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Controlling actions and experiencing control: the influence of movement execution and goal achievement on the Sense of Agency

FINAL DISSERTATION

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Table of contents

To Francesca M.

1. Introduction

One of the most distinctive features of human beings, as compared to other animals, lies in their ability to exert a purposeful and flexible control over their movements and on the external environment (Bandura, 2001). People are constantly engaged in performing actions, which are generally directed at obtaining a certain goal. This can be more or less significant for the individual. For instance, pressing a button can result in various outcomes: from turning on a light, to donating a certain amount of money to a charity, to showing appreciation or disapproval of a certain content on social media. Investigating human cognition from the perspective of the disposition to perform finalized actions can help to understand some of its basic underlying principles. In the early age of experimental psychology, William James already pointed at the relevance of the desire to obtain certain events in the outside world to understand voluntary behavior: intentional actions require a representation of their effects, a theory that has been termed "ideo-motor" (Elsner & Hommel, 2001; Haggard, 2005; Hommel, 2009; James, 1890). A century later, theories of motor control refined this idea by framing it in terms of the predictive capacity of the brain: future and desired states in the external world are represented, and the brain selects the best course of action to translate predictions in actual events (Blakemore & Frith, 2003; Wolpert, Ghahramani, & Jordan, 1995). Given the central role of goal-directed actions in the cognitive architecture, it is perhaps not surprising that humans have also evolved feelings and conscious thoughts about control, that is, the Sense of Agency. The Sense of Agency can be defined as the experience that arises when individuals control their actions and their consequences in the external environment (Haggard, 2017. But see paragraph 1.1 for other definitions). Its role in everyday life and in the functioning of the society is crucial, despite people rarely reflect about it. Indeed, the Sense of Agency is intimately connected with a sense of responsibility over one's own actions and their effects (Frith, 2014). Its relevance becomes dramatic when crimes are committed: in law courts, individuals are typically punished if they were experiencing a feeling of control over their actions at the time they committed the crime (Haggard, 2017).

The importance of the Sense of Agency also becomes apparent when errors prevent individuals from obtaining a desired outcome, or when clinical conditions alter the way in which actions are commonly experienced. Interestingly, the centrality of agency in human cognition can also be found in the fact that the brain developed the capacity to monitor difficulties in obtaining the goal of the action: an error monitoring system, centered on the activity of the Medial Frontal Cortex, has been proposed to signal deviations between the desired and actual external outcome (Ullsperger, Danielmeier, & Jocham, 2014). This system would enable a flexible control of actions and allow to overcome environmental constraints.

As I will argue throughout the thesis, different processes might contribute to the Sense of Agency, and the brain might use different sources of information to modulate it. My research during my Ph.D. was mostly dedicated to understanding the contribution of two types of information: the control of one's own movements and the control of events (i.e., goals) in the external environment. As argued before, the goal-directed nature of behavior seems to be a crucial aspect of human cognition. Hence, it is not surprising that previous research focused on the effects of a success or of a failure to obtain a desired outcome for the Sense of Agency. In other words, on the *end* of the action. Additionally, previous research also investigated how the Sense of Agency is influenced by controlling one's own body. Interestingly, some studies (e.g. Daprati et al., 1997; van den Bos & Jeannerod, 2002) investigated the contribution of movement information per se, measuring participant's Sense of Agency over movements that did not cause any consequence in the environment. However, movements can be viewed as the primarily *means* that are employed to achieve a certain goal. The question of which of these two aspects – the means or the ends - is more relevant for the Sense of Agency was rarely addressed.

Before tackling this specific issue, I will first introduce the Sense of Agency by reporting some of definitions that different authors have given about it (section 1.1). Then, I will describe some models that were proposed to explain the Sense of Agency and the sources of information that were found to influence it (section 1.2). Finally, I will focus on previous experiments that inspired the investigation of the respective influence of movement and goal information for the Sense of Agency (section 1.3).

1.1 Definition(s) and components of the Sense of Agency

A formal and common definition of the Sense of Agency is the following: It is "the experience of controlling one's own motor acts and, through them, the course of external events" (Haggard, 2017). However, other definitions were proposed, which might sound different. The reason of the discrepancies between them might lie in the focus on a certain component of the Sense of Agency over the others.

For instance, De Vignemont and Fourneret proposed that the Sense of Agency might include a reference to the *Self*, and define it as "the ability to refer to oneself as the author of one's action" (De Vignemont & Fourneret, 2004). Gallagher (2000) made a similar proposal and extended it to include the concept of causation and agency for conscious thoughts: the Sense of Agency would be "the sense that I am the one who is causing or generating an action. For example, the sense that I am the one who is causing something to move, or that I am the one who is generating a certain thought in my stream of consciousness". (Gallagher, 2000)

Also Haggard agrees that causation is relevant for the Sense of Agency. This is apparent when he states that "the sense of agency is the feeling of making something happen" and that it is "the sense that our actions cause effects in the outside world" (Haggard, 2017).

Tsakiris and Haggard additionally pointed at the relevance of conscious *intentions* for the Sense of Agency, which would be "the sense of intending and executing an action" (Tsakiris & Haggard, 2005). The same researchers also highlighted the importance of free will and of voluntary actions for the Sense of Agency. In the same article, Tsakiris and Haggard suggest that "only voluntary actions can produce a Sense of Agency" (in contrast to Sense of Ownership, see below).

Another aspect that is frequently associated to the Sense of Agency is the capacity to distinguish between outcomes generated by the oneself from those generated by other actors, which hints at the idea that the Sense of Agency also involves the capacity to operate a “self-other” distinction (David et al., 2007, 2009; David, Newen, & Vogeley, 2008) and that it might rely on a specific cognitive process dedicated to performing this distinction, the “who system” (De Vignemont & Fourneret, 2004; Georgieff & Jeannerod, 1998).

Summarizing, these different definitions (and many others) seem to disagree with respect to which components should be considered fundamental for the Sense of Agency. Different concepts such as “causation”, “intentions”, “voluntary action”, “authorship” “Self” and “Other” might be viewed as crucial to explain the Sense of Agency by one researcher and as not essential by another. It is possible different components might contribute to the Sense of Agency, and recent theoretical models proposed that the Sense of Agency is a multi-faceted experience that relies on multiple sources of information (Moore & Fletcher, 2012; Synofzik, Vosgerau, & Newen, 2008a, 2008b). Additionally, one way in which the Sense of Agency can be understood is by contrasting it with the Sense of Ownership, i.e. the sense that my body belongs to me and that I am the one who is undergoing a certain sensory experience (Gallagher, 2000; Tsakiris, Longo, & Haggard, 2010; Tsakiris, Schu, & Gallagher, 2007). Indeed, the Sense of Agency is often identified by comparing the different sensations associated to voluntary and involuntary movements: involuntary movements and passive movements induced by external forces would only involve a sense of ownership, while voluntary movements would include both. The fact that both sensations might be present during the execution of an action created an additional difficulty for Sense of Agency research: to measure the Sense of Agency over one’s body without confounding it with the Sense of Ownership (Gallagher, 2013). In spite of this methodological issue, the two experiences seem to be qualitatively different and to rely on the activity of different neural circuits (Tsakiris et al., 2010).

Wittgenstein famously asked: “What is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?” (Wittgenstein, 1958). One response to this question would be: a Sense of Agency (Haggard, 2017), that is, the awareness that I am controlling the movement of the arm.

1.2. Explanatory models of Sense of Agency

In this section I will describe some models that were proposed to explain the Sense of Agency, namely how this experience is generated and how it is sometimes lost. I will first illustrate one the most influential accounts – the comparator model – which was derived from models of motor control and that for its elegance and simplicity was employed for a long time to explain Sense of Agency both in healthy and clinical conditions. I will then review recent studies that suggest that the Sense of Agency might also depend on action selection, before any movement is performed – the so-called "prospective" Sense of Agency. Then, I will report an account that was initially developed to explain how "free will" might be an illusion, and that shows that the Sense of Agency might depend also on inferential processes that are partly independent from action execution. Finally, I will describe two recent theories that explain how different, motor and non-motor cues might contribute to the Sense of Agency.

1.2.1 Comparator model

When an individual is performing an action, the brain is constantly engaged in forming predictions about the way in which actions will unfold and in checking that those predictions were accurate. This idea was proposed to explain some characteristics of animal perception and behavior, such as their ability to maintain perceptual stability despite moving, their ability to perform fast corrections when unpredicted events occur and to learn new motor skills (Blakemore & Sirigu, 2003; Sommer & Wurtz, 2008). Early evidence that predictive representations of movements and of their sensory consequences are formed in the phase of motor planning was first provided by Sperry and by von Holst and Mittelstaedt (Sperry, 1950; von Holst & Mittelstaedt, 1950) who claimed that when the brain programs the execution of eye-movements (saccades) it also produces a "Corollary Discharge", a "copy of a motor command sent to other brain areas for interpreting sensory inflow" (Sommer & Wurtz, 2008). Corollary discharges are also known as "efference copies", and evidence for their existence was also found for other types of movements, such as those performed with hands (Wolpert & Ghahramani, 2000; Wolpert et al., 1995). Efference copies might work as inputs for *forward models*, neural systems which have the function to predict future states of the moving body and of the sensory consequences of actions.

Evidence in favor of the existence of forward models also comes from the finding of "sensory attenuation" of self-generated outcomes (Blakemore, Frith, & Wolpert, 1999; Blakemore, Wolpert, & Frith, 2000; Burin, Pyasik, Salatino, & Pia, 2017; Desantis, Weiss, Schütz-Bosbach, & Waszak, 2012; Kühn et al., 2011). Indeed, when an outcome is generated by one's own actions, this is perceived as less intense as compared to outcomes that have an external origin. This is also accompanied by a reduction of the neural responses to self-produced outcomes (Hughes & Waszak, 2011; Kühn et al., 2011).

Similarly, Haggard and colleagues (2002, 2003) found that when an outcome is the result of a voluntary action, this is perceived sooner than an identical outcome produced by external causes (Haggard & Clark, 2003; Haggard, Clark, & Kalogeras, 2002). Additionally, the onset of a voluntary action is perceived later than a passive movement. This results in a time compression between action and outcome in voluntary actions, termed Intentional Binding, which is considered an implicit marker of the Sense of Agency (see Moore & Obhi, 2012 for a review). Intentional Binding is commonly interpreted as the result of the predictions formed by the brain when it is programming a voluntary action (Haggard et al., 2002)[1].

Forward models, sensory attenuation and Intentional Binding were proposed as a mechanism by which the brain might distinguish self-generated from other-generated events, leading the individual to experience a Sense of Agency.

[1] It should be noted, however, that other factors have been shown to modulate Intentional Binding, such as priming (Moore, Wegner, et al., 2009), social context (Caspar, Christensen, et al., 2016) and belief about the existence of free will (Desantis, Weiss, et al., 2012). Desantis and colleagues (2012) criticized the predictive interpretation of Intentional Binding and suggested that it might be due to the mere presence of an action rather than to prediction (Desantis, Hughes, et al., 2012). In line with this, intentional binding has also been shown for observed actions (Poonian & Cunnington, 2013).

In particular, Frith (Blakemore, Wolpert, & Frith, 2002; Frith, Blakemore, & Wolpert, 2000) proposed that the same mechanism operating in the generation and in the control of actions could also explain the way in which individuals experience, or lose, the feeling of controlling their actions. In his account, forward models form predictions related to the executed movement and to the sensory consequences of the action. The brain monitors the actual consequences of actions and compares them with the predicted events. If they match, the individual experiences control. Conversely, if unexpected events occur the brain generates an error signal, which reduces the Sense of Agency. Given that this model relies on a comparison between predictions and actual consequences of actions, it was given the name "comparator model" (see **Figure 1**). It was suggested that this model might account not only for the Sense of Agency in healthy individuals, but also for Sense of Agency disturbances and for other types of abnormalities in the awareness of actions (Blakemore et al., 2002; Frith et al., 2000). For instance, a disturbance of Sense of Agency can be found in the case of Schizophrenia: patients often report "passivity experiences" - the feeling reported by many patients that their actions and thoughts are controlled by an external force. Passivity experiences could be explained by a deficit to predict the consequences of one's actions (Frith et al., 2000). In other words, schizophrenic individuals might be able to form intentions and to control their actions appropriately, but they might lack the awareness of having initiated the action or the ability to recognize the predictions that they formed.

Another example of how a failure at a specific level of the comparator model might lead to a distortion of the awareness of actions can be found in "anosognosia for hemiplegia". In this case, the disturbance is not strictly related to the Sense of Agency, but rather to "motor awareness", i.e., the conscious knowledge that, when performing an action, a certain part of one's body is moving (Berti & Pia, 2006). Indeed, some hemiplegic patients (generally in the left part of their body) are unaware that they cannot perform movements anymore and claim that they can still move, generally after a right-hemispheric (or bilateral) lesion (Berti et al., 2005; Pia, Neppi-Modona, Ricci, & Berti, 2004). This deficit was explained by a failure to monitor one's own actions: patients with anosognosia for hemiplegia might still be able to form motor predictions, but the lesion might impair their capacity to compare predicted and actual events. The predicted consequences of action would not be disconfirmed due to a failure of the monitoring system caused by the brain lesion, and the individual would erroneously perceive that he performed the movement (Berti et al., 2005).

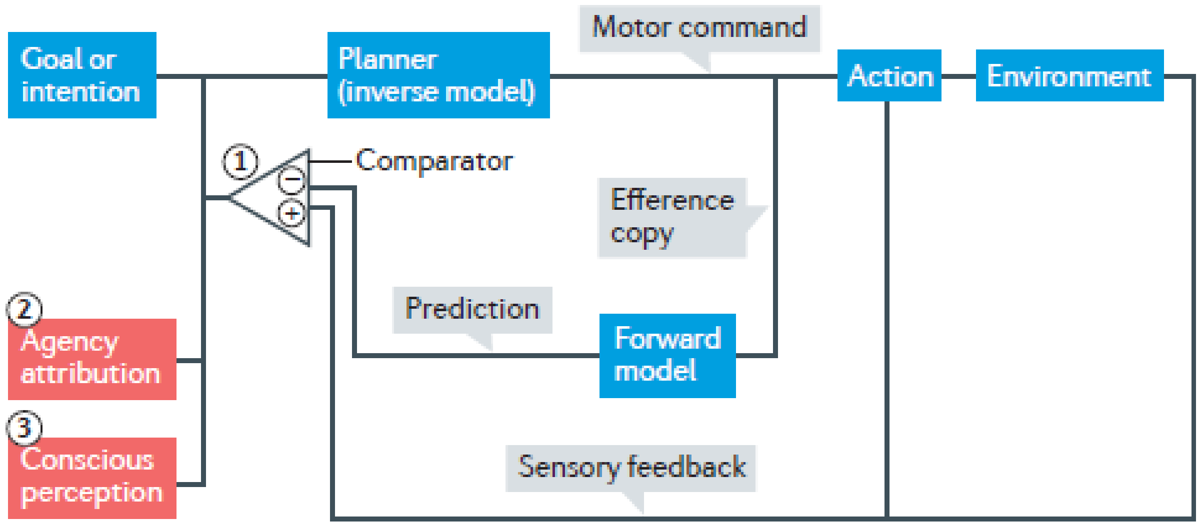

Figure 1. Comparator model of the Sense of Agency. The brain selects the motor command that most likely will allow to fulfill a certain intention or achieve a goal. Then, an efference copy is generated and sent to the forward model, which predicts the sensory consequences of actions. Predictions are compared with the sensory feedback. When predicted and actual events match, the individual experiences control. Conversely, unpredicted events reduce the Sense of Agency (Figure from Haggard, 2017).

Despite its popularity, the Comparator Model has received criticism in the last decade: some researchers have raised the point that it might lack the capacity to explain different aspects of the Sense of Agency and proposed alternative models (see section 1.2.4). For instance, the comparator model might fail to explain situations where the individual still experiences a sense of control despite the presence of small deviations between predictions and actual events; it might also fail to explain the finding that individuals can experience a "vicarious" Sense of Agency for observed actions in absence of movements (Tieri, Tidoni, Pavone, & Aglioti, 2015; Wegner, Sparrow, & Winerman, 2004); additionally, this model does not appear to be suitable to explain how individuals can attribute actions to specific other agents, and the Sense of Agency for thoughts (Synofzik et al., 2008a).

In sum, even if it is generally accepted that a mismatch between predicted and actual consequences of actions leads to a Sense of Agency reduction, the Comparator Model might not account for other aspects of the agentic experience.

1.2.2 Prospective Sense of Agency

As described above, the Comparator Model might include both predictive and retrospective components: indeed, the model assumes that the experience of agency might result from a comparison between predicted states and ensuing sensory information. This has generated ambiguity with respect to whether the Sense of Agency might be primarily a predictive or postdictive experience. Recently, Haggard and Chambon (2012) proposed that the Comparator Model might explain a *retrospective* component of the Sense of Agency, since the individual has to wait that a comparison between predicted and actual consequences of action takes place before being able to experience control (Haggard & Chambon, 2012).

However, Haggard and Chambon suggested that individuals might also feel a Sense of Agency even before the beginning of the action and termed this component *prospective* Sense of Agency. This hypothesis is driven by recent studies that showed that individuals might experience a Sense of Agency already at the stage of action selection.

Wenke and colleagues (2010) devised a paradigm where participants performed button presses with their left and right index fingers, which resulted in several possible outcomes – i.e., circles of different colors – on a screen (Wenke, Fleming, & Haggard, 2010). Participants could either freely choose which action to perform, or they could receive an instruction – an arrow pointing to the left or to the right – that indicated which finger they should use. In each trial they also received a masked subliminal prime that could either *facilitate* action selection – an arrow pointing in the same direction of the instruction – or make it more difficult – an arrow pointing in the opposite direction. Importantly, the color of the outcome depended on the compatibility between prime and instruction: for instance, it was blue if both the prime and the instruction pointed towards the left, and yellow if the prime pointed towards the left and the instruction towards the right. Sense of Agency was measured by means of a combination of ranking and rating procedures. At the end of each experimental session, participants were first asked to order colored tokens (representing the colors they observed on screen during the experimental session) on a vertical scale, ranging from most control to least control. Then, for each color they had to express how much control they experienced on a scale ranging from 0 (no control) to 100 (complete control). Participants reported that they experienced more control over outcomes of colors (e.g. blue) associated to compatible rather than incompatible (e.g. yellow) primes. The authors concluded that the fluency of action selection might contribute to the Sense of Agency, by fostering a feeling of control even before the beginning of the action.

This pattern of results was replicated in a study that involved recording of brain activity by means of fMRI (Chambon, Wenke, Fleming, Prinz, & Haggard, 2013). Additionally, it was found that the Angular Gyrus - a region of the parietal cortex that was shown to code for mismatches between expected and actual consequences of actions (Farrer et al., 2008) - became more active both when primes where incompatible with the instruction, which resulted in reduced fluency of action selection, and when participants reported a lower sense of control over the outcome. This suggests that the brain might monitor the simplicity of action selection and adjust the Sense of Agency accordingly. These results might be consistent with the view that the Sense of Agency might be a default assumption of the brain, which would be reduced in case of errors and unpredicted outcomes (Chambon, Sidarus, & Haggard, 2014; Chambon et al., 2013; Frith et al., 2000). This might also suggest that the Sense of Agency might not be an illusory experience, as proposed by the theory of "apparent mental causation" described in the following section.

1.2.3 Apparent mental causation

The fact that the Sense of Agency might not depend exclusively on mechanisms related to motor control was suggested by the theory of "apparent mental causation" proposed by Wegner (Wegner, 2003, 2004; Wegner & Wheatley, 1999). Wegner considered the experiences of conscious will and of causation “illusory” and independent of the actual influence that individuals exert on the external environment. To use Wegner’s words, free will and mental causation would be the “mind’s best trick” (Wegner, 2003). According to his view, the Sense of Agency would not be a genuine experience, but it would be the result of an inference that the brain makes in the attempt to understand the causes of actions and of the resulting events, which would actually be unconscious. However, under some specific conditions, humans might be induced to believe that their thoughts were the causes of events. Wegner identified three principles that can foster the impression of free will: priority, consistency and exclusivity. In particular, if the thought on an action occurs before moving (*priority*), is consistent with the performed action (*consistency*) and no other explanation for that action is present (*exclusivity*), an individual will attribute the authorship of the action and the resulting event to himself. Indeed, some evidence exists that individuals might erroneously assume that they caused an event, despite having no actual role in the causal chain.

For instance, in a famous experiment Wegner and Wheatley asked their participants to move a cursor on a monitor until a stop signal occurred (Wegner & Wheatley, 1999). Pictures of different objects were represented on the screen. The cursor was controlled by means of a mouse together with another individual, who unbeknownst to the participant, was a confederate. While performing the task, participants wore a pair of headphones and heard a series of words, some of which were primes, since they corresponded to objects available on the screen. Importantly, in some trials, the *confederate* took control of the cursor and stopped it on the primed object. At the end of each trial, participants were asked to rate how much they had intended to make each stop, irrespective of their partner’s intentions, by putting a mark on a scale that had as endpoints “I allowed the stop to happen” (no intention) and “I intended to make stop” (full intention). The experimenters then converted the marks to percentages representing the intensity of participants’ intention for a certain trial. The results of the study indicated that participants often reported that they intended to make the cursor stop on the object, despite it was not them to exert control. Wegner and Wheatley experiment suggested that the mere correspondence between a prior intention (or thought) and an effect can induce an illusory sensation of causing the event.

This pattern of results was later confirmed by other studies that found that the Sense of Agency over certain outcomes is enhanced by corresponding primes presented before the action (Linser & Goschke, 2007; Moore, Wegner, & Haggard, 2009; Sato, 2009). A higher feeling of control over primed outcomes was observed both when the Sense of Agency was assessed by means of implicit (i.e., Intentional Binding. Moore, Wegner, et al., 2009) and explicit (i.e., questionnaires and likert scales ranging from no control to full control. Linser & Goschke, 2007; Sato, 2009) measures. As explained by Wegner himself, the theory of apparent mental causation does not necessary imply that conscious will cannot cause actions, but rather that "the mind's own system for computing causal relations […] is no more than a rough-and-ready guide to such causation" (Wegner, 2003) In essence, Wegner theory suggested that processes independent of motor control, such as inference and prior expectations can contribute to the Sense of Agency. The point that prior expectations can shape the Sense of Agency was recently developed in cue-integration theories, that view the Sense of Agency as a multi-faceted experience that involves different levels of subjective experience.

1.2.4 Cue-integration Theories

Recent theories extended previous proposals so that different explanations and components of the experience of agency could be integrated. These can be defined as "cue-integration" theories, since they all suggest that the Sense of Agency relies on a wide number of motoric and non-motoric cues. Hence, these theories suggest that neither the comparator model, nor other theories alone can fully explain the Sense of Agency.

The necessity of an integrative approach was already put forth by Wegner and Sparrow (2004). These authors suggested that that an individual might rely on different sources of information to decide whether she\he or someone else was the cause of a certain event. These might include sensorimotor information, information about social context and action-relevant thoughts (Wegner & Sparrow, 2004).

Recently, two formal models were proposed: the “Two-Step Account” (Synofzik et al., 2008a, 2008b) and the “Cue-integration” model (Moore & Fletcher, 2012).

The Two-Step Account suggests that the Sense of Agency cannot be considered a unitary experience, but rather that it might comprise two levels (see **Figure 2**): the Feeling of Agency and the Judgment of Agency.

At the level of the Feeling of Agency, the individual perceives to be the author of the action without being able to form an explicit attribution of the action to himself. The feeling of agency includes a non-conceptual, sensorimotor representation that an action is or isn’t performed by oneself. Perceptually, the feeling of agency results in a “rather diffuse sense of a coherent, harmonious ongoing flow of action” (Synofzik et al., 2008a). A reduction of the feeling of agency results in experiencing the action as “strange, peculiar and not fully done by me”.

On the other hand, Judgments of Agency would be explicit and conceptual representations of being the author of an action. At this level, the individual makes conscious inferences that allow him to attribute causality to himself or to another specific agent.

These two levels might interact in a hierarchical fashion. People mostly do not need to form explicit judgments of agency. Under normal circumstances individuals only experience a feeling of agency, which suffices to inform them that actions are leading to the intended consequences. However, in certain occasions the individual might need to form explicit judgments to decide if he is or is not in control. For instance, unexpected consequences of actions and ambiguous situations, such as those involving other actors, might generate the need for the individual to reason about the causes of a certain event.

On the other hand, judgments of agency could also influence the perceptual level: for instance, the belief that one could not be responsible for an action could reduce the feeling of agency.

This view of the Sense of Agency cannot be explained by the Comparator Model alone. Indeed, the two-steps account is accompanied by a profound criticism of the comparator model, as it might fail to explain circumstances where individuals experience control despite unpredicted events, or how causality is attributed to other specific individuals (as discussed in section 1.2.1). The presence of error signals might indeed reduce the Sense of Agency, but other sources of information might contribute to it. At the level of the feeling of agency, motor cues might be integrated by means of a weighting process. This weighting process might inform other modules, such as beliefs and conceptualization, when evidence in favor of oneself as responsible for action is insufficient. On the other hand, beliefs and attitudes could also modulate this weighting process. The Sense of Agency would thus arise by a combination of bottom up and top-down processes.

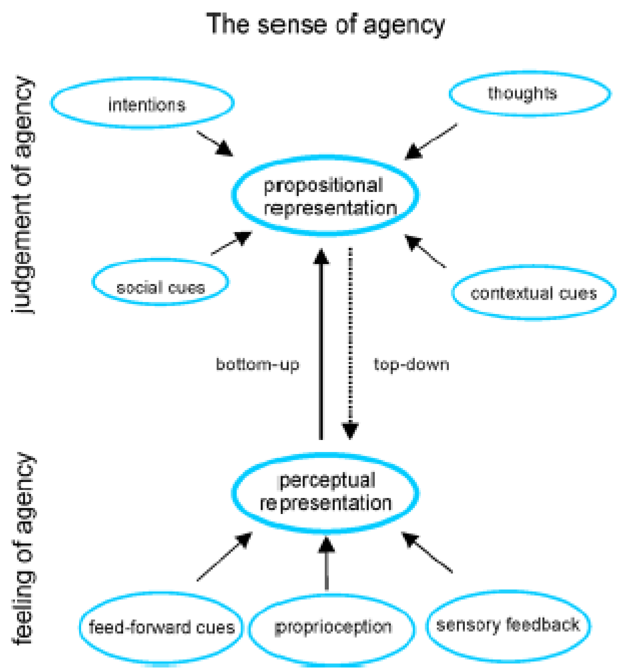

Figure 2. The two-step account of agency. Sense of Agency might be composed of two interactive levels: a non-conceptual and perceptual level – the Feeling of Agency – and a conceptual and explicit level that is involved in the attribution of causality to oneself or to other specific agents - Judgments of Agency.

The idea that multiple cues could might be integrated to generate and modulate the Sense of Agency was further developed in the "Cue-Integration" model by Moore and Fletcher (2012). These authors proposed that multiple cues might contribute to the Sense of Agency, such as internal sensorimotor information (Blakemore et al., 2002) and external cues (Wegner, 2003). To explain how different sources of information might be combined, Moore & Fletcher were inspired by recent Bayesian models of perception. Moore and Fletcher suggest that information from different sources of information is integrated by attempting to minimize uncertainty with respect to whether an individual was the agent of an action and the cause of the resulting events. Different cues individually carry information about the probability that oneself is the cause of an event. By combining these cues, the brain tries to estimate the probability associated to the fact that the individual was causally involved in determining a certain outcome. Additionally, a certain source of information might be considered more or less *reliable* and weighted accordingly. As a consequence, not all sources of information are equally relevant: for instance, it was suggested that internal sensorimotor information might be a stronger cue as compared to external sources of information (Moore, Wegner, et al., 2009). But under some conditions, such as experimental settings or, more dramatically, in some clinical disorders such as Schizophrenia, the reliability of sensorimotor cues could be reduced, leading the individual to rely more or external information (Moore & Fletcher, 2012). One important insight of this theory is that, by referring to a Bayesian framework and to the concept of reliability, it supports the idea that prior *expectations* might be fundamental for the Sense of Agency.

The relevance of prior expectations and the idea that multiple cues might contribute to the Sense of Agency are crucial in the two studies that I will present in chapters 2 and 3. Indeed, our experimental questions were related to how the violation of expectations relative to two action cues – respectively movement and the achievement of the goal of the action – contribute to modulate the Sense of Agency.

1.3. Effects of different action cues on the Sense of Agency

As suggested by cue-integration theories, multiple motor and non motor sources of information might contribute to the shape the Sense of Agency. In my doctoral studies, we addressed this issue by devising a novel paradigm that allows the manipulatation of multiple action features at the same time.

We reasoned that only by means of a simoultaneous manipulation of different action cues it is possible to understand their relative contribution to the Sense of Agency. In other words, whether the *means* (the movements) are as important as the *ends* (the goal) for the Sense of Agency.

In doing this, we were inspired by previous studies that found a connection between the error monitoring system and the experience of control. As descibed before, the fact that errors lead to a reduction of the Sense of Agency was one of the main proposals of the the Comparator Model. Despite the criticism that this model received, even the most recent cue-integration theories of the Sense of Agency agree that errors and *prediction errors* are likely to influence the experience of agency. Prediction errors can be defined as a mismatch between prior expectation and reality (den Ouden, Kok, & de Lange, 2012). In the context of motor cognition, they can be viewed as the difference between the predicted and actual outcome of an action (Haggard, 2017).

Indeed, the influence of errors and of prediction errors on the Sense of Agency was strongly supported by empirical research (e.g. Caspar, Desantis, Dienes, Cleeremans, & Haggard, 2016; Daprati et al., 1997; David, Skoruppa, Gulberti, Schultz, & Engel, 2016; Farrer et al., 2008; Kühn et al., 2011; Pavone et al., 2016; Pezzetta, Nicolardi, Tidoni, & Aglioti, 2018; Sato & Yasuda, 2005). I will provide a detailed description of previous evidence of this in the introduction of the first experiment reported in this manuscript (section 2.2).

Interestingly, most Sense of Agency studies seem to i) neglect the fact that actions are generally performed to obtain a certain goal in the external environment and ii) focus on the influence of a specific cue, without considering that in everyday actions people might rely on different sources of information to decide whether they are in control. Here I will focus on the description of some previous studies that inspired our main experimental question: whether in a goal-directed action, information about movement execution and goal achievement is equally relevant for the Sense of Agency.

1.3.1 Violated expectations *either* related to the movement or the outcome reduce the Sense of Agency

Previous studies provided evidence that violated expectations concerning either movement execution or goal achievement impair the Sense of Agency. Typically, these studies focused on one or the other action cue.

Studies that investigated the role of movement control for the Sense of Agency typically introduced visual information that was inconsistent with participants expectations: for instance, when participants performed a movement with their index, they could observe a movement with the thumb or a movement with a different trajectory (e.g. Farrer, Franck, Georgieff, et al., 2003; Farrer, Franck, Paillard, & Jeannerod, 2003; Padrao, Gonzalez-Franco, Sanchez-Vives, Slater, & Rodriguez-Fornells, 2016; van den Bos & Jeannerod, 2002). Additionally, participants could also observe delays between the executed and observed action (Daprati et al., 1997; Farrer et al., 2008; Franck et al., 2001). Typically, these studies investigated explicit aspects of the Sense of Agency: in some cases, participants were asked to provide a "yes" or "no" answer to questions such as if "the observed movement was the one they performed or if it was someone else's movement" (Farrer et al., 2008; Farrer, Franck, Georgieff, et al., 2003; Farrer, Franck, Paillard, et al., 2003; Franck et al., 2001); in other cases, participants were asked to complete questionnaires, where the items (e.g., "Most of the time, the movements of the virtual hand seemed to be my movements") assessed their experience of control under conditions of congruent and incongruent movement observation. In these studies, answers were collected by means of Likert scales, ranging from strongly disagree (e.g., -3) to strongly agree (e.g., +3) (Padrao et al., 2016). The results of these studies indicated that incongruent movements consistently reduced the Sense of Agency over the observed action. However, it should be noted that these studies involved the execution of a movement that did not result in any outcome in the external environment.

