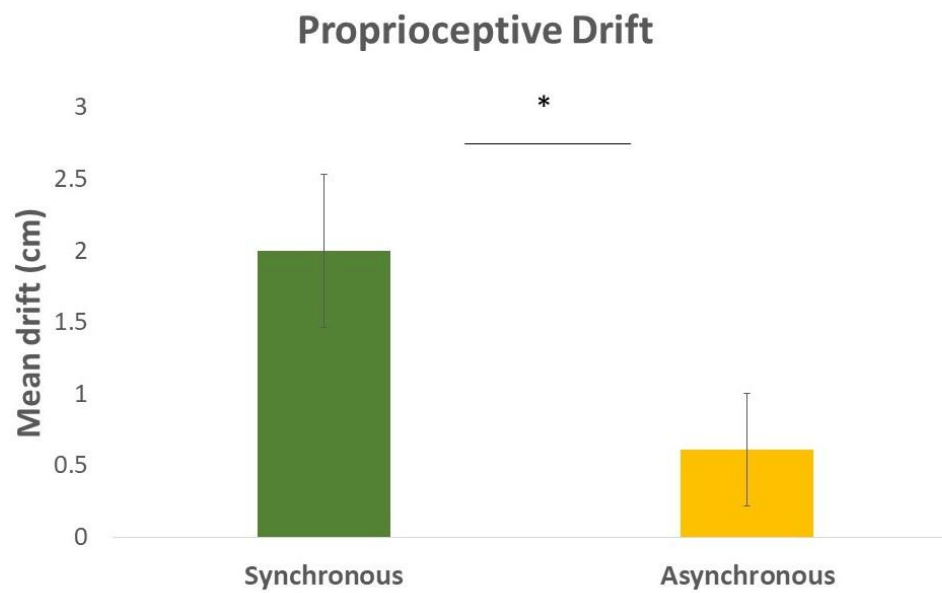


Figure 7.5. Mean proprioceptive drift shown by participants following synchronous and asynchronous stimulations. Participants showed significantly greater drift towards the artificial hand after synchronous stimulation. Error bars represent standard deviation.

Vicarious agency task

The effect of Condition (Match vs Mismatch) on 'Anticipation' ratings was examined using a Wilcoxon signed ranks test. Participants reported significantly higher anticipation in the match conditions compared to the mismatch conditions in both the vicarious agency task following synchronous RH stimulation ($z = -4.73$, $p < .001$) and asynchronous RH stimulation ($z = -4.84$, $p < .001$) (Figure 4.7a). This shows that differences in attention to the actions or instructions, or any response bias, are unlikely to explain agency or ownership effects.

The effect Condition (Match vs Mismatch) on 'Agency' ratings was examined using a Wilcoxon signed ranks test. Participants reported significantly higher sense of agency in the match compared to the mismatch conditions in the vicarious agency task following synchronous RH stimulation ($z = -4.78$, $p < .001$) and asynchronous RH stimulation ($z = -4.76$, $p < .001$) (Figure 7.6b).

The overall effect Condition (Match vs Mismatch) on 'Ownership' ratings was examined using a Wilcoxon signed ranks. Participants reported significantly higher sense of ownership in the match compared to the mismatch conditions in both the vicarious agency task following synchronous RH stimulation ($z = -4.63$, $p < .001$) and asynchronous RH stimulation ($z = -4.46$, $p < .001$) (Figure 7.6c). These results show the established effects induced by the vicarious agency task.

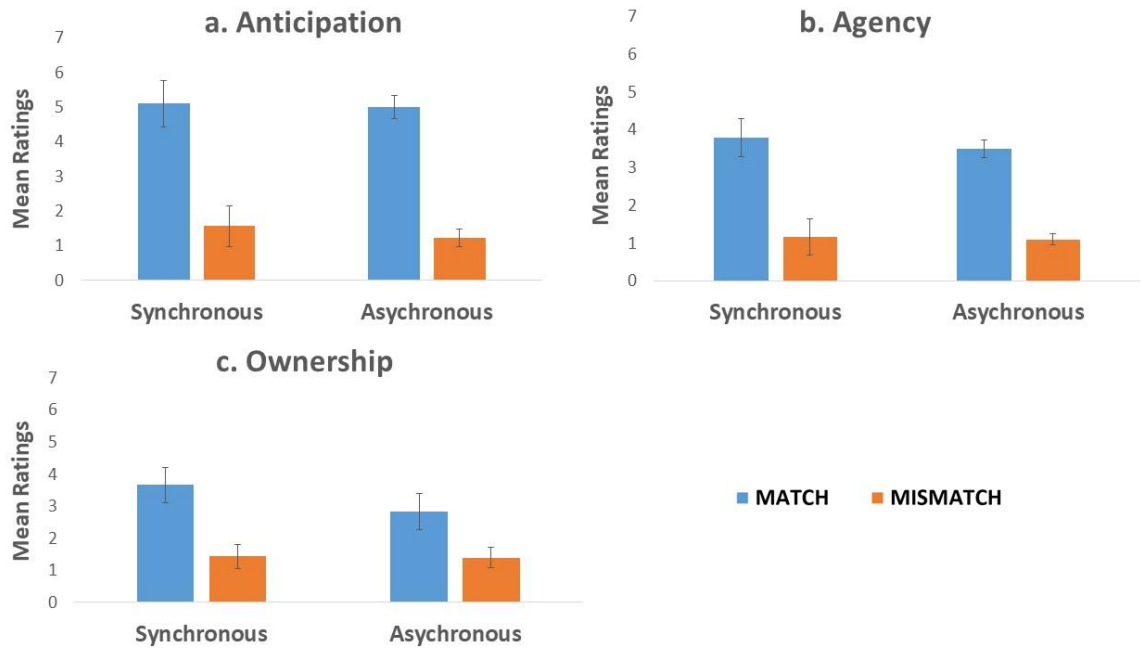


Figure 7.6. Mean ratings for Anticipation (a), Agency (b) and Ownership (c) at the vicarious agency task, following both synchronous and asynchronous stimulations. Error bars represent standard deviation.

Rubber Hand Illusion + Vicarious Agency Task

To examine the effect of the RHI stimulation (Synchronous vs Asynchronous) on the magnitude of vicarious agency illusion, we calculated the difference between match and mismatch trials for the agency question (Agency effect) and the difference between match and mismatch trials for the ownership question (Ownership effect). The difference between match and mismatch trials for the anticipation question (Anticipation effect) was also calculated. The Agency, Ownership and Anticipation effects were calculated separately for ratings that followed the synchronous and the asynchronous conditions.

These were entered into a Friedman's ANOVA, which revealed that the magnitude of the Agency and Ownership effects in the synchronous and asynchronous conditions was significantly different ($\chi^2(5) = 59.76, p < .001$). Subsequent pairwise comparisons (using Wilcoxon signed rank tests) showed that synchronous stimulation induced a significantly greater illusion of ownership compared to asynchronous stimulation ($z = -2.71, p = .007$) (SO Synchron: $av = 2.23, sd = 1.22$; SO Asynchron: $av = 1.43, sd = 1.04$). Although a trend can be observed, there was no significantly greater illusion of agency following the synchronous stimulation compared to the asynchronous stimulation ($z = -1.66, p = .089$) (SoA Synchron: $av = 2.63, sd = 1.01$; SoA Asynchron: $av = 2.4, sd = 1.2$), (Figure 7.7). This suggests that the rubber hand

manipulation selectively modulated the sense of ownership on vicarious agency task.

As predicted, the type of stimulation did not influence the ratings for the check question (i.e. Anticipation), as shown by a Wilcoxon signed rank test between anticipation effect in synchronous vs asynchronous stimulation ($z = -1.07$, $p > .250$) (Anticipation Synch: $av = 3.53$, $sd = 1.57$; Anticipation Asynch: $av = 3.77$, $sd = 1.19$), (Figure 7.7).

To further investigate whether SO influenced SoA, we ran separate linear regressions between the SO mean ratings obtained immediately following the RHI and differences in the Agency effect shown during the vicarious agency illusion, after both synchronous and asynchronous stimulations. The results showed that SO ratings did not predict the Agency effect in neither the synchronous nor the asynchronous conditions ($p > .250$). Similarly, mean proprioceptive drift measures did not predict the Agency effect in neither the synchronous nor the asynchronous conditions ($p > .250$)

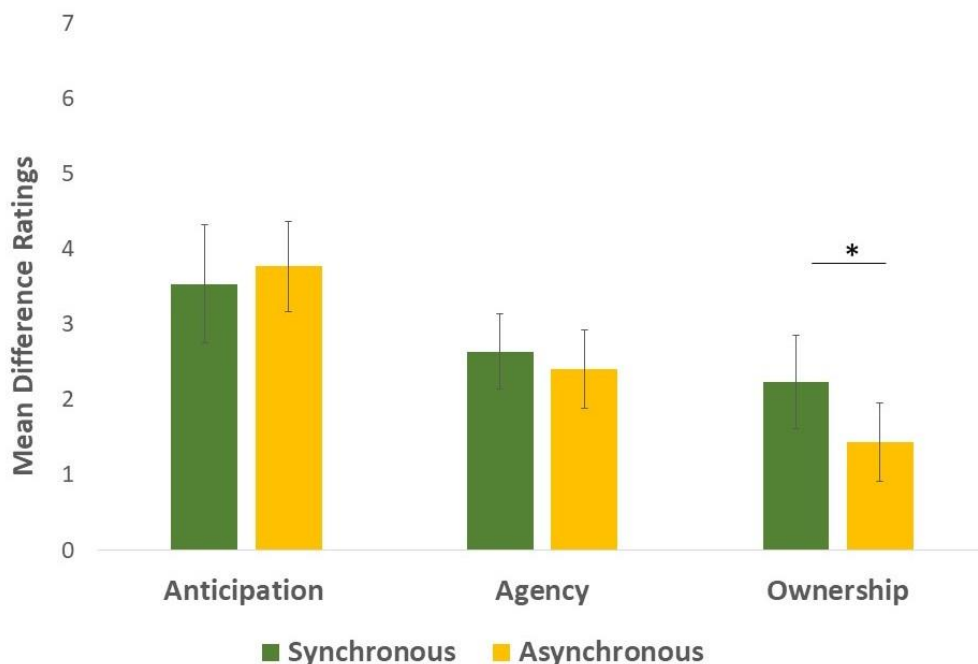


Figure 7.7. Mean difference ratings (match-mismatch) reported in the vicarious agency task for Anticipation, Agency and Ownership following RHI synchronous and RHI asynchronous stimulation. Participants reported greater SO over the hands in the vicarious agency task following synchronous compared to asynchronous stimulations. No difference was found in Anticipation and Agency ratings. Error bars represent standard deviation.

Discussion

This work sought to shed light on the relationship between sense of ownership and sense of agency. While this relationship has been extensively investigated, it remains unclear (Ma & Hommel, 2015; Tsakiris et al., 2010, 2006).

Here we investigated whether the subjective experience of ownership towards a hand can influence the subsequent illusory experience of agency towards the 'same' hand on a separate task. We did so by combining two well-established paradigms: the Rubber Hand Illusion (Botvinick & Cohen, 1998) and the Vicarious Agency illusion (Wegner, Sparrow, & Winerman, 2004). Participants were tested on two occasions: they underwent the RHI synchronous condition followed by the vicarious agency task in one occasion and, on a separate occasion, they underwent the RHI asynchronous condition followed by the same vicarious agency task.

Our study was able to replicate the well-established effects of both paradigms. Participants felt higher SO towards the rubber hand after synchronous, compared to asynchronous stimulations. Equally, the proprioceptive drift towards the rubber hand was greater following synchronous compared to asynchronous stimulations. With regards to the vicarious agency task, participants reported higher Anticipation (check question), Sense of Agency and Sense of Ownership in the match conditions, compared to the mismatch conditions. These effects were shown in the vicarious agency task sessions following both the RHI synchronous and asynchronous stimulation sessions. By looking at the differences in the vicarious agency experience following synchronous or asynchronous stimulation, we found that illusory SO elicited by the RHI did not influence the illusory experience of control in the vicarious agency task. Interestingly, the illusory SO elicited by the RHI did influence SO towards the moving hands of the vicarious agency task. That is, participants felt greater SO in the vicarious agency task after synchronous RHI stimulation, compared to asynchronous RHI stimulation.

At first glance, our results seem to support the idea of the 'independent model' of SoA and SO, which suggests that SoA and SO are two separate experiences. This

model is supported by behavioural studies showing modulating SoA does not affect the SO (e.g. Dummer et al., 2009; Sato & Yasuda, 2005) and that SoA and SO play different roles in structuring body awareness (Tsakiris et al., 2006). Neuroimaging evidence also shows different neural activation for the SoA compared to SO (Tsakiris et al., 2010). In line with this view, our results seem to suggest that SO and SoA are, at least partially, independent experiences. Were SO to exert an influence on the SoA, we would expect that synchronous stimulation in the RHI would influence the vicarious SoA. Instead, we did not find such modulation.

However, there are a few aspects that should be considered. Firstly, our investigation was limited to explicit judgments of agency: in the RHI we collected a measure of implicit SO (i.e. proprioceptive drift), but we did not collect a measure of implicit SO and SoA in the vicarious agency task. In light of previous results showing a dissociation between implicit and explicit agency (e.g. Dewey & Knoblich, 2014), it is possible that illusory SO would exert a different influence on explicit compared to implicit agency. However, recent findings suggest that dissociation between SoA and SO is also valid at an implicit level (Braun, Thorne, Hildebrandt, & Debener, 2014; Kalckert & Ehrsson, 2014). For example, Braun and colleagues (2014) incorporated the intentional binding paradigm into the traditional RHI in order to measure the interplay between SO and SoA also at an implicit level. Their results showed that an absence of SO towards the hand did not lead to an absence of SoA towards its movements, and vice versa, supporting the idea of a dissociation between SoA and SO also at an implicit level.

Secondly, our aim was to investigate whether illusory SO would influence illusory SoA. It is possible that the relationship between SoA and SO goes in the opposite direction, with illusory SoA having an influence on SO. While we hypothesised that SO would be a cue for SoA it might be the case that SoA is a cue for the SO, reflecting the role that agency plays in the construction of SO (Ma & Hommel, 2015; Tsakiris et al., 2006) or in the self-recognition of one own's body (e.g. Van Den Bos & Jeannerod, 2002). Future studies should investigate this, perhaps by swapping the order of the tasks: vicarious agency task followed by the RHI.

In conclusion, our results show that subjective ownership does not seem to have an influence on subjective agency. However, further behavioural and anatomo-physiological evidence is needed in order to understand this complex relationship.

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CHAPTER EIGHT

General discussion

In this thesis, I have presented a set of novel findings on explicit sense of agency (SoA) in different groups. This work was conducted with two principal aims. Firstly, to gain a better understanding of SoA and how it is created in light of the cue integration approach to SoA. Secondly, to improve our understanding of agency changes in groups where there has been little, or no, agency research.

These two objectives bring mutual gains to each other: by investigating agency in groups that deviate from those normally studied (i.e. young neurotypical adults) we gain unique insight into the mechanisms of agency processing. At the same time, improving our understanding of the basic mechanisms involved in sense of agency will help us better understand, and remedy, agency processing problems.

In chapter 2, we built on the extensive literature of agency in schizophrenia to look at the relationship between the schizotypy personality trait and susceptibility to the vicarious experience of agency. We found that a greater susceptibility to external agency cues predicted higher schizotypy scores.

In chapter 3, we showed that SoA in patients with anosognosia for hemiplegia (AHP) is largely dominated by their intention to move, while external agency cues are discounted. Importantly, we showed that this disturbance of SoA extends to the healthy limb.

In chapter 4, we focused on healthy older adults. Our results suggested that older adults tend to rely more on internal agency cues and discount external cues. Moreover, we showed that older adults may discount external cues because of increased reliance on internal agency cues.

In chapter 5, for the first time, we investigated changes in SoA in people with Mirror-touch synaesthesia (MTS). Our results showed that the experience of agency in MT synaesthetes is more malleable than in non synaesthetes and that this may be due to an enhanced saliency of external cues in the creation of the SoA.

Chapter 6 sought to investigate the role of the right temporo-parietal junction (rTPJ) in agency attribution in healthy adults; specifically looking at its contribution in integrating different agency cues. Our results failed to speak more on this but are useful in directing future research on this topic.

Lastly, chapter 7 investigated the relationship between sense of agency and sense of ownership (SO), which was indirectly explored throughout the experiments presented in the other chapters. Our results showed that illusory SO did not have an influence on the illusory SoA, suggesting that SO and SoA are, at least partially, independent.

Here I will discuss what are the implications of these findings, when taken together, as well as future directions.

Cue integration approach as a common basis to understand the sense of agency

The cue integration approach to SoA proposes that SoA is created by optimally integrating a large variety of internal and external cues. Importantly, these cues are interactive and their relative influence depends on their reliability (Moore & Obhi, 2012; Synofzik, Vosgerau, & Lindner, 2009). This approach has a strong explanatory power and sets itself as a conceptual basis for understanding SoA in healthy subjects, as demonstrated by Moore et al. (2009), and in groups where the experience of agency may be disrupted, as suggested by Moore & Fletcher (2012). Throughout this work we have tested specific predictions developed on the basis of this approach and demonstrated its validity across a variety of cases.

We showed that, according to our predictions, patients with anosognosia over-rely on cues associated with their intention to move and under-rely on visual feedback (chapter 3). These results are significant in that they provide the first evidence that certain neuropsychological disorders can be characterised by changes in the way the various agency cues are integrated. We have shown that SoA can be a key factor in neuropsychological syndromes and that taking this approach can advance our understanding of these conditions. Future studies can build on our work using this approach to investigate other

neuropsychological conditions, such as alien hand or anarchic hand syndromes (Bundick & Spinella, 2000; Della Sala, Marchetti, & Spinnler, 1991).

While this work on AHP has shown the validity of this approach with a clinical group that presented a well-demarcated disruption of SoA, we have also shown that the approach can predict and explain changes in SoA that are much subtler (chapters 2, 4 and 5).

We demonstrated that the weighting given to external visual cues predicted schizotypy scores (chapter 2). This offers a new research direction: it shows not only that SoA changes can relate to individual differences, but also that this framework is a useful tool to detect them and understand them. For example, studies have shown that disruptions of SoA play an important role for patients with obsessive compulsive disorder (Gentsch, Schtz-Bosbach, Endrass, & Kathmann, 2012) as well as agoraphobia (Gallagher & Trigg, 2016). Here I suggest that future research should work towards identifying links between SoA changes and individual differences that predispose to the development of those pathologies (Mrazek & Haggerty, 1994).

We have shown that changes in the weighting of different agency cues occur with older adulthood. This raises new questions about the changes in SoA during the lifespan. Our findings in older adulthood have demonstrated that experimentally manipulating different agency cues is a viable route to detect age-related changes in the SoA. To date, only two studies have looked at SoA in childhood (Cavazzana, Begliomini, & Bisiacchi, 2014; Metcalfe, Eich, & Castel, 2010) and very little is known about agency processing in children and adolescents. Examining cue integration in children and adolescents is likely to provide us with insights into their agency processing and, in turn, inform us on the development of this fundamental aspect of cognition.

In chapter 5, we have found that mirror-touch synaesthetes (MTS) present exaggerated SoA. Based on the evidence that MTS is characterised by a difficulty in inhibiting the others (Santiesteban, Bird, Tew, Cioffi, & Banissy, 2015), we suggested this could be linked to stronger weighting placed on external cues than on internal signals. Our work on MTS helps narrow the gap between social and individual aspects of cognition. Previous studies

investigating SoA using social scenarios suggest that not only do we have SoA for our own actions but our SoA may extend to other agents' actions in social contexts (e.g. Obhi & Hall, 2011; Pfister, Obhi, Rieger, & Wenke, 2014). Although speculative, this 'extended agency' may be the result of the integration of various cues. Recent research on SoA and autism seems to support this suggestion. Lafleur and colleagues (2016) suggested that a lack of reliability in sensorimotor agency cues may explain alternations in SoA found in people with autism. They also went on to suggest that part of the changes in social and interpersonal abilities that characterise autism may ensue from altered SoA. Future work should consider using the cue integration approach as a framework to understand agency also in social contexts.

The cue integration theory was initially supported by results obtained by manipulating the implicit experience of agency in healthy adults (Moore et al., 2009). Very few studies have looked at the role of external and internal agency cues on explicit SoA (e.g. Sato, 2009; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Wegner, Sparrow, & Winerman, 2004). Crucially, our set of findings speaks about the *explicit* SoA. We have expanded previous work and shown that the cue integration approach is a valid framework to explain not only implicit but also explicit aspects of SoA (chapters 2-5). This has significant conceptual implications. While implicit and explicit aspects of agency are dissociable (e.g. Dewey & Knoblich, 2014), it was also proposed that they are not fully independent (Moore, Middleton, Haggard, & Fletcher, 2012; Synofzik, Vosgerau, & Newen, 2008). Although speculative, the findings presented in this thesis support this view and, moreover, suggest that implicit and explicit aspects of agency may be the result of a similar process, namely the integration of different agency cues. Importantly, future work should look at whether our findings on explicit SoA in the populations examined are confirmed with regards to the implicit SoA.

Taken together, these findings prove that the cue integration approach to SoA is a valid and testable approach to understand SoA in many contexts. This work lays the groundwork for detailing studies aimed at systematically investigating SoA within a unifying framework. In particular, the mechanisms that are responsible for differences in cue weighting discussed in this work

(chapters 2-5) should be more closely examined. That is, future work should test whether these changes in agency cue weighting are a *direct* consequence of differences in their reliability. We have partially addressed this in chapter 4, where we investigated the relationship between the susceptibility to the manipulation of external cues in older adults and the ability to interpret internal cues (i.e. interoception and proprioception) in both younger and older adults. Our findings suggested that the decreased reliance on external cues shown by older adults is linked to an increased reliability on internal agency cues. Future work should build on this and continue exploring the mechanisms behind the difference in agency cues weighting. This will allow us to achieve a deeper understanding of SoA processing.

Self-agency and self-other distinction

A difficulty within SoA research consists of defining what it is meant by SoA, and what the measures used are actually measuring. As proposed in the introductory chapter, explicit and implicit measures of agency are likely to be both valid but measuring different aspects of sense of agency. How much the explicit SoA is representative of the overall SoA is an unanswered question, and it is likely to depend on the nature of the action being performed (Synofzik et al., 2008). Even within the categories of implicit and explicit measures of agency, what aspects of SoA are actually measured can be different.

In this thesis, I have investigated the explicit aspects of SoA. The tasks that have been used created ambiguous situations in which participants had to report the amount of vicarious control exerted over movements (vicarious agency task) or identify whether movements belonged to them or someone else (action recognition). Crucially, both tasks are characterised by the presence of another agent. These paradigms differ from those where an agency judgment is asked but there is no alternative agent involved in the action (e.g. Sato & Yasuda, 2005). The presence of another agent adds an important component to the agentic situation. That is, judging agency in these contexts involves to some extent recognising oneself (Haggard & Tsakiris, 2009). The paradigms used in this work have emphasized the fundamental role that agency plays in distinguishing oneself from another. Differentiating actions that are self-generated from those that are performed by others gives

rise to a self-other distinction in the domain of action and contribute to the experience of a distinct self (David, Newen, & Vogeley, 2008; Georgieff & Jeannerod, 1998).

Strikingly, we have shown the tight relationship between self-other distinction and SoA in chapter 5. We found that the blurring in self-other distinction processes that characterises mirror touch synaesthetes (Banissy & Ward, 2013; Ward & Banissy, 2015) is significant for their SoA. While we have not focused on the role that agency plays in self-other distinction, our studies have measured the SoA in contexts where the agents were required to make self-other distinctions. Future work could directly investigate the role that SoA plays in the construction self-awareness.

Sense of agency and Sense of ownership

As discussed in the introductory chapter and in chapter 7, the relationship between SO and SoA has been extensively investigated but still remains unclear (Ma & Hommel, 2015; Tsakiris, Prabhu, & Haggard, 2006). Throughout this thesis, the relationship between SoA and SO has been an underlying theme (chapter 2-6). This was then explored directly in the experiment presented in chapter 7. Here I summarise what our data tell us about the interplay between SoA and SO and discuss future directions for research on this topic.

In chapter 2, we found that changes in the vicarious experience of agency, and not of ownership, were uniquely predictive of schizotypy scores. In chapter 3, patients with anosognosia for hemiplegia showed an altered SoA, while their SO did not differ from those of controls. These results suggest that SoA and SO are, at least partially, independent. In particular, they show that alterations of SoA are not necessarily linked with a significant disturbance of SO. In chapter 6, we found that hyperactivating the right temporo parietal junction did not have any effect on self-other agency attribution, but seemed to have led to a more robust sense of ownership (experiment 2). Although this result should be further investigated, it suggests that SoA and SO are underpinned by different neural mechanisms. Lastly, we have investigated whether illusory SO induced by the synchronous stimulation, in the RHI paradigm, influenced

illusory SoA over the same hand in the vicarious agency task. We found that SO did not influence SoA in the vicarious agency task, but boosted the illusory SO towards the hand in the same task. This finding supports the view that SO and SoA are independent.

All the findings mentioned so far are compatible with each other, in that they support the view that SoA and SO are two separate aspects of self-awareness and may even stem from different processes (Sato & Yasuda, 2005; Tsakiris, Longo, & Haggard, 2010; Tsakiris et al., 2006). However, some of our other findings point towards a much closer relationship between SO and SoA. For example, when we looked at changes in SoA in older adults (chapter 4), we found that older adults were less susceptible to vicarious experience of control compared to younger adults. Their SO was also reduced. We then found that a greater susceptibility to vicarious experience of both agency and ownership was correlated with reduced interoceptive and proprioceptive awareness. These results suggest that SoA and SO may be somewhat related. In Chapter 4 we also suggested SO seems to be the primary aspect of self-awareness to be disturbed in MTS but that this primary disturbance of SO may lead to the alterations of SoA that we observed. These results support the accounts of agency processing that argue that the experience of agency is predicated on the sense of ownership (Gallagher, 2000).

To summarise, our results on the one hand (chapters 2-3-6 and 7) seem to support the independence model, but on the other hand (chapter 4) seem to be in line with an additive view of SO and SoA, for which SO and SoA are more closely linked. While these results add to the understanding of SoA and SO, especially within the single populations studied, the relationship between these two components of self-awareness remains elusive. There may be a few reasons behind the contradictory results presented in the literature and in this thesis.

Firstly, different studies may define SoA and SO in different ways. For example, often studies investigating SO do not distinguish between the feeling of recognising the body as one's own, and the feeling that the body *is* one's own. While these two aspects are undoubtedly linked, they may rely on different

processes. A second source of confusion may lie in the distinction between explicit and implicit aspects of both SoA and SO. Many studies have investigated implicit and explicit aspects of SO and only explicit aspect of SoA (e.g. Kalckert & Ehrsson, 2012, 2014) and only a few studies have looked at both implicit and explicit aspects of SoA and SO (e.g. Braun, Thorne, Hildebrandt, & Debener, 2014; Burin, Pyasik, Salatino, & Pia, 2017). As a consequence of these issues, the measures used to capture SO and SoA may also be responsible for the heterogenous results. Equally, the equipment used to induce SO or SoA varies incredibly, going from traditional rubber hands (e.g. Dummer, Picot-Annand, Neal, & Moore, 2009), to robotic hands (e.g. Caspar et al., 2015), to Virtual Reality (e.g. (Kokkinara & Slater, 2014; Ma & Hommel, 2015). It is plausible that all these methods give rise to very different experiences.

Lastly, the conflicting findings of the literature may reflect the complexity of the interplay between SO and SoA. So far, there has been a generalised effort to categorise these two aspects of awareness as independent or entirely linked (Tsakiris et al., 2010). However, it is possible that this relationship is much more nuanced. While SO and SoA *could* be completely independent or completely related, these are just the two extremes of a continuum. Where on the continuum and how the SO-SoA interplay develops may depend on different factors such as the context of the investigations or the populations investigated, as we have seen throughout this thesis.

To conclude, future work is needed to disentangle the relationship between SoA and SO and taking into account these points may provide fruitful directions.

Concluding remarks

In every chapter of this thesis, I have listed and discussed the different implications that our studies have for each of the groups investigated. Here, I aim to reflect on the overall impact of this work.

As highlighted by Moore (2016), the majority of the applied work around SoA is still in its infancy and it is at times difficult to articulate the relevance of SoA research. This thesis provides examples of the potential applications for agency research.

In this work, I have presented studies that range from clinical, to atypical and typical populations. Our findings have shown how SoA research can have a substantial impact on the health and well-being of the groups investigated. As SoA is such a fundamental feature of our daily lives, research aimed at understanding it and uncovering its changes across different groups or contexts, has the potential to bring great benefits, not only to those groups but to all of us.

In this thesis, I have investigated sense of agency in clinical, atypical and typical populations. Our results have brought a new understanding of sense of agency processing and of each of the groups investigated. While we have answered many questions, many others have arisen. This work represents one more piece of the puzzle.

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