I control it, but does it mean it is part of me? How the relationship between body movements and controlled object movements influences the sense of agency and the sense of ownership

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The influence of the relationship between body movements and object movements on sense of agency and sense of ownership

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1. Zusammenfassung

Der “Active Self”-Ansatz sagt aus, dass jedes Objekt, welches wir willentlich und vorhersehbar manipulieren, Teil unseres „Selbst“ wird in dem Sinne, dass wir Kontrolle über dieses Objekt empfinden (Sense of agency) und es als zu unserem eigenen Körper zugehörig erleben (Sense of ownership). Während es eine beträchtliche Menge an Evidenz dafür gibt, dass wir tatsächlich sowohl Sense of agency als auch Sense of ownership für eine breite Vielfalt an Objekten empfinden können, wenn wir diese durch unsere Handlungen kontrollieren, wurde der Ansatz auch dafür kritisiert die Flexibilität des menschlichen Selbst über zu strapazieren. In dieser Arbeit untersuche ich den Einfluss, den die Beziehung zwischen den Körperbewegungen, welche ein Objekt kontrollieren, und den Bewegungen des Objekts selbst auf den Integrationsprozess eines Objekts in das Selbst hat. Ich demonstriere, dass ein Objekt vollständig zu kontrollieren nicht ausreichend ist, damit es in das Selbst integriert wird, da sowohl explizite als auch implizite Maße für Sense of agency und Sense of ownership weniger oder keine Integration zeigen, wenn Körperbewegungen in invertierte Objektbewegungen transformiert werden. Darüber hinaus zeige ich, dass solche Invertierungen zur Herunterregulierung sensorischer Signale entweder vom Körper oder vom kontrollierten Objekt führen, um mit der konfligierenden multisensorischen Information umzugehen, wenn solche Handlungen ausgeführt werden. Ich argumentiere, dass diese Herunterregulierung der zugrundeliegende Faktor ist für die verringerte oder eliminierte Integration invertierter Körper- und Objektbewegungen und ich diskutiere weitere Richtungen für mögliche zukünftige Studien, die auf diesen Befunden aufbauen.

2. Summary

The “active self” approach suggests that any object we manipulate voluntarily and foreseeably becomes part of our “self” in the sense that we feel control over this object (sense of agency) and experience it as belonging to our own body (sense of ownership). While there is considerable evidence that we can indeed experience both a sense of agency and a sense of ownership over a broad variety of objects when we control these through our actions, the approach has also been criticized for exaggerating the flexibility of the human self. In this thesis, I investigate the influence that the relationship between the body movements controlling an object and the movements of the object itself has on the process of integrating an object into the self. I demonstrate that fully controlling an object is not sufficient for it to be integrated into the self since both explicit and implicit measures of the sense of agency and the sense of ownership indicate less or no integration when body movements are transformed into inverted object movements. Furthermore, I show that such inversions lead to the downregulation of sensory signals either from the body or from the controlled object in order to deal with the conflicting multisensory information when performing such actions. I argue that this downregulation is the underlying factor behind the diminished or eliminated integration of inverted body and object movements and I discuss further pathways for possible future studies building up on these findings.

3. The self and the body

I have a self. How do I know this? Well, I just know that I have one because of my subjective experience of myself as a conscious and perceiving entity. One might say that this is quite a poor argumentation: What is the value of using a subjective, self-referential argument to claim the existence of a concept that is inherently subjective and dependent on a first-person perspective as well? However, as a response to this, one might argue that nothing could give a more precise description of such a concept than the individual, subjective and introspective experience of a person. This idea is prominently captured by the "phenomenological" approach to the self (e.g., Henry, 1963; Zahavi, 2003). This self-experience based on immediate perception does not need to be conscious. For example, I do not need to reflect about who or what I am, my past, my future, my values, attitudes or opinions to still have the experience of existing and experiencing right now at this point in time. This idea of an unconscious, ever-present self-experience is what Gallagher (2000) has called the "minimal self". According to Gallagher (2000), one's experience of a minimal self must be tightly linked to one's body since the body essentially is the source of all our perceptions and experiences. So in order to answer the question how the sense of having a self emerges in a person, let us first turn to the question how one perceives one's body.