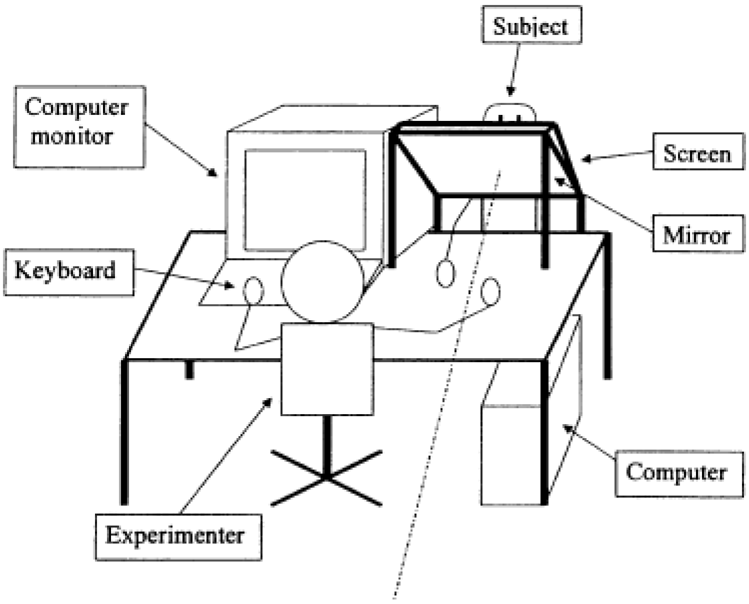

Figure 3 Typical example of manipulation of movement information. Typically, studies that investigated the Sense of Agency for movements involved the observation of a moving hand from a first-person perspective. Participant real hand was generally hidden by a monitor, and visual information could be congruent or incongruent with participant's action. As an example, this image was taken by Van den Bos and Desmurget (2002) and represents their experimental set-up.

Other studies focused on understanding how the occurrence of an unexpected outcome would impair the Sense of Agency, without manipulating movement information (Barlas & Kopp, 2018; Kühn et al., 2011; Sato & Yasuda, 2005; Spengler, von Cramon, & Brass, 2009).

One way in which this issue was investigated is by means of priming (e.g. Linser & Goschke, 2007; Moore, Wegner, et al., 2009; Sato, 2009). In these studies, participants were presented with a prime indicating which outcome would have followed the action (for instance, left pointing arrows). The effect of the action could either be the primed outcome (left pointing arrows) or a different one (e.g. right pointing arrows). These studies found that both implicit and explicit levels of the Sense of Agency (see paragraph 1.2.3 for more information about the measures employed by these studies) were reduced when the effect of the action was not the one that was primed, suggesting that expectations about which outcome will follow one's action modulate the experience of control.

Another way in which expectations about outcomes can be violated is found in studies that included an association phase, where participants learned that a certain action (e.g. button press with the left index finger) would be followed by a specific outcome (e.g. high-pitch tone) (Kühn et al., 2011; Sato & Yasuda, 2005). Then, in the experimental phase participants were presented with the previously associated tone or a different one (e.g. a low-pitch tone). These studies measured explicit levels of the Sense of Agency: at the end of each trial, participants reported if they believed it was them or the experimenter to produce the tone, by means of a visual analogue scale ranging from 1 ("Me") to 100 ("Somebody else"). These studies found that unexpected outcomes - as they were incompatible with respect to the previous association - reduced the Sense of Agency.[2]

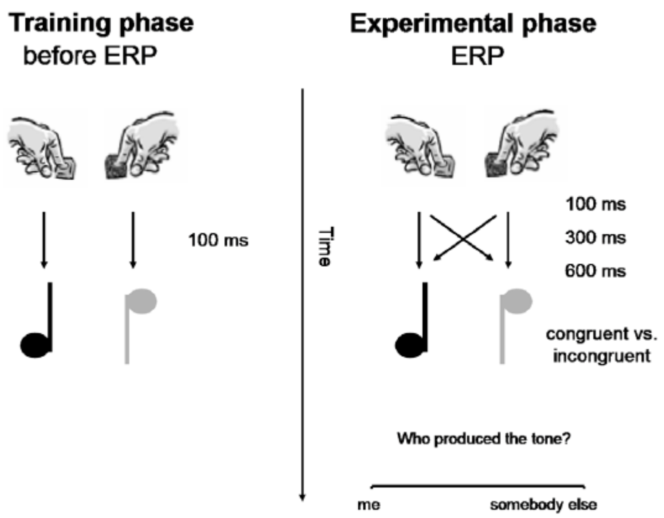

Figure 4 Typical example of outcome manipulation. A common procedure to evaluate the influence of expectations about the outcome on the Sense of Agency involves the presentation of an unexpected outcome following participant's action. For instance, in a study by Kuhn and colleagues (2011) participants learned a mapping between a left\right index button press, and a following low\high pitch tone. In the experimental phase, participants heard a congruent or incongruent tone with respect to the learned mapping. Sense of Agency

[2] It should also be noted that some studies that employed intentional binding as a measure of Sense of Agency failed to find a modulation of the identity of the outcome – whether it was congruent or incongruent with previous mapping – on implicit Sense of Agency (Desantis, Hughes, et al., 2012; Haering & Kiesel, 2014). Hence, despite some studies indicate that predictions about the outcome of the action can modulate the Sense of Agency, their conclusions should receive further support by means of new studies, measuring both implicit and explicit aspects of the Sense of Agency.

was lower when the action was followed by the unexpected as compared to the expected tone (Figure from Kuhn et al., 2011).

Hence, previous studies suggest that both unpredicted movements and outcomes are associated to a reduction of the Sense of Agency. However, at least two remarks can be made with respect to these findings. The first one is that these studies manipulated *either* movement or outcome information. The implication of this is that it is remains unclear whether these action-cues are equally important for the Sense of Agency. Only two previous studies (Caspar, Desantis, et al., 2016; David et al., 2016) tackled this issue by combining manipulation of movement and outcome information. A detailed description of the procedures and results of these two studies can be found in the introduction and in the discussion of the first behavioral study reported in the thesis (sections 2.2 and 2.5). In summary, while David and colleagues finding suggested that information about the outcome of the action might be more relevant than movement information, Caspar and colleagues found that both might influence the Sense of Agency.

However, another fundamental aspect to be considered - with respect to these two studies and to previous ones that manipulated the outcome of the action - is whether their outcome can be considered a "goal". Indeed, the outcome of the studies reviewed in this section was associated with a certain movement by means of a learning procedure, or by means of priming. Thus, whether in these studies participants *intended* to produce a certain outcome, or rather simply expected that a specific outcome would follow their movement remains uncertain. As I will argue in the next section, some studies focused on the investigation of the Sense of Agency in genuine goal-directed actions.

1.3.2 Sense of Agency in goal-directed actions

Some studies investigated the Sense of Agency in goal-directed actions. In these studies, the performed (or observed) actions were aimed at obtaining a specific goal in the external environment, which is similar to what happens in most daily actions. These studies generally involved tasks where participants had to control a cursor on a monitor using a joystick, a mouse or keypresses in order to reach a certain target (the goal) on the screen (Kumar & Srinivasan, 2017; Metcalfe, Eich, & Miele, 2013; Metcalfe & Greene, 2007; Wen, Yamashita, & Asama, 2015b, 2015a). The experimenters generally manipulated responsiveness of the input device to the commands of the participants (for instance introducing lags between keypress and movement of the cursor), which made achieving the goal more difficult. Although these studies reported slightly different patterns of results, they generally agree that both reduced responsiveness to commands and a failure to achieve the goal are associated to a reduction of the Sense of Agency, both at implicit (i.e. intentional binding, e.g. Kumar & Srinivasan, 2017) and explicit levels. In this latter case, participants reported how much control they experienced in a certain trial by choosing a value comprised between 1 (no control) and 9 (full control) (Wen, Yamashita, & Asama, 2015b) or between 1 (no control) and 100 (full control) (Wen, Yamashita, & Asama, 2015a). In particular, these studies suggest that achieving the goal of the action might not be enough to generate a Sense of Agency, if intermediate steps between motor commands and distal outcomes do not take place as expected. In other words, also the proximal consequences of the action might inform the Sense of Agency (Metcalfe et al., 2013; Metcalfe & Greene, 2007; Wen et al., 2015b). A more detailed description of some of these studies (Metcalfe et al., 2013; Metcalfe & Greene, 2007) can be found in the discussion of the first study reported in this manuscript (section 2.5).

However, it should be noted that these studies manipulated the proximal results of a movement – the responsiveness of input devices to motor commands – rather than information about movement itself.

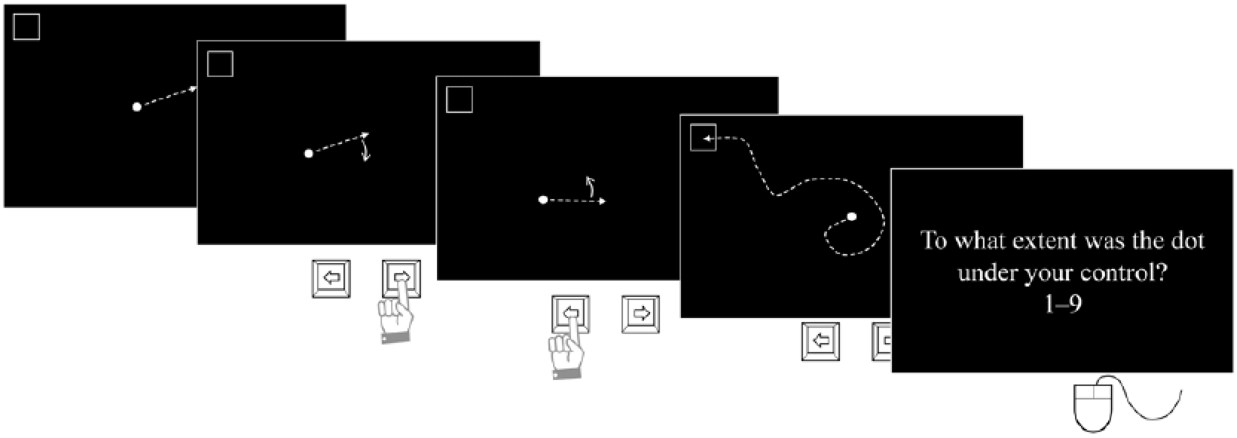

Figure 5. Investigation of the Sense of Agency in a goal-directed action. Experiments studying the Sense of Agency in a genuine goal-directed action typically involve the control of an object on a screen in order to reach a target. The achievement of the goal of the action can be made more or less easy by means of experimental manipulations, such as the introduction of noise in the control of the object. After each trial the participant reports a subjective rating of how much in control she\he felt in that trial (figure from Wen et al., 2015a).

Additionally, a recent line of studies (Pavone et al., 2016; Pezzetta et al., 2018) in fully immersive virtual reality explored the way in which a success or failure to achieve the goal of the action modulates the Sense of Agency. Pavone and colleagues (2016) and Pezzetta and colleagues (2018) asked their participants to observe a virtual body performing goal-directed actions – grasping a glass with the right hand - both from a first and a third-person perspective. In some trials, the virtual hand deviated from the expected trajectory and missed the glass, thus making an error. After observing the virtual action, participants were either asked to report their Sense of Embodiment (Sense of Ownership + Sense of Agency), by answering to the question "how much did you feel the avatar's arm belonged to you?" by uttering a number between 1 ("not mine") and 5 ("mine") (Pavone et al., 2016); or their Sense of Agency and Sense of Ownership separately (Pezzetta et al., 2018). In the study by Pezzetta and colleagues, participants were asked an explicit evaluation of their Sense of Agency by judging how much they felt in control of the arm by means of a visual analogue scale ranging from 0 (no control) to 100 (maximal control). In analogy with previous studies that found that a vicarious Sense of Agency can be experienced for movements of limbs that are in an anatomically plausible position with respect to one's own limbs (Tieri et al., 2015; Wegner et al., 2004), the mere observation of a successful reach-to-grasp from a first-person perspective elicited a feeling of control over the virtual action. Conversely, observation of an erroneous reach-to-grasp movement reduced the Sense of Agency. However, one important point with respect to these studies is the following: it is not clear whether the Sense of Agency was reduced by the unexpected trajectory of the arm or by the failure to grasp the glass. In other words, whether it was the unexpected movement or the failure to achieve the goal of the action to impair the Sense of Agency.

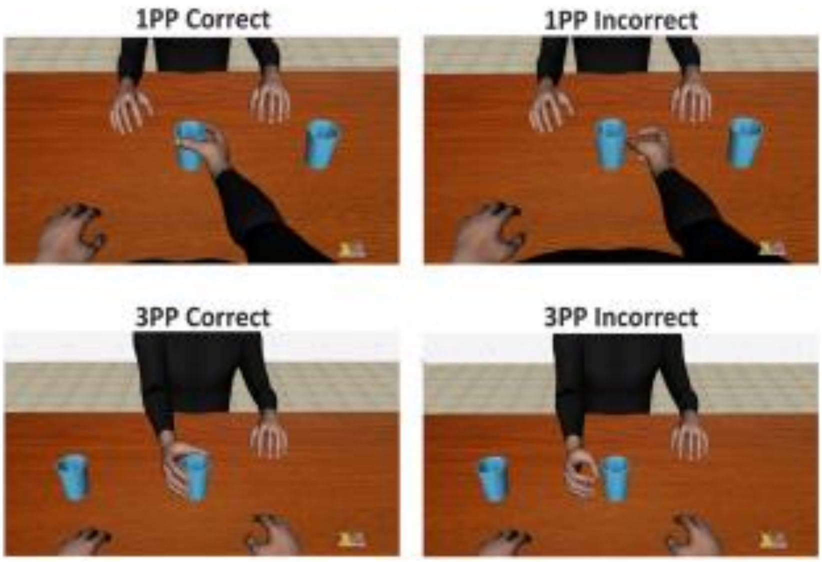

Figure 6. Observation of a correct or erroneous goal-directed action of a virtual avatar. The manipulations introduced by Pavone and colleagues (2016) and Pezzetta and colleagues (2018) in the virtual scenario. On the panel on the top-left, a correct reach-to-grasp movement from a first-person perspective is represented. The top-right panel shows an erroneous reach to grasp from the same perspective. Correct (bottom-left) and erroneous (bottom-right) reach to grasp movements could be observed also from a third-person perspective. Figure from Pavone et al., 2016.

1.4. Aims of the present thesis

As argued in the introduction, some recent theoretical models of the Sense of Agency suggest that this experience might rely on the integration of various cues. However, only a few studies (Caspar, Desantis, et al., 2016; David et al., 2016) manipulated in the same paradigm information about movement and information about the outcome of the action. Additionally, studies that involved the investigation of genuine goal-directed actions typically manipulated the responsiveness of input devices to commands, rather than movement information itself. Hence, the respective roles of information about movements and about achievement of the goal of the action remains uncertain. To disentangle the relative contribution of these two action components for the Sense of Agency, we devised a novel paradigm where participants perform a simple goal-directed action – pressing a button of a certain color – while they observe a virtual hand performing an action in a virtual scenario from a first-person perspective. The virtual action can be similar or different with respect to the one executed by the participant, and information about movement and the achievement of the goal of the action can be independently and simultaneously manipulated. A detailed description of the paradigm, and the results of two behavioral studies where we employed it are reported in chapters 2 and 3.

In the first study (Chapter 2) we sought to understand how violated predictions concerning movement execution and the achievement of the goal of the action can influence the Sense of Agency.

In the second study (Chapter 3), we compared the effects of movement and goal achievement manipulation respectively in freely chosen and cued actions. In particular, we were interested in understanding whether these two action cues exert the same or a different influence when the individual can choose the goal of the action, or when it is defined by an instruction.

Additionally, a second aim of these two studies was to understand whether unexpected movement and goal related information - i.e., prediction errors - would also affect participant’s behavior and lead to behavioral adjustments, similarly to the commission of real errors (Danielmeier & Ullsperger, 2011)

Finally, in the Appendix I report preliminary results of an experiment where we investigated the neurocognitive processes underlying a different but related topic: the capacity of the individuals to exert agency, i.e., to control one's own ocular movements when one is exposed to potentially distracting social stimuli (other's gaze). We used a non-invasive brain stimulation technique (i.e., Transcranial Magnetic Stimulation) to investigate the neural correlates of controlling oculomotor movements when exposed to others' gaze movements. In particular, we used a dual pulse Transcranial Magnetic Stimulation paradigm to temporary interfere with the activity of the right Frontal Eye Fields (rFEF) and of the right Posterior Parietal Cortex (rPPC), which have been shown to contribute in controlling the influence of distracting gaze and hand-gestures, respectively. We measured participant's oculomotor behavior by means of an eye-tracker. Our preliminary results suggest that control over one's own gaze is reduced when the model moved his eyes in the opposite direction with respect of the cue. Additionally, we provide initial evidence that stimulation of FEF resulted in worse performance.

2. Violation of expectations about movement execution and goal achievement leads to Sense of Agency reduction

2.1 Abstract

The controlling of one's own movements and their impact on the external world generates a feeling of control referred to as Sense of Agency (SoA). SoA is experienced when actions match predictions and is reduced by unpredicted events. The present study investigated the contribution of monitoring two fundamental components of action -movement execution and goal achievement- that have been most often explored separately in previous research. We have devised a new paradigm in which participants performed goal-directed actions while viewing an avatar's hand in a mixed-reality scenario. The hand performed either the same action or a different one; simultaneously or after various delays. Movement of virtual finger and goal attainment was manipulated so that they could match or conflict with the participants' expectations. We collected judgments of correspondence (an index of SoA that overcomes the tendency to over-attribute actions to oneself) by asking participants if the observed action was synchronous or not with their action. In keeping with previous studies we found that monitoring both movement execution and goal attainment is relevant for SoA. Moreover, we expanded previous findings by showing that movement information may be a more constant source of SoA modulation than goal information. Indeed, an incongruent movement impaired SoA irrespective of delay duration, while a missed goal did so only when delays were short. We suggest that the ability to simultaneously manipulate multiple action features makes our novel paradigm suitable for investigating the contribution of different sub-components of action in healthy and clinical populations to SoA.

2.2 Introduction

The controlling of one's own movements and their impact on the external world generates a feeling of control referred to as *Sense of Agency* (SoA; Moore & Fletcher, 2012; Tsakiris, Longo, & Haggard, 2010). SoA is put forth as a key element of the Self (Daprati et al., 1997; Gallagher, 2000) and is fundamental to the development of a feeling of responsibility that fosters social cohesion (Frith, 2014). Both "prospective" and "retrospective" accounts have been proposed to explain SoA (see Haggard, 2017 for a review). Prospective accounts suggest that SoA is generated by processes that take place before action execution, such as action selection, which shows SoA to be higher when action selection is smooth (Chambon et al., 2013; Sidarus, Vuorre, & Haggard, 2017a; Wenke et al., 2010). Retrospective accounts focus on the role of processes that take place after action execution; such as monitoring the consequences of actions, which shows higher SoA to be experienced when actions unfold as predicted (Blakemore, Frith, & Wolpert, 1999, 2001; Blakemore, Oakley, & Frith, 2003; Blakemore, Wolpert, & Frith, 2000; Frith, Blakemore, & Wolpert, 2000; Wegner & Wheatley, 1999). In spite of the differences between these accounts, it is widely acknowledged that detection of discrepancies between planned and actual consequences of the action leads to a decrease of SoA. However, little is known about how and to what extent different types of prediction errors (e.g., related to the correctness of the movement, to the actual achievement of the targeted goal) affect SoA. Consider the case of a soccer player about to shoot a penalty: the player plans the shot and expects to score. If the planned movement is correctly performed and the goal is scored, no mismatch is identified by the player. However, the player may have to deal with occasional errors that could involve the execution of the movement (e.g., a clumsy performance), the achievement of the goal (e.g., the goalkeeper catches the ball), or both.

Will the player experience the same level of agency in each scenario?

The idea that some errors may impair SoA more deeply than others can be found in the renowned example of Maradona who scored a goal by touching the ball with his hand. In doing so, the

Argentinian champion lead his team to win the world cup by scoring with an unconventional (and forbidden) movement. Under the assumption that he hit the ball with his hand involuntarily, the example begs the question: how much control is experienced when a goal is achieved with an unplanned movement?

Apart from football, we constantly perform goal-directed actions in everyday situations, which can be as simple as grasping a glass. By failing in completing such actions, we experience a discernible reduction in our feeling of control (Pavone et al., 2016; Spinelli, Tieri, Pavone, & Aglioti, 2017). As in the case of the soccer player, we may fail or succeed in the presence of a clumsy motor performance or changes in the external environment.

Although this type of dissociation may bear theoretical and practical implications, previous research does not resolve the incertitude regarding whether the reason behind the failure makes any difference to SoA.

This is due to the fact that the link between action monitoring and SoA was traditionally addressed by selectively investigating the effects of either movement information *or* goal achievement. The contribution of movement information to SoA has been traditionally studied by manipulating the degree of correspondence (i.e., congruency) between an executed and an observed movement (Daprati et al., 1997; Farrer et al., 2008; Fourneret & Jeannerod, 1998; Padrao et al., 2016; van den Bos & Jeannerod, 2002). A reduction of SoA has been consistently reported for incongruent movements. The influence of goal achievement on SoA has been investigated with tasks resembling videogame interfaces. The experimenters systematically varied the ease by which a target depicted on a computer screen could be reached by means of an input device (Kumar & Srinivasan, 2017; Metcalfe et al., 2013; Metcalfe & Greene, 2007): failure to achieve the goal was associated with a loss of SoA. Direct manipulation of the outcome of the action (e.g., a sound or a visual event following participant's action) reduces SoA when the outcome is different than predicted (Kühn et al., 2011; Sato & Yasuda, 2005) or when the outcome is delayed with respect to movement execution (e.g., Farrer, Valentin, & Hupé, 2013; Spengler, von Cramon, & Brass, 2009).

Despite the importance of manipulating movement and goal information within the same experiment in order to understand their impact on SoA, to the best of our knowledge only two recent studies on this issue have been published thus far. In the first, David and colleagues (2016) asked participants to observe a virtual hand depicted on a monitor (David et al., 2016). A movement of the hand was reproduced in the virtual environment, and a tap with the index finger was associated with an outcome: either in the form of a sound or of a color change in the VR scenario. In each trial, the experimenters manipulated the lag between movement execution and i) movement observation *or* ii) outcome occurrence. Participants were asked to judge if the action they observed was or was not their own. Participants were found to be less likely to attribute the action to themselves when delays were introduced with respect to outcome observation. This led the authors to conclude that SoA is more sensitive to outcome than to movement information. Importantly, the authors manipulated movement and goal separately and incongruence took place only in the time domain (both the observed movement and the outcome were correct but they could occur later than expected).
In the second study, Caspar and colleagues (2016) asked participants to associate two finger movements to two successive tones (Caspar, Desantis, et al., 2016). In the experimental phase participants decided freely which finger to move and the action was followed by the expected or unexpected tone. As in the Intentional Binding paradigm (Haggard et al., 2002), perceived latency of the tone was taken as an implicit measure of SoA. Importantly, while performing the task participants observed a robotic hand moving the same or another finger. The authors found that binding between action and tone was stronger for congruent than incongruent tones only if the robot movement was also congruent. These findings suggested that SoA was sensitive to both movement and outcome information.

It is worth noting that in Caspar and collaborators (2016) participants observed a robotic instead of a humanlike hand and their action was not clearly identifiable as goal-directed, since participants may not have intended to produce certain tones, but rather they expected a specific tone to occur following the movement of a certain finger as learned in preceding training blocks. Importantly, the manipulation of movement and outcome were not simultaneous: outcomes did not immediately follow movement execution (delays between action and outcome were at least 300 ms), while the robotic hand moved immediately after the real hand movement. Thus, the roles of specific types of prediction errors in reducing SoA remain unclear.

In order to fill this gap, we sought to investigate how SoA is modulated when monitoring two fundamental subcomponents of the action at the same time, namely the congruency between performed and observed movement and the achievement of the goal. We reasoned that the simultaneous manipulation of the two sub-components in the context of an intuitive goal-directed action would allow a straightforward comparison of their respective roles for SoA.

We thus devised a novel task that involved simple goal-directed actions (i.e., to press, by raising or lowering the right index, one of two colored buttons) while participants observed actions performed by a virtual humanlike hand. The choice to use a virtual hand – instead of representing participants' real hand, for instance, by filming them with a camera – was supported by previous evidence and was aimed at simplifying our experimental setup (but see paragraph 4.4 for more considerations on this issue). Although SoA over a virtual action might not be identical to SoA over one's own limbs, previous studies suggest that individuals can experience SoA over actions performed by a virtual body (David et al., 2016; Padrao et al., 2016; Pavone et al., 2016; Pezzetta et al., 2018; Tieri et al., 2015) and that SoA is reduced when a virtual hand performs an incongruent or delayed movement with respect to participant's actual movement (David et al., 2016; Padrao et al., 2016). Hence, we reasoned that participants would be likely to experience higher SoA over congruent as compared to incongruent virtual movements. It is reasonable to assume that similar results could be obtained by showing participants congruent or incongruent movements of their own hand. However, it should be considered that by using a virtual hand we could isolate the contribution of movement information on SoA from the influence of other sources of information, such as the morphological appearance of participant's real hand. This strategy is similar to previous studies that employed gloves to minimize the possibility that morphological information could be used as a cue to agency (Daprati et al., 1997;

Imaizumi & Asai, 2015; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005; Weiss, Tsakiris, Haggard, & Schütz-Bosbach, 2014). In line with this, the use of identical virtual stimuli for all participants would also had the advantage to minimize the possible differences between participants with respect to their reliance on the morphological appearance of their hand to modulate their SoA. In our task, virtual actions could be congruent or incongruent with participants' real actions in terms of movement execution and/or the resulting outcome. Moreover, in order to investigate the temporal dynamics of the effects of movement and goal on SoA, we introduced delays between action execution and action observation. Causality perception and time perception are known to be closely linked and to influence each other (Desantis, Waszak, Moutsopoulou, & Haggard, 2016; Shimada, Qi, & Hiraki, 2010; Stetson, Cui, Montague, & Eagleman, 2006; Timm, Schönwiesner, SanMiguel, & Schröger, 2014; Walsh & Haggard, 2013). Indeed, representing one's own actions as the cause of certain outcomes biases time perception of the events associated with these actions (Desantis, Roussel, & Waszak, 2011; Desantis et al., 2016). For instance, expecting that specific visual stimuli will follow one's own actions (as an effect of a previous learning phase) induces the tendency in the participants to perceive the onset of the visual stimuli as occurring after their own actions (Desantis et al., 2016). Vice versa, temporal cues are known to contribute to the perception of causality and to SoA: time gaps between action and outcome reduce the sensation that the outcome results from one's own action (David et al., 2016; Franck et al., 2001; Sato & Yasuda, 2005; Shanks, Pearson, & Dickinson, 1989; Weiss et al., 2014). Hence, the introduction of delays allowed us to measure SoA by means of judgments of temporal correspondence (Weiss et al., 2014) between the executed and the observed action (henceforth called Synchrony Judgments). We chose this measure since Synchrony Judgments rely on the same information employed to attribute an action to oneself or to someone else (Weiss et al., 2014). This may be suggested by interesting fMRI data (Farrer et al., 2008) that the inferior parietal cortex is activated both when participants notice delays between their action and visual feedback of their action (i.e., temporal discrepancy) and when they attribute the visual feedback to someone else (i.e., action authorship discrepancy). Reporting a discrepancy between an action and its outcome may thus be equivalent to expressing an agency judgment (Weiss et al., 2014). Besides that, it is possible that Synchrony Judgments might capture also variations in the Sense of Ownership (SoO) - *the experience that my body is 'my own' and that I am the one who is undergoing an experience* (Gallagher, 2000; Tsakiris et al., 2010) - of the participants. The point of a possible confusion between different aspects of SoA and SoO was also reported for previous studies that investigated SoA with measures similar to the one we employed (Gallagher, 2012, 2013; Gallagher & Zahavi, 2007). The choice of Synchrony Judgments might be associated to two more issues. First, individuals might in principle experience control over effects that are delayed with respect to their action, despite recognizing the asynchrony between action and effect; conversely, they might not feel in control of events that take place shortly after their actions. However, it should be considered that several previous studies showed that individuals tend to report higher Sense of Agency over events that immediately follow their actions and lower Sense of Agency for identical outcomes, if the time gap between action and outcome is increased (David et al., 2016; Franck et al., 2001; Sato & Yasuda, 2005; Shanks et al., 1989; Weiss et al., 2014). Second, it is possible that Synchrony Judgments might fail to fully capture the possible variations of the feeling of control induced in the participants by our experimental manipulations, or they measure other aspects of action awareness not related to the feeling of control. This may be due to the fact that Synchrony Judgments are an indirect measure of SoA: contrary to direct measures – which are generally in the form of questions such as "was the observed movement the one you performed or was it someone else's movement?" (e.g. Farrer et al., 2008; Farrer, Franck, Georgieff, et al., 2003; Farrer, Franck, Paillard, et al., 2003; Franck et al., 2001) to which the participant answers with a "yes" or "no", or of likert scales or Visual Analogue Scales that participants use to report how much control they experienced under a certain experimental condition (e.g., Padrao et al., 2016; Pezzetta et al., 2018; Tieri et al., 2015) - Synchrony Judgments do not require participants to make an overt reference to their feeling of control. However, it should be noted that another indirect, time-related measure – i.e., Intentional Binding – is often reported a reliable marker of the Sense of Agency. Intentional Binding consists of a time compression between action and outcome, resulting from the fact that a) a self-produced outcome is perceived sooner than an identical outcome produced by external causes, and b) that a voluntary movement is perceived later than a passive movement (Haggard & Clark, 2003; Haggard et al., 2002). This effect has been replicated in numerous following studies (see for instance Moore & Obhi, 2012, for a review). Interestingly, "interval estimations" have been recently used as a proxy for intentional binding (Barlas & Kopp, 2018; Caspar, Christensen, Cleeremans, & Haggard, 2016; Moore, Wegner, et al., 2009): participants are asked to report the amount of time (in milliseconds) that passed between their action and an outcome. Shorter estimated intervals are considered to indicate higher SoA. We reasoned that similarly to interval estimation, higher SoA should be associated to higher perceived synchrony between real and executed action; lower SoA should be associated to lower perceived synchrony. Additionally, choosing Synchrony Judgments as a measure of SoA may facilitate the comparison of our results with those of similar studies, possibly reducing the influence of self-attribution bias, which had been reported for explicit agency judgments (Tsakiris et al., 2005; Wegner & Wheatley, 1999; Weiss et al., 2014).

Hence, despite the limitations described above, we decided to employ Synchrony Judgments as a measure of SoA (but see paragraphs 2.7 and 4.4 for further considerations on this issue). We expected that Synchrony Judgments would be differently influenced by the type of observed action and by the introduction of incongruences.

In keeping with previous studies, we predicted that observation of both an incongruent movement (compared to congruent) and a missed (compared to an achieved) goal would lead to a reduced perceived synchrony between the participant's action and the one shown in the virtual scenario, which would indicate a diminished SoA.

Research suggests that information relative to movement kinematics may not be adequately monitored as long as the visual feedback is coherent with the goal of the action (Fourneret & Jeannerod, 1998). Therefore, we predicted that observing a failure in reaching the goal should be more relevant in diminishing SoA than observing an incongruent movement. This prediction remains consistent with the conclusions of David and collaborators.

Finally, the introduction of delays allowed us to further investigate the temporal dynamics of movement and goal monitoring on SoA.

2.3 Materials and methods

2.3.1 Participants

Thirty healthy volunteers took part in the study (fifteen males; age range: 20-32 years; mean ± standard error of the mean [s.e.m.]: 24.1 ± 0.538). All participants were right-handed, had normal or corrected-to-normal visual acuity and were naive as to the purposes of the experiment. Explanations of the experimental hypotheses were provided only after the end of the experiment. The experimental protocol was approved by the ethics committee of Fondazione Santa Lucia (Prot. CE/PROG.557) and was performed in accordance with the 1964 Declaration of Helsinki. All participants provided a written informed consent to take part in the study and received a refund of € 7.50/h.

2.3.2 Apparatus

The experiment was run by means of a Matlab (The MathWorks, Inc.) custom script and relied on the use of a mixed-reality scenario (**Figure 7, panel A**). A virtual response box (composed of two dark gray buttons attached to the upper and lower part of a transparent structure) and a virtual humanoid right limb (forearm + hand) were depicted on a computer screen.

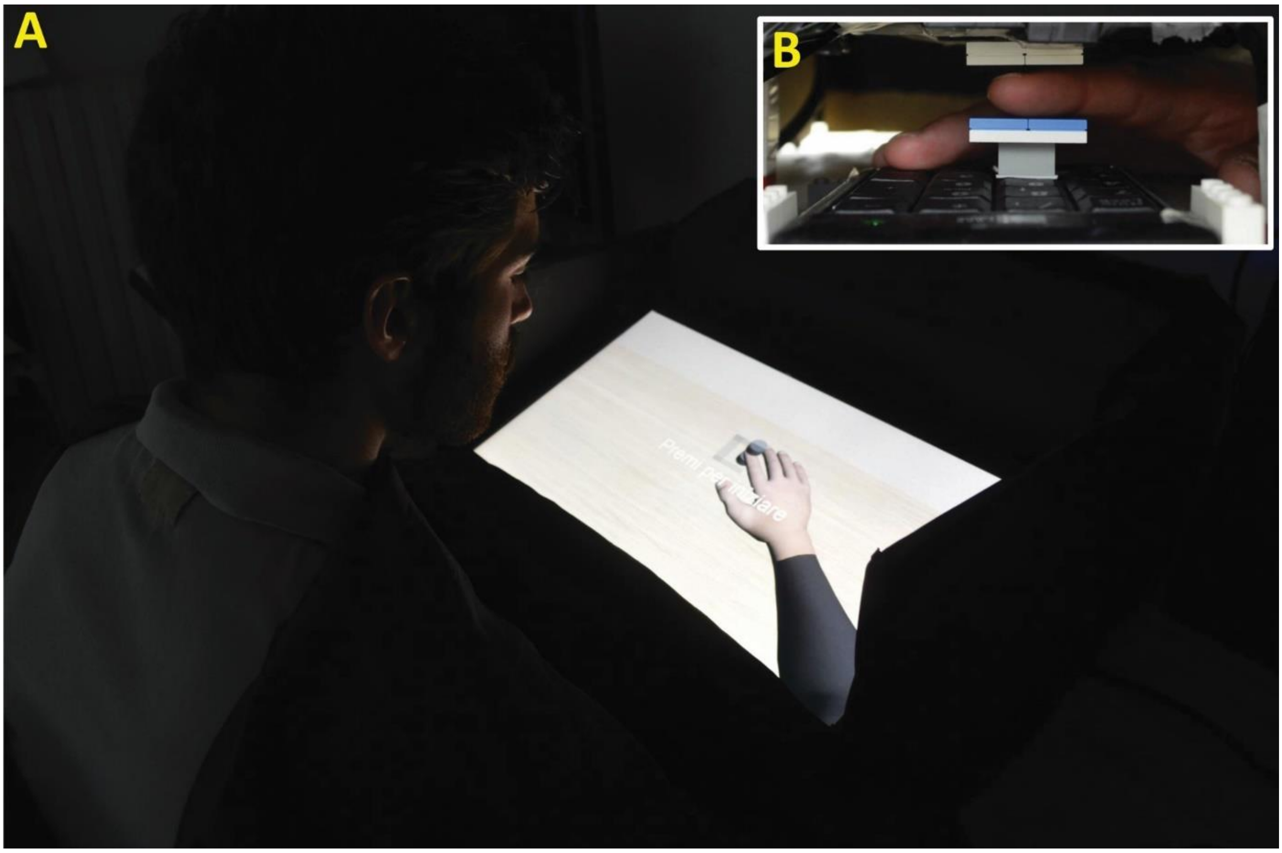

Figure 7: *Experimental set-up*. Participants sat on a chair in front of an inclined PC monitor. The virtual environment represented a virtual right limb resembling a human hand. Participant's right arm rested on the table and matched the position of the virtual limb, with the index resting between the two buttons of the real response box (A). The C-shape response box with two buttons facing each other allowed participants to perform goal directed actions (B). A keyboard on the left (not visible to the participants) allowed us to collect responses to the Synchrony Judgment questions (see main text for details). Answers were provided by pressing two keys (labeled with "S" for Synchronous, and "A" for Asynchronous) with the index and middle finger of the left hand.

The index of the virtual hand laid between the two virtual buttons of the response box. Virtual stimuli were created with 3DS Max 2011 (Autodesk, Inc) and were presented on a led monitor (Benq GL 2250-T; refresh rate: 60 Hz, resolution set to 1280 x 720 pixels) sustained in an inclined position (12.7° with respect to the horizontal plane) by a wooden structure located on a table. A rectangular hole (7.50 x 5.8 cm) at the front of the structure allowed participants to lay their right hand on the table, under the monitor and hidden from sight. A custom-made C-shaped response box, designed to record downwards and upwards movements of the index, was placed on the desk below the monitor

(**Figure 7, panel B**). This was composed of two identical numeric keypads that allowed two button presses with opposite movements. A plastic support fixed to the table (height: 7 cm) sustained the upper keypad so that the keys of the two devices were facing each other's. To facilitate input acquisition, two plastic buttons (height: 1.5 cm) with a squared, flat top face (side length: 3.2 cm) were fixated to single keys of the two keypads and aligned. The distance between the surfaces of the two buttons was adapted for each participant by inserting paper supports below the lower keypad, until the dorsal part of the distant phalanx of the index touched the superior button, while the ventral part rested on the inferior button. In this way, the key features of the virtual response box closely matched the features of the physical response box. A keyboard (not visible to participants) was positioned on the table to the left of the monitor and allowed participants to express Synchrony Judgments (see *Action-Outcome manipulation* and Figure 7 for details).

2.3.3 Procedure and Task

The study was performed in a dimly lit room. Participants sat comfortably on a chair in front of a table, at a viewing distance of approximately 40 cm from the center of the screen. They were asked to lay their right arm on the table trying to match the position of the virtual limb and to insert their index in the space between the two buttons of the response box. A black cloth covered the shoulders and the elbow joint preventing any visual discontinuity between the virtual arm and participant's real limb. Participants were asked to perform goal-directed movements following a color-based rule (see below for details and **Figure 8, panel A** for a graphical representation of a typical trial). For each trial, the two dark gray virtual buttons turned respectively to blue and or yellow. Participants were instructed to press as fast as possible the button corresponding to a given target color (blue or yellow). Importantly, for each trial the target color change could involve the upper (pressed by lifting the index finger) or the lower button (pressed by lowering the index finger).

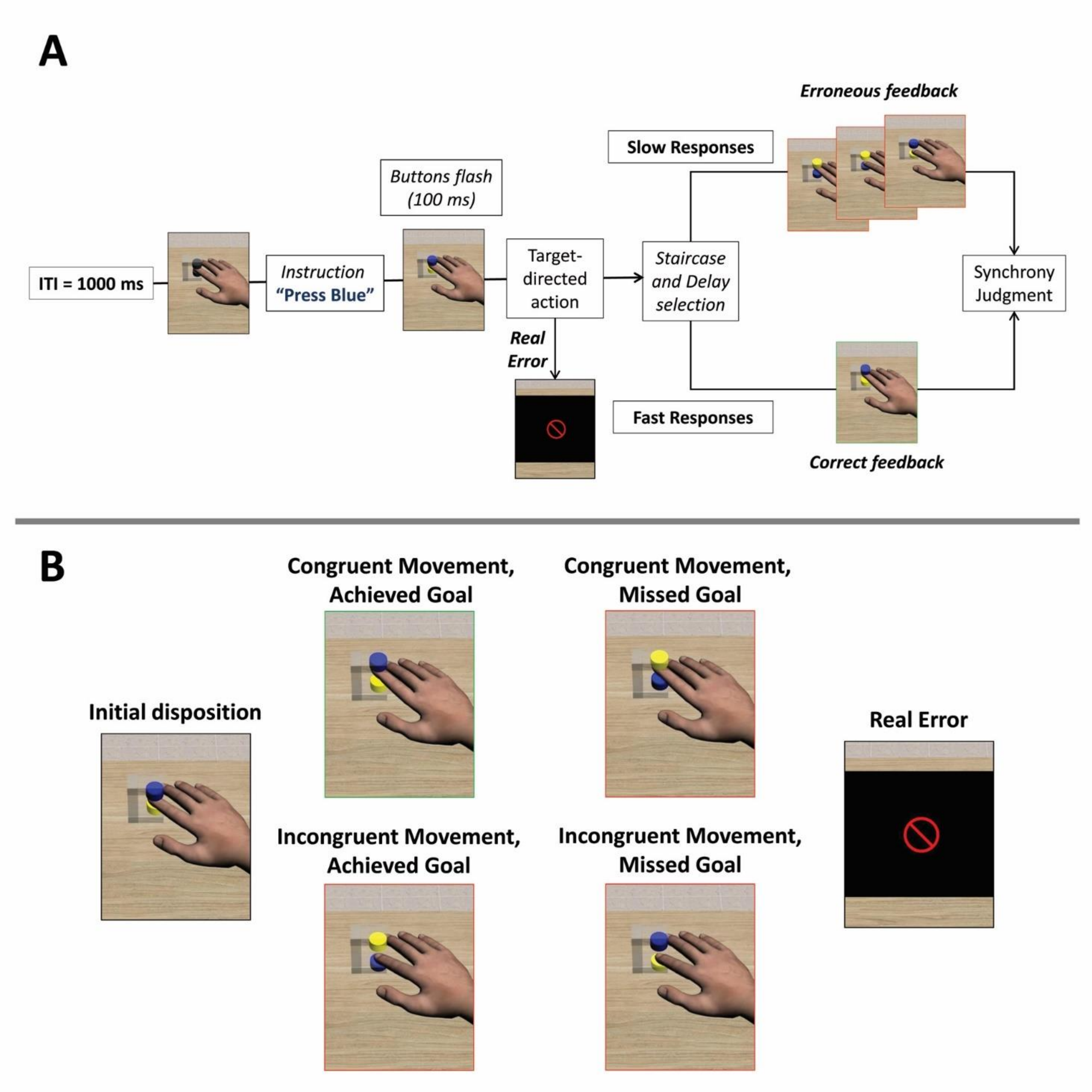

Figure 8: a) Timeline of a typical trial. For explanatory purposes, we show only the case where the color of the target button was blue. At the beginning, the color of the buttons was dark gray. After 1000 ms a text instruction reminded participants about the color of the target. After a random interval comprised of between 1000 and 1500 ms the buttons flashed once to yellow and blue for 100 ms with a random disposition. Feedback in the virtual scene was shown after a temporal delay (0, 75, 150, 225, 300 ms) only if participants pressed the correct button. The feedback consisted in a congruent (M+) or incongruent (M-) movement with respect to the one performed by the participant where the goal (i.e., pressing the target color) was achieved (G+) or missed (G-). The type of feedback depended on participant performance as evaluated by a staircase procedure. A fast press was associated with *correct* feedback (M+G+), while a slow press was associated with one of the types

of *erroneous* feedback (M+G-, M-G+, M-G-). In case of a real error, a prohibition sign appeared on screen and the current trial was aborted. Feedback was shown for 500 ms: a black rectangle covered the virtual hand and the response box, and participants were asked to provide Synchrony Judgments. Trials were separated by an inter-trial interval of 1000 ms. **b)** This panel represents the possible types of feedback participants observed after pressing a button of the response box. For explanatory purposes, we report only the case where the color of the target button was blue and where it appeared above the index, but the manipulation of movement and goal information was the same for when participants were asked to press the yellow button and when the disposition of colors was reversed. On the far left of the figure the initial disposition of the colors is reported. On the center of the figure the four possible types of feedback that followed a correct button press are displayed: one type of feedback was fully *correct* (M+G+) and was viewed if participants provided a fast response, while the remaining types of feedback were *erroneous* (M+G-, M-G+, M-G-) and one of them was observed if they provided a slow response. The panel on the right represents the prohibition sign participants viewed if they pressed the wrong button.

At the beginning of each trial an instruction is presented for one second reminding participants about the target color (i.e., "Press Yellow/Blue"). After a random interval (between 1000-1500 ms) the two buttons changed from dark gray to yellow and blue for 100 ms with a random disposition (see **Figure 8, panel A**). The color change signaled to participants to press the target button as fast as possible. In trials where participants followed the instructions correctly, the button press triggered an action of the virtual hand (i.e., a visual feedback in the virtual scene; see *Action-Outcome Manipulation* section). In trials where participants followed the instructions erroneously (e.g., the target color was "Blue" and they pressed the "Yellow" button) a prohibition sign was displayed for 2 seconds (see **Figure 8, panel B**). After this signal, the current trial was aborted and a new trial begun.

Participants performed two blocks in which the color of the target was fixed. Thus, the color of the target remained the same for the entire duration of the first block but was changed in the following block. The block order was quasi-counterbalanced across participants (16 and 14 participants started the first block with the blue and yellow color as target, respectively).

Due to the adaptive algorithm employed to determine the type of visual feedback participants observed in the virtual scene (*Staircase Procedure*. See *Action-Outcome Manipulation* for more details), the number of trials of the two blocks was not identical for each participant. Participants performed on average 247 trials (range: 223-271; s.e.m.: 1.89) in the first block and 246 trials (range: 224-281; s.e.m.: 2.12) in the second block. Hence participants performed on average 493 trials (range: 447-547; s.e.m.: ± 3.33) in the whole experiment.

Before starting each block, participants performed a practice session to familiarize themselves with the task. During the practice session, they pressed the target color that would be used in the next block. Participants performed on average 24 practice trials (range: 18-30; s.e.m.: 0.62) before the first block and 22 trials (range: 15-29; s.e.m.: 0.65) before the second block.

2.3.4 Action-Outcome Manipulation

The visual feedback was presented at different delays after participants' actual button press (0, +75, +150, +225, +300 ms). The feedback consisted of a button press in the virtual scenario, where the observed movement could be congruent or incongruent with the one participants performed (M+/M-) and the disposition of the colors of the two virtual buttons could be the same as the one preceding their input, or reversed (**see Figure 8, panel B**). Thus, by changing the disposition of the colors after the button press, the goal of the action could be either achieved or missed (G+/G-). Overall, we manipulated action-outcome expectations in four different ways: congruent movement with achieved/missed goal (M+G+ & M+G-) and incongruent movement with achieved/missed goal (M-G+ & M-G-). Therefore, one type of feedback was fully *correct* (M+G+), while the remaining types of feedback were *erroneous* (M+G-, M-G+, M-G-), since they could conflict with participants' expectations about the observed movement and/or about goal achievement. Whether participants observed correct or erroneous feedback depended on their reaction time. An adaptive algorithm (staircase procedure) was used to set up the limit to classify fast and slow responses for each trial (Walentowska, Moors, Paul, & Pourtois, 2016). The mean of the reaction times in the last two trials (the current trial and the previous one) was computed and if the reaction time in the current trial was lower or equal to the mean value we considered it a "fast" response, while if it was higher than the mean value we considered it a "slow" response. Fast responses were associated with the observation of correct feedback, while trials in which participants provided slow responses were associated with the observation of erroneous feedback. The advantage of this procedure was that the response deadline was updated throughout the experiment, which prevented habituation and fatigue while motivating participants to actively attend to the external stimulus (Walentowska et al., 2016).

Each type of erroneous feedback (M+G-, M-G+, M-G-) was presented 80 times (16 times for each delay, 8 per block), for a total amount of 120 trials per block and 240 trials for the entire study. The order of appearance of the different types of erroneous feedback was fully randomized. However, due to the characteristics of the staircase procedure, the appearance of the correct feedback (M+G+) depended on participant's reaction time. This meant that the number of M+G+ observations was not identical for each participant. Participants observed on average an M+G+ feedback 239 times (range 198-272; s.e.m.: 2.78. See Data Handling for more details). The order of delays for M+G+ was randomized.

In each of the two blocks, the first four correct button presses were always followed by the observation of a M+G+ feedback. This allowed participants to acclimatize and to start the staircase procedure for stimuli presentation. The feedback lasted on screen for 500 ms followed by the appearance of a black rectangle covering the virtual hand and the virtual response box. Participants had to judge whether the visual feedback was synchronous or asynchronous with their movement (*Synchrony Judgment* question, henceforth SJ). Participants were explicitly instructed to focus on the temporal correspondence between their movement and the feedback showed on screen, irrespective of the specific kind of feedback they observed. Answers were collected by pressing two keys (labeled with "S" for Synchronous, and "A" for Asynchronous) with the index and middle finger of the left hand. The associations between the two judgments (S and A) and the fingers (index and middle) used to provide the response were counterbalanced across participants.

2.3.5 Data Handling

We excluded from the analysis the first 4 trials of each block (i.e., trials where the staircase procedure was not operating). Trials where participants committed a real error by pressing the wrong button according to instructions (range: 0-27; mean ± s.e.m.; 5.83 ± 1.13; mean percentage of real errors across participants: 1.18%) and trials where participants failed to provide any response after buttons flashed into yellow and blue (e.g., they did not notice the disposition of the colors) were aborted (range: 0-4; 0.6 ± 0.189). This left on average 479 valid trials per participant (range: 438-512; s.e.m.: ± 2.76). In half of these trials (mean ± s.e.m.; absolute value: 239 ± 2.78; percentage value: 49.94% ± 0.298%) participants viewed a M+G+ feedback, while the remaining trials were equally divided among the three types of erroneous feedback (M+G-: absolute value: 80 ± 0.056; percentage value: 16.70% ± 0.101%; M-G+: absolute value: 80 ± 0.92: percentage value: 16.67% ± 0.099%; M-G-: absolute value: 80 ± 0.92: percentage value: 16.70% ± 0.100%). Thus, in order to perform the statistical analysis on the same number of trials per condition we implemented an algorithm to select a subset of trials equally spaced for each action-outcome*delay manipulation. By applying this algorithm, an equal number of trials for each condition was obtained for each participant (absolute value: 15.7 ± 0.085; range: 15-16).

Two dependent variables were taken into account: a) the proportion of "synchronous" answers to the Synchrony Judgments (SJs) per each experimental condition; b) the amount of time participants took to provide a SJ after receiving visual feedback on the screen. This variable will be referred to with the term Judgment Times (JTs). Moreover, the reaction times (RTs) between target appearance and button press were analyzed in order to check staircase procedure effectiveness.

The mean values of these variables were calculated for each participant for all the 20 experimental conditions, which resulted by manipulation of three factors: Movement (2 levels: M+/M-); Goal (2 levels: G+/G-); Delay (5 levels: 0/75/150/225/300 ms).

Normality was not met for some conditions when both the Kolmogorov-Smirnov test was significant and the z-scores for Skewness and Kurtosis were not between -2.58 and +2.58 (Field, Miles, & Field, 2012). To correct for this, SJs mean values underwent an intra-subjects standardization by means of an ipsatization procedure (Tieri et al., 2015). A reciprocal transformation ($1/x$) was applied to JTs and RTs, since several conditions were not normally distributed. After applying these transformations, we found no deviations from normality for the dependent variables. Transformed variables were then entered into separate 2x2x5 repeated measures analyses of variance (ANOVAs) with Movement, Goal and Delay as within-subjects factors. Tukey correction was applied for all post-hoc comparisons.

2.4 Results

2.4.1 Staircase Procedure

The 2x2x5 Anova on transformed RTs was performed to check that the staircase procedure was effective in splitting fast and slow presses and in associating the observation of erroneous feedback only to slow reaction times. According to the algorithm we set, fast RTs should have been followed by M+G+, while slow RTs should have been followed by one type of erroneous feedback. Hence, RTs should be, on average, faster in trials where M+G+ was viewed, compared to trials where one type of erroneous feedback (M+G-, M-G+, M-G-) was viewed. Consequently, these should not differ one from another. Indeed, we found significant main effects of factors Movement ($F(1, 29) = 143.38$, $p = .000$, $\eta_p^2 = .832$) and Goal ($F(1, 29) = 223.59$, $p = .000$, $\eta_p^2 = .885$). Importantly, a significant Movement x Goal interaction was also found ($F(1, 29) = 183.44$, $p = .000$, $\eta_p^2 = 0.863$). Post-hoc comparisons showed that M+G+ observations (2.14 ± 0.061) were preceded by faster RTs compared to M+G- (mean ± s.e.m.: 1.69 ± 0.058; $p = .000$; $d = 1.37$), M-G+ (1.71 ± 0.063; $p = .000$; $d = 1.26$) and M-G- (1.70 ± 0.059; $p = .000$; $d = 1.33$). All the other comparisons did not differ (all *p*s > .845, all *ds* < .057). This pattern of results confirms that fast responses were followed by M+G+, while slow responses were followed by one of the three types of erroneous feedback.

The Anova did not show any other significant main or interaction (all Fs < 1.32; all *p*s > .266, all η_p^2 < .044) effects.

2.4.2 Synchrony Judgments (SJs)

The 2x2x5 Anova on the mean scores of ipsatized SJs showed a significant main effect of factor Movement (F(1, 29) = 4.47, *p* = .043, η_p^2 = .134; **Figure 9, panel A**). Perceived synchrony was higher when participants viewed a congruent movement (M+: (mean ± s.e.m.) 0.043 ± 0.021) compared to when they viewed an incongruent movement (M-: - 0.043 ± 0.021; *d* = .772). Not surprisingly, the Anova also revealed a main effect of the Delay (F(4, 116) = 81.445, *p* = .000, η_p^2 = .737; **Figure 9, panel C**) explained by higher SJs for shorter delays compared to longer delays (delay 0: 0.253 ± 0.026; delay 75: 0.158 ± 0.020; delay 150: 0.003 ± 0.014; delay 225: -0.165 ± 0.018; delay 300: -0.248 ± 0.024; all *ps* < .039; all *ds* > .737). The only exception of delays were 225 and 300 which did not differ from one another (*p* = .095; *d* = .717). Importantly, the Anova revealed a significant interaction between factors Goal and Delay (F(4, 116) = 4.06, *p* = .004, η_p^2 = .123; **Figure 9, panel B**). Post-hoc comparisons revealed that at delay 0 participants perceived the feedback as more synchronous when goal was achieved compared to when it was missed (*p* = .015; *d* = .358). The same comparison was marginally significant (*p* = .054; *d* = .380) also at delay 75. SJs were not different when goal was achieved or missed at delays 150, 225 and 300 (all *ps* > .999, all *ds* < .087; see **Table 1** for mean ± s.e.m. for each Goal*Delay level. It is intesting to note that the analogous interaction between factors Movement and Delay was not significant (F(4,116) = 0.806, p = .524, η_p^2 =.027). Thus, in contrast to information about goal achievement, incongruent movements were associated with lower perceived synchrony, irrespective of the duration of the delay (main effect of factor Movement).

The Anova did not show any other significant main or interaction (all Fs < 0.906; all *ps* >.349; all η_p^2 < .031) effects.

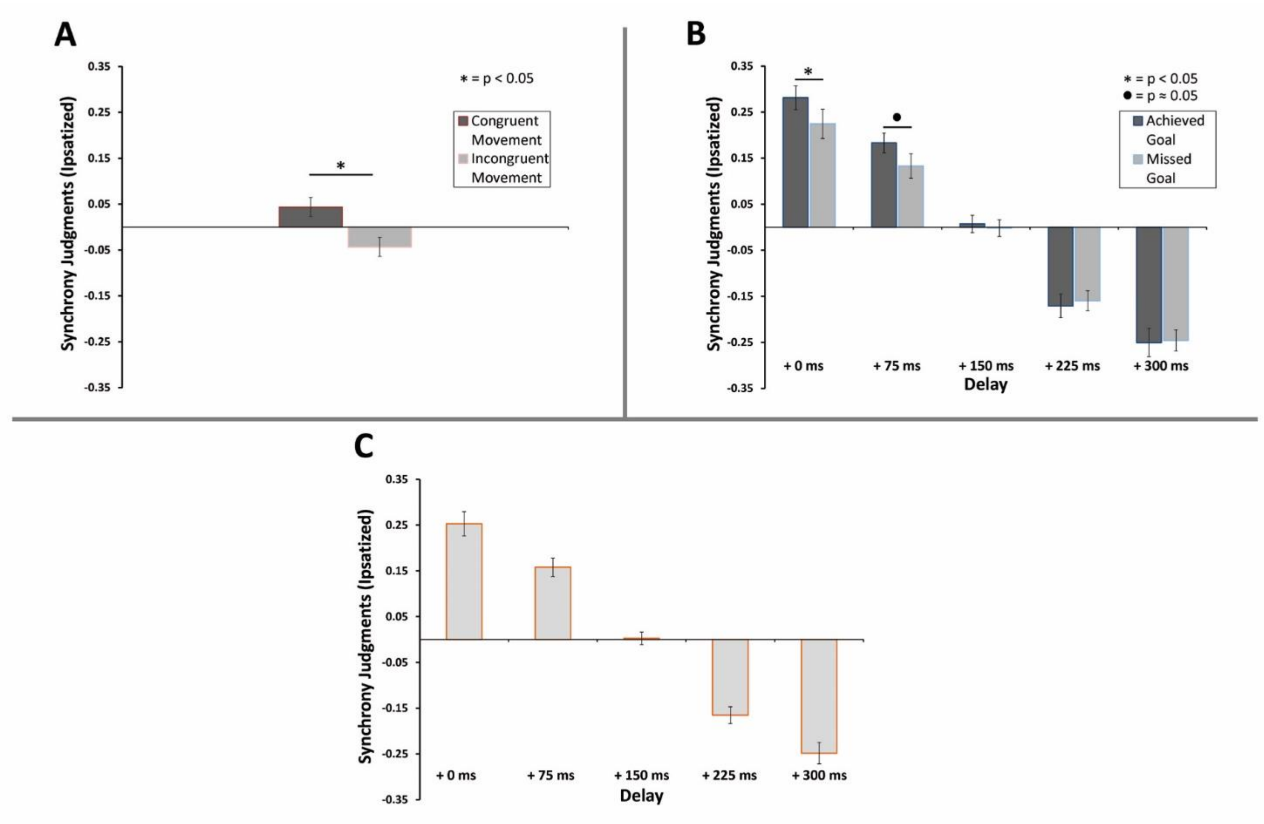

Figure 9. This figure represents the mean ipsatized scores of Synchrony Judgments (SJs) **a)** after the observation of a congruent (M+) or incongruent (M-) movement, **b)** after the observation of feedback where goal was achieved (G+) or missed (G-) for each delay (0, +75, +150, +225, +300 ms. Only significant differences between G+ and G- within each delay are plotted) and **c)** for each delay irrespective of the type of observed feedback. Vertical bars denote mean ± standard error of the mean (s.e.m).

	+ 0 ms	+75 ms	+150 ms	+225 ms	+300 ms
Achieved Goal	0.281 ± 0.026	0.183 ± 0.021	0.007 ± 0.019	-0.171 ± 0.026	-0.250 ± 0.030
Missed Goal	0.224 ± 0.032	0.133 ± 0.026	-0.002 ± 0.018	-0.159 ± 0.022	-0.246 ± 0.023

Table 1. Mean ipsatized scores ± standard error of the mean (s.e.m) of Synchrony Judgments after the observation of feedback where goal was achieved (G+) or missed (G-) for each delay.

2.4.3 Judgment Times (JTs)

The 2x2x5 Anova on transformed JTs revealed that participants were significantly faster in providing SJs when they observed visual feedback that was fully congruent with what they expected in terms of movement direction and goal achievement (M+G+). The Anova showed a significant main effect of factor Delay ($F(4, 116) = 4.748$, $p = .001$, $\eta_p^2 = .141$). Post hoc comparisons on factor Delay revealed that participants were significantly faster in providing a JT when the delay was 300 ms (mean ± s.e.m.: 1.58 ± 0.112) compared respectively to 0 ms (1.39 ± 0.110; $p = .003$; $d = .319$), 75 ms (1.41 ± 0.105; $p = .016$; $d = .283$) and 150 ms (1.42 ± 0.097; $p = .030$; $d = .273$). No other comparison was significant (all *ps* > .110; all *ds* < .213). We found a significant main effect of Movement ($F(1, 29) = 15.91$, $p = .000$, $\eta_p^2 = .354$) and a main effect of Goal ($F(1, 29)=18.085$, $p = .000$, $\eta_p^2 = .384$). Importantly, the interaction between Movement and Goal was significant as well ($F(1, 29) = 25.054$, $p=.000$, $\eta_p^2 = .463$; **Figure 10**). Post-hoc comparisons revealed that participants were significantly faster in providing a SJ when they viewed M+G+ (mean ± s.e.m.:1.64 ± 0.116) compared to M+G- (1.41 ± 0.101; $p = .000$, $d = .395$), M-G+ (1.39 ± 0.010; $p = .000$; $d = .434$) and M-G- (1.41 ± 0.101; $p = .000$; $d = .387$) respectively. All the other comparisons were not significant (all *ps* > .887; all *ds* < .049).

The Anova did not show any other significant main or interaction (all Fs < 0.854; all *ps* > .494; all $\eta_p^2 < .029$) effects.

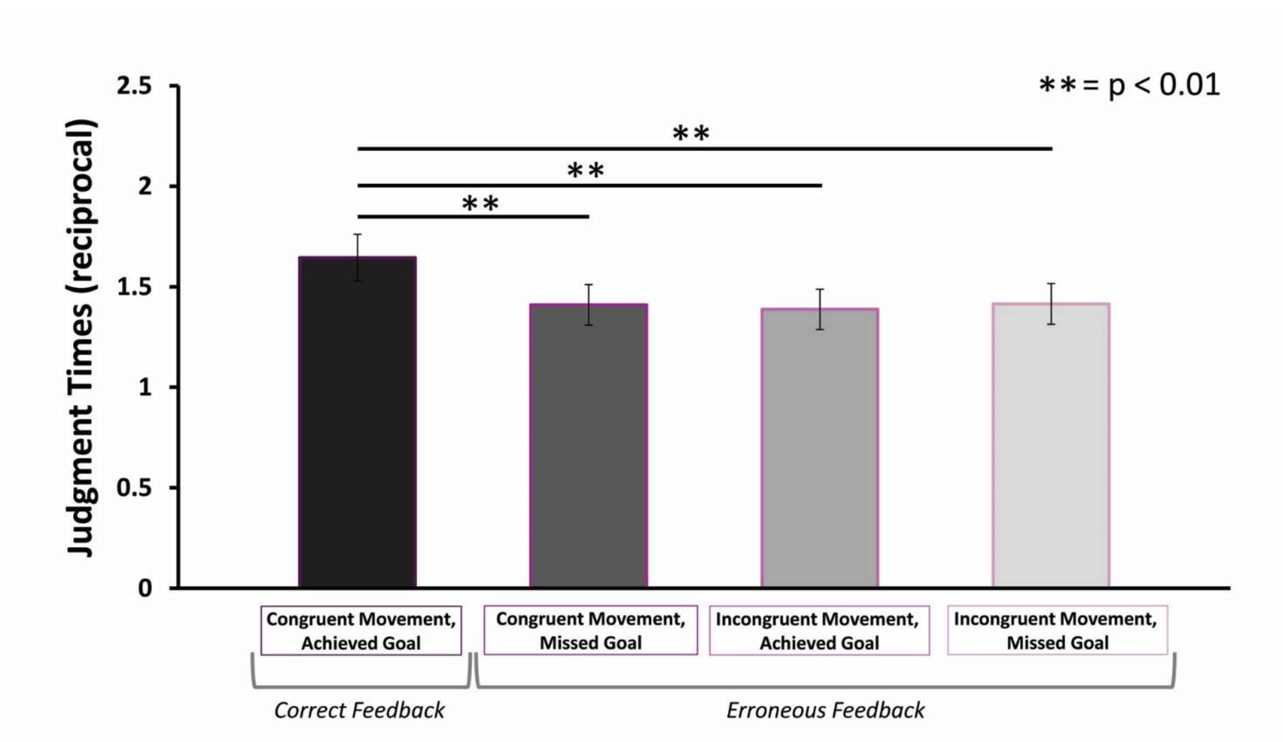

Figure 10 Graphical representation of the inversed mean values (1/x) of the time required to express a Judgment Time (JT) after the observation of each possible feedback. Vertical bars denote mean ± standard error of the mean (s.e.m).

2.5 Discussion

We investigated how violating expectations about movement execution or goal achievement influences the Sense of Agency (SoA). We reasoned that to understand their relative contribution to SoA, the monitoring of movement execution and goal achievement should be manipulated simultaneously in the context of an intuitive goal-directed action. To do this, we devised a novel paradigm that combined the execution of simple goal-directed actions (i.e., pressing a button of a target color by lifting or lowering the index finger) with observation of virtual actions that fitted or violated the participants' expectations about the performed and observed actions. Virtual actions could be congruent or incongruent with participants' actions. Incongruences concerned the level of movement and/or goal and could occur at different time delays: a feature of the task that allowed us to investigate the temporal dynamics of their effects on SoA. Participants were asked to evaluate the synchronicity between the executed and the observed actions, i.e., *Synchrony Judgments*, which might be equivalent to express a judgment of agency.

Our results indicate that both movement and goal errors impair SoA. However, we show for the first time that movement monitoring may be a more constant source of modulation of SoA than goal monitoring.

2.5.1 Modulations of SoA: influence of movement, goal and delays between action execution and action observation

The analysis of SJs showed a significant main effect of Delay. This is coherent with the results of previous studies that found a reduction of SoA when the latency of events resulting from one's own actions differs from what one expects (e.g., David et al., 2016; Franck et al., 2001; Weiss et al., 2014). In the specific case of our study this also indicates that participants correctly understood the task: they successfully identified increasing delays between their action and the visual feedback in the virtual scenario.

Interestingly, the analysis of SJs showed that participants tended to perceive the visual feedback in the virtual scenario as more synchronous with their own action when they observed a movement that was congruent with the one they executed, compared to when they observed an incongruent movement, as indicated by the main effect of factor Movement. This was true regardless of the specific delay we introduced between the observed and executed action and irrespective of whether the goal was or was not achieved (both the interactions Movement*Delay and Movement*Goal were not significant). The feedback in the virtual scenario was also perceived as more synchronous when the goal was attained compared to when it was missed. However, this happened only for simultaneous (0 ms) feedback or after short delays (75 ms) with respect to the button press as revealed by the post hoc analysis ran for the significant Goal x Delay interaction on the SJs.

These results suggest that information regarding the congruency of the movement and the achievement of the goal are both relevant for experiencing SoA. One may note that: i) participants' SoA decreased when they observed a movement that was incongruent with their own, irrespective of when they observed it; and ii) the observation of a failure to achieve the goal was also effective in reducing SoA, but only when the feedback was contemporary to or immediately followed action execution. However, these results do not indicate that movement information is more relevant than goal information for SoA since no interaction between factors Movement and Goal was found. The time-limited sensitivity to goal manipulation found in our study, as compared with the constant reliance on movement information, may be compatible with the findings by two studies by Metcalfe and collaborators. Metcalfe and colleagues (2013) asked their participants to play a videogame in which their task was to touch downward scrolling targets with a cursor controlled through a mouse. Success in touching the target was associated with a change in its visual appearance ("explosion"). The cursor responsiveness to commands ("proximal action") and the probability that the target would “explode” after a hit ("distal outcome") were manipulated. At the end of each trial, participants reported how much control they experienced by moving an indicator bar to a desired point of a visual analogue scale, where the left end indicated no control and the right end indicated full control. SoA was more affected by introduction of perturbation that affected the responsiveness to commands, than by diminishing probability of causing the explosion of the target. Congruently, in a previous study that employed a similar procedure and an analogous measure of SoA, Metcalfe & Greene's (2007) found that SoA was modulated by the degree of control participants were allowed to exert over the outcomes. When no perturbation in the control of the cursor was introduced, their judgments of control corresponded to their success in causing the distal outcome: they were high when they hit many targets, and low when they did not succeed in the task. When noise in the control of the cursor was introduced, or when target or distractors were "magically" hit despite the cursor being distant from said target, people relied less on how often they succeed in hitting the targets, and more on the monitoring of the performed action. Taken together, the results of these two studies from Metcalfe and collaborators suggest that people are generally capable of tracking information about their movements and that monitoring of proximal actions is at least as relevant as obtaining an expected outcome for generating SoA. As in Metcalfe and colleagues studies, our results suggest that information relative to one’s own movement is relevant for feeling control over actions which aim at attaining a goal.

All together our results are in line with the hypothesis that the observation of an incongruence between the executed and the observed action -either related to the movement or to the goal-will generally reduce SoA, but they do not support the hypothesis that a failure to achieve the goal will more strongly affect SoA than the observation of an incongruent movement. In fact, movement information induced a more constant modulation of SoA than goal information: the influence of the latter began to vanish when introducing very short delays. On first sight our results may seem in contrast with findings by David and colleagues (2016) who found that SoA was crucially affected by the final outcome of the action more than by other features related to the action itself. However, we think that methodological differences may have played a role. In our case, participants could observe the virtual finger moving in the opposite direction (incongruent movement) and/or pressing the button of a different color than their target (missed goal). In the study by David and colleagues (2016) expectations about the course of the action were violated only by introducing delays between executed and the observed movement, or between the executed action and the final outcome. In other words, the observed movements were always congruent and the final outcome was always obtained, but both were shown at different latencies. Additionally, in our study, manipulation of both movement and goal took place simultaneously, while in David and colleagues' experiment manipulation of movement and goal could not occur in the same trial. Finally, in David and colleagues' study, participants were asked to explicitly express if they or someone else produced the action observed in the virtual scenario, while in our study SoA was assessed through judgments of correspondence (i.e., judgments about the synchronicity between the executed and the observed action).

Our results are in line with those reported by Caspar and colleagues (2016). In their study, binding between action and outcome was higher for congruent than for incongruent tones only if the robot moved the same finger used by the participant. Therefore, similarly to our findings, Caspar and colleagues reported that information about the execution of the movement and the outcome of the action contribute to SoA. Importantly, we expand their findings by adding that movement information may contribute to SoA for a more extended temporal window than goal information.

2.5.2 Salience of the Goal

One possible limitation of our study concerns the seemingly low influence of the goal, which was time-limited as compared to the extended influence of movement manipulation. This unexpected result may be due to the fact that achieving (or missing) the goal was not associated to any relevant consequence for the participant (e.g., in the form of a monetary gain/loss) that might have reduced the "salience" of the goal. Notably, we deliberately selected a "neutral" goal to measure its contribution to SoA in order to avoid any emotional or rewarding effect associated to a salient outcome. This procedure may have reduced the influence of the goal on SoA compared to the other components of the action we manipulated here, i.e., movement and time. However, our procedure allowed us to compare our findings with those published by other groups. A neutral outcome for example was employed in the original version of the intentional binding paradigm (Haggard & Clark, 2003; Haggard et al., 2002), and in Metcalfe & Greene experiment (2007) where targets simply disappeared after a hit. Moreover, a neutral outcome was employed also in the more recent studies using similar procedures to the ones proposed here (Caspar, Desantis, et al., 2016; David et al., 2016). Was then the goal we employed *too* neutral to the point that participants did not attend to it and therefore did not notice when the virtual finger pressed the wrong target? The idea that participants did not pay attention to the target while executing the task is very unlikely. In fact, the observation of any virtual action (either congruent or incongruent) was fundamental for the correct execution of the task, which implied locating the target color and pressing the correct button in the response box. Given the low number of incorrect responses with respect to the total amount of trials, we argue that participants could successfully identify the location of the target most of the time, and respond appropriately.

In support of that, the analysis on the amount of time participants took to provide a SJ (i.e., Judgment Time) revealed an important interaction between factors Movement and Goal. This interaction shows that participants were significantly faster in providing a SJ when they observed a fully congruent action (M+G+), while all other types of feedback were associated with longer JTs and did not differ. Thus, after erroneous feedback participants noticed a discrepancy between the executed and the observed action, which led them to wait longer to respond to the SJ question. This may be similar to the behavioral adjustments that occur after erroneous responses (e.g., post-error slowing Rabbitt, 1966) as reported in studies on performance monitoring (see Danielmeier & Ullsperger, 2011 and Ullsperger, Danielmeier, & Jocham, 2014 for extensive reviews). Interestingly, this was also true for M+G-, where the observed movement was congruent and goal was missed. If the goal was truly irrelevant, JTs for M+G- should not differ from JTs for M+G+ or should be at least lower than M-G-. However, this was not what we found. Indeed, our data supports the idea that participants actually noticed when the goal was not attained. SJs at 0ms delay were higher when the goal was achieved compared to when it was missed (and tended to be higher when delay was equal to 75 ms), suggesting that participants recognized an unexpected change in the observed outcome. For all of these reasons, we believe that both movement and goal manipulations were salient for the participants and both modulate SoA.

2.6 Conclusion

To explore how different components of actions modulate SoA we devised a novel paradigm where the congruency between the expected and observed movement and the success to attain the goal, can be simultaneously manipulated. Previous investigations of SoA tended to focus on specific features of action (either movement execution or goal achievement). However, the actions we perform every day involve both: we use our bodies to achieve desired goals.

By combining the manipulation of movement and goal information within the same study, we confirm that they are both relevant for SoA as previously reported. However, we expand current knowledge by showing that the former may be more constant that the latter in influencing SoA. We suggest that the advantage of the paradigm presented here is that it allows a straightforward comparison of the contribution of different sub-components of action (e.g. movement, goal and time) to SoA (Sidarus, Vuorre, & Haggard, 2017b). The paradigm could be easily combined with other known measures of the Sense of Agency – like the intentional binding (Haggard & Clark, 2003; Haggard et al., 2002) – to better specify the conditions under which this central feature of the Self is experienced, and, at times, lost. Importantly, the paradigm could also help clarify which aspects of action monitoring are involved in conditions associated to an impairment of SoA, such as schizophrenia, utilization behaviour, the alien-hand syndrome (Moore & Fletcher, 2012) or obsessive-compulsive disorder (Gentsch, Schütz-Bosbach, Endrass, & Kathmann, 2012).

2.7 Interim conclusions on the influence of Movement Execution and Goal achievement on the Sense of Agency

The behavioral study described in this chapter was based on a new paradigm where information about different action features – movement execution, goal achievement, and the timing of these action-related events – can be simultaneously manipulated. This allowed to directly compare their relative influence on the Sense of Agency.

The results of this study led us to conclude that Movement information might exert an influence on the Sense of Agency for a more extended temporal window than goal achievement. This suggests that individuals might rely mostly on the former as compared to the latter to establish whether they are in control of their actions.

However, this study also had some limitations that needed to be tackled.

Firstly, in the study described above only cued actions were possible: participants always performed actions following an instruction, and the goal of the action was never chosen by the participants. From the one hand, this limited our conclusions to cued actions. On the other hand, both theoretical and empirical work suggest that the Sense of Agency be higher for freely chosen outcomes (Barlas & Obhi, 2013; Beck, Di Costa, & Haggard, 2017; Borhani, Beck, & Haggard, 2017). Hence, we reasoned that a comparison between free and cued actions within our paradigm might allow to understand if the influence of goal-related information on the Sense of Agency might differ in freely chosen and in cued actions; additionally, this comparison might help to clarify if the relevance of goal achievement in freely chosen actions might be similar, or even higher, with respect to movement related information.

Secondly, in the study described above we obtained only an indirect measure of Sense of Agency by means of Synchrony Judgments: by doing this, we relied on previous evidence (Weiss et al., 2014), suggesting that synchrony judgments might be equivalent to explicit agency judgments. However, this study prevented us from obtaining a direct measure of participants feeling of control. We reasoned that this limitation prevented us from obtaining a complete picture of participants Sense of

Agency in our task.

To tackle these two points, we decided to run a new study. We adapted our paradigm so that it allowed participants to perform both freely chosen and cued actions, and we added a second measure of SoA: in addition to Synchrony Judgments, we asked participants to rate their sensation of causing the virtual action by means of a Visual Analogue Scale.

3. Freedom to act enhances the Sense of Agency, while movement and goal-related prediction errors reduce it and lead to behavioral adjustments.

3.1 Abstract

The Sense of Agency (SoA) is the experience of controlling one's movements and their consequences in the external environment. Accumulating evidence suggests that freedom to act enhances SoA, while prediction errors are known to reduce it. These two aspects were mostly explored separately in previous research. Here, we sought to understand if prediction errors exert the same influence on SoA during free and cued actions, and if they both lead to behavioral adaptations. Participants performed free or cued goal-directed actions - pressing a button of a selected color - while observing a virtual hand executing the same or a different action, simultaneously of after various delays. The virtual hand moved in the same or in the *opposite* direction – i.e. movement-related prediction error - and the goal could be achieved or *missed* – i.e., goal-related prediction error. To investigate implicit and explicit levels of SoA, we collected both indirect (i.e. Synchrony Judgments between the executed and observed action) and direct (i.e. reports of the subjective feeling of causation) measures. We investigated behavioral adaptations by analyzing reaction times. We found that participants judged a virtual action as more synchronous when they were free to act. Additionally, both perceived synchrony and feeling of causation were reduced by movement-related prediction errors, while goal-related prediction errors impaired only the feeling of causation. Slower reaction times were observed following both types of prediction errors. Our data suggest that that freedom to act might enhance SoA, and that movement and goal-related prediction errors might reduce it and lead to behavioral adaptations both in free and in cued actions.

3.2 Introduction

The Sense of Agency (SoA) is the experience of controlling one's movements and their consequences in the external environment (Aarts et al., 2012; Moore & Fletcher, 2012; Tsakiris et al., 2010). Recent theoretical models suggest that SoA might be a multi-faceted experience that comprises both implicit and explicit components (Moore & Fletcher, 2012; Synofzik et al., 2008a, 2008b; Synofzik, Vosgerau, & Voss, 2013; Wegner & Sparrow, 2004). It has been proposed that SoA involves a non-conceptual level – i.e. *feeling of agency* – that relies mostly on sensorimotor information, and a conceptual and interpretative level – i.e. *judgments of agency* – that relies on a belief formation process about the causes of actions and their consequences (Synofzik et al., 2008a, 2008b). This distinction implies that SoA might not depend on a single process, but rather on a set of multiple cues. This view was recently translated in a Bayesian model of SoA inspired by theories of perception (Moore & Fletcher, 2012; Synofzik et al., 2013). The brain might use multiple action cues to modulate SoA, such as prior beliefs about one's own agency, contextual information, and a comparison between predicted and actual consequences of actions. This work focuses on the contribution of two possible sources of SoA modulation, and on how they might interact: the free choice of the individual about the action she\he intends to perform; and the effects of prediction errors on SoA.

Free choice has been often put forth as the core of the experience of agency. Despite that, there is still no consensus to date about what characterizes voluntary actions (Fried, Haggard, He, & Schurger, 2017). Traditionally, voluntary actions have been identified by contrasting them to reflexes and to actions guided by external cues, i.e. cued actions (Fried et al., 2017; Frith, 2013). Indeed, a central notion of voluntary actions is considered their "freedom from immediacy" (Fried et al., 2017; Haggard, 2017) which implies that they are internally generated and independent from environmental influences. As such, voluntariness is often viewed as a fundamental cue to SoA (Haggard, 2017), since being an autonomous agent would require freedom of choice as a prerequisite (Barlas & Obhi, 2013). Possibly, individuals can still feel responsible to some extent for actions they performed and that they did not choose, but accumulating evidence suggests that freedom to act enhances SoA. For instance, Wenke and colleagues (2010) asked their participants to press one of two buttons with either the left or the right index to obtain a visual outcome on screen (Wenke et al., 2010). Two conditions were possible: in one condition participants freely selected which button to press in 75% of the trials, while in the remaining 25% they received an instruction; and a second condition in which the proportion of free (25%) and instructed (75%) actions was reversed. Participants reported higher control over the visual effect when they were free to act most of the times, as compared to when they mainly relied on external cues.

In a series of studies, Barlas and colleagues (Barlas, Hockley, & Obhi, 2017, 2018; Barlas & Obhi, 2013) studied the influence of freedom of choice on SoA by comparing conditions in which participants could choose between a different number of action alternatives to conditions where they to responded to external cues. Specifically, their task was to press one of the buttons of a response pad to produce a tone. The button could be defined by a cue (i.e. no choice) or could be selected by the participant among an increasing number of options (e.g. 3 or 7 buttons). Freedom of choice was associated to stronger binding – i.e., a time compression between action and tone that is considered an implicit marker of SoA (Haggard et al., 2002; Moore & Obhi, 2012). The same trend was also observed when participants provided explicit reports of their feeling of control (Barlas et al., 2017, 2018). Overall, these studies indicate that freedom to act might increase SoA both at an implicit and explicit level.

Importantly, recent studies also suggested that SoA might also be reduced by limitations to one's freedom to act induced by the social context. Caspar and colleagues (2016, 2017, 2018) had pairs of participants act in turn (Caspar, Christensen, et al., 2016; Caspar, Cleeremans, & Haggard, 2018; Caspar, Vuillaume, Magalhães De Saldanha da Gama, & Cleeremans, 2017). In each turn, one participant could deliver electrical shocks to the other by performing a button press, which was associated to economic gain. Alternative, she\he could cause the other economic harm – i.e. they would take money from the other participant – without shocks being delivered. Importantly, actions could be executed in a context of freedom of choice, or they could be demanded by the experimenter (i.e., coercive condition). Participants heard a tone simultaneously to the harmful outcome, which allowed to measure SoA by means of intentional binding. Binding was significantly reduced when participants were coerced to perform an action. Taken together, these studies bring additional evidence that freedom to act is crucial for SoA.

A second source of information consistently associated to modulation of SoA are prediction errors. Prediction errors can be defined as a mismatch between prior expectation and reality (den Ouden et al., 2012). In the context of motor cognition, they can be viewed as the difference between the predicted and actual outcome of an action (Haggard, 2017). It is generally assumed that the brain forms prediction about how the action will unfold and about its sensory consequences (Blakemore & Frith, 2003; Blakemore & Sirigu, 2003; Wolpert et al., 1995). Predictions are then compared with the actual events. If they match, no prediction error is generated, and the individual likely experiences SoA. Conversely, unpredicted events reduce SoA. The role of errors and of prediction errors in modulating SoA was consistently confirmed by previous research. As argued in chapters 1 (paragraph 1.3.1) and 2 (paragraphs 2.2 and 2.5), individuals experience higher SoA when their actions are followed by a predicted outcome, as compared to when outcomes are different than predicted (i.e., incongruent) (Caspar, Desantis, et al., 2016; Kühn et al., 2011; Sato & Yasuda, 2005). Similarly, a decrease of SoA was also observed for unpredicted (i.e., incongruent) movements observed from a first-person perspective. This finding was obtained when participants observed a human (Daprati et al., 1997; David et al., 2016; Farrer et al., 2008; van den Bos & Jeannerod, 2002), a robotic (Caspar, Cleeremans, & Haggard, 2015; Caspar, Desantis, et al., 2016) or a virtual hand (Padrao et al., 2016; Villa, Tidoni, Porciello, & Aglioti, 2018). As reviewed before, also the mere observation of a virtual arm failing to perform a simple goal-directed movement - such as reaching movement to grasp a glass – reduces SoA (Pavone et al., 2016; Pezzetta et al., 2018).

However, whether movement and goal-related prediction errors exert the same influence on SoA both in free and cued actions was rarely investigated. In a previous study, Barlas and Kopp (2018) asked their participants to press one of four buttons, corresponding to a left, right, down or up arrow (Barlas & Kopp, 2018). Pressing one of the four buttons was associated to the observation of an outcome on screen – i.e. an arrow pointing in the same or in one of the alternative directions with respect to the selected one. Importantly, the authors also manipulated participants' freedom of choice: they could be instructed about which button to press or they could choose between 2, 3 or 4 buttons. SoA was measured by means of intentional binding and subjective ratings of the feeling of control. SoA was reduced both by limitations to participants freedom to act and by the observation of incongruent outcomes – i.e. arrows pointing in an unexpected direction. However, freedom of choice and outcome congruency did not interact and independently affected participants SoA. In their task, Barlas and Kopp presented participants with only one type of prediction error - i.e the outcome of the action could be different than expected.

However, in a previous study (Villa et al., 2018) we argued that the SoA might rely on at least three types of action-related cues: information about movement execution; information about the achievement of the goal of the action; and predictions about the time in which these events should occur. As described in chapter 2, to assess the contribution of these different cues to SoA, we devised a paradigm in which participants perform simple goal-directed actions while they observe a virtual hand performing the same or a different action from a first-person perspective. Importantly, the virtual action can violate different types of expectations. It can generate a movement related prediction-error, - i.e, the virtual finger moves in the opposite direction with respect to the participant - and/or a goal-related prediction error - i.e. the color of the target is different than expected. Additionally, the virtual action can occur with different delays with respect to action execution. Tellingly, our data indicated that movement and goal related prediction errors might not impair SoA in the same way: observation of an incongruent movement disrupted SoA irrespective of delay duration, while a missed goal did so only when we introduced short delays between the executed and the virtual action. Hence, our data indicated that movement information might be a more constant source of SoA modulation than goal information.

In our previous version of the task the goal of participant's action was defined by an external cue: they had to press the button that turned to a specific color. Hence, it is unclear whether the same effects could be observed also for freely chosen actions. Here, we adapted our paradigm so that participants could perform actions both under conditions of free choice or following cues in two separate blocks. This way, we sought to directly compare the effects of movement, goal and time-related prediction errors when the individual performs free or cued actions.

As mentioned before, SoA might include implicit and explicit components. To capture the effects of our manipulations on these two levels of SoA we employed two measures. In a first part of the experiment, as in the study reported in chapter 2 we employed Synchrony Judgments as an indirect measure of SoA (Farrer et al., 2008; Weiss et al., 2014). The reasons for the choice of this measure, along with some of its potential limitations, were already discussed in paragraphs 2.2 and 2.7 and will be further addressed in paragraph 4.4. However, here we were also interested in obtaining a direct measure of participants' SoA. To do this, in a second part of the experiment we asked them to rate their sensation of causing the virtual action by means of a Visual Analogue Scale (Pavone et al., 2016; Pezzetta et al., 2018). Firstly, we hypothesized that participants would experience a decrease of SoA after observing both movement and goal-related prediction errors and we expected to obtain similar results to our previous study when participants performed cued actions. Secondly, we hypothesized that freely chosen actions would be associated to higher SoA as compared to cued actions. Thirdly, we expected that information about achievement of the goal of the action would influence SoA more in free as compared to instructed action. Indeed, recent studies suggest that freely chosen outcomes might be linked to stronger binding (Beck et al., 2017; Borhani et al., 2017). Finally, we expected differences between implicit and explicit agency measures: given that individuals tend to self-attribute successful outcomes (Arkin, Appelman, & Burger, 1980; Miller & Ross, 1975), achievement of the goal of the action might be more relevant for SoA at an explicit level. Additionally, we were interested in measuring the possible effects of prediction errors on motor performance. Making an error is known to affect performance in following trials, which is generally referred to as "post-error adjustments" (Danielmeier & Ullsperger, 2011; Fusco et al., 2018; Ullsperger et al., 2014). For instance, participants perform actions more slowly in trials following an error, an effect known as Post-Error Slowing (PES). Post-error adjustments were also reported after prediction errors and unexpected visual consequences of actions (Gentsch, Ullsperger, & Ullsperger, 2009; Wessel & Aron, 2013; Wessel, Danielmeier, Morton, & Ullsperger, 2012). However, whether movement and goal related prediction-errors operate in the same way in generating behavioral adaptations is not clear. In the study described in chapter 2, we found initial evidence for the presence of behavioral adjustments also in our paradigm, when participants observe an unpredicted movement or a failure to achieve the goal of the action. Here, we measured behavioral adaptations by calculating the amount of time participant took a) to provide synchrony judgments and b) to perform a new action after observation of every type of virtual action. We expected that movement and goal related prediction errors would be associated to increased reaction times for both measures. A difference in reaction times would hint at a different severity of the two types of prediction errors.

3.3 Materials and Methods

3.3.1 Participants

A total of 46 volunteers participated in the study (23 males; age range: 19-43 years old; mean ± standard error of the mean (SEM): 24.3 ± 3.9). All participants were right-handed, had no prior history of neurological disorders, had normal or corrected to normal visual acuity and were not color-blind. Participants were naïve with respect to the purposes of the study, and explanation of the hypotheses were provided only after the end of the experiment. The experimental protocol was approved by the ethics committee of Fondazione Santa Lucia (Prot. CE/PROG. 686) and was performed in accordance with the 1964 declaration of Helsinki. All participants provided written informed consent to take part in the study. Six participants were excluded from the final sample and from the analyses since they failed to meet pre-defined exclusion criteria (see "excluded participants" for more details). The final sample was thus composed of 40 participants (20 males; age range 19-31 years; mean ± standard error of the mean (SEM: 23.7 ± 0.408). The order of blocks (Free\Cued) and the finger used to respond "Synchronous" to the synchrony judgment question (Index\Middle) was fully counterbalanced across participants.

3.3.2 Apparatus

The apparatus employed in this study were the same described for the study reported in chapter 2 (Villa et al., 2018). Hence, I will describe it shorty in this paragraph. Full details can be found in paragraph 2.3.2.

A Matlab custom script (The MathWorks, Inc) was used to run the experiment. A virtual scenario (**Figure 11**) was represented on a monitor. This included a virtual humanoid right-limb (forearm + arm) and a virtual response box, composed of two dark grey buttons respectively attached to the top and to the bottom of a transparent structure. The index of the virtual arm rested between the two buttons of the virtual response box. 3DS Max 2011 (Autodesk, Inc) was used to create the virtual stimuli.

The monitor was sustained by a wooden structure located on the table. Participant inserted their right arm in a rectangular hole at the front of the structure. They were asked to lay their arm on the table matching the position of the virtual arm. The presence of the screen prevented participants to observe their real arm. A custom-made response box, closely matching the features of the virtual response box, was placed on the table below the monitor. The response box was C-shaped and included two buttons that allowed to record upwards and downwards movements of the index. Before starting the experiment, the distance between the surfaces of the two buttons was adapted for each participant so that the dorsal part of the distant phalanx of the index touched the superior button, while the ventral part rested on the inferior button, and the two buttons were aligned. Finally, a standard USB keyboard was placed to the left of the monitor and allowed participants to answer to the specific question that appeared on screen at the end of a trial (See "Procedure and task" and Figure 11 for more details).

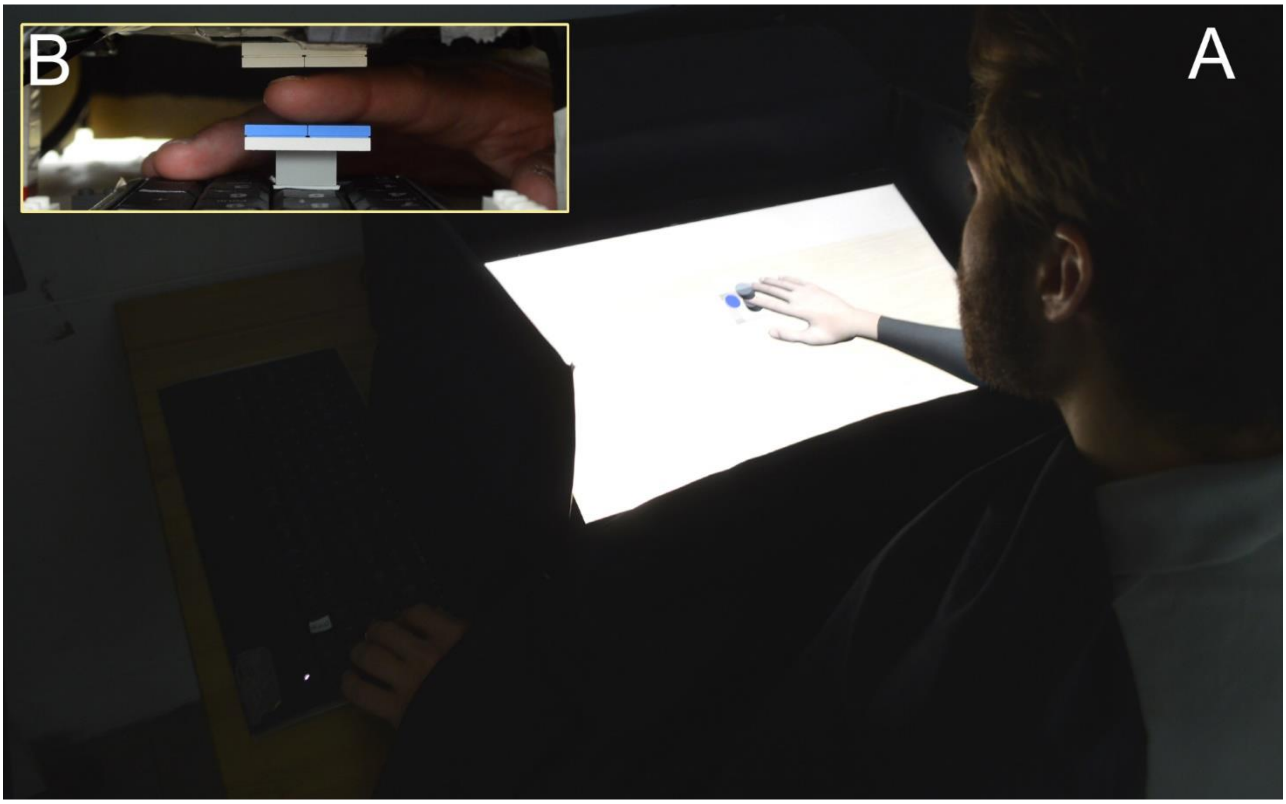

Figure 11. Experimental set-up. Participants performed simple goal-directed actions – pressing a button of a selected color (blue or yellow) - and observed a virtual hand performing their same or a different action from a first-person perspective (**panel a**). A screen was placed on a wooden structure in an inclined position, and a hole at the front of the structure allowed participants to place their hand under the screen and hidden from sight. Participants inserted their finger between two buttons of a custom-made response box (**panel b**), which allowed to collect downward and upwards movements. In separate blocks, participants could either freely select which color to press (free actions) or follow a cue (cued actions. As an example, the image represents the cue that participants received when they were instructed to press blue). The virtual action could be simultaneous (+0 ms) or delayed (+150, +300 ms) with respect to button press. This allowed to collect Synchrony Judgments as indirect measure of SoA in the first part of the experiment. Responses were given by means of a keyboard on the left of the structure. In the second part of the experiment the same keyboard was used to collect ratings of the subjective feeling of causation expressed by means of a Visual Analogue Scale appearing on the screen at the end of each trial.

3.3.3 Procedure and task

The experiment was performed in a dimly lit room. Participants sat comfortably on a chair, at a viewing distance of approximately 40 cm from the center of the screen. They were asked to lay their arm on the table and under the screen. Then, they inserted their index between the two buttons of the response box and adjusted the position of their arm to match the position of the virtual arm. A piece of black cloth was used to cover the shoulders and the elbow joint, which prevented any visual discontinuity between the virtual limb and participant's body.

During the experiment, the two buttons turned to yellow and blue, respectively. Participants' task was to select one of the two buttons according to its color (see below for details) and to press it as fast as possible, by performing an upward or downward moment. Pressing the button triggered the observation of an action in the virtual scenario. This could be similar or dissimilar to the one performed by the participant and could take place with different possible delays with respect to button press (see action-outcome manipulation section). An indirect (Synchrony Judgments) or direct (VAS) measure of SoA was then collected (see **figure 12, panel A**). In the first part of the experiment, participants provided an indirect measure of SoA by judging as fast as possible if the observed visual change in the virtual scenario took place simultaneously to their action or if it was delayed – i.e. Synchrony Judgments. They were informed that by "change in the virtual scenario" we referred to the fact that contingently to their button press, they would observe the virtual index pressing a button of a certain color. We considered that using this terminology - instead of "observed action" - would not bias participants to focus on a certain action feature over another (for instance movement of the finger over the color of the target). The experimenter made sure that each participant understood the meaning of the above terminology by providing examples before starting practice and by asking the participant to explain its meaning. Synchrony judgments were collected by means of keypresses with the left hand. Participants were also asked to respond to the question irrespective of the type of observed action, focusing solely on the temporal contiguity between their action and the visual change in the virtual scenario. A failure to adhere to this request would determine the exclusion of the participant from the final sample of the study. Two keys of a keyboard were respective labeled "S" for Synchronous and "A" for Asynchronous, and participants used the index and the middle fingers to respond. Mapping between the keys and the fingers used to respond was counterbalanced across participants. Additionally, to check that participants were aware of the disposition of the colors when performing a button press, we added a control question. In a sub-set of trials, instead of providing a synchrony judgment, participants were asked to report if "the final disposition of the colors - observed following the virtual action - was reversed with respect to the initial one - observed before performing the action." (see action-outcome manipulation for more details). To answer to this question participants used the same fingers and keys as for synchrony judgments. They pressed S for Yes (the final disposition was reversed with respect to the initial one) and A for No (the disposition of the two colors did not change).

In the second part of the experiment participants provided a direct measure of SoA. They were asked to rate how much they felt they had caused the visual change in the virtual scenario after each virtual action observation by means of a 100 points Visual Analogue Scale (VAS) spanning from 0 ("Not at all") to 100 ("Completely"). As for synchrony judgments, we referred to the visual change to avoid that participants would focus on a certain action feature (e.g. movement) over another. Participants were asked to move a cursor (initially appearing at the neutral position 50) to the position that they felt that was more representative of their sensation in that trial. To do this, they pressed two keys of the USB keyboard respectively labelled with a left and a right arrow. Pressing the left arrow moved the cursor toward 0, while the right arrow moved it toward 100. Participants were informed that they could choose between all the values of the VAS and that they had to press a third key, labelled "enter", to confirm their answer. Control questions were not collected in the second part of the experiment, since we considered that data obtained in the first (and longer) part would be sufficient to establish participants ability to notice the initial disposition of the colors. Both parts of the experiment were additionally sub-divided in two blocks, which differed in how participants selected the target color (see **Figure 12, panel A**). In one block participants pressed one of the two colors following an instruction – hence they performed a "cued" action; in the other block they were free to press a color of their choice – hence they performed a "free" action.

In the "Cued" blocks the structure of a typical trial was as follows (see **Figure 12, panel B**). At the beginning of the trial the virtual hand was still and the color of the two virtual buttons was dark gray. A tone signaled the beginning of the trial, and at the same time a blue or yellow circle appeared at the left of the virtual response box, at the same height of the virtual index and at equal distance from the two virtual buttons. The color of the circle instructed participants about which button they should press in the current trial - i.e. if yellow, they had to press the button that turned to yellow; if blue, they had to press the button that turned to blue. The circle remained visible for 1000 ms and then disappeared. After a random time included between 1000 and 1500 ms the two buttons flashed for 120 ms, one of them turning blue and the other yellow. The two possible dispositions of the colors (yellow up, blue down and vice-versa) were presented an equal number of times, and their order of presentation was randomized for each participant. The color of the two buttons then returned dark gray, and participants had to press the button corresponding to the position of the cued color with an upward or downward movement. If no response was provided within three seconds the current trial was aborted and it was repeated at the end of the block. If the participant pressed the wrong button (e.g. the target color appeared above the virtual index finger, but the participant pressed the lower button) a "prohibition sign" was displayed for 2000 ms; the current trial was then aborted, and it was repeated at the end of the block.

When participants pressed the correct target button they observed a visual *feedback* in the virtual scenario – i.e. a virtual action that could be the same performed by the participant or a different one, simultaneous or delayed with respect to the button press (see Action-Outcome manipulation and **Figure 12, panel C**). The visual feedback remained visible for 500 ms. After that, the virtual hand and the virtual response box were covered by a black (for Synchrony Judgments and VAS) or grey (for control questions) rectangle and participants were asked to respond to the current question. The inter-trial interval (ITI) was set to 1000 ms.

The structure of a typical trial in the "Free" blocks was similar to the one employed in "cued" blocks. However, here the color of the circle appearing at the beginning of the trial was half yellow and half blue. The orientation of the circle (whether the left half was yellow or blue. See **Figure 12, panel B**) was random for each trial and participants observed an equal number of times the two types of circles (blue-yellow/yellow-blue). This symbol was introduced to maintain a perceptual similarity with respect to the “Cued” block, and participants were asked to use it as a reminder that they should decide which color to press in that trial. Participants were asked to: i) freely choose which color to press in each trial but to ii) refrain from using a predefined strategy (e.g. alternating between yellow and blue presses) and to iii) avoid pressing always the same color. Adherence to these constraints was assessed at the end of the experiment for each participant and was considered a prerequisite for the inclusion of the participants in the final sample of the study. The structure of each trial was then the same as for the “Cued” block. As for the cued block, the two possible dispositions of the colors (yellow up, blue down and vice-versa) were presented an equal number of times, and their order of presentation was randomized for each participant. The type of feedback shown at the end of each trial was decided online depending on which button -hence which color- was chosen by the participant in that trial (see Action-Outcome manipulation).

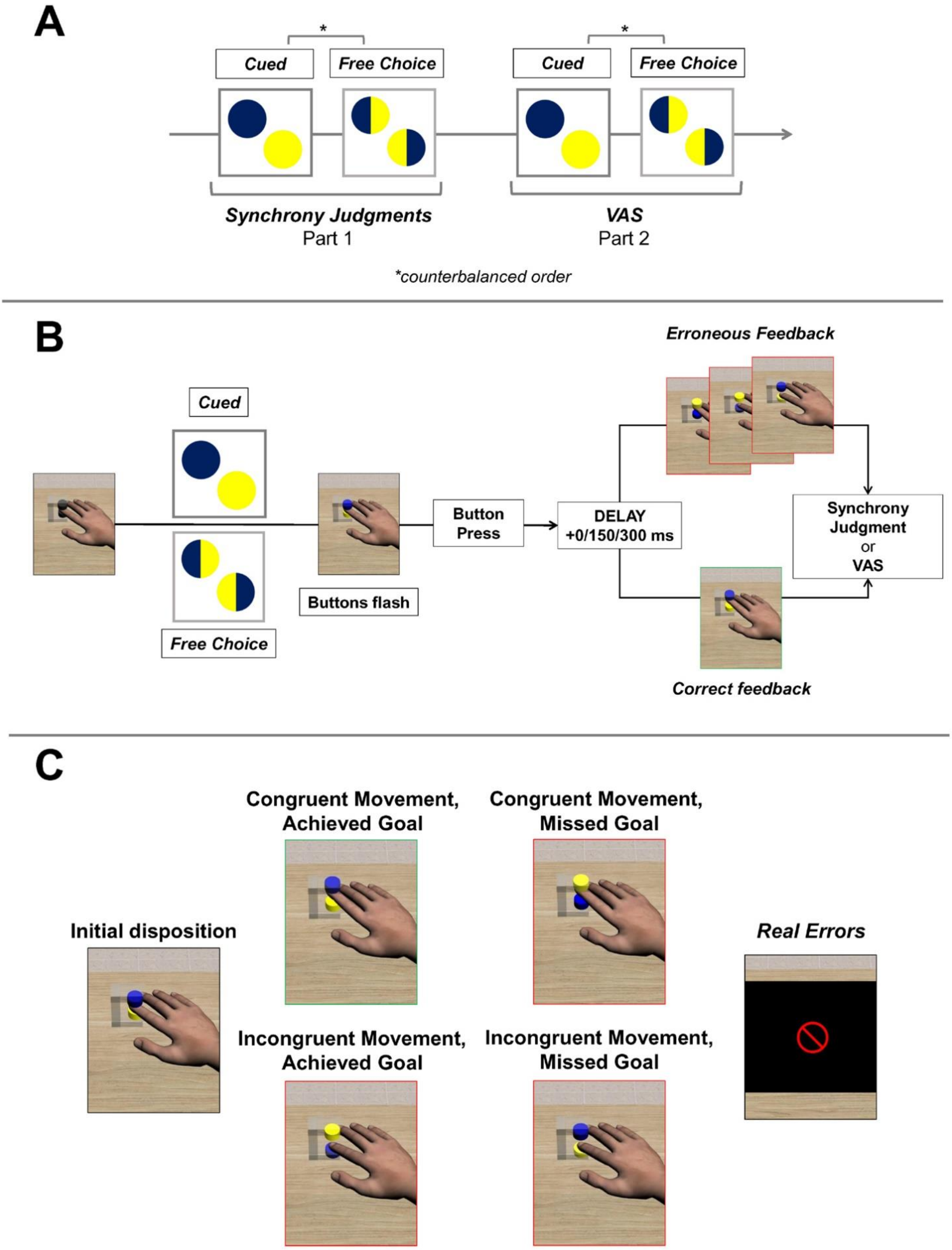
A
*
Cued
Free Choice
*
Cued
Free Choice
Synchrony Judgments
Part 1
VAS
Part 2
*counterbalanced order
B
Erroneous Feedback
Cued
Button
Press
DELAY
+0/150/300 ms
Synchrony
Judgment
or
VAS
Buttons flash
Free Choice
Correct feedback
C
Congruent Movement,
Achieved Goal
Congruent Movement,
Missed Goal
Initial disposition
Real Errors
Incongruent Movement,
Achieved Goal
Incongruent Movement,
Missed Goal

Figure 12. Experimental procedure and virtual stimuli. The experiment was divided in two parts (**panel A**): in the first part participants were asked to provide Synchrony Judgments between the virtual action and the observed visual change (i.e. the virtual action) occurring in the virtual scenario; in the second part participants provided ratings of the subjective feeling of causing the virtual action by means of a Visual Analogue Scale. The two parts of the experiment were divided in two sub-blocks: in one participants performed freely chosen actions, in the other they followed cues. The order of free and cues blocks was counterbalanced across participants in both parts of the experiment. The structure of each trial was identical for free and cued actions (**panel B**), with the only exception of the type of symbol that appeared at the beginning of the trial: in the cued block, a yellow or blue circle indicated to the participants which color they had to press; in the free block, the circle was half blue and half yellow and reminded participants to choose which color to press. The circle remained visible for 1000 ms and then disappeared. After a random time comprised between 1000 and 1500 ms the two buttons flashed for 120 ms, one of them turning blue and the other yellow. Participants pressed the button corresponding to the position of the selected color with an upward or downward movement and observed a visual *feedback* in the virtual scenario – i.e. a virtual action which took place simultaneously (+0 ms) or delayed (+150, +300 ms) with respect to the button press. The visual feedback remained visible for 500 ms. After that participants were asked to respond to the agency question (Synchrony Judgments or VAS, respectively in the first and second part of the experiment). The inter-trial interval (ITI) was 1000 ms, during which the hand remained still and the two virtual buttons were dark grey. The possible types of visual feedback are reported in **panel C**. To the left, the initial disposition of colors is reported. For explanatory reasons we represent only the case where blue is up and yellow is down, but in half of the trials the disposition of the colors was reversed and the same manipulations were applied. At the center of the panel the four possible types of feedback (M+G+, M+G-, M-G+, M-G-) are represented. To the right of the panel we report the prohibition signal that participants observed in the cued block if they pressed the wrong button (*real error*).

3.3.4 Action-Outcome Manipulation

Pressing one of the two buttons of the response box was associated to a visual feedback (i.e. a virtual action) in the virtual scenario. The feedback could be presented after various delays with respect to button press (0 ms, + 150 ms, +300 ms). Importantly, the virtual finger could move in the same (M+) or in the opposite (M-) direction with respect to participant’s movement, and the goal (pressing the selected color) could be achieved (G+) or missed (G-). The combination of movement and goal manipulations resulted in four possible types of feedback: one was fully *correct* (M+G+), while three were *erroneous* (M+G-, M-G+, M-G-), as they could be congruent or incongruent with participant’s action (See **figure 12, panel C** for a graphical representation of the four types of feedback).

In each part of the experiment (Synchrony Judgments\VAS) and in each block (Free\Instructed), the order of appearance of each feedback x delay combination was randomized. In the cued blocks, where the color of the target was determined by an instruction at the beginning of the trial, the specific virtual action (e.g. upward movement resulting in pressing the blue button) that corresponded to the pre-determined feedback for the current trial (e.g. M+G+) were known before the participant performed the action. In the free blocks, where the target color was freely selected by the participant, the specific type of virtual action corresponding to the planned feedback in the current trial was determined online according to the button pressed by the participant. For instance, if the planned feedback was M+G+ and participant pressed the yellow button below the index, the script determined that in that trial the virtual index would move downwards and press the yellow button. Vice-versa, if participant pressed the blue button above the index, the script determined that the virtual finger would move upwards and press the blue button. The same happened for all the remaining types of feedback.To help participants acclimatize to the experimental procedure, the first 4 button presses in of the two parts of the experiment and in each block were always followed by fully correct feedback (M+G+). These trials were later excluded from the analysis. During the first part of the experiment, where SoA was measured by means of Synchrony Judgment, each feedback x delay combination (es M+G+, delay 0, for a total of 12 possible combinations) was viewed 24 times, for a total of 144 trials in each block (free/cued) and of 288 trials for the first part of the experiment. Additionally, in 16 trials (8 per block, 2 per each type of feedback) participants were asked to respond to the control question aimed at assessing participants' awareness of the disposition of the colors. No delays between action and feedback were introduced when participants were required to respond to the control question. Before starting each of the two blocks that composed the first part of the experiment, participants performed practice trials. In these trials, the first 2 button presses were always followed by the observation of an M+G+ feedback; in twelve trials participants observed each of the possible feedback X delay combinations, and in 1 trial participants responded to the control question. Since participants could make errors, fail to perform an action within the given response window, or need to adjust the position of the hand to facilitate button presses, the overall number of trials during practice was not the same for all participants. They performed on average 15 trials (range: 15-17; ± S.E.M.: 0.106) before starting the free block and 16 trials (range: 15-24; ± S.E.M.: 0.277) before starting the free block. Data from practice trials were not included in the analysis.

During the second part of the experiment, where SoA was measured by means of VAS, each feedback x delay combination was viewed 8 times, for a total of 48 experimental trials per block (free/cued) and of 96 trials for the first part of the experiment. No practice trials were performed before the free and cued blocks in the second part of the experiment, since both conditions were known to the participants and only the question appearing at the end of the trial was different.

3.3.5 Excluded Participants

Before starting the analysis of the collected data, we excluded from the sample a total of six participants. These exclusions were motivated by methodological and theoretical concerns. Specifically, two participants were excluded for declaring during the debriefing that they had used a predefined strategy in selecting the target color in the "Free" block: they relied on the color of the right half of the circle that appeared at the beginning of the trial to decide which color to press. We reasoned that this criterion contrasted with one of the instructions that participants were given - i.e., to refrain from using a predefined strategy - and implied that these two participants performed cued rather than freely chosen actions also in the free block. This created a difference with respect to the rest of the sample: indeed, none of the other participants reported using any strategy in the choice of the color in the free block. Importantly, this prevented us from observing in these two participants potential differences in their Sense of Agency linked to the different type of action (free or cued) they were performing.

Two more participants were excluded from the analyses for always responding "Synchronous" to the Synchrony Judgment question, hence showing no modulation of delays and suggesting a difficulty in understanding the task (which was to judge the synchrony between the executed action and the visual change in the virtual scenario). The exclusion of these participants was performed in accordance with previous studies that reported a similar exclusion criterion, i.e., a failure to recognize time gaps of increasing duration between action and outcome (Barlas et al., 2017, 2018; Caspar, Christensen, et al., 2016) .

One more participant was excluded because his/her age was strongly different than the rest of the sample (43 years old, +4.83 SD with respect to the sample mean). By excluding this participant, we wanted to control for potential age-related differences in the Sense of Agency (Cavazzana, Begliomini, & Bisiacchi, 2017; Cioffi, Cocchini, Banissy, & Moore, 2017; Metcalfe, Eich, & Castel, 2010) with respect to the rest of the sample.

Finally, one participant was excluded for declaring that she\he responded to the Synchrony Judgment question by relying on the movement of the virtual finger instead of delays between action and feedback - i.e. she/he responded Synchronous if he observed a congruent movement; Asynchronous if the movement was incongruent. This participant did not understand the Synchrony Judgment question and aggregating her\his data to those obtained by the rest of the sample would have implied the introduction of a spurious difference between the sample means of perceived synchrony respectively under conditions of congruent and incongruent movement observation.

3.3.6 Data Handling

Although the number of trials for each feedback x delay combination was known in advance in both parts of the experiment (Synchrony Judgements/VAS), the total number of trials was not identical for each participant (for instance, they could perform real errors in the instructed blocks, or they could fail to perform an action within the given response window of 3 seconds). They performed on average 318 trials in the first part of the experiment (i.e. **SJs** trials: range: 312-348; SEM: ± 1.137. Free block:

range: 156-166. Mean ± SEM = 157 ± 0.274; Cued block: range: 156-191. Mean ± SEM = 161 ± 1.022), and 106 trials in the second part (i.e. **VAS** trials: range: 104-113; SEM: ± 0.342. Free block: range: 52-53. Mean ± SEM = 52 ± 0.053; Cued block: range: 52 ± 61. Mean ± SEM = 54 ± 0.328). The first 4 trials of each block (where participants always observed a fully *correct* feedback with no delay) in both parts of the experiment were removed from the analysis. Additionally, real errors (which were possible only in cued blocks. **SJs**: range: 0-35. mean ± SEM: 6.3 ± 0.993. **VAS**: range: 0-9. mean ± SEM: 1.7 ± 0.325) were removed from the analysis. We also excluded from the analysis trials where participants did not perform an action within the given time window (**SJs**: range: 0-11. Mean ± SEM = 1.3 ± 0.391. Free block: range: 0-10. mean ± SEM: 0.650 ± 0.274; Cued block: range: 0-10. mean ± SEM: 0.625 ± 0.288; **VAS**: range: 0-4. Mean ± SEM: 0.350 ± 0.127. Free block: range: 0-1. mean ± SEM: 0.125 ± 0.053; Cued block: range: 0-4. mean ± SEM: 0.255 ± 0.110) and trials where the experiment was momentarily suspended to adjust the position of participant's index finger to favor optimal reception of button presses (**SJs**: range: 0-3. Mean ± SEM = 0.150 ± 0.084; Free block: range: 0-1. Mean ± SEM = 0.050 ± 0.035; Cued block: range: 0-3. Mean ± SEM = 0.100 ± 0.078; **VAS**: range: 0-1. Mean ± SEM = 0.050 ± 0.035; Free block: range: 0-1. Mean ± SEM = 0.025 ± 0.025; Cued block range: 0-1. Mean ± SEM = 0.025 ± 0.025). Finally, control questions (16 in total in the first part of the experiment. See section 3.3.4.5) were analyzed separately with respect to Synchrony Judgments.

After removing these trials, analyses were performed on 288 trials per participant for the first part of the experiment (except for 2 subjects, for whom the number of trials was 287) and on 96 trials for the second part (except for 2 subjects, for whom the number of trials was 95).

We took into account a total of four dependent variables: three for the first part of the experiment (Synchrony Judgment trials) and one for the second part (VAS trials). For Synchrony Judgment trials, for each condition we calculated 1) the proportion of "Synchronous" answers to the synchrony judgment question (Synchrony Judgments, abbreviated SJs) 2) the mean amount of time participants took to provide a synchrony judgment after observing a visual feedback in the virtual scenario

(Judgment Times, abbreviated JTs) and 3) the mean amount of time participants took to perform a new action in the trial that followed the observation of each specific type of feedback (post observation Reaction Times, abbreviated poRTs). For VAS trials we calculated the mean reported feeling of causing the virtual action for each condition. Mean values were calculated for each dependent variable, for each subject in each of the 24 conditions resulting from the combination of 4 independent variables: Action Type (Free/Cued), Movement (Congruent, Incongruent), Goal (Achieved/Missed) and Delay (+0 ms, +150 ms, +300 ms). Before running parametrical statistical tests, we checked that the normality assumption was met by verifying that at least one of these two criteria was met (Field et al., 2013): a) that Kolmogorov-Smirnov test was not significant and that b) z-scores for skewness and kurtosis were included between -2.58 and +2.58. Several conditions were not normally distributed for all dependent variables except from VAS, where no condition violated the abovementioned criteria. To correct for this, mean SJs values were transformed by means of an ipsatization procedure: we calculated the mean reported synchrony for each subject across conditions, and we subtracted it from the individual values obtained in each condition (Tieri et al., 2015). For JTs and poRTs we applied a square root transformation to the raw mean values. For SJs, 4 out of 24 conditions were still not normally distributed after the ipsatization procedure. Given the small number of conditions not meeting the normality assumption and that the number of participants was relatively high ($N = 40$), we decided to proceed with parametrical testing. For JTs and poRTs we found no deviations from normality following transformations. SJs, JTs, poRTs and VAS data were entered into 4 separate 2x2x2x3 repeated measures Analysis of Variance (ANOVAs), with Action Type, Movement, Goal and Delay as within-subjects factors. The level of significance was set to .05 and Tukey correction was applied to all post-hoc comparisons.

3.3.4 Results

3.3.4.1 Synchrony Judgments (SJs)

The 2x2x2x3 Anova on the mean scores of ipsatized Synchrony Judgments revealed a main a main effect of factor Delay (F(2, 78): 74.830, p = .000, η_p^2 = .657. **Figure 13, panel C**). Although not surprising, this result confirms that participants correctly understood the meaning of the synchrony judgment question and that they could successfully discriminate increasing delays, which were all different from each other as confirmed by post-hoc comparisons (delay_0: mean ± SEM: 0.250 ± 0.029; delay_150: 0.015 ± 0.016; delay_300: -0,264 ± 0,026. All *ps* < .001; all *ds* > 1.608). Importantly, the Anova showed a main effect of factor Movement (F(1,39) = 7.581, p = .009, η_p^2 = .163. **Figure 13, panel A**). Participants perceived a congruent movement (M+: 0.062 ± 0.023) as more synchronous than an incongruent movement (M-: -0.062 ± 0.023, d = 0.871). Interestingly, the Anova also revealed a main effect of factor Action Type (F(1, 39) = 6.052; p = .018, η_p^2 = .134. **Figure 13, panel B**): participants perceived the visual feedback as more synchronous in the free (Free: 0.017 ± 0.007) than in the cued block (Cued: -0.017 ± 0.007, d = 0.778). Importantly, the effects of factors Action Type and Delay were further explained by an Action Type x Delay interaction (F(2, 78) = 5.221, p = .007, η_p^2 = .118. **Figure 13, panel D**). Post-hoc comparisons revealed that participants could discriminate increasing delays in both blocks (all *ps* < .001 and *ds* > 1.328 for all within-blocks comparisons. See **Table 2** for mean ± SEM for each Action Type x Delay level). Importantly, a feedback in the virtual scenario was perceived as more synchronous in the free block than in the instructed block when it was observed after a delay of 150 ms (p = .041, d = 0.367), and of 300 ms (p = .000; d = 0.354). No difference between free and cued actions was observed when no delay was introduced after button press (p = .999. d = .012). The Anova on Synchrony Judgments did not reveal any other significant main or interaction effects (all *Fs* < 2.573, all *ps* > .083, all η_p^2 < 0.062).

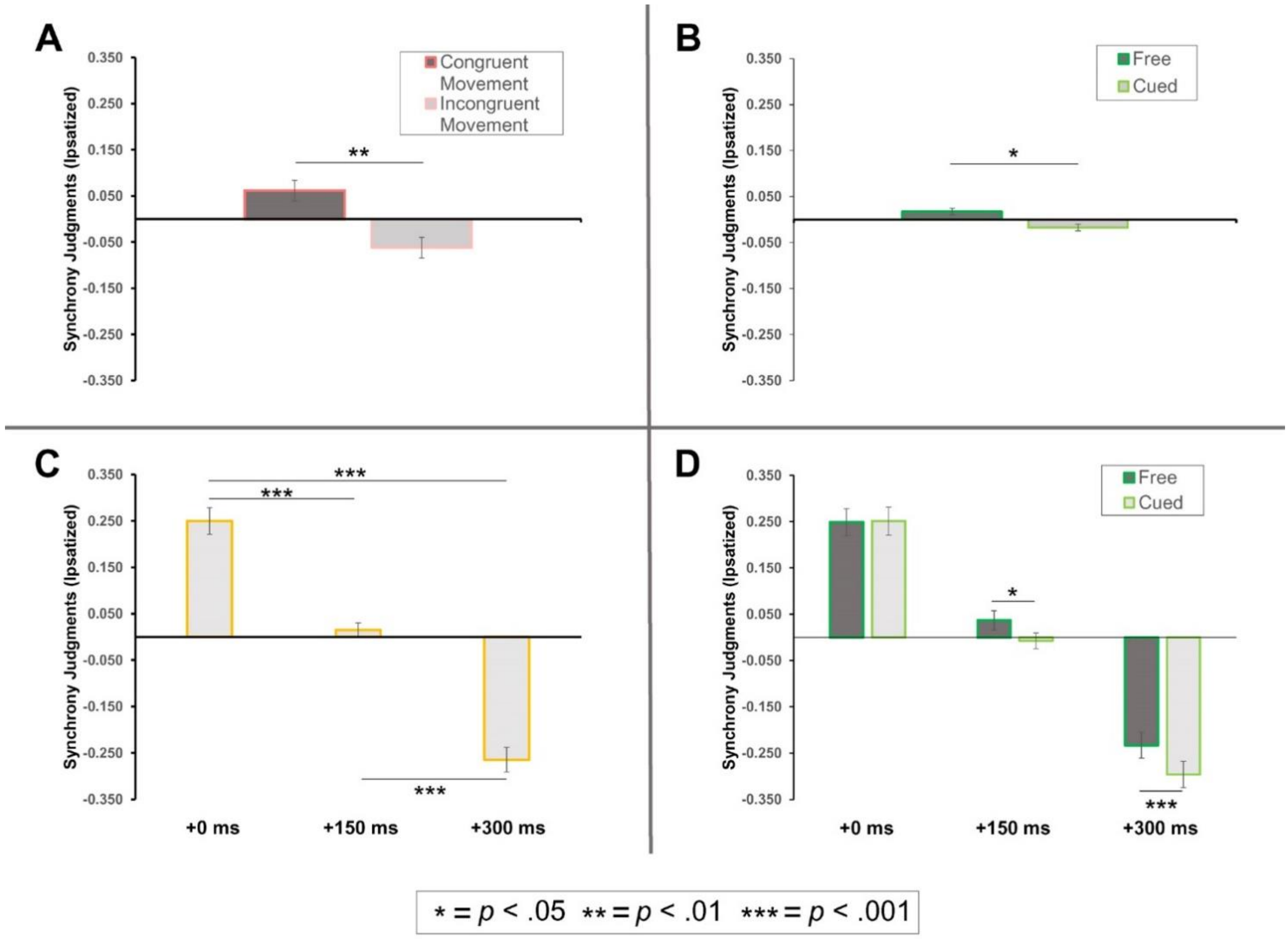

Figure 13 Effects of movement, goal and delay manipulations on Synchrony Judgments. The analysis of Synchrony Judgments revealed a main effect of factor Movement (**panel A**), indicating that participants perceived a virtual action as more Synchronous when the virtual index finger moved in their same direction as compared to when it performed an opposite movement. Additionally, a main effect of factor Action Type was found (**panel B**): participants reported on average higher perceived synchrony for free as compared to cued actions. A main effect of factor delay (**panel C**) indicated that participants could discriminate delays of increasing duration. Finally, an Action Type X Delay interaction was found (**panel D**): freely chosen actions were perceived as more synchronous with respect to cued actions when delays of 150 ms or 300 ms were introduced between real and virtual actions, but not when virtual actions took place simultaneously to button press (+ 0 ms). Error bars represent the Standard Error of the Mean in all panels.

	+ 0 ms	**+ 150 ms**	**+ 300 ms**
Free	**0.249 ± 0.029**	**0.037 ± 0.021**	**-0.233 ± 0.028**
Cued	**0.251 ± 0.030**	**0.007 ± 0.017**	**-0.296 ± 0.028**

Table 2. The table reports the mean ± Standard Error of the Mean (SEM) of ipsatized Synchrony Judgments for all levels of the interaction between factors Action Type (Free\Instructed) and Delay (+0 ms, + 150 ms, + 300 ms).

3.3.4.2 Judgment Times (JTs)

The 2x2x2x3 Anova on Judgment Times (JTs) revealed a main effect of factor Delay (F(2, 78) = 14,892, p = .000, η_p^2 = .276. **Figure 14, panel A**). Post-hoc analysis showed that participants were significantly faster in providing a synchrony judgment when the delay between action and virtual feedback was of 300 ms (Delay_300: 0.828 ± 0,016), as compared to delays 0 (Delay_0: 0.865 ± 0,017. p = .000, d = .351) and 150 (Delay_150: 0.880 ± 0,018. p = .000, d = .482). Delays 0 and 150 did not show any significant difference (p = .119, d = .140). A significant main effect of factor Goal was also found (F(1, 39)=30.218, p = .000, η_p^2 = 0.437**. Figure 14, panel B**). JTs were significantly higher when participants observed that the virtual hand pressed the button of the unexpected color (G+: 0,871 ± 0.017), as compared to when the virtual hand pressed the selected color (G-: 0.845 ± 0.016. d = 0.252). Importantly, the effects of goal manipulation on JTs are further explained by a significant interaction between factors Movement and Goal (F(1, 39) = 20,088, p =.000, η_p^2 = .340. **Fig 4, panel C**). Participants where significantly faster in providing a Synchrony Judgment after observing a fully congruent virtual action (M+G+: 0,829 ± 0,015) as compared to when they observed any of the possible types of erroneous feedback (all ps < .008; all ds > .272). Importantly, significant differences were also found for JTs following specific types of erroneous feedback. JTs were significantly slower when the movement was congruent and the goal was missed (M+G-: 0,884 ± 0,017) as compared to when movement was incongruent and the goal was missed (M-G-: 0,857 ± 0,017, p = .027, d = 0.244) and to when movement was incongruent and the goal was achieved (M-G+: 0.860 ± 0.018, d = 0.215), even though this difference was only marginally significant (p = .055). Finally, JTs following M-G+ and M-G- observation did not differ (p = .991, d = 0.023). The Anova also showed that the interaction between factors Motivation and Goal approximated significance (F(1,

39) = 3.8854, p = .056, η_p^2 = 0.091). However, this interaction was not further explored, as the p-value was higher than the significance level (.05). The Anova on JTs did not show any other significant main or interaction effects (all Fs < 2,390, all ps > .130, all η_p^2 < 0.058).

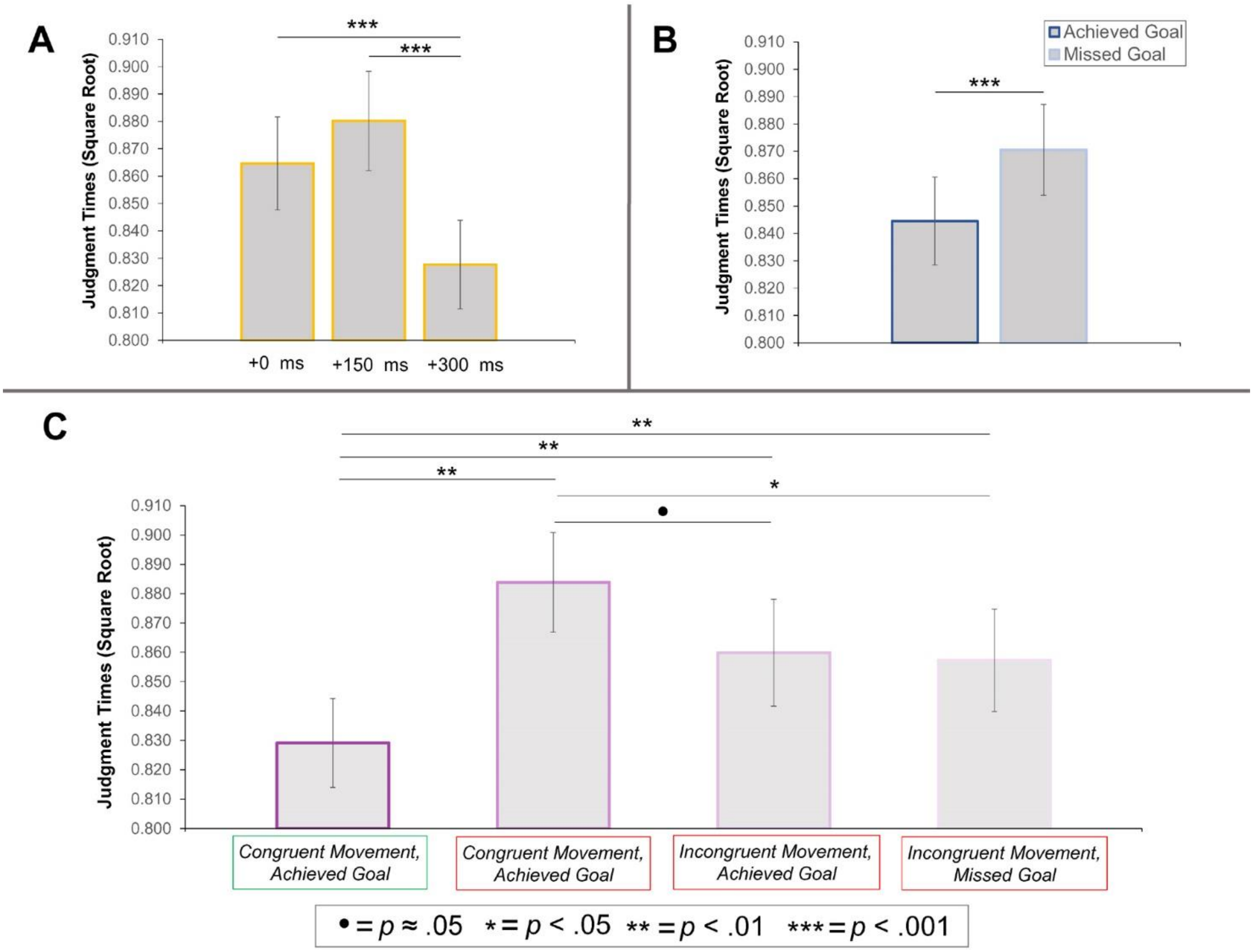

Figure 14. Effects of movement, goal and delay manipulations on Judgment Times. The analysis of the amount of time participants took to respond to the Synchrony Judgment question – i.e. Judgment Times – revealed a main effect of factor Delay (**panel A**): participants were significantly faster in providing a Synchrony Judgment when a delay of 300 ms was introduced between real and virtual action, as compared to when the delay was of 150 ms or when no delay was introduced (+0 ms). Additionally, a main effect of factor Goal was found (**panel B**). Judgment Times were significantly lower when participants observed that the goal of the action was achieved as compared to when it was missed. This effect is further explained by a significant interaction between factors Movement and Goal: the condition associated to lower Judgment Times was the one where participants observed a fully congruent virtual action (the virtual index finger moved in the same direction of the participant, pressing the selected color), which was significantly faster as compared to all the types of erroneous feedback. Additionally, one erroneous feedback was associated to slower Judgment Times as compared to the others: the one where participant observed a congruent movement, but the goal of the action

was missed (M+G-). Please note that the difference between M+G- and M-G+ approximated significance (p = .055). Error bars represent the Standard Error of the Mean in all panels.

3.3.4.3 Post Observation Reaction Times (poRTs)

The Anova on post observation Reaction Times (poRTs) revealed three main effects. Firstly, we found a main effect of factor Movement (F(1, 39) = 5.3176, p = .027, η_p^2 = .120. **Figure 15, panel A**): participants were significantly slower in executing an action in trials that followed the observation of an incongruent movement (M-: 0.772 ± 0.018) as compared to when they observed a congruent movement (M+: 0,768 ± 0.018. d = .039). Secondly, the Anova revealed a main effect of factor Goal (F(1, 39) = 5.0922, p = .030, η_p^2 = 0,115 **Figure 15, panel B**): participants were significantly slower in executing an action in the trial immediately following the observation of a failure to press the selected color (G-: 0,773 ± 0.018) as compared to when they observed the virtual hand pressing the selected color (G+: 0,767 ± 0.017, d = 0.047). Finally, the Anova also revealed a main effect of factor Action Type (F(1, 39) = 4.5896, p =.038, η_p^2 = .105). This suggests that participants might have generally been faster in performing a button press in the cued as compared to the free block. To check for this, we compared the reaction times in the two blocks, without sorting them according to the type of observed outcome in the previous trial. We performed this comparison by means of a paired samples t-test on the mean reaction times for each subject in the two blocks (square root transformation was applied, consistently with other analyses on RTs). The t-test was significant (t(39) = 2.218, p = .032, d = .247) indicating that participants performed actions faster in the cued block (Cued: 0.756 ± 0.016) than in the free block (Free: 0.786 ± 0.022). The Anova on poRTs did not reveal any other main or interaction effects (F < 2.121, p > .153, η_p^2 < .052).

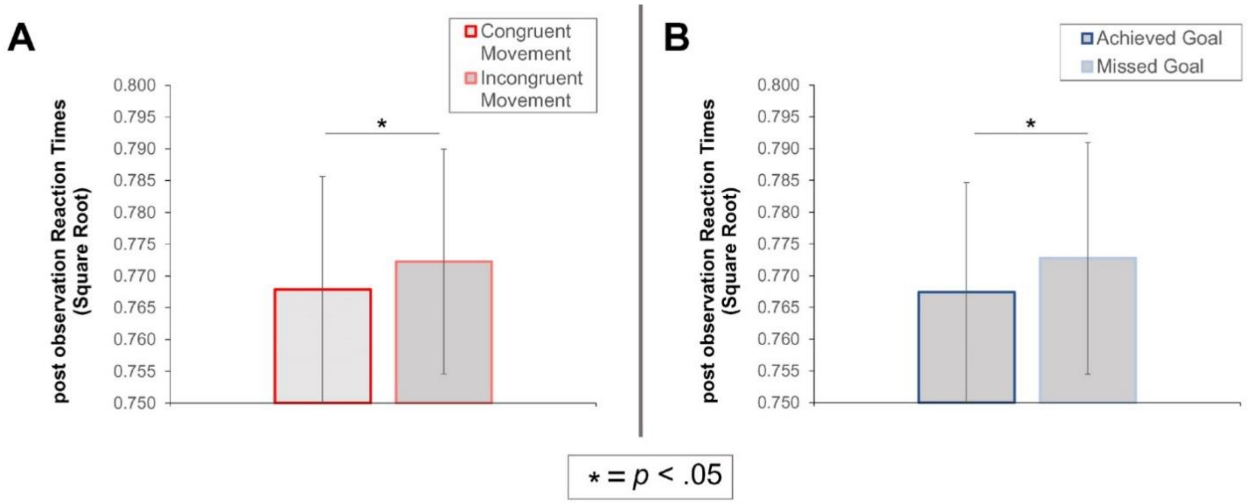

Figure 15. Effects of Movement and Goal manipulations on reaction times in the following trial i.e. post observation Reaction Times. The analysis of post observation Reaction Times revealed a main effect of factor Movement (**panel A**): participants were significantly slower at performing a button press after observing an incongruent movement as compared to a congruent movement. Additionally, a main effect of factor Goal was found (**panel B**): participants were significantly slower to perform a new action after observing that the virtual hand pressed the button of the color they did not select as compared to when they observed that the virtual hand pressed the selected color. Error bars represent the Standard Error of the Mean in all panels.

3.3.4.4 Feeling of Causation (VAS)

The 2x2x2x3 Anova on mean reported feeling of causing the virtual action (obtained in the second part of the experiment, where synchrony judgments were replaced by VAS) revealed three main effects.

Firstly, we found a main effect of factor Delay (F(2, 78)=15.463, p =.000, η_p^2 = .284. **Figure 16, panel A**): participants reported a stronger feeling of causing virtual feedbacks that immediately followed their actions as compared to delayed feedback. Post-hoc comparisons revealed that the three delays (delay_0: 52.141 ± 3.432; delay_150: 44.509 ± 2.547; delay_300: 36.815 ± 2.771) were all significantly different (all *ps* < .020, all *ds* > .399), with lower feeling of causation for increasing delays. Secondly, we found a main effect of factor Movement (F(1, 390) = 28.074, p =.000, η_p^2 = .419. **Figure 16, panel B**): participants reported a stronger feeling of causation when the virtual finger moved in the same direction as the participant's (M+: 53.070 ± 2.942), as compared to when the virtual finger moved in the opposite direction (M-: 35.907 ± 2.971, *d* = 0.918). Lastly, we found a main effect of factor Goal (F(1, 39) = 4.446, *p* = .041, η_p^2 = .102. **Figure 16, panel C**): participants reported a stronger sensation of causing the virtual feedback when the virtual hand pressed a button of the expected color (G+: 45.928 ± 2.592), as compared to when it pressed the alternative color (G-: 43.048 ±. 2.539, *d* = .177). The Anova did not reveal any other significant main or interaction effects (all *Fs* < 3.173, all *ps* > .083, η_p^2 > 0.075).

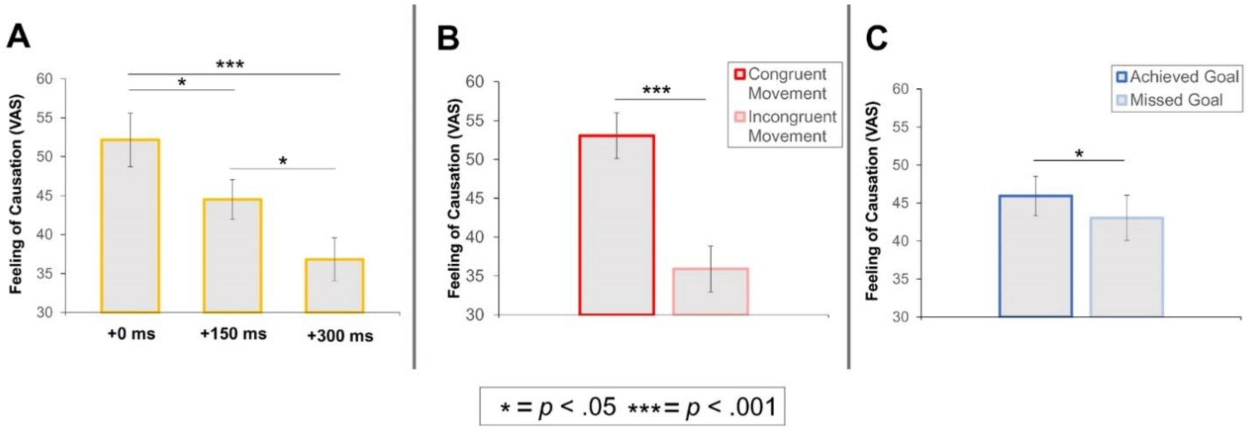

Figure 16 Effects of Movement, Goal and Delay manipulations on the subjective feeling of causation (VAS). The analysis of VAS revealed three main effects: firstly, a main effect of factor Delay (**panel A**), indicating that participants experienced lower SoA for longer delays between real and virtual action. Secondly, a main effect of factor Movement (**panel B**), indicating that participants experienced lower SoA when they observed that the virtual index finger moved in the opposite direction as compared to when it moved in their same direction. Lastly, a main effect of factor Goal was found (**Panel C**), which suggest that SoA was lower when the virtual finger pressed the button of the color they did not select, as compared to when it pressed the selected color.

3.3.4.5 Control question Analysis

To check that participants were aware of the disposition of the colors when they performed a button press, we conducted an analysis of the answers they gave to the control question ("was the final disposition of the colors - observed following the virtual action - reversed with respect to the initial one?") collected during the first part of the experiment (i.e. Synchrony Judgments blocks). We calculated the accuracy for each participant in both free and cued blocks. Participants' responded correctly to the control question on average 77.3% (± SEM: 3.1%) of the times in the free block and 71.1% (± SEM: 2.7 %) of the times in the cued block. We then compared accuracy scores for both free and cued blocks against chance (50%) by means of two separate one-sample t-tests. Participants were significantly better than chance in answering to the control question both in free ($t(39) = 8.891$, $p = .000$, $d = 1.406$) and in the cued blocks ($t(39) = 7.917$, $p = .000$, $d = 1.252$), which suggests that they were aware of disposition of the colors when they performed a button press both in free and cued blocks.

3.5 Discussion

The aim of this study was to investigate the effects of movement and goal-related prediction errors on SoA when the individual performs freely chosen or cued actions. Additionally, we investigated if the same manipulations lead to behavioral adjustments. To do this, we modified the paradigm described in chapter 2 (Villa et al., 2018) so that both free and cued actions were possible. Participants performed simple goal-directed actions – pressing a button of a chosen or cued color – and observed a virtual action represented on a screen from a first-person perspective. The virtual index finger could move in the same or in the opposite direction with respect to the participant, which generated a movement-related prediction error. The color pressed by the virtual hand could be the selected one or a different one, which resulted in a goal-related prediction error. Additionally, different delays between the executed and virtual action were introduced. We collected both indirect (i.e. Synchrony Judgments) and direct (subjective reports of the feeling of causation) measures of SoA. We also calculated the amount of time participants took to provide Synchrony Judgments (i.e. Judgment Times) and to perform a new action after observing each type of virtual action (post observation Reaction Times) to evaluate the presence of behavioral adaptations following prediction errors.

Our results suggest that freedom to act might enhance SoA. Additionally, movement-related prediction errors might reduce both implicit and explicit SoA, while goal-related prediction errors might impair SoA only at an explicit level. Analysis of Judgment Times and of post observation Reaction Times further suggests that adaptations might occur for both types of prediction errors. Interestingly, our results suggest that movement and goal-related prediction errors might exert a similar effect on SoA and lead to behavioral adaptations both in free and cued actions.

3.5.1 Effects of Freedom to act and Prediction Errors on the Sense of Agency

As expected, the analysis of Synchrony Judgments revealed that SoA decreased when a delay was introduced between the executed and observed action (main effect of factor Delay). Importantly, the same analysis revealed other main effects and interactions.

Firstly, we observed a main effect of factor Movement. Participant perceived a virtual action as more synchronous to their own when the virtual finger moved in their same direction, and as less synchronous when the virtual finger moved in the opposite direction. This effect was observed irrespective of the presence of delays, of the achievement of the goal of the action and of whether the performed actions were freely chosen or cued, as suggested by the fact that no interaction between factors Movement, Goal and Action Type was found.

Secondly, we observed a significant main effect of factor "Action Type", which was further explained by an Action Type X Delay interaction. Participants tended to perceive a virtual action as more synchronous to their own action when they freely decided which action to perform, as compared to when they received an instruction. Interestingly, this effect was observed only when a delay of 150 or 300 ms was introduced between real and virtual action and not when the virtual action was immediately triggered by their button press.

Summarizing, when SoA was measured indirectly by means of Synchrony Judgments, three sources of information appeared to modulate the experience of control: the presence of delays between the observed and virtual action; the congruency between the performed and the observed movement; and whether participants were free or cued about which action to perform. These results partly overlapped with those obtained when we collected direct measures of agency – subjective reports of the feeling of causing the virtual action by means of Visual Analogue Scales (VAS). Indeed, the analysis of VAS revealed three main effect.

Firstly, a main effect of factor Delay, indicating that participants SoA decreased when longer delays between real and virtual action were introduced. Secondly a main effect of factor Movement, indicating that participants feeling of causation was higher when the virtual finger moved in the same as compared to the opposite direction. This effect did not depend on delay duration, goal achievement or whether participants chose which action to perform or were guided by a cue. Thirdly, we also observed an interesting main effect of factor Goal: participants experienced higher control over the virtual action when they observed that the virtual hand pressed the button of the expected color as compared to when they observed a failure to achieve the goal. This effect was independent of the presence of delays, of congruency between the executed and the observed movement, and of whether participants freely selected the goal of the action or followed a cue.

Overall, our data offer an interesting representation of how different action cues might influence implicit and explicit aspects of SoA.

3.5.1.1 Freedom to act enhances implicit, but not explicit Sense of Agency

The analysis of Synchrony Judgments revealed that participants partly relied on information about the origin of the action (free choice vs external cues) to decide whether the virtual action was synchronous to their own. Indeed, Synchrony Judgments were on average higher when participants were free to decide which action to perform. This was observed when delays of 150 ms or 300 ms were introduced between real and virtual action. We thus confirm that SoA is enhanced by freedom to act as reported by other recent studies. Interestingly, we did not observe a similar effect when SoA was measured by means of VAS: freedom to act did not influence the feeling of causation. Overall, our data suggest that implicit, but not explicit SoA is enhanced by freedom of choice.

Our data are thus compatible with results of recent studies that reported stronger binding between action and outcome – and hence stronger implicit SoA - under conditions of free choice, as compared to actions performed following instructions (Barlas et al., 2017, 2018; Barlas & Kopp, 2018; Barlas & Obhi, 2013; Caspar, Christensen, et al., 2016; Caspar et al., 2018, 2017). We obtained similar results by employing a different measure - Synchrony Judgments instead of Intentional Binding – which contributes to strengthen the notion that freedom to act enhances implicit SoA. In particular, the interaction between factors Action Type and Delay is strikingly similar to the one reported by Barlas and colleagues (2017): in their case stronger binding was observed for free as compared to cued actions, but this effect was observable only when the delays between action and outcome were longer. This might suggest that information about the origin of actions (free choice vs environmental demands) might contribute to SoA when evidence in favor of oneself as the cause of actions is reduced by other factors, such as low temporal contiguity between one's action and the external consequences. However, our data do not provide support to the notion that freedom to act might enhance SoA also at an explicit level, as reported by previous studies (Barlas et al., 2017, 2018; Barlas & Kopp, 2018; Wenke et al., 2010). Some methodological differences might account for this. For instance, in previous studies participants performed actions finalized at producing outcomes in the external environment, such as a tone or the appearance of an outcome on screen. Here, participants performed actions while observing a virtual action from a first-person perspective. The virtual action could represent different types of incongruent information, concerning not only the outcome of the action (Barlas & Kopp, 2018) but also the observed movement. Hence, it is possible that movement related information, together with information concerning the achievement of the goal of the action and the presence of delays, might have been a strong cue to explicit SoA, to the point that freedom to act might have not exerted a positive effect on the feeling of causation.

3.5.1.2 Movement-related prediction errors reduce both implicit and explicit SoA, while goal-related prediction errors only impair explicit SoA

Overall, our data suggest an interesting pattern: some action-cues contribute to SoA both at an implicit and an explicit level, while the influence of others is limited to one level.

Two cues appear to influence both implicit and explicit SoA: information about movement and the temporal contiguity between action and the resulting effect. This is suggested by the fact that the main effects of factors Movement and Delay were observed both in the analysis of Synchrony Judgments and of VAS.

With respect to the role of movement, our data show that both perceived synchrony between the executed and the virtual action and the subjective feeling of causation were reduced by the occurrence of a movement-related prediction error – i.e. by the observation of an opposite movement. Hence, information about movement might be a pivotal source of SoA modulation. This is consistent with previous studies that found that information about movement congruency influenced SoA, both when indirect (Caspar, Desantis, et al., 2016) and direct measures of SoA were employed (Daprati et al., 1997; Farrer et al., 2008; Fourneret & Jeannerod, 1998; Padrao et al., 2016; van den Bos & Jeannerod, 2002). Here, we show that both indirect and direct measures yield the same result within the same paradigm, suggesting that movement-related prediction might reduce implicit and explicit SoA.

Delays between real and virtual action also appear to influence both implicit and explicit SoA: evidence for a reduction of SoA was found both when it was measured with Synchrony Judgments and VAS. This is also consistent with the results of previous studies that show a reduction of SoA when introducing a delay between executed and observed action, and between an action and its outcome (Farrer et al., 2008; Franck et al., 2001; Sato & Yasuda, 2005; Shanks, Pearson, & Dickinson, 1989; Weiss et al., 2014). However, it should be noted that in the first part of the experiment participants' task was to evaluate whether the virtual action was synchronous or not with their own action: hence, a possible limitation to our interpretation of the role of temporal contiguity on implicit SoA might be that the main effect of factor Delay simply reflects the fact that participants could successfully discriminate delays of increasing duration.

Additionally, we obtained evidence that two other action-cues might influence SoA, respectively at an implicit and explicit level: freedom to act might enhance implicit SoA; information about goal achievement might influence mostly explicit agency judgments. The role of freedom to act was discussed in the previous section (3.4.1.1). The fact that a failure to achieve the goal of the action did not reduce SoA at an implicit level might be surprising. Indeed, previous studies that employed intentional binding suggest that unexpected outcomes of the action reduce the implicit SoA (Caspar, Desantis, et al., 2016; David et al., 2016; Kühn et al., 2011; Sato & Yasuda, 2005). However, it should also be noted that other studies failed to find any effect of outcome identity on intentional binding (Desantis, Hughes, & Waszak, 2012; Haering & Kiesel, 2014). Our data are in line with the results of these latter studies. However, whether implicit SoA is modulated by goal-related prediction errors remains an open issue that should be further investigated in future studies. In particular in the study described in chapter 2 (Villa et al., 2018) we reported that a failure to achieve the goal of the action reduced implicit SoA, but only when delays between real and virtual action were short. Here we did not observe the same result, but some methodological differences might account for this. First, here both free and cued actions were possible, while our previous procedure only allowed cued actions. Second, here only 3 delays between real and virtual action were possible (+0, +150, +300 ms), while in our previous study we used 5 delays (+0, +75, +150, +225, +300 ms), which might have made it easier for participants to identify delays between real and virtual action in the present study: this could have led them to rely less on events occurring in the virtual scenario (e.g. success or failure to achieve the goal) to provide a Synchrony Judgment. Third, in this study the goal of the action in the cued block was assigned randomly in each trial, while in our previous study the goal of the action was fixed within a block: in other words, in our previous study participants were asked to press a button of a certain color (blue\yellow) for a long series of trials (around 250) before aiming for a different goal. Lastly, in this study each type of virtual feedback was observed an equal number of times (25% of trials), while in the previous study participants observed a fully correct feedback (M+G+) in 50%

of trials, and each type of erroneous feedback (M+G-, M-G+, M-G-) in 16% of trials. Consistently with a cue-integration theory of SoA (Moore & Fletcher, 2012. See below), in our previous study participants might have considered information about goal achievement as sufficiently reliable to inform implicit SoA, while here participants might have failed to form a stable association between action and outcome. Overall, our previous and present studies show different patterns of results concerning goal achievement that could be accounted for by methodological differences.

Interestingly, goal-related prediction errors were instead effective in modulating the subjective feeling of causation, as revealed by the analysis of VAS. This is consistent with the proposal that inferential processes are involved in the formation of explicit beliefs about causation and self-attribution (Synofzik et al., 2008a, 2008b; Wegner & Wheatley, 1999), which can be independent from statistical contingency between action and outcome and from learning of associations. In line with this, this result might be compatible with the fact that individuals tend to view themselves as the cause of successful outcomes, and to attribute failures to external factors (Arkin et al., 1980; Miller & Ross, 1975). Additionally, this result is in line with those of a recent study by Pezzetta and colleagues (2018), who reported that when participants passively observed a goal directed action in a fully immersive virtual scenario – a reaching movement to grasp a glass – they experienced more control over the virtual action when the virtual hand successfully grasped the glass as compared to when it failed to do so (Pezzetta et al., 2018). Importantly, the proportion of failures (75%) was higher than the proportion of successes (25%), which suggests that individual can experience explicit SoA even when the probability of success is low.

Overall, the different effects of movement and goal information might be compatible with recent models that explain SoA in terms of the contribution of various sources of SoA modulation (Moore & Fletcher, 2012; Synofzik et al., 2008a, 2008b). For instance, Moore and Fletcher (2012) proposed a Bayesian model in which multiple action cues are weighted according to their reliability. Given our experimental design, the probability of observing a movement or goal-related prediction error was 50%. This might have different implications respectively for movement and goal information and for implicit and explicit SoA. With respect to movement information, participants might have had strong prior predictions about the way movement would unfold once they performed the action. Indeed, control of one's own body is part of everyday experience. On the other hand, control of events in the external environment – especially new events such as in the case of our study – might require a reliable association between action and outcome through a learning phase. In the absence of this, participants might have disregarded information about achievement of the goal to modulate implicit SoA, which might depend more on a stable action-outcome association (Moore, Lagnado, Deal, & Haggard, 2009) but not explicit SoA, which might be partly independent from action-outcome associations.

3.5.1.3 Freedom to act and prediction errors independently affect SoA

Our study does not provide support to the possibility that movement and goal-related prediction errors might exert a different influence of SoA respectively in free and cued actions. Indeed, we did not find any significant interactions between factors Action Type, Movement and Goal in neither analysis of Synchrony Judgments or VAS. Although conclusions from null results should be extremely cautious, it is nonetheless interesting to note that a similar pattern of results was also reported by Barlas and colleagues (2018). In their study, freedom to act and congruency between expected and actual outcome exerted an independent influence on SoA: freedom to act enhanced SoA, while observation of an unexpected outcome reduced it.

Here we report a similar pattern of results by means of a different paradigm. First, here actions were performed in a virtual scenario, while in their case participants were asked to press a button and observe an expected or unexpected outcome on a screen. Secondly, here not only the external outcome, but also the observed movement could be unexpected. Hence, our results are in line with those of Barlas and colleagues and extend them, by showing that also movement related prediction errors do not exert a different influence on SoA in free and cued action. Freedom to act and action monitoring might be two independent sources of SoA modulation.

This is especially interesting with respect to monitoring of goal achievement. Indeed, voluntary actions are often viewed as goal-directed and primarily concerned with the achievement of an intended event in the external environment. For instance, ideomotor theories, as well as models of motor control, assume that movements are selected on the basis of the consequences they should bring about in the external environment (Haggard, 2008; Herwig, Prinz, & Waszak, 2007). Hence, we expected that achievement of the goal of the action would be especially relevant in a context of freedom of choice. This expectation was further motivated by recent studies by Borhani and colleagues (2016) and Beck and colleagues (2017), who showed that participants experienced stronger SoA for freely selected outcomes as compared to outcomes that were determined by an external cue (Beck et al., 2017; Borhani et al., 2017). However, this is not what we found. One important difference with respect to previous studies is that in their studies the outcome of the action was a painful or non-painful electrical stimulation that the participant delivered to him\herself by means of his\her own keypress. Their outcome is clearly different than ours for at least two reasons: firstly, our outcome (pressing a button of a certain color) was visual, instead of a painful or non-painful cutaneous stimulation; secondly, our outcome lacks any emotional value, while in their studies the outcome could be more or less pleasant for the participant. Additionally, it should be noted that our study is not the first that doesn't find an interaction between freedom to act and outcome of the action. For instance, in a series of studies, Caspar and colleagues demonstrated that binding between action and outcome is reduced by the presence of a context of coercion, and its enhanced by freedom to act (Caspar, Christensen, et al., 2016; Caspar et al., 2018, 2017). However, this effect appeared to be independent from the actual type of outcome that participants produced by means of their actions - whether their actions resulted in a more or less severe event for another individual. Thus, our results align with those Caspar and colleagues, suggesting that freedom to act itself might be linked to an enhancement of SoA, irrespective of its consequences in the external environment.

3.5.2 Behavioral adaptations following movement and goal-related prediction errors

In addition to modulation of participants' SoA, we obtained evidence that manipulation of movement and goal information had an influence also on their motor performance.

First, the analysis of Judgment Times - i.e. the time participants took to provide a Synchrony Judgment - revealed a significant main effect of factor Goal, further explained by significant interaction between factors Movement and Goal. Post-hoc analysis of this interaction revealed that participants were faster in providing a Synchrony Judgment when they observed a fully correct feedback - the goal was achieved with the expected movement – as compared to all types of erroneous feedback (M+G-, M-G+, M-G-). Interestingly, the condition that was associated to slower Judgment Times was the one where participants observed a congruent movement and the goal of the action was missed (M+G-). This indicates that participants noticed when the virtual hand pressed the button of the unexpected color, and hence that a goal-related prediction error occurred. This is also confirmed by the analysis of the control question both in the free and instructed blocks: participants could discriminate if the disposition of colors following the virtual action was reversed with respect to the beginning of the trial.

Evidence for behavioral adjustments following movement and goal related prediction errors also comes from the analysis of post-observation Reaction Times – the time participant took to perform a new action after observing a specific type of action in the virtual scenario. Here, two main effects were especially interesting, respectively of factors Goal and Movement: they indicate that participants were slower in performing a new action after observing a failure to achieve the goal of the action and an opposite movement in the previous trial, respectively.

Overall, the analysis of Judgment Times and of post observation Reaction Times suggest that not only SoA, but also participants behavior was affected by prediction errors. The slowing observed in both measures might be similar to the behavioral adjustments that occur after a real error, in particular Post Error Slowing (Danielmeier & Ullsperger, 2011; Fusco et al., 2018; Ullsperger et al., 2014).

Interestingly, despite movement appeared a more relevant cue to SoA as compared to goal achievement (at least for implicit SoA), the latter appeared to exert a strong influence in behavioral adaptations, even stronger than that of movement execution as suggested by the analysis of judgment times.

Previous evidence suggests that prediction errors and unexpected visual events that resulted from action lead to behavioral adaptations (Gentsch et al., 2009; Wessel & Aron, 2013; Wessel et al., 2012). Here, we show that post error adaptation can occur also when prediction errors are generated by the observation of a virtual hand from a first-person perspective, performing an unexpected movement or failing to achieve the goal of the action.

Finally, we did not find any evidence of a significant interaction between movement and goal-related prediction errors and the type of performed action – free or cued. This suggests that the consequences of free and cued actions might lead to similar behavioral adaptations.

3.6 Conclusion

In this study we investigated the effects of movement and goal-related prediction-errors on the Sense of Agency and on behavioral adaptations in freely chosen and cued actions. To do so, we adapted a paradigm described in the previous chapter (Villa et al., 2018) where participants execute simple goal directed actions while they observe a virtual action from a first-person perspective. The virtual action can be similar or dissimilar to the real action. Manipulations occurring in the virtual scenario allow to violate participant's expectations about movement, goal achievement and timing of these two action-cues. We collected both indirect (Synchrony Judgments) and direct (subjective ratings about the feeling of causation) measures of SoA, and we looked for possible behavioral adaptations following each type of action. Our data suggest that movement prediction errors – both at an implicit and explicit level – and goal prediction errors – only at an explicit level – reduce SoA, both in free and instructed actions. Additionally, they suggest that freedom to act might enhance implicit, but not explicit SoA. Finally, both movement and goal-related prediction errors might lead to behavioral adjustments in free and instructed actions.

Our data depict an interesting pattern of how different action cues contribute to SoA. Firstly, we provide support to the notion that freedom to act enhances SoA. Secondly, movement execution appears to be a central cue to SoA, while goal achievement appears to mostly influence explicit judgments of agency. However, it is possible that the contribution of goal information to implicit SoA might increase in case of a more reliable association between action and outcome (Moore, Lagnado, et al., 2009). The influence of goal achievement might also be enhanced if it was endowed with an affective or rewarding valence (Takahata et al., 2012; Yoshie & Haggard, 2013). Future studies might tackle these issues. Finally, we showed that prediction errors pertaining movement and goal information might both lead to behavioral adjustments. However, the suggestions from this behavioral study should be further explored by means of suitable neuroimaging techniques, such as electroencephalography (EEG), which could allow to identify specific event-related potentials (e.g. ERN/FRN) or modulation of the activity of specific bands of frequency (e.g. Theta/Delta) often associated to identification of errors or of prediction errors (Cavanagh & Frank, 2014; Ullsperger et al., 2014). The application of EEG recording to our paradigm might allow to understand whether movement and goal related prediction errors generate similar or different brain potentials (Krigolson & Holroyd, 2006, 2007) and how these signals might specifically be associated to behavioral adjustments and to modulation of the Sense of Agency.

4. General conclusions

4.1 General discussion: effects of movement execution, goal achievement and freedom to act on the Sense of Agency

In this thesis I reported the results of two behavioral studies that employed the novel paradigm I described in chapters 2 and 3, which allows an independent and simultaneous manipulation of visual information about movement execution and goal achievement. Our initial aim was to understand the effects of violation of expectations about these two actions-cues on the Sense of Agency (chapter 2). We then sought to understand the influence of movement and goal-related prediction errors on the Sense of Agency in free as compared to cued actions (chapter 3). These studies were led under the assumption, supported by previous evidence, that a strong link exists between the detection of unpredicted events (i.e. prediction errors) by the action monitoring systems and modulation of the Sense of Agency. We expected that prediction errors would also have led participants to adjust their behavior.

Consistently with our hypotheses, we found evidence in both studies that our manipulations had an influence on the Sense of Agency and led to behavioral adjustments.

In the first study (chapter 2), we found that observation of an opposite movement with respect to the performed one reduced the Sense of Agency. Additionally, the observation of a failure to achieve the goal of the action reduced the Sense of Agency, but only when delays between action and outcome were short. We concluded that movement information might be a more constant source of Sense of Agency modulation than goal information. Additionally, we found that the observation of an unexpected movement and a failure to achieve the goal of the action both led to an increase of the time participants took to provide a judgment of agency (i.e. Judgment Times), which might be similar to the post-error slowing observed when individuals make an error (Danielmeier & Ullsperger, 2011).

In the second study, we found that both implicit and explicit levels of the Sense of Agency are influenced by movement information: this is suggested by the fact that movement-related prediction errors reduced both the perceived synchrony between the executed and the virtual action (i.e., Synchrony Judgments, indirect measure of the Sense of Agency) and the subjective feeling of causing the virtual action (direct measure of the Sense of Agency). On the other hand, we found that information about goal achievement influenced the Sense of Agency only at this latter, explicit level. The effects of the two action cues did not differ in free and cued actions. With respect to freedom to act, the results of the second study further suggest that it might enhance the Sense of Agency. The second study also provided further support that behavioral adjustments might occur for both movement and goal-related prediction errors. Indeed, similarly to the first study, we found that Judgment Times were slower when either the observed movement or the color pressed by the virtual hand were unpredicted. Additionally, participants were also slower in executing an action in the trial that immediately followed the observation of an opposite movement or a failure to achieve the goal of the action. These effects were observed both in freely chosen and in cued actions.

In both studies, information about movement appeared to consistently influence the Sense of Agency. Indeed, observation of a different movement with respect to the executed one impaired the Sense of Agency, both at an implicit and explicit level, and in freely chosen and cued actions.

An equally important role appears to be played by the timing of action related events. Indeed, delays between action and outcomes are known to reduce the Sense of Agency (David et al., 2016; Franck et al., 2001; Sato & Yasuda, 2005; Shanks, Pearson, & Dickinson, 1989). Although the effects of delays on our indirect measure of Sense of Agency - Synchrony Judgments - might simply reflect the fact that participants could discriminate gaps of increasing duration between the executed and observed action, the fact that participants reported a reduced feeling of causation for increasing delays supports the notion that the Sense of Agency is reduced when the timing of action-related events is different than predicted.

Additionally, in our second study we found evidence that freedom to act might enhance the Sense of Agency. This is in line with previous studies that found that the Sense of Agency might be increased by higher freedom of choice (Barlas et al., 2017, 2018; Barlas & Kopp, 2018; Barlas & Obhi, 2013) and reduced by a social context of coercion (Caspar, Christensen, et al., 2016; Caspar et al., 2018, 2017). However, this effect was only observed when the Sense of Agency was measured by means of Synchrony Judgments, and not when we asked participants a direct subjective report of their feeling of causation, as reported by previous studies (Barlas et al., 2017, 2018; Barlas & Kopp, 2018; Wenke et al., 2010). Interestingly, the role of freedom to act might be dependent on the temporal contingency between action and effect: when the effect takes place with an unexpected delay, the individual might rely on the information about the origin of the action – free choice or external cue - to decide whether she\he is in control. In other words, freedom to act might contribute to the Sense of Agency when the objective control of actions is reduced by the presence of noise, such as delays. Interestingly, no interaction was found between freedom to act and goal achievement. This suggests that individuals might not experience a higher Sense of Agency for freely chosen outcomes, as compared to identical outcomes generated following an external cue. This might be surprising with respect ideomotor theories of motor control, that suggest that actions are programmed to achieve a certain desired goal, and with respect to the common idea that Free Will and Sense of Agency are strongly connected (Haggard, 2008; Herwig et al., 2007). However, previous studies offer an inconsistent pattern of results with respect to this issue. Some studies (Borhani et al., 2016; Beck et al., 2017) find evidence for a higher sensation of control over freely chosen outcomes, while others do not corroborate this finding (Caspar, Christensen, et al., 2016; Caspar et al., 2018, 2017). Our results do not suggest that freely chosen outcomes might have a special status in influencing the Sense of Agency with respect to outcomes indicated by external instructions.

Finally, the role of the achievement of the goal of the action in our studies was not consistent. In the first study, goal attainment was associated to higher Sense of Agency as compared to a failure to attain the goal only when delays between executed and virtual action were short. In the second study, this effect on synchrony judgments was not visible. However, when synchrony judgments where replaced by visual analogue scales, participants reported a stronger feeling of causing the virtual action when the goal was achieved as compared to when it was missed, suggesting that explicit Sense of Agency might be influenced by goal information.

I provided some possible explanations of the different effects of a failure to achieve the goal of the action on Synchrony Judgments found in our two behavioral studies in section 3.5.1.2. In brief, consistently with a Bayesian cue integration-theory of the Sense of Agency (Moore & Fletcher, 2012), an explanation might be related to the reliability of the information relative to the achievement of the goal of the action. Indeed, in the first study the proportion of successes in attaining the goal was higher than in the second study. This might have led participants in the second study to disregard information about the goal of the action as a source of modulation of their implicit Sense of Agency. Taken together, our two studies seem to suggest that the relevance of achieving the goal of the action might be limited, either in time domain (first study) or to an explicit level of the Sense of Agency (second study).

In our two studies, we did not find any evidence for an interaction between factors movement and goal that could further explain their respective roles for the Sense of Agency. This prevents us from showing a hierarchy of the importance of these two action cues for the experience of control. Nonetheless, our data strongly suggest that information about movement execution might be a more reliable source of Sense of Agency modulation than goal achievement. This conclusion is supported by the fact that while movement information exerted an influence irrespective of the slight differences between the design of our two studies and of the adopted measures of Sense of Agency (Synchrony Judgments\subjective reports of the feeling of causation) the influence of goal achievement appears to be limited by specific parameters in our experimental design (first study) or by the use of an explicit measure of the Sense of Agency (second study).

However, it is interesting to note that both movement and goal-related prediction errors led to behavioral adjustments, as described above. This result was consistent across the two studies. From the one hand, these findings support the notion that movement and goal-related prediction errors, and not only actual error commission, might result in behavioral adjustments. From the other hand, they suggest that that participants could notice both manipulations of movement and goal achievement, which led them to adjust their behavior. This was not mirrored by analogous modulations of the Sense of Agency, as discussed above.

4.2 General conclusions: how these results fit (and do not fit) with previous evidence and theoretical models of the Sense of Agency

Taken together, the result of the two behavioral studies provide some indications with respect to the roles of movement execution, goal achievement and freedom to act for the Sense of Agency in goal-directed actions. Although these should be taken with caution, they might contribute to rethink previous ideas about the roles of different action components for the feeling of control and generate further questions.

Our results suggest that when participants perform simple goal-directed actions in a virtual scenario where different types of unpredicted events can take place, they appear to be mostly affected by movement and time-related prediction errors, rather than by goal-related prediction errors. This might be surprising with respect to studies that manipulated the correspondence between the intended and actual outcome of the action, and that found that the Sense of Agency was reduced when actions were followed by an unexpected event (e.g. Kühn et al., 2011; Sato & Yasuda, 2005).

Indeed, the Sense of Agency is believed to be strongly influenced by the match between the intended and desired effect in the outside world – i.e., goal achievement (Blakemore et al., 2002; Haggard, 2017). The relevance attributed to goal achievement for the feeling of control might have its roots in the renowned "ideo-motor" theory of voluntary behavior, according to which intentional actions require a representation of their effects (Elsner & Hommel, 2001; Haggard, 2005; Hommel, 2009; James, 1890). Current theories of the Sense of Agency view voluntariness as a central cue (Haggard, 2017), an hypothesis that has received support in recent research (Barlas et al., 2017, 2018; Barlas & Obhi, 2013; Caspar, Christensen, et al., 2016; Caspar et al., 2018, 2017; Wenke et al., 2010). However, it is interesting to note that these studies seem to agree on the fact that the Sense of Agency is enhanced by the mere possibility of choosing which action to perform, rather than on the *achievement* of a freely chosen goal. In this sense, the absence of a clear indication that freely chosen outcomes foster a stronger Sense of Agency as compared for instance, to outcomes determined by a external instruction, casts doubts on the idea that goal achievement might be a crucial aspect for the Sense of Agency (see paragraph 3.5.1 for a more detailed discussion of this issue). Even more important is the fact that previous studies of the Sense of Agency in goal-directed actions did not generally involve manipulations of the executed movement. Only a few studies investigated in the same experiment both motor related-cues – by means of manipulation of the responsiveness of input devices to motor commands – and goal achievement (Metcalfe et al., 2013; Metcalfe & Greene, 2007; Wen et al., 2015a). However, it should be noted that these studies did not involve the direct manipulation of movement information (for instance, by showing a congruent or incongruent visual feedback of participant movement), but rather of its proximal consequences. Tellingly, some other studies manipulated both visual feedback about the movement and congruence of the *outcome* – rather than the *goal* - of the action (Caspar, Desantis, et al., 2016; David et al., 2016). Strikingly, most of these studies found that the presence of unpredicted motor-related information (unresponsive input devices\distorted visual feedback of the movement) reduced the Sense of Agency to a similar extent, if not even higher, than a failure to obtain the expected action effect (one exception can be found, for instance, in the study by David and colleagues, as discussed in paragraph 2.5).

In line with these findings, in our two behavioral studies we did not find evidence that goal achievement might be more relevant than accurate movement execution for Sense of Agency modulation. On the contrary, it appears that intermediate steps between the generation of an intention and the effect in the external environment – i.e., the executed movements and time gaps between action and outcome – might be crucially involved in the modulation of both implicit and explicit aspects of the Sense of Agency. As discussed in the previous paragraph, only when some conditions are met – e.g. the presence of specific delays between action and outcome, or the use of direct measure of the Sense of Agency – individuals seem to make use also of other sources of information, such as goal achievement and freedom to act, to modulate their feeling of control.

Importantly, our findings were obtained by means of a paradigm that combines the investigation of different action cues for the Sense of Agency (as in Caspar, Desantis, et al., 2016; David et al., 2016) with the presence of a simple goal-directed action (as in Metcalfe et al., 2013; Metcalfe & Greene, 2007; Wen et al., 2015a). Our novel line of research thus extends the finding that controlling one's own movements is crucial for experiencing a Sense of Agency in a goal-directed action, by showing that unpredicted movements of a virtual hand consistently reduce the feeling of control.

The conclusion that movement and time related information might be the most relevant sources of Sense of Agency modulation should be taken with caution: indeed, they are driven by the attempt to reconcile the results of the two studies in a general view, rather than on a significant statistical interaction between factors Movement, Goal, and Freedom to act, which we did not find neither of our two studies and with neither indirect nor direct measures of Sense of Agency: this does not allow to define a precise hierarchy of their relevance for the Sense of Agency. Nonetheless, our results appear to be partly discrepant with the idea that goal achievement and freedom to act might be the most relevant factors in generating a feeling of control. In this sense, our results might contribute to generate both theoretical debate and new studies aimed at disentangling the role of different action cues for the Sense of Agency.

A possible explanation for the more reliable role of movement information as compared to goal achievement for the Sense of Agency might be found by considering the way in actions unfold. In goal-directed actions, controlling one's own movements is a fundamental prerequisite to obtain the desired change in the external environment. Importantly, imprecise movement execution is likely to cause also a failure to achieve the goal of the action, despite under some circumstances environmental changes might compensate for motor errors. However, individuals do not generally rely on luck or on external assistance: the latter might be the case, for instance, when people permanently or transitorily lost the possibility to effectively control their bodies. But individuals without neurological or movement disorders (as the participants to our studies) might consider the fine control over their body a fundamental mean to achieve their desired goals, and as a consequence a crucial cue to their Sense of Agency. As a consequence, our results cast doubt on the assumption that goal achievement is sufficient to foster the Sense of Agency, if movements do not unfold as planned. Additionally, our results also suggest that the idea that freedom to act enhances the Sense of Agency should be taken with caution: although we found evidence for this in our second study, it should also be considered, as discussed above, that being free to decide which action to perform might contribute only to implicit levels Sense of Agency, and when evidence in favor of oneself as the cause of a certain event is reduced, for instance by the presence of delays between action and outcome. Furthermore, we did not find evidence that freely chosen outcomes might be associated to higher Sense of Agency than outcomes obtained following an external cue: hence, our results do not provide strong support to the hypothesis that Free Will and Sense of Agency are intimately connected (Barlas & Obhi, 2013; Haggard, 2017).

Importantly, our results might contribute to refine the way in which prediction errors are thought to influence the Sense of Agency. Indeed, the fact that prediction errors reduce the Sense of Agency is generally accepted and is one of the key assumptions of the Comparator Model (Blakemore et al., 2002; Frith et al., 2000). However, our results show that the severity of movement and goal-related prediction errors might not necessarily be mirrored in an equally severe reduction of the Sense of Agency. This is suggested by of our studies, which show different effects of movement and goal-related prediction errors respectively on measures of behavioral adjustments and of Sense of Agency: indeed, movement and goal manipulations led to similar behavioral adjustments, but the same manipulations did not result in analogous effects on the Sense of Agency. This is particularly interesting with respect to goal-related prediction errors, that consistently led to behavioral adjustments, without resulting in a similar reduction of the Sense of Agency. This suggests that the idea that prediction errors reduce the Sense of Agency should be taken with caution: the effects of prediction errors on the feeling of control might also depend on their informativeness, as suggested by cue-integration theories (Moore & Fletcher, 2012; Synofzik et al., 2008a).

Interestingly, we did not find any evidence in the second study that the type of performed action (free vs cued) and the monitoring of the consequences of one's action might interact. As shown in chapter 3, the fact that both freedom to act and prediction errors contribute to modulate the Sense of Agency has received wide support by lines of research that were mostly independent one from the other. To my knowledge, only one previous study has attempted to combine their investigation before (Barlas & Kopp, 2018). Our second study adds evidence that freedom to act and prediction errors might independently influence the Sense of Agency, and extends the conclusion of Barlas & Kopp to movement-related prediction errors.

Our novel line of research also offers some methodological novelties in the study of Sense of Agency in goal-directed actions.

Firstly, our results were obtained by means of a paradigm where participants performed genuine goal-directed actions, in the sense that participants did not need to associate a certain action to a certain consequence (e.g. a tone). Our task might be similar to simple everyday actions, such as turning on a light. This appears to be different than previous studies where participants learned that a certain action would be followed by a certain event in training sessions, which generates uncertainty with respect to whether participants simply expected that a certain event would follow their actions, or genuinely intended to produce those events (e.g. Kühn et al., 2011; Sato & Yasuda, 2005). Secondly, our studies employed virtual humanlike stimuli to manipulate movement-related information: this is different than previous studies that used robotic hands (e.g., Caspar, Cleeremans, & Haggard, 2015; Caspar, Desantis, et al., 2016), or that manipulated responsiveness of input devices to motor commands (e.g., Metcalfe et al., 2013; Metcalfe & Greene, 2007; Wen et al., 2015a).

Finally, our results show the intriguing possibility that behavioral adjustments might occur not only for real errors (Danielmeier & Ullsperger, 2011; Fusco et al., 2018; Ullsperger et al., 2014), but also for prediction errors relative to movements or outcomes. However, these results are only preliminary and should be corroborated by further studies specifically aimed at the investigation of the effects of prediction errors on participants behavior.

4.3 Current development: investigating the neural signatures of movement and goal-related prediction errors, and their effects on the Sense of Agency

Our two behavioral studies provided evidence that movement and goal-related prediction errors did not only reduce the Sense of Agency: they also led participants to adjust their behavior. Evidence for behavioral adjustments occurring in our paradigm suggests that our manipulations might recruit neural systems dedicated to the monitoring of one's actions. This encouraged us to explore brain responses to movement and goal-related prediction errors, and how these might be related to the modulation of the Sense of Agency. We are currently investigating these issues in a study that combines our paradigm with electroencephalography (EEG).

The error (or action) monitoring system is a neurocognitive function dedicated to the detection of errors in goal-directed actions (Cavanagh & Frank, 2014; Ullsperger et al., 2014). Neuroimaging studies have revealed that this system might be centered on the Medial Frontal Cortex (MFC), in particular on the Anterior Cingulate Cortex (ACC) (Cavanagh & Frank, 2014; Ridderinkhof & Ullsperger, 2004; Ullsperger et al., 2014). The activity in this region would signal the need for cognitive control due to errors that prevent the individual from achieving the desired goal of the action. This would result in a re-organization of behavior that might allow to overcome the obstacle that prevented the individual from obtaining the goal. Electrophysiological studies revealed that the brain responds to errors by generating specific signals. In the time domain (i.e., Event-Related Potentials), two components have been consistently observed: the Error-Related Negativity (ERN), a negative deflection peaking approximately 80 ms after the commission of an error and that is generally found with a fronto-central distribution; and the Error Positivity (Pe), a later component consisting in a positive deflection which peaks around 300 ms and which is generally associated to a central-posterior distribution (Pezzetta et al., 2018; Ullsperger et al., 2014). In the time-frequency domain, detection of errors have been associated to a the modulation of the activity of some specific frequency bands, such as Theta, which shows an increase in power after an error is made (Cavanagh & Frank, 2014).

Recent studies revealed that also prediction errors might recruit the same monitoring system and similar brain regions involved in the detection of real errors and lead to behavioral adjustments (Gentsch et al., 2009; Joch, Hegele, Maurer, Müller, & Maurer, 2017; Wessel & Aron, 2013; Wessel et al., 2012). For instance, Joch and colleagues (2017) found that mere violation of predictions relative to the course of action might recruit the same neural activity observed following real errors. This was suggested also by Gentsch and colleagues (2009) who observed that when participant's action was followed by the observation of a fake error – i.e. the outcome of the action was unexpectedly wrong due to an experimental manipulation – brain activity was similar and had an analogous scalp distribution as compared to when the participant committed a real error. However, "fake" errors resulted in a similar but different component, possibly the feedback related negativity (FRN), that has a delayed latency with respect to real errors.

Additionally a recent line of studies found that the mere observation in an immersive virtual environment of an avatar making an error from a first person perspective generates brain responses overlapping with those observed when an individual makes an error, such as the ERN, the Pe and an increase of power of the Theta band (Pavone et al., 2016; Pezzetta et al., 2018; Spinelli et al., 2018). Hence, we hypothesized that also the observation of a movement or goal-related prediction error would be detected by the action monitoring system resulting in the generation of components in the EEG signal such as the ERN\FRN and the Pe, and in a modulation of the activity of the Theta Band. However, whether the two types of prediction error might result in analogous brain signals is not clear. For instance, Padrao and colleagues reported that the observation of an avatar moving his hand in the opposite direction with respect to the participant resulted in a negative deflection analogous to the N400 that was mostly observable in parietal regions (Padrao et al., 2016). It is thus possible that the observation of an opposite index finger movement of the virtual hand might result in a similar component. In addition to this, previous studies found that unexpected outcomes of an action might generate an FRN and an in increase in the power of the Theta Band (Balconi & Crivelli, 2009, 2010), which suggests that something similar could happen in our paradigm when the virtual hand presses a button of the unexpected color.

Hence, it is possible that movement and goal-related prediction errors might generate dissociable brain components. Evidence for this comes from a series of studies by Krigolson and Holroyd (Krigolson & Holroyd, 2006, 2007). These authors provided evidence that movement and outcome errors might generate different signals and involve different systems. At a neural level, the ACC would monitor incongruences between the intended and the actual outcome of the action. On the other hand, PPC would identify discrepancies between planned and executed movements, which might be similar to the finding by Padrao and colleagues that unexpected movements might involve the activity of the parietal cortex.

However, previous studies either did not involve the use of virtual stimuli (Balconi & Crivelli, 2009, 2010, Krigolson & Holroyd, 2006, 2007) or they did not include the execution of a goal directed action (Padrao et al., 2016; Pavone et al., 2016; Pezzetta et al., 2018; Spinelli et al., 2018). Hence, we decided to run a new study, in which we could apply EEG recording to our novel paradigm (**Figure 17)**. We reasoned that this would allow us to investigate the brain potentials respectively associated to movement and goal-related prediction errors, and how these potentials might relate to variations of the Sense of Agency and to behavioral adjustments.

The design of this EEG study is very similar to the one described in chapter 2. However, since the number of trials required to for an EEG experiment is higher than the one advised for a behavioral study, we decided to employ a simpler design. We removed the cued block, since we did not find any evidence of any interaction between free\cued actions and visual manipulation of movement and\or goal information. Additionally, we decided to use only the indirect measure of Sense of Agency (i.e.

Synchrony Judgments). These changes resulted in a 2x2x3 design, given by our manipulation of factors Movement (Same\Opposite), Goal (Achieved, Missed), and Delay (+0, +150, +300) ms. The combination of these factors gives a total of 12 conditions, each of which is observed in 32 different trials, for a total of 384 trials.

On the basis of previous evidence, we hypothesize that both movement and a goal-related prediction errors will be detected by the error monitoring system and generate components that were reported by similar previous studies. In particular, in the time domain we predict that a negative deflection in the recordings will be observed for both types of prediction errors. The latency of this negative component might be comparable to the observed ERN or to the FRN, but it might also depend on the type of prediction error. In line with the results of previous studies that manipulated both motor and outcome-related information (Krigolson & Holroyd, 2006,2007), we also expect to observe a different scalp distribution of these components: goal-related prediction errors might involve the activity of frontal sites, while movement related prediction errors might be associated to the generation or components in posterior sites overlapping with the parietal cortex.

Additionally, we expect that the presence of these components might be, to a certain extent, inversely correlated with the Sense of Agency. This would be in line with models that posit a link between the presence of error signals and the reduction of the Sense of Agency. However, it should be noted that both cue-integration theories of the Sense of Agency (Moore & Fletcher, 2012; Synofzik et al., 2008b, 2008a) and the results of our two behavioral studies suggest that error signals might not suffice to modulate the Sense of Agency, and that reliability of information from these different sources might be a crucial factor. Hence, one possibility is that the Sense of Agency might not be affected by goal-related prediction errors, despite the presence of goal-related error signals in the EEG recordings. Unfortunately, data from participants who already participated in the study (N = 10) in the study was not analyzed yet, and for this reason they were not included in the thesis.

Nonetheless, I considered it would be useful to add this paragraph, so that I could offer an idea of the evolution of my project, and of the hypotheses that I developed from my previous studies.

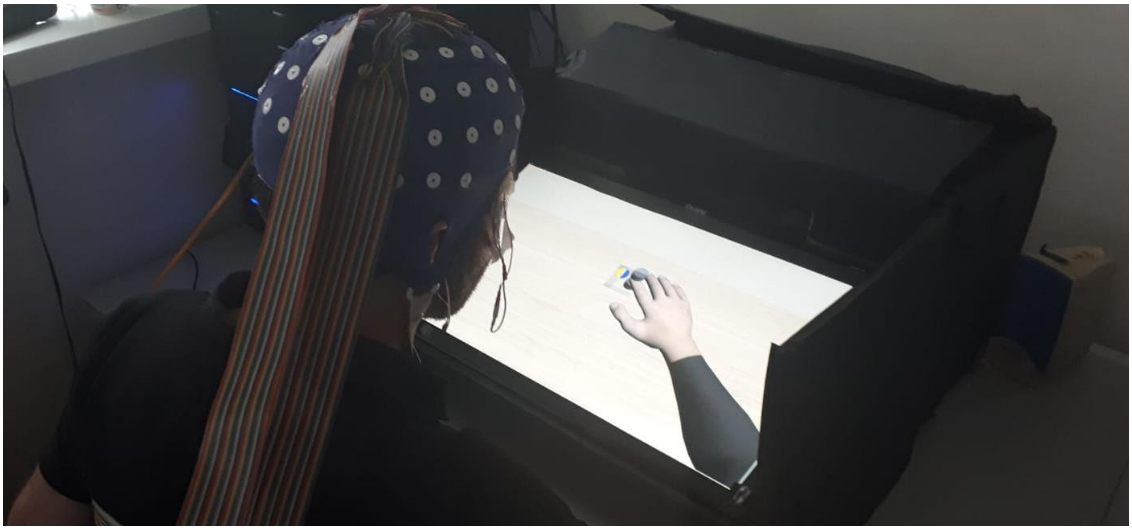

Figure 17. the experimental set up of our current study, that combines our novel paradigm with recording of brain activity by means of electroencephalography (EEG).

4.4 Future directions and applications

In this thesis I presented a novel paradigm which was designed to allow the comparison of the influence on the Sense of Agency of different action cues – movement, goal and time-related – by means of their simultaneous manipulations. The paradigm was employed in two behavioral studies so far (chapters 2 and 3) and is currently being used in a new study, where it is combined with EEG recording (paragraph 4.3). Additionally, other studies could be led in the future, which might aim at solving some of the potential current limitations of the paradigm, or at understanding how the different action cues contribute to the Sense of Agency in clinical conditions and in actions resulting in a significant outcome for the participants.

One possible future study might aim at understanding whether the observation of *real* actions, rather than the ones performed by a virtual humanlike hand, would yield the same results. The choice of using virtual stimuli in our previous studies was motivated by several reasons (as argued more extensively in paragraph 2.2): firstly, it was found that individuals can experience control over virtual actions (e.g., Pezzetta et al., 2018; Tieri et al., 2015); secondly, we wanted to isolate the influence of movement manipulation from the potential influence of the morphological appearance of participant's real hand on our Sense of Agency measures; lastly, the use of identical virtual stimuli allowed to simplify our experimental setup. Nonetheless, this paradigm could be adapted so that participants could observe their own hands, rather than virtual ones. This could be achieved for instance, by first filming participant upwards and downwards movements by means of a video-camera. The video-recordings could later be used as stimuli in the experimental session. Depending on the direction of participant movements – upwards, downwards – participants could be presented with the video-recording of his own hand performing the same or opposite movement, in this latter case generating a movement-related prediction error. By comparing conditions in which participants observe virtual stimuli to conditions where they observe movements of their own hand, it would be possible to compare whether individuals experience the same feeling of control for virtual hands and real hands, and to compare the effects of movement related prediction errors in these two scenarios. This comparison might be intriguing, especially in an age where virtual reality is becoming part of everyday life, and individuals perform actions in virtual scenarios that have real consequences. Indeed, nowadays virtual reality is being employed in many fields, such as in work environments, education and medical training.

Another future methodological study might aim at understanding whether Synchrony Judgments are as effective as other measures to capture variations of the Sense of Agency. As argued in paragraph 2.2, the choice of this measure was driven by previous studies (Farrer et al., 2008; Weiss et al., 2014) and aimed at minimizing the possibility of self-attribution bias. We obtained evidence, in the two studies presented here, that Synchrony Judgments are capable to measure changes in participants' Sense of Agency. However, as argued in paragraph 2.2, some issues might be associated to Synchrony Judgments, such as that they might not be capable to fully capture variation of the Sense of Agency given by the experimental manipulation; they might not be immune to the influence of changes in the Sense of Ownership; and individuals might still experience a Sense of Agency over effects that are delayed with respect to the action. To provide further support to the validity of Synchrony Judgments as a measure of Sense of Agency, a new methodological study could be performed, where Synchrony Judgments are compared with other known indirect measures of the feeling of control, such as Intentional Binding or sensory attenuation (Blakemore et al., 1999, 2000; Burin et al., 2017; Desantis, Weiss, et al., 2012; Kühn et al., 2011). Given the complexity of our virtual scenario, the combination of our paradigm with measures of sensory attenuation might be complicated. However, a future study might aim at understanding if Synchrony Judgments and Intentional Binding yield the same results. To do so, our paradigm could be slightly modified so that after each trial participants could be asked, under one experimental condition, to provide a Synchrony Judgments; under another, to provide an estimate of the time interval in milliseconds between the real and the virtual action - i.e., interval estimations. Indeed, interval estimation has been used as a simplified measure of intentional binding in recent studies (Caspar, Christensen, et al., 2016; Caspar et al., 2015, 2018; Caspar, Desantis, et al., 2016; Caspar et al., 2017). It could be hypothesized that when movement or goal-related prediction errors occur, participants might report both a reduced perceived synchrony between real and virtual action – when the Sense of Agency is assessed by means of Synchrony Judgment - and a longer interval estimate, suggesting reduced binding - when interval estimations are employed. The two measures might hence be correlated: the higher the perceived synchrony between real and virtual action, the lower the estimated interval (which would suggest higher Intentional Binding). This future methodological study might help to provide stronger support for the use of Synchrony Judgments as an indirect measure of Sense of Agency.

In addition to the potential methodological studies described above, the characteristics of our novel paradigm might make it particularly useful to study the Sense of Agency in clinical conditions and in actions that have an affective value.

Many psychological and neurological disorders have been associated to an impairment of the Sense of Agency and of the experience of action. These include schizophrenia, obsessive-compulsive disorder, depression, anosognosia for hemiplegia, utilization behavior or the anarchic hand syndrome (Blakemore et al., 2002; Frith et al., 2000; Moore & Fletcher, 2012).

For instance, previous studies observed that schizophrenic patients tend to interpret events as they were caused by their actions more than healthy controls (Daprati et al., 1997; Franck et al., 2001; Metcalfe, Van Snellenberg, DeRosse, Balsam, & Malhotra, 2014). This over-attribution effects have been explained as a consequence of the reliance of schizophrenic patients on external cues, rather than on their own internal forward signals (Frith et al., 2000; Metcalfe et al., 2014; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Voss et al., 2010). Consistently, passivity experiences in schizophrenia – i.e. the tendency of some participants to view their actions and thoughts as externally generated - has been often linked to either a deficit in the capacity to predict the consequences of actions or to recognize the existence of those predictions (Frith et al., 2000). Similarly, the disturbance of the Sense of Agency in Obsessive Compulsive Disorder have been explained as a result of a deficit in the predicting the consequences of actions (Gentsch et al., 2012).

However, no study so far systematically investigated which sub-components of these predictions are compromised in these disorders. In other words, are both movement and goal-related predictions compromised in these patients? Our paradigm might help to understand which aspects of self-monitoring and of the Sense of Agency – either related to the control of one’s movements or to the achievement of a desired goal – are compromised in this and in other clinical conditions.

Another potential application of this paradigm might be related to the study of the Sense of Agency in actions that have an emotional or affective value. As Gentsch and Synofzik recently observed: “Emotions are the force initiating and guiding behavior by making people act in certain ways in order to achieve or avoid significant outcomes, and actions in turn change how we are feeling and give rise to particular emotional states” (Gentsch & Synofzik, 2014). However, most of the studies on the Sense of Agency (including ours) have focuses on actions that did not have any significant outcome for the participant. Previous research avoided affective dimensions to understand the basic principles of the Sense of Agency by employing simple experimental settings. Nonetheless, actions outside laboratories are endowed with a meaning, which might be related to the emotional value of the outcome or to the social context in which actions are performed (Di Costa, Théro, Chambon, & Haggard, 2017; Gentsch & Synofzik, 2014). By adapting our paradigm, it would be possible to understand whether the relevance of movement and goal related information for the Sense of Agency is modulated by the presence of a meaningful goal. For instance, Takahata and colleagues found that when participants performed actions that resulted in monetary loss the Sense of Agency was reduced, as compared to when the action led to monetary gain (Takahata et al., 2012). Yoshie and Haggard found that hearing a negative emotional vocalization following one's action was associated to Sense of Agency reduction (Yoshie & Haggard, 2013). Hence, it could be hypothesized that succeeding or failing to attain a meaningful goal would have a stronger impact for the Sense of Agency with respect to our previous data, where the goal was neutral with respect to affective of rewarding dimensions. Additionally, it would be interesting to understand if the relevance of different action-cues would change with respect to our previous findings, if the action was embedded in a relevant social context, such as one of coercion, which has been shown to reduce the Sense of Agency for outcomes of the action (Caspar, Christensen, et al., 2016; Caspar et al., 2018, 2017). However, whether coercion also results in a reduction of the experience of control over one's movements is unclear. The combination of our paradigm with those of Caspar and colleagues could help to shed light on this issue. With this respect, the inclusion of Sense of Ownership measures in our paradigm could also help to understand if individuals also experience a reduced sensation of owning a body under a threatening social context.

Finally, one potential application of this paradigm could be related to the study of individuals of lost the possibility to control upper limbs, and amputees. This might allow to understand what fundamental part of the experience of acting they are missing: the possibility to control their body, or the capacity to change their environment according to their needs. Results of these experiments might help engineers to design devices that are more likely to restore not only the objective capacity to exert agency, but also the sensations deriving from it.

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APPENDIX – Neurocognitive processes underlying the control of oculomotor behavior: A dual-pulse TMS study

A1. Abstract

The capacity of the individuals to exert agency, i.e. control of one's own ocular movements might be reduced when one is exposed to potentially distracting social stimuli (other's gaze). In this study, participants were asked to perform saccades towards the left or the right starting from a central position, following an imperative cue (i.e., the color change in blue or red respectively of a central square). Just before the appearance of the imperative cue, participants also observed a human model moving his eyes in the same or in the opposite direction with respect to the one indicated by the cue. We expected that participants would be automatically captured by the model's gaze, and that this would have resulted in slower reaction times and impaired performance in case the model gazed in the opposite direction with respect to the cued one. By using a non-invasive brain stimulation technique (i.e., Transcranial Magnetic Stimulation) we also investigated the neural correlates of controlling oculomotor movements when exposed to others' gaze movements. Previous work has shown that both Frontal Eye Fields (FEF) and Posterior Parietal Cortex (PPC) might contribute to reduce the influence (i.e., the re-orienting of attention) of distracting social stimuli when these are incompatible with one's current task and that this is mapped in the brain according to a somatocentric frame of reference. Therefore, we hypothesized that interfering with the normal activity of FEF would enhance the influence of the gaze of another individual more that when interfering with PPC normal activity, being PPC more involved in controlling the attentional capture mediated by hand gestures. Therefore, we expected that TMS stimulation of FEF would increase the tendency to follow the gaze of the other individuals, and hence reduce the control over one's own oculomotor behavior. We measured participant's oculomotor behavior by means of an eye-tracker and a dual pulse Transcranial

Magnetic Stimulation paradigm to temporary interfere with the activity of the right FEF and of the right PPC while participants were asked to perform saccadic movements. Our preliminary results suggest that control over one’s own gaze is reduced when the model moved his eyes in the opposite direction with respect of the cue. Additionally, we provide initial evidence that stimulation of FEF resulted in worse performance.

A2. Introduction

Perceiving another person's gaze direction rapidly orients one's own attention to the gazed-at location (Driver et al., 1999; Friesen, and Kingstone, 1998) reflexively (Frischen et al., 2007) and, to a large extent, independently from awareness (Sato et al., 2007; Xu et al., 2011). The reactivity to social cues indexed by covert shifts of attention or eye movements triggered by others' gaze (i.e. gaze-following, GF) is foundational to the development of other sophisticated social skills such as joint attention and theory of mind (Baron-Cohen, 1995; Emery, 2000; Itier, and Batty, 2009). GF is found in many species of animals, e.g. birds (Bugnyar et al., 2004; Jaime et al., 2009); dogs (Téglás et al., 2012) and tortoises (Wilkinson et al., 2010), as well as in non-human and human primates (Deaner, and Platt, 2003; Tomasello, et al., 1998). In humans, GF emerges early in life (Brooks and Meltzoff, 2005; Moll and Tomasello, 2004) and is often dysfunctional in neurodevelopmental disorders like autism (Senju et al., 2004; Zilbovicius et al., 2006).

Although largely automatic (Ricciardelli et al., 2012) shifts of attention driven by averted gaze are influenced by higher-order variables, e.g. social status of the gazing face (Dalmaso et al., 2012) and observer-distractor perceived similarities in personality (Liuzza et al., 2013, 2011) or physical appearance (Porciello et al., 2014b; Hungr and Hunt, 2012).

Functional neuroimaging studies have explored the neural correlates of voluntary shifts of visuo-spatial attention triggered by endogenous cues and of reflexive shifts of visuo-spatial attention triggered by highly salient, but non-informative peripheral cues. Findings from these studies report activation of a dorsal frontoparietal network in which the principal nodes are the intraparietal sulcus (IPS)/superior parietal lobule (SPL) and the frontal eye field (FEF) and of a ventral frontoparietal network, the principal nodes of which are the temporo-parietal junction (TPJ), the ventral frontal cortex as well as the insula (see Corbetta et al., 2008 for a review).

Whether the control of social attention recruit specialized neural mechanisms is still an open and hotly debated question. Some studies, for example, report that social and non-social stimuli bring about increase of neural activity in overlapping regions (Sato et al., 2009; Tipper et al., 2008). However, specific activations triggered by gaze have also been reported suggesting that shifts of attention triggered by social stimuli may be mediated by neural systems at least partially different from those mediated by non-social stimuli (Engell et al., 2010; Hietanen et al., 2006). Over the past few years, we have explored whether reflexive orienting mediated by body-related distractors (gaze and pointing hands) influences voluntary shifts of attention and the coordinate systems used for implementing such shifts at both the behavioral (Crostella et al., 2009; Ricciardelli et al., 2002) and neural (Cazzato et al., 2012; Porciello et al., 2014a) level. The behavioral results showed that the magnitude of the interference mediated by social distractors depended on the type of overt directional response that participants used to perform the task. Indeed, previous work suggests that agency, i.e. the control over one's own ocular or hand movements, is reduced by the observation of a biological, effector-specific social stimulus. In particular, averted gaze interfered more when participants performed saccadic movements, and directional hands interfered more when pointing movements were requested (Crostella et al., 2009). Using fMRI we found that the magnitude of the attentional capture mediated by the social stimuli, contingent upon the distractor-effector link, specifically modulated the BOLD signal in the fronto-parietal attentional network with increased FEF activity for averted gaze during the saccadic task and increased IPS activity for distracting hands in the hand-pointing task (Cazzato et al., 2012). Whether the selective increase of fronto-parietal activity is crucial for the effector-based mapping of reflexive social attention or it is merely epiphenomenal remains largely unknown. Recent TMS evidence (Porciello et al., 2014a) suggests a causal role of the PPC in mediating the control of hand pointing distracting stimuli when participants used pointing gestures to respond to the color change of an imperative cue. However, no studies thus far have explored whether frontal regions are in turn actively involved in controlling attentional shifts triggered by gaze when the onlookers perform saccadic movements. If this is found to be true, it would complement and expand the notion that the fronto-parietal networks control social attention according to body-effector centered co-ordinate systems as predicted by our somatotopic model of social attention (Cazzato et al., 2012; Crostella et al., 2009; Porciello et al., 2014a). To explore this hypothesis, we conducted a study in which healthy participants performed leftward or rightward saccadic movements following a central imperative cue, while observing a human model moving his eyes in the same or in the opposite direction with respect to the one indicated by the cue. We expected that the observed, directional gaze would impair participant's performance in the task. Using an event-related dual-pulse TMS paradigm we transitorily interfered with the neural activity of two areas crucially involved in the orienting and re-orienting of social and non-social visuo-spatial attention: FEF and posterior parietal cortex (PPC). TMS pulses were delivered at two different time intervals: the first one was delivered simultaneously with the appearance of the directional distractors (i.e. 75 ms before the imperative cue); the second one 100 ms later (25 ms after the imperative cue), a condition in which interference effects were found (Porciello et al., 2014a). Based on fMRI (Cazzato et al., 2012) and TMS (Porciello et al., 2014a) findings, we predicted that interfering with FEF, but not with PPC would selectively impair agency over one's oculomotor behavior, due to an increase of the attentional capture mediated by the distracting gaze of the human model.

A3. Materials and Methods

A3.1 Participants

17 participants took part so far to the study (6 males, age range: 19-26, mean ± standard error of the mean (SEM): 22.44 ± 0.48). All participants were right-handed, had normal or corrected to normal vision, no problems with color perception and were naïve to the purposes of the study. The experimental procedures, in accordance with the ethical standards of the 1964 Declaration of Helsinki, were approved by the Ethics Committee of the Department of Psychology. None of the participants had neurological, psychiatric, other medical problems or any contraindication to TMS (Rossi et al., 2009). No discomforts or adverse effects due to the TMS were reported or noticed by participants.

A power analysis conducted with GPower 3.1 (Faul et al., 2007) with the following parameters: estimated effect size f: 0.25, $\alpha = .05$, Power: .80 - suggested that for observing a small-medium of the Congruence x Stimulation Site interaction (see below) we should collect data from a total of 24 participants. For this reason, results from this study should be considered preliminary.

A3.2 Experimental Procedure

The study was performed in a quiet room with medium illumination (about 64 cd/m2). Participants sat in front of an LCD monitor, positioned at about 60 cm from their eyes. Each trial started with the appearance of a black central fixation cue (0.21° x 0.21°) presented in the center of a distracting non-directional image – a human model with a straight gaze - centered in turn on a light gray background (about 47 cd/m2), and two black squares (0.43° x 0.43°) presented at 10.2° of eccentricity in the left and right visual field. After 575 ms, the color of the central cue changed to either blue or red. The color change was the imperative signal for making a fast and accurate saccade toward the left (change into blue) or the right (change into red) lateral target square. The imperative signal remained visible until the end of the trial. 75 ms before the onset of the imperative cue a directional stimulus consisting of a color digital picture (6.38° X 6.76°) depicting the human model performing a leftwards of rightwards directional gaze (**Figure A1**), replaced the image depicting the human model with a straight gaze. Distracting gazes were hence animated by two frames presented in rapid sequence: the second frame (lasting 875 ms) depicting a leftward or rightward gaze replaced the first non-directional frame (lasting 500 ms).

The direction of the distractor and the direction indicated by the imperative cue were either congruent (both left/right -ward) or incongruent (one leftward and the other rightward or viceversa). Importantly, participants were repeatedly instructed to ignore the distracting stimuli, uninformative of the upcoming location indicated by the imperative cue, and to focus their attention only on the central cue. This engaged automatic processes by minimizing expectations. Moreover, to avoid possible anticipations of the stimuli, a random inter-trial interval (ITI) ranging from 1500 to 3000 ms was inserted.

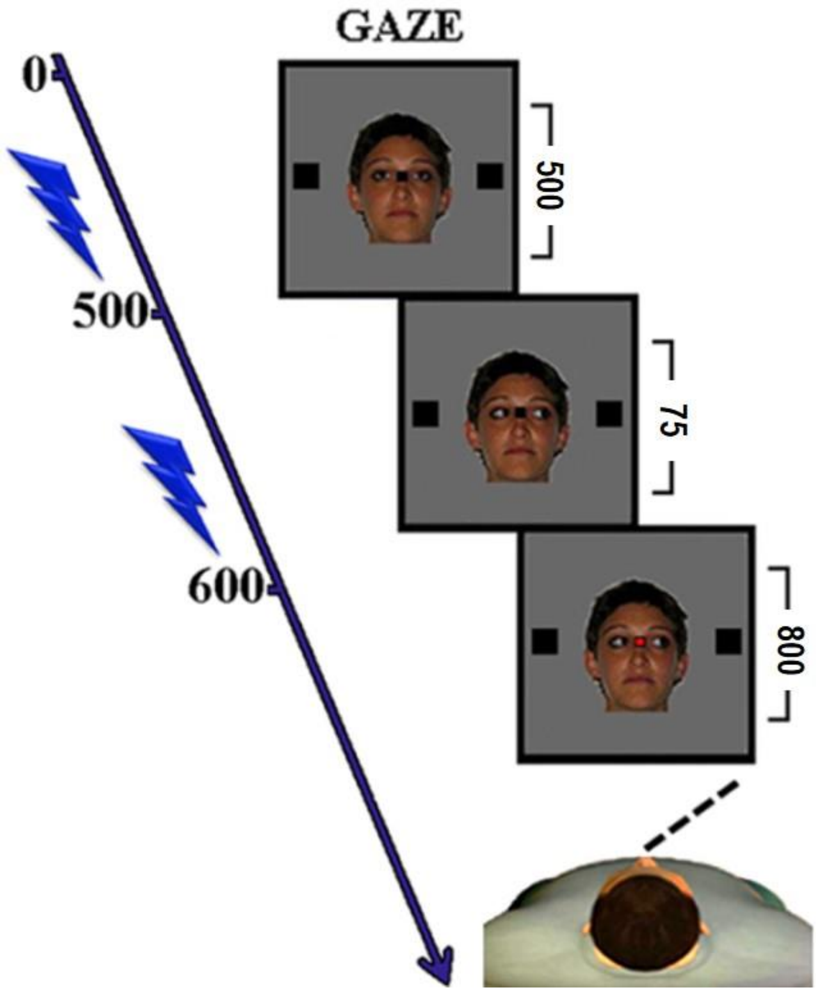

Figure A1. Structure of a typical trial of the gaze-following task. Participants had to make saccades from the central black cue to the right or to the left later black target, as quickly and accurately as possible, according to the change in color (into red or blue) of the central cue. Red signaled to gaze right, blue signaled to gaze left. Dual-pulse transcranial magnetic stimulation (dpTMS) with an interstimulus interval (ISI) of 100 ms, was delivered supra-threshold on one of the three cortical sites (FEF or PPC) in each trial at 500 ms, simultaneous with the onset of the directional gaze (congruent or incongruent with the direction indicated by the central imperative cue)

Participants were tested in two identical separate blocks to minimize fatigue. Additionally, to allow that the dpTMS could be applied on FEF and PPC in a consecutive number of trials without changing the position of the coil, hence facilitating the precise stimulation of our target areas, each block was additionally divided in fours sub-blocks (order counterbalanced across participants), where only FEF or PPC was stimulated. In each sub-block, the two imperative cues (left/right -ward) and the direction expressed by the distractor (congruent or incongruent respect to the imperative cue) were equally probable (50%) and presented in a random sequence. Each of the 4 possible combinations was repeated 12 times in each sub-block, for a total of 48 trials per block and of 96 trials in the whole experiment.

To measure the oculomotor behavior, eye position and movements were measured monocularly in real-time by means of an infrared video-based system (SMI RED 500, SensoMotoric Instruments, GmbH, Germany). Gaze position was determined by analyzing video field collected at 240 Hz with an accuracy of 0.5°, using the combined Purkinje-Pupil reflection as a tracking method, and measured with a spatial resolution of about 0.25° visual angle. All the analyses were based on the horizontal eye position. Calibration and drift correction of the position signal were repeated every 12 trials. Slight head movements were compensated by the system.

Following our previous results (Porciello et al., 2014a), dpTMS was delivered simultaneously to the appearance of the oriented distractor (first pulse 75 ms before and second pulse 25 ms after the imperative cue) to transiently disrupt the hypothesized the re-orienting of the attention triggered by directional gaze. The two target sites of stimulation, FEF and PPC, were stimulated in separate sub-blocks. The timing and delivery of visual and dpTMS stimuli were controlled with E-Prime (version 1.2, Psychology Software Tools, Inc., Pittsburgh, PA). Full detail of the TMS stimulation procedure can be found in the next paragraph.

A3.3 Dual-pulse TMS procedure

Participants wore a tightly fitting bathing cap on which the stimulation points of the scalp were marked. Stimulation sites were identified on each participant's scalp with SofTaxic Navigator system (EMS, Bologna, Italy), as in our previous TMS studies (Avenanti et al., 2013; Avenanti et al., 2007; Porciello et al., 2014a; Urgesi et al., 2007a). Skull landmarks (nasion, inion and two preauricular points) and about 60 points providing a uniform representation of the scalp were digitized using a Fastrak Polhemus digitizer (Polhemus, Colchester, VT). Coordinates in Talairach space (Talairach and Tournoux, 1988) were automatically estimated by the SofTaxic Navigator from a standard MRI-constructed stereotaxic template.

The scalp locations best corresponding to FEF (Paus, 1996) and PPC (see for a review Iacoboni, 2006) coordinates for the right hemisphere were identified and marked with a pen. Mean (± SEM) coordinates of the stimulation sites were $x = 30.8 \pm 0.23$, $y = -1.53 \pm 0.12$, $z = 46.41 \pm 0.12$ for right FEF, and $x = 26.24 \pm 0.43$, $y = -53.47 \pm 0.47$, $z = 55.88 \pm 0.36$ for right PPC. Although the fronto-parietal attention network is bilaterally distributed, several neuroimaging and clinical studies point at a prominent role of the right hemisphere in controlling attentional orienting and re-orienting functions (Corbetta and Shulman, 2011). Thus, also in view of the need to control the length of each experiment, we chose to stimulate only the right hemisphere.

To interfere with the target areas (FEF, PPC) we used dual-pulse TMS (dpTMS). dpTMS may produce facilitatory and inhibitory effects on participants' performance depending on different stimulation parameters and behavioral contexts (Kapoula et al., 2011; O'Shea et al., 2004; Wip et al., 2001). Crucially inhibitory effects in reflexive social attention paradigms were obtained using stimulation parameters similar to those used in the present study (Porciello et al., 2014a). Moreover, inhibitory effects of dpTMS were found by stimulating frontal, parietal, and occipito-temporal regions, during body processing tasks (Candidi et al., 2008; Urgesi et al., 2007b). dpTMS was applied by connecting two Magstim Model 200 stimulators with Bistim module (The Magstim Company, Carmarthenshire, Wales, UK), with a 70-mm figure-eight stimulation coil (Magstim polyurethane-coated coil) in separate blocked conditions (i.e the sub-blocks where only FEF or PPC was stimulated). Two supra-threshold pulses were delivered with an interstimulus interval of 100 ms. Stimulation intensity was 120% of the resting motor threshold (defined as the lowest intensity able to evoke 5 of 10 motor-evoked potentials with amplitude of at least 50 mV, recorded from the first dorsal interosseous muscle of the right hand with surface Ag/AgCl electrodes placed in a belly-tendon montage) for both pulses and ranged from 38% to 68% (mean value = 53.06%) of the maximum stimulator output. The same pulse delay and the individual stimulation intensity were used for each stimulation site. It is held that a relatively high intensity of TMS may reduce the focality of stimulation causing direct spread of excitation to other oculomotor areas. However, previous TMS studies on oculomotor control used the same or even higher stimulation intensities and still produced regional specific effects on the initiation of eye movements (Müri et al., 1995; Nyffeler et al., 2007; Olk et al., 2006).

During dpTMS, the coil was held by hand tangential to the scalp, with the handle pointing backward and medially at a 45° angle from the middle sagittal axis of the participants' head. The position of the coil with respect to the marks was checked continuously. During the stimulation, participants wore commercial earplugs to protect their hearing. None of the participants reported phosphenes or muscular twitches after the stimulation.

A3.4 Data Handling

We calculated reaction times (RTs) and accuracy (percentages of correct responses) of participants' saccadic responses in each condition.

Directional accuracy was calculated by focusing on the first horizontal saccade that followed the imperative cue with an amplitude larger than 2°. Only correct RTs were considered. Trials in which the reaction time was lower than 100 ms (anticipations) and trials where the reaction times were higher than 500 ms (delays) were excluded from the analysis. Additionally, reaction times respectively lower than -3DS and higher than +3DS with respect to the participant mean in a specific condition were excluded from the statistical analysis.

The combination of our 2 experimental factors – Stimulation Site (FEF\PPC) and Congruence (Congruent\Incongruent direction of the observed gaze with respect to the imperative cue) determined a 2x2 experimental design and a total of four possible conditions. For each condition and for each participant we calculated the mean accuracy and the mean reaction time of the saccadic movements.

Once ascertained that both dependent variables were normally distributed in all conditions using the Kolmogorov-Smirnov test, we analyzed mean accuracy and mean RTs separately by means of two 2x2 repeated measures ANOVAs with Simulation Site and Congruence as within subjects factors. Moreover, we explored possible interactions between our two dependent variables – Accuracy and RTs – as a function of the stimulation site. We first calculated an index for each subject of the interference effect (IE) induced by the distracting stimuli on participants' accuracy, by subtracting the mean values for congruent and incongruent conditions separately for the two stimulation sites. This index, termed "Accuracy IE", allowed us to combine the performance at the congruent and incongruent trials in terms of interference, i.e. costs-plus-benefits (see also Liuzza et al., 2011; Wiese et al., 2012 for a similar approach). We then obtained an index of the of the overall distracting effect of incongruent gaze on reaction times for each participant – the "Overall RTs IE" – by calculating the difference between incongruent and congruent conditions across stimulation sites. This index should reflect the tendency of the participant to be distracted by the model's gaze, since it is independent of stimulation site. This second index was used as a covariate in an ANCOVA with Stimulation Site as within subjects factor and "Accuracy IE" as dependent variable. We expected that participants who were most likely to be distracted by the model's gaze would also be the ones who would be mostly affected by the temporary disruption of FEF, which would result in a reduction of accuracy.

All statistical tests were performed with STATISTICA 8 (StatSoft, Tulsa, OK, USA). Newman-Keuls was used to correct for possible post-hoc comparisons.

A4. Results

A4.1 Accuracy

The 2x2 Anova on Accuracy revealed a main effect of factor Congruence ($F(1, 16) = 21.642$, $p = .000$, $\eta_p^2 = .575$. **Figure A2**). Participants were significantly less accurate in following the imperative cue when the human model gazed in the incongruent (Mean ± SEM: 0.946 ± 0.014) as compared to a congruent (Mean ± SEM: 0.756 ± 0.043) direction. The effects of factors Stimulation Site ($p > .38$) and the interaction Stimulation Site X Congruence ($p > .610$) were not significant.

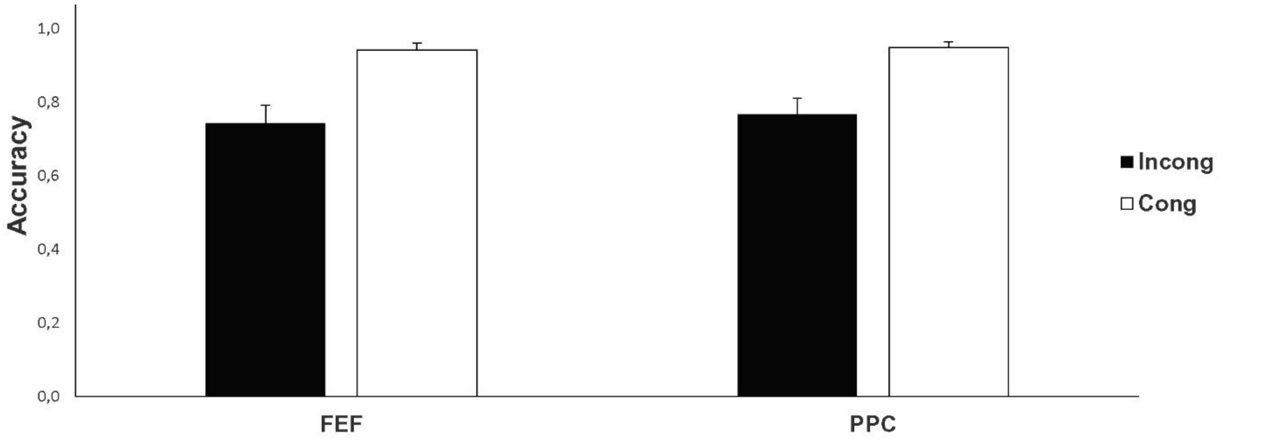

Figure A2. Effect of distracting gaze on accuracy. Observing the human model performing a saccade in the opposite direction with respect to the imperative cue (*Incong*) was associated to a significant decrease of participants' accuracy to follow the instruction as compared to when the observed saccade was in the same direction as the cued one (*Cong*), as indicated by the main effect of factor Congruence. Participants' accuracy did not change when dpTMS was applied over FEF or PPC. Error bars represent the Standard Error of the Mean.

A4.2 Reaction Times

The 2x2 Anova on Reaction Times revealed a main effect of factor Congruence ($F(1, 16) = 27.484$, $p = .000$ $\eta p2 = .632$ **Figure A3**). Participants were significantly slower in executing correct saccades when the human model gazed in the incongruent (Mean ± SEM: 314.2 ± 7.86) as compared to a congruent (Mean ± SEM: 288.34 ± 7.24) direction with respect to the imperative cue. The effects of factors Stimulation Site ($p > .80$) and the interaction Stimulation Site X Congruence ($p > .674$) were not significant.

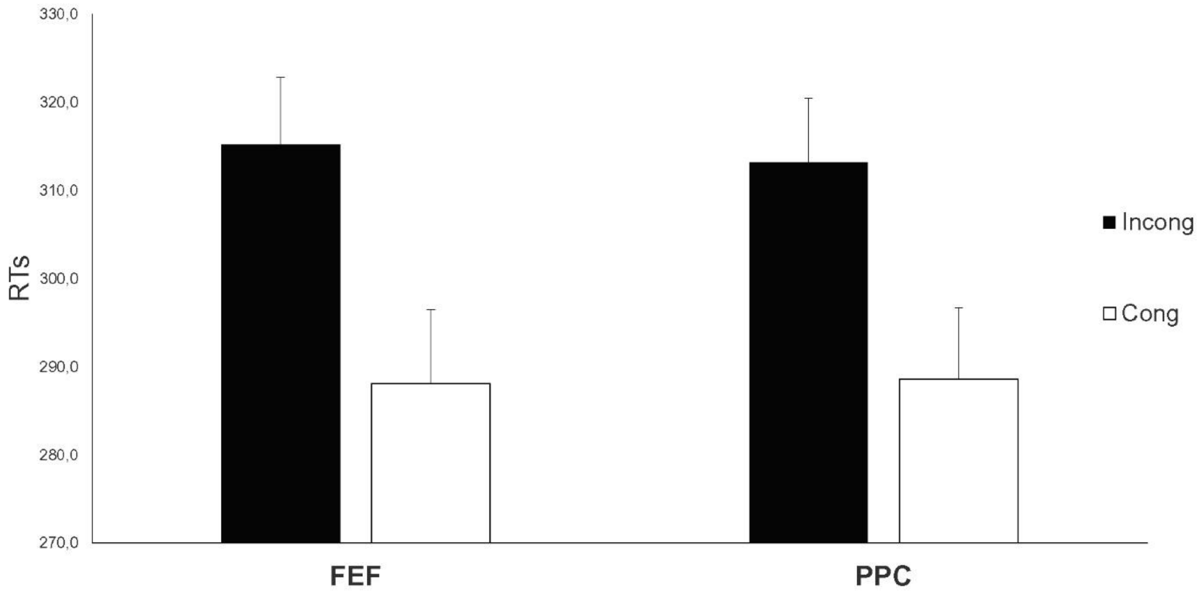

Figure A3. Effect of distracting gaze on Reaction Times. Observing the human model performing a saccade in the opposite direction with respect to the imperative cue (*Incong*) was associated to a significant increase of participants reaction times, as compared to when the observed saccade was in the same direction as the cued one (*Cong*), as indicated by the main effect of factor Congruence. Participants'reaction times did not change when dpTMS was applied over FEF or PPC. Error bars represent the Standard Error of the Mean.

A4.3 Accuracy - Interference Effect

The ANCOVA lead with "Accuracy IE" as dependent variable, "Overall RTs IE" as continuous predictor, and "Stimulation Site" as within subjects factor did not reveal any significant main or interaction effect. Indeed, neither the main effect of "Overall RTs IE" ($p > .26$), nor the main effect of "Stimulation Site" ($p > .16$) was significant. However, the interaction between these two factors approximated significance ($p = .068$). We decided to perform an explorative analysis of this interaction. To do this, we subtracted the Accuracy IE for PPC, from that of FEF, thus obtaining an index of the interference effect due to the stimulation site ("Overall Stimulation Site IE"): a higher value of this index suggests that stimulation of FEF compromised participant's accuracy more than stimulation of PPC. We then performed a correlation of this index with the "Overall RTs IE". Although not significant ($r = .482$, $p = .068$, $r^2 = .233$. **Figure A4**), this correlation suggests that the slower participants were in performing a correct saccade when they were exposed to an incongruent distracting gaze, the more the stimulation of FEF decreased their accuracy. In other words, the effect of selective FEF stimulation on disrupting oculomotor control might depend on the general tendency of the participants to imitate a distracting gaze, as reflected by the "Overall RTs IE" index.

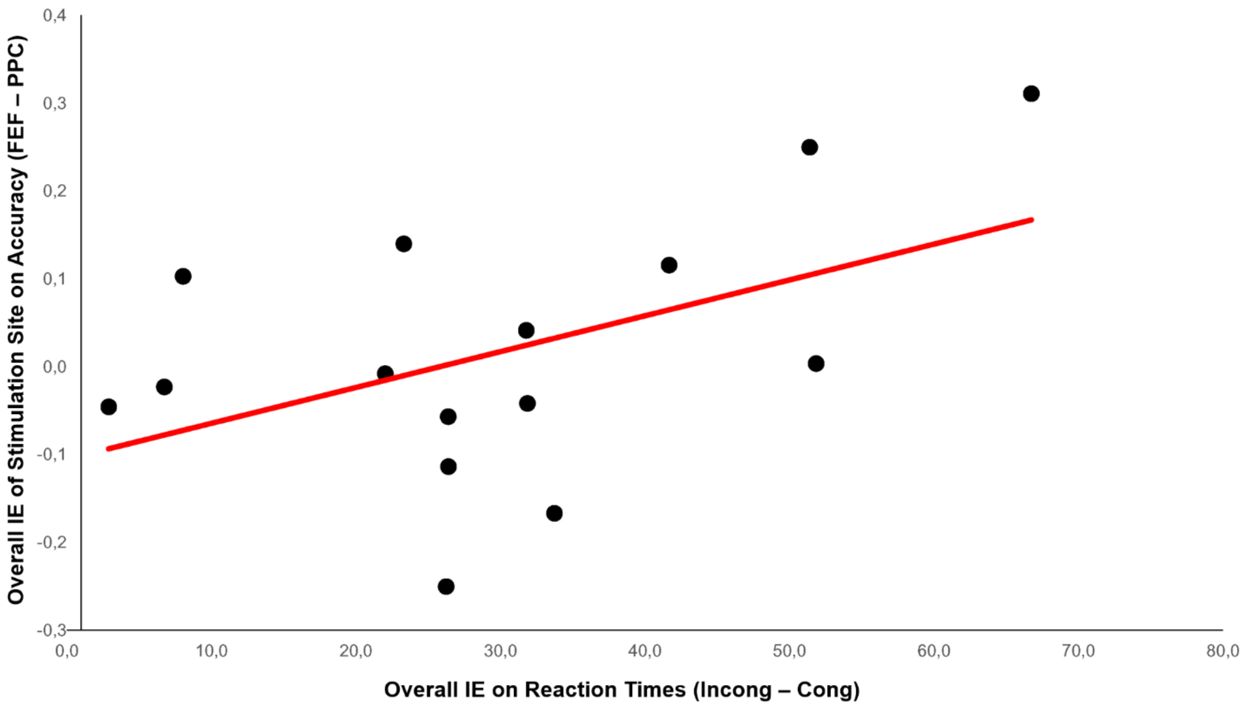

Figure A4. Correlation between the Overall Interference effect on Reaction times and the Overall Interference effect of Stimulation Site on Accuracy (IE = Interference Effect). This almost significant correlation (p = .068) suggests that those individuals who were more likely to be distracted by the direction of the human model's gaze, as reflected by the "Overall RTs IE" index, were also those whose accuracy was mostly reduced by stimulation of FEF as compared to PPC, as reflected by the "Overall Stimulation Site IE".

A6. Discussion

In this study, we combined an online event-related dpTMS protocol with a gaze-following task to investigate the causative role of the right-FEF and right-PPC in controlling oculomotor behavior when the individual is performing cued-saccades in the presence of a distracting human gaze. We found that control of participants' oculomotor behavior was impaired by the observation of a human model that moved his eyes in the opposite direction with respect to the one indicated by the imperative cue. This was suggested by the main effect of Congruence found both in the analysis of Accuracy and in the analysis of Reaction Times.

Contrary to our predictions, in neither analysis we found evidence of a main effect of Stimulation Site or of an interaction between Stimulation Site and Congruence. The explorative analysis (ANCOVA) we led to observe potential correlations between the tendency of the participants to be interfered by the model's gaze (as reflected by the "Overall RTs IE" index) and the impact of the stimulation site on accuracy revealed that accuracy of the saccadic movements changed across the two stimulation sites when we considered in the analysis the strength of the gaze-mediated interference on the RTs. A follow-up correlation analysis on this interaction showed that the participants who were more distracted by the observation of an incongruent gaze also showed a reduced accuracy linked to the stimulation of FEF, rather than of PPC.. However, it should be considered that this interaction only approximated significance. Additionally, our number of participants is relatively small (N = 17) and only an extension of the sample size might reveal whether this effect is genuine.

A6.1 Other-gaze reduces control over one's own ocular behavior

Our combined analyses of accuracy and reaction times indicates that the observation of a human model performing a distracting directional gaze reduced participants' control over one's own ocular behavior.

Previous studies suggest that by observing gaze direction of conspecifics, people automatically direct their attention toward the gazed-at location (Itier and Batty, 2009; Klein et al., 2009). Previous evidence also shows that that people respond more quickly to targets signaled by conspecifics, even when social cueing is brief or consistently misleading (see Frischen et al., 2007 for a review). Our results are in line with previous evidence showing that observation of a task-relevant biological distractor (i.e. gaze) reduces the capacity to control one's own motor behavior in the corresponding effector (Crostella et al., 2009; Ricciardelli et al., 2002; Porciello et al., 2014). This is in line with our our somatotopic model of social attention (Cazzato et al., 2012; Crostella et al., 2009; Porciello et al., 2014a), which claims that the control of social attention is exerted according to a body-effector centered co-ordinate system, where biological distractors (e.g. gaze) are more likely to affect one's response if the same effector (e.g. eyes) is used to perform the action. However, it should be noted that our paradigm did not include other kinds of biological or non-biological distractors. At the neural level re-orienting of attention that allows to control for the automatic influence of distractors if these are not compatible with the task at hand, has been linked to the activation of a fronto-parietal network that maps a variety of attentional functions, including covert and overt reorienting of attention to non biological stimuli (Corbetta et al., 2008; Corbetta and Shulman, 2002; Sato et al., 2009; Tipper et al., 2008), as well as following the direction of someone else's gaze (Grosbras et al., 2005). Our preliminary data seem to suggest that frontal areas (i.e. FEF) rather than parietal areas (i.e. PPC) might be crucial in the control of oculomotor behavior, when observing the distracting gaze of another individual automatically leads the individual to look in the same direction. It is worth noting that the pivotal adaptive role of gaze-following in understanding other's mental states (Baron-Cohen, 1995) implies also a dynamic perception-action coupling between interacting agents with possible involvement of mirror-like mechanisms. The notion that the mirror systems may play a role in the oculomotor domain is supported by human brain-imaging studies showing that overlapping fronto-parietal and temporal regions are recruited during the execution and the observation of eye movements (see Grosbras et al., 2005 for a meta-analysis). Moreover, a recent single-cell recording study in monkeys reported increased activity of specific populations of neurons, not only when the monkey orients his attention towards a specific receptive field, but also when he observes another monkey orienting to the same direction (Shepherd et al., 2009). Given the intimate relationship between spatial attention and control of eye movements (Corbetta, 1998; Nobre et al., 2000) it is not surprising that anatomical connections in the oculomotor system may overlap with those for attentional re-orienting when an oculomotor response is required (Umarova et al., 2010).

This mechanism seems to be largely lateralized to the right hemisphere (Anderson et al., 2011) and rely on FEF.

A6.2 FEF might contribute to control the attentional capture triggered by the gaze of others

FEF, located in the anterior bank of the arcuate sulcus, is typically associated with oculomotor control (Pierrot-Deseilligny et al., 2004). FEF neurons are either visual, motor (saccadic) or visuomotor (Bruce et al., 1985; Schall, 1991). Since they fire just before the beginning of ocular movements (Segraves and Park, 1993) the suggestion is made that these neurons are involved in triggering saccades (see Wardak et al., 2011 for a review). Moreover, FEF is a crucial part of the fronto-parietal network, known to be involved in attentional re-orienting (Corbetta et al., 2008; Grosbras et al., 2005) and in the selection of stimuli and responses for different goal-directed actions. Importantly, specific nodes within this network seem to be differentially activated when participants plan and perform different biological movements (Connolly et al., 2003; Corbetta and Shulman, 2002). Although fMRI studies indicate that the human FEF may be similarly involved in attending, looking and pointing to external stimuli (Astafiev et al., 2003; Hagler et al., 2007) with only weak lack effector specificity (Levy et al., 2007), lesions of this region in monkeys produce disruptions of saccade generation (Latto and Cowey, 1971; Rizzolatti, 1983) and electrical stimulation evokes saccadic movements in humans (Godoy et al., 1990; Rasmussen and Penfield, 1948). It is worth noting that FEF seems to be particularly involved in controlling saccadic movements in conflictual situations as indicated by the increase of right FEF activity during erroneous saccadic movements (Ptak et al., 2011). Moreover, single-pulse TMS over rFEF delivered before the onset of the target has been found to increase the cost of invalid cueing mediated by directional distractors (Grosbras and Paus, 2002).
In keeping with previous evidence, the correlation – approximating significance – between the tendency to be captured by the distracting directional gaze (Overall RTs Interference Effect) and the

reduction of accuracy due to the application of dpTMS over FEF with respect to PPC (Overall Stimulation Site Interference Effect) might show how the transient disruption of the FEF neurons in an oculomotor task actively and specifically modulates the saccadic responses to a central cue in the presence of distracting gazes. Although preliminary, this result might suggest that FEF activity contributes to re-orienting of attention and to resume control over one's ocular behavior even under the influence of distracting social stimuli, specifically the directional gaze of another individual.

A7. Conclusions and future directions

We showed that participants control over their oculomotor behavior was reduced by the observation of an incongruent directional gaze, and we provided initial evidence that individuals who show a higher tendency be distracted by the observed gaze might be also those who are mostly interfered by stimulation of FEF, rather than of PPC. This might be in line with a role of rFEF in controlling reflexive shifts of attention triggered in onlookers by someone else's gaze. However, this possible effect should be further explored by increasing the size of our sample, which at the current moment is relatively low (N=17).

Additionally, an interesting future step might be related to the exploration of how individuals experience control over their eye movements when performing an ocular task under the influence of distracting social stimuli. Interestingly, Stephenson and colleagues have recently reported that participants experience higher Sense of Agency for ocular movements that guide the ocular behavior of another individual (Stephenson et al., 2018). It would be intriguing to understand to what extent the guided onlooker experiences control over his own eye movements.

A8. References

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