3.1. The sense of (body) ownership

What is part of our body? For most healthy people this seems to be a fairly easy, if not trivial, question to answer. Every human being has a clearly circumscribed biological body, which is objectively separable from the bodies of others, other objects and the environment around it. Furthermore, if not restricted by pathological conditions, humans can more or less constantly perceive their biological body and are thus affirmed of its presence; for example by visual information about the position of one's limb and torso and by "feeling" the location and configuration of one's body parts through proprioception. However, despite the objective clarity and the knowledge of people what is part of their body, the subjective experience of what belongs to one's body is often surprisingly fuzzy and malleable and does often not reflect the objective simplicity of this question. This is most prominently captured in the so called "rubber hand illusion" (e.g., Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; de Haan et al., 2017; Ehrsson, Spence, & Passingham, 2004; Kalckert, Bico, & Fong, 2019a; Kalckert, Perera, Ganesan, & Tan, 2019b; Lloyd, 2007; Samad, Chung, & Shams, 2015; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005) in which participants are misled to perceive a rubber hand as being part of their body. This sensation is induced by placing the rubber hand next to the participant's real hand on a table in front of them and stroking both of the hands simultaneously with a soft brush while the participant only has a free view on the rubber hand. Within the first half minute after such synchronous stroking, the great majority of participants reports to subjectively feel the stroking of the brush on the rubber hand as if the rubber hand was their own hand (Ehrsson et al., 2004; Lloyd, 2007). Furthermore, when asked to localize their real, unseen hand, participants' judgments are usually biased into the direction of the rubber hand, an effect that has been labelled as "proprioceptive drift" (Dummer, Picot-Annand, Neal, & Moore, 2009; Kalckert & Ehrsson, 2012; Rohde, Di Luca, & Ernst, 2011). Finally, also various neural (Ehrsson et al., 2004; Makin, Holmes, & Ehrsson, 2008) or physiological responses (Armel & Ramachandran, 2003; Hohwy & Paton, 2010; Ma & Hommel, 2013, 2015a; Moseley et al., 2008; van Stralen et al., 2014) supporting these subjective experiences have been observed which suggest that afferent visual information from the rubber hand is indeed processed similarly to afferent sensations stemming from the own body. For example, a cooling of the real hand can be observed during the illusion suggesting its physiological "replacement" with the rubber hand (Hohwy & Paton, 2010; Moseley et al., 2008; van Stralen et al., 2014), and when the rubber hand is "threatened" by a knife or another potentially harmful object, participants often show increased skin conductance responses (Armel & Ramachandran, 2003; Ma & Hommel, 2013, 2015a). Importantly, none of these effects occurs, or only to a much smaller degree, when the stroking of the real and the rubber hand is performed asynchronously.

But how does the experience of "ownership" for the rubber hand emerge in this situation? In the rubber hand illusion and also in almost any situation a person might be confronted with in their everyday life, the sensory input perceived by this person can be classified into two different categories: On the one hand the “resident” or “interoceptive” sensations which are always and only generated by the biological body itself, such as kinesthetic, proprioceptive or tactile perception. On the other hand, there are also “remote” or “exteroceptive” sensations, which describe the perception of “signals that originate from locations other than that of the sensors which encode them” (Liesner, Hinz, & Kunde, 2021, p. 2).[1] When remote signals, such as the visual signals from seeing the rubber hand being stroked, match with simultaneous resident signals, such as the tactile sensations of the brush on one’s own hand, these two multisensory signals can become integrated because they are attributed to the same common cause (Blanke, 2012; Blanke, Slater, & Serino, 2015; Samad et al., 2015; Tsakiris, 2010, 2017). In the situation of asynchronous stroking, the resident and remote signals are not ascribed the same common cause and therefore also no integration of them takes place. This integration of multisensory signals from different sensory modalities can be observed in many different situations and with different combinations of sensory signals (e.g., Ernst & Banks, 2002; Spence, 2007; Talsma, Senkowski, Soto-Faracao, & Woldorff, 2010). One example for such multisensory integration in perception is the popular “ventriloquist effect” where visual and auditory stimuli from slightly different directions are experienced in the same location (e.g., Alais & Burr, 2004; Bertelson, Vroomen, De Gelder, & Driver, 2000; Bonath et al., 2007). However, just because sensory signals from different modalities are integrated, it does not mean that also a sense of illusory ownership for the sources of these sensory signals would be experienced. For example, it would be highly surprising if a test person experiencing the previously mentioned ventriloquist effect would suddenly report to experience ownership over the source of the visual or auditory stimulus. To experience a

[1] While other authors often use the terms “interoception” and “exteroception” to refer to the distinction I want to make here, I will consistently use the terms “resident” and “remote” sensations throughout this dissertation. The reason for this is the inconsistent use of the former terms in the literature, especially of “interoception”, which is sometimes restricted to sensations stemming exclusively from inside the body such as sensations from visceral organs (e.g., Craig, 2009; Tsakiris, 2017). The terms “resident” and “remote” reflect that the source of the sensory signals is either residing in or on the biological body or remote from the biological body and will be used as defined in the main text. Other terms used by different authors to make a similar, though not always exactly equivalent, distinction between different sensory signals are for example “proximal” vs. “distal” or “body-related” vs. “body-external”.

feeling of ownership, the presence of resident sensory signals is indispensable since these are uniquely diagnostic for a person in signaling the presence of the own body given that no other object or source in the world can generate these sensations (e.g., Cassam, 1995; Gallagher, 2013; Liesner & Kunde, 2021). If remote sensory signals or their source are thus to be experienced as “owned” by a person’s body, they must necessarily be accompanied by fitting resident sensory signals. This necessity is impressively demonstrated by the reports of so called “deafferented” patients who have lost most or all of their proprioceptive and tactile sensation while maintaining efferent control over their body (e.g., Gallagher & Cole, 1995; Renault et al., 2018). These patients sometimes describe their biological body as something alien that they have control over but that does not “belong” to them (Cole & Paillard, 1995). Furthermore, similar experiences of “bodylessness” have also been reported by users of drugs which reduce or eliminate proprioceptive sensations (Millière, Carhart-Harris, Roseman, Trautwein, & Berkovich-Ohana, 2018).

4. The active self

Resident and remote sensations however cannot only be generated by external stimulation, such as when feeling a touch on one's body or seeing two objects touching each other. They can also be generated as the effects of efferent signals, i.e. of motor actions. For example, when moving one's arm a person can feel the proprioceptive sensation of that movement, but can also observe the movement visually. The former of these sensations can be construed a resident action effect while the latter can be classified as a remote action effect (James, 1890/1981).

The fact that efferent activity typically produces (matching) resident and remote sensations which is crucial to experience a sense of ownership has motivated researchers to investigate the role of efferent activity for the emergence of a sense of ownership. For this purpose, various adaptations of the classical rubber hand illusion paradigm have been introduced in which the appearance of an external object changes in response to movements of the test person (Dummer et al., 2009; Kalckert & Ehrsson, 2012, 2014a, 2017; Kirsch, Pfister, & Kunde, 2016; Ma & Hommel, 2013; 2015a, b; Pfister, Klaffehn, Kalckert, Kunde, & Dignath, 2021; Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010; Zopf, Polito, & Moore, 2018). Most prominent, in the "active rubber hand illusion" participants can move their own hand and these movements are transformed into the movements of a rubber hand, again with only the rubber hand visible (e.g., Dummer et al., 2009; Kalckert & Ehrsson, 2014a; Pfister et al., 2021). Given the broad range of possibilities for introducing such contingencies between the real hand and its "fake" counterpart in virtual reality, this version is often also applied as a "virtual hand illusion" (e.g., Sanchez-Vives et al., 2010; Ma & Hommel, 2013, 2015b). Overall, the results from such body illusions grounded on active movements resemble very much the results from studies in which the illusion is induced through external, passive stimulation. When participants in these experiments start moving their occluded real hand and see the synchronous movement of the artificial or virtual hand in response to this, this usually produces the same effects that can also be observed in the passive rubber hand illusion: Participants "feel" as if the fake hand is the hand they are actively moving (Dummer et al., 2009; Kalckert & Ehrsson, 2012, 2014a, 2017; Ma & Hommel, 2013, 2015b; Sanchez-Vives et al., 2010; Zopf et al., 2018), they show a judgment bias towards the fake hand when asked to localize their real hand (Kalckert & Ehrsson, 2012, 2014a; Ma & Hommel, 2015b; Sanchez-Vives et al., 2010) and physiological measures also support the “incorporation” of the fake hand (Ma & Hommel, 2013, 2015b). Similarly, just like with passive induction methods, ownership induced by active movements is disrupted by asynchrony between the resident and remote sensations and by increasing distance between the real hand and the virtual or artificial hand (Dummer et al., 2009, Kalckert & Ehrsson, 2012, 2014a; Ma & Hommel, 2013, 2015b).

4.1. The sense of agency

However, one factor in which active and passive inductions of ownership experiences clearly differ is in the actual and perceived controllability of the sensory signals experienced during the illusions. This experience of control for changes in afferent signals based on motor activity is commonly referred to as “sense of agency” (Gallagher, 2000; Haggard, 2017) and is seen as a second aspect of the minimal self, besides the sense of ownership (Gallagher, 2000). Gallagher (2000, p.15) defines the sense of agency as “The sense that I am causing or generating an action. For example the sense that I am the one who is causing something to move […]”. Forming one aspect of the minimal self, this sense of control does not need to be represented explicitly in consciousness, but it can also emerge in a pre-reflective manner as a general attribution of an observed sensory change to one’s own efferent activity. This differentiation between two different “levels” of the sense of agency has been addressed by distinguishing between an explicit “judgment of agency” and an implicit “feeling of agency” (Bayne & Pacherie, 2007; Gallagher, 2006; Pacherie, 2008; Synofzik, Vosgerau, & Newen, 2008b; Tsakiris, Schütz-Bosbach, & Gallagher, 2007; Wegner, 2003). Similar as with the rubber hand illusion for the sense of ownership, different paradigms and measures have been introduced to grasp these two different kinds of sense of agency. The most common way to assess the explicit sense of agency is to simply ask people to rate how much they felt that they "caused", were "responsible" for or "in control" over a certain event in the world (e.g., Ebert & Wegner, 2010; Kalckert & Ehrsson, 2012, 2014a, b; Ma & Hommel, 2013; 2015a, b; Schwarz, Weller, Klaffehn, & Pfister, 2019; Weller, Schwarz, Kunde, & Pfister, 2017). For the implicit sense of agency, a paradigm called "intentional" or "temporal binding" is most commonly used to assess the feeling of agency without explicitly reminding participants to think about their subjective experience (e.g., Buehner, 2012; Cao, Steinborn, Kunde, & Haendel, 2020; Desantis, Hughes, & Waszak, 2012; Haggard, Clark, & Kalogeras, 2002; Kirsch, Kunde, & Herbort, 2019; Majchrowicz & Wierzchoń, 2018; Moore, Lagnado, Deal, & Haggard, 2009; Ruess, Tomaschke, & Kiesel, 2017; Suzuki, Lush, Seth, & Roseboom, 2019).

While being a fast growing field of research, the concept of the sense of agency as well as the equivalence of its different explicit and implicit measures have also been subject to criticism in recent years. In a very general criticism of the concept of the sense of agency, Hommel (2018) argues that this concept only functions as a social role when communicating the experience and ascription of control over a certain event to oneself or another person. Accordingly, he argues that the sense of agency as measured by explicit questions in many studies is also nothing more than a response to these questions without a veridical perception of this subjective agency that would also be present in the absence of the questions. Similarly, also other authors have criticized the artificiality of the concept of the sense of agency (e.g., Hofstede, Hofstede, & Minkov, 2010). This viewpoint is obviously in stark contradiction to the phenomenological approach to the self as introduced in section *3. The self and the body* (e.g., Henry, 1963; Zahavi, 2003). It would be beyond the scope and purpose of this dissertation to dig into this rather philosophical than empirical conflict in depth, however I believe that it is hard to completely deny the existence of the phenomenological aspect of the sense of agency and of other forms of self-experiences. Therefore, I believe that also the study of these concepts is justified since, even if these experiences do not originate from any new or special mechanisms (Hommel, 2021), the way in which these mechanisms shape the phenomenology is an interesting field to study.

A more empirically motivated criticism of the sense of agency, or rather the measures used to assess it, has been put forward both against explicit measures such as questionnaires and implicit measures such as temporal binding. The criticism against the former often concerns so called “demand characteristics” (Orne, 1962), i.e. participants’ different responses to different experimental conditions rather because they think they are expected to respond differently to them than because of actual differences in their experiences. This is a problem that notoriously applies to all questionnaire measures and that can only be circumvented by researchers carefully choosing and designing experimental conditions and drawing interpretations from their results with caution. Regarding temporal binding, there is a growing body of studies that has casted some doubt on whether this method actually measures the sense of agency. Instead studies that have shown intentional binding for involuntary actions or have failed to show correlations between explicit and implicit measures of the sense of agency rather suggest some other more basic mechanism of multisensory integration as its basis (e.g., Buehner, 2012; Kirsch et al., 2019; Majchrowicz & Wierzchoń, 2018; Moore et al., 2009; Schwarz et al., 2019; Suzuki et al., 2019). It might however also be that these measures capture different aspects of the sense of agency. I will come back to these points when discussing the results of Experiments 3 & 4 (section *7.4. Spatial action-effect binding depends on type of action-effect transformation - General discussion*) and in the theoretical integration (section *10.3.2. Differentiating between the sense of agency, the sense of ownership and different aspects of the two*).

Taking its existence for granted for a moment, according to most theorists, the sense of agency is caused by the comparison of predicted sensory states in a given situation and the actually experienced sensory states which has become known as the so called “comparator model” of the sense of agency (Carruthers, 2012; Haggard, 2017; Haggard & Chambon, 2012; Zaadnoordijk, Besold, & Hunnius, 2019). The comparator model states that an agent can predict the sensory outcomes of any voluntary action based on the intended goals of this action and the motor output generated to achieve these goals. There are different views in the literature by authors with different theoretical backgrounds on how exactly these sensory outcomes are predicted based on action goals and/or motor actions (e.g., Hommel, 2013; James, 1890/1981; Koch, Keller, & Prinz, 2004; Miall & Wolpert, 1996; Shin, Proctor, & Capaldi, 2010; Waszak, Cardoso-Leite, & Hughes, 2012; Wolpert, 1997; Wolpert & Flanagan, 2001).

According to prediction-based theories, an agent aims at establishing a certain sensory goal state through their actions. Based on this sensory state a motor command is then chosen in order to produce an action which should result in the intended sensory goal state. The activation of this motor command however not only triggers the efferent activity itself, but also an additional simulation of it, a so called "efference copy" (e.g., Miall & Wolpert, 1996; Wolpert, 1997; Wolpert & Flanagan, 2001). This efference copy is essentially the prediction of the intended sensory goal state according to these models which is subsequently compared with the actually observed sensory states after the action has been performed. Based on this comparison, a sense of agency is then said to be inferred according to this "comparator model" (e.g., Carruthers, 2012; Haggard & Chambon, 2012; Figure 1A).

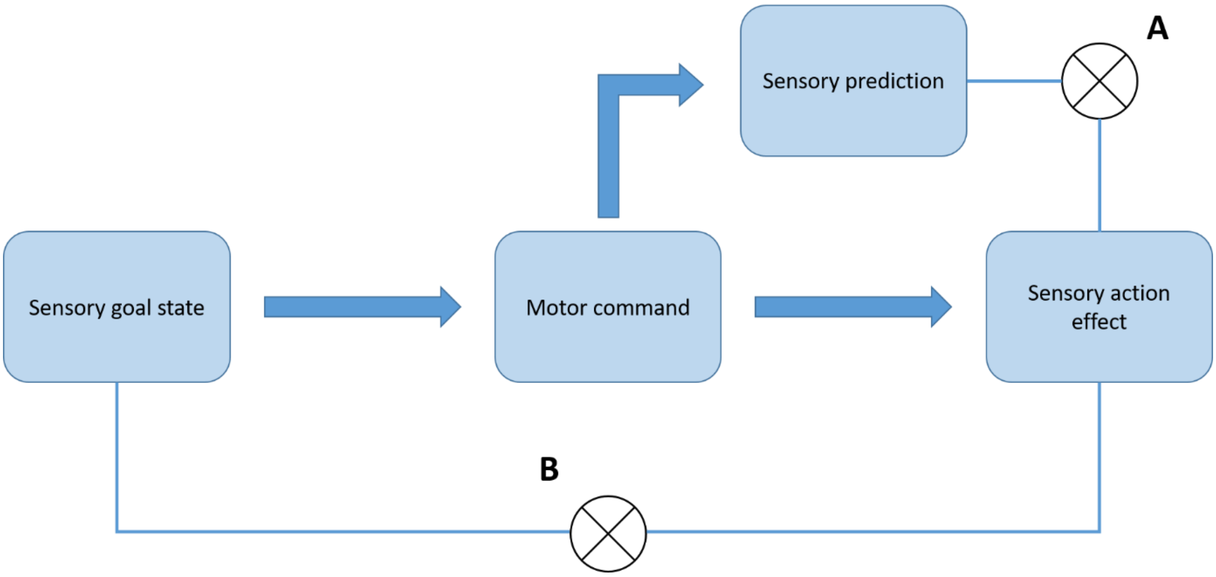

Figure 1. The comparisons made during actions based on which a sense of agency is inferred according to prediction-based approaches (A) and ideomotor action control approaches (B).

Ideomotor action control models however argue that a sensory prediction in the form of an efference copy based on an activated motor pattern is not only superfluous but also pointless in the process of action generation. According to this approach, there is a direct bidirectional connection between motor commands and sensory effects. The presence of an intended sensory goal state should therefore automatically trigger the motor commands which are linked to this goal state and which should therefore be capable to produce the intended sensory state (e.g., Hommel, 2013; James, 1890/1981; Koch et al., 2004; Shin et al., 2010; Waszak et al., 2012). Ideomotor models however do not assume any further sensory predictions on top of the activated motor commands since these predictions could not provide any further information to the organism different from the information which is already provided by the intended sensory goal state. Therefore, the sense of agency is, according to these models, directly inferred from a comparison between the intended sensory goal state and the feedback from the actually observed sensory state (Hommel, 2015; Wiener, 1948; Figure 1B).

Despite the different viewpoints on the role of sensory action effects for motor planning, most authors would agree that a prediction or anticipation of the sensory consequences of the action takes place in some form and at some point during action planning or action generation. If the perceived sensory changes match the predicted ones, a sense of agency is experienced for these changes and they are regarded as the consequences or effects of one's motor actions (Wegner, 2017).

4.2. Extending the self through action

Actively and predictably controlling afferent signals triggers a sense of agency for these signals, but does this mean that sense of agency is experienced by a person for all signals which are controlled by them? Actually, recent approaches on sensorimotor action control go even further by suggesting that active control of an external object does not only create a sense of agency for the controlled object but also leads to an even broader integration of this object into one's self in terms of a sense of ownership (e.g., Ma & Hommel, 2015a; Verschoor & Hommel, 2017). As Verschoor & Hommel (2017, p. 139) have put it: "adults tend to accept artificial virtual events as belonging to their body if only the behavior of these events is synchronous with their own movements". This suggests that such ownership experiences based on correlating own actions and perceived environmental effects might not be restricted to external objects that visually or functionally resemble the body, but that any event, which is controlled by efferent activities, can become part of the self in terms of both sense of agency and sense of ownership, which has been labelled as the "active self" approach. This is in stark contrast with studies demonstrating that such ownership experiences for objects not resembling the biological body cannot be induced by passive visuotactile stimulation alone (Guterstam, Gentile, & Ehrsson, 2013; Kalckert et al., 2019a; Tsakiris et al., 2010; Tsakiris & Haggard, 2005; though see Armel & Ramachandran, 2003, for a frequently cited yet criticized exception). Indeed, an accumulating number of studies has by now been able to demonstrate that different kinds of objects, such as tools or virtual objects, which are actively controlled by a person, can be experienced by that person as belonging to their body (e.g., Kirsch et al., 2016; Ma & Hommel, 2015a, b; Maravita, Spence, Kennett, & Driver, 2002; Weser, Finotti, Constantini, & Proffitt, 2017). Based on these findings it has been suggested that a sense of self is constructed in a bottom-up fashion by active movements so that any perceptual changes which are accompanied by voluntary motor actions get integrated with these (e.g., Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Ma & Hommel, 2015a).

However, the results from two groundbreaking studies by Ebert & Wegner (2010) and Farrer et al. (2003) speak against such a bottom-up approach of self-construction through which any object controlled by voluntary actions of an agent becomes part of that agent's self. Farrer et al. (2003) had participants perform joystick movements that triggered movements of a virtual hand holding a joystick on a screen. Importantly, the virtual movements did not always exactly mirror the actual movements of the participants, but in some blocks, angular deviations of different intensity were introduced or the virtual movements were controlled completely by another person. The task of the participants was to indicate after every block whether the virtual movements had been produced by themselves directly, by themselves with a distortion or by another person. Interestingly, while performance was perfect in the undistorted and other person condition, participants were less accurate in identifying their own control for the virtual movements in the distorted conditions. Similarly, Ebert & Wegner (2010) also used joystick movements that were translated into visual effects on a screen to investigate the sense of control that participants experienced for these effects. Their participants had to produce push or pull movements that triggered an increase or decrease in the size of an object on the screen to reflect a movement of the object either towards or away from the participant. The authors observed that with “inconsistent” relationships between joystick movements and object movements (e.g., when a push movement increased the size of the object) the sense of agency of participants was lower than with “consistent” movements (e.g., when a push movement decreased the size of the object). This was reflected both in explicit ratings of control experience and in a decrease in the perceived time interval between their movement of the joystick and the movement of the object on the screen.

A further problem regarding the discussed bottom-up approaches of sensorimotor self-experience is that they lead to a blurring of the differentiation between the sense of agency and the sense of ownership as two related but different aspects of the (minimal) self. Indeed, some authors (e.g., Ma & Hommel, 2015a, b) have even equalized the two even though there is a considerable amount of studies and theoretical notions demonstrating their difference (Gallagher, 2000; Jeannerod, 2003; Kalckert & Ehrsson, 2012; Riemer, Kleinböhl, Hölzl, & Trojan, 2013; Tsakiris, Prabhu, & Haggard, 2006; Tsakiris et al., 2007). While such an integrative account of the two phenomena seems to hold for controlled objects, which have little to no similarity with the biological body and where an experience of ownership might depend on a concurrent experience of agency (Kirsch et al., 2016; Ma & Hommel, 2015a, b; Maravita et al., 2002; Weser et al., 2017), the two phenomena seem to be able to emerge more independently with body-similar objects (Riemer et al., 2013; Tsakiris et al., 2006).

4.3. A model accounting for and explaining the limitations of extending the self through action

The active self approach suggests that any object which is voluntarily controlled by the actions of a person becomes integrated into the self of that person in terms of sense of agency and sense of ownership. However, some of the studies reported above have demonstrated that this is not a universal phenomenon accounting for all objects or regardless of the way in which the controlling body movement is transformed into the object movement (Ebert & Wegner, 2010; Farrer et al., 2003). This raises the question to what extent the situations, in which body-external controlled objects are integrated into the self, differ from those situations in which the controlled objects are not integrated into the self.

In the discussed studies by Ebert & Wegner (2010) and Farrer et al. (2003), sense of agency was negatively affected by increasing discrepancy between the movement trajectories of the controlled object and of the hand controlling this object. But why do the discrepancies in movement trajectories have this detrimental effect on self-integration while other discrepancies between body and body-external object such as, for example, their spatial offset (Kalckert & Ehrsson, 2014b; Kalckert et al., 2019b; Lloyd, 2007), visual dissimilarity or the fact that one is virtual and one is “real” (Kirsch et al., 2016; Ma & Hommel, 2015a, b; Maravita et al., 2002; Weser et al., 2017) do not seem to disrupt the sense of agency and/or the sense of ownership similarly? To answer this question, it is necessary to first take a look at how agents generate voluntary actions in the first place and how these generation processes in turn act back on perception processes again.

According to ideomotor theory, humans perform voluntary movements by the anticipation of their sensory effects (e.g., Elsner & Hommel, 2001; Hommel, 2013; James, 1890/1981; Koch et al., 2004; Kunde, 2001; Shin et al., 2010; Waszak et al., 2012). This requires that a person must have sufficient knowledge about the sensory effects, which are typically produced by an action, to use these action-effect associations for generation of efferent activities. Establishing these associations is assumed to happen based on the observation of sensory effects of exploratory movements, which over time stamps in the links between motor patterns and the effects they usually produce (Elsner & Hommel, 2001; Paulus, Hunnius, van Elk, & Bekkering, 2012). As explained above (section *4. The active self*), motor actions produce both resident and remote effects (James, 1890/1981, see Figure 2). In most situations, these effects widely overlap in their spatiotemporal dynamics such that, for example, the visual and proprioceptive effects of moving one’s hand do not provide much, if any, different information about the location, direction or other movement characteristics for the agent. If one however controls body-external objects, such as tools, virtual hands or mouse cursors, through motor activities, then the distinction between resident and remote action effects becomes more obvious and also more relevant for the agent since the information transferred by them might differ to a greater extent. For example, when controlling a virtual object on a screen, the visual remote effect of the object movements and the proprioceptive resident effect of the hand movements provide sensory information about different, non-overlapping components of the same action. Theoretical and empirical work has suggested that humans can use both resident and remote effects to generate motor actions, given that the links between motor patterns and codes of the sensory effects have been established to a sufficient degree (Memelink & Hommel, 2013; Mocke, Weller, Frings, Rothermund, & Kunde, 2020; Pfister, 2019). Thus, human agents seem to have some flexibility how to represent their actions.

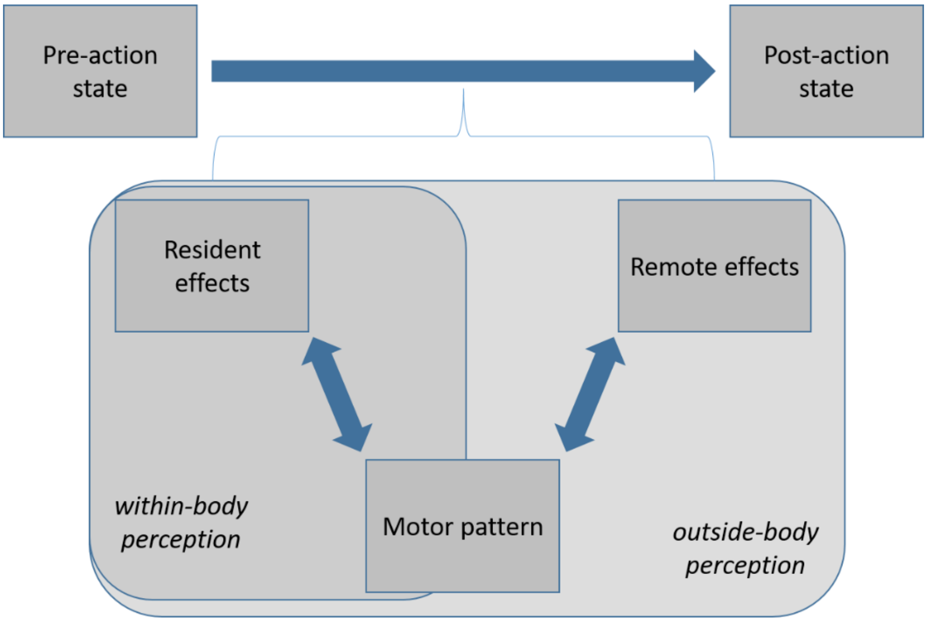

Figure 2. The mental representation of actions and their effects according to ideomotor theory (e.g., Hommel, 2013; James, 1890/1981; Koch et al., 2004; Shin et al., 2010; Waszak et al., 2012). Based on sensorimotor experience when performing actions and perceiving the perceptual changes that accompany these, bidirectional links are learned between motor patterns and the sensory effects usually produced by them. This accounts both for resident effects and remote effects. In order to generate a goal-directed movement, the sensory effects associated with this movement are anticipated which leads to an activation of the motor codes linked to these effects and thus produces the movement.

The assumption that links are formed between actions and the effects that are typically produced by them inevitably opens up the question what happens when confronted with a situation where these typical action effect links are violated. Participants in the previously discussed experiments of Ebert & Wegner (2010) and Farrer et al. (2003) encountered such a situation since the common everyday experience that objects which are controlled by a body effector should move in the same direction as the effector itself, was violated here. There is a large number of studies that have demonstrated that the initiation of actions foreseeably leading to such “incompatible” resident and remote effects comes with performance costs such as slower initiation times and movement errors (e.g., Crothers, Gallagher, McClure, James, & McGuian, 1999; Kunde, 2001; Kunde, Müsseler & Heuer, 2007; Kunde, Pfister, & Janczyk, 2012; Müsseler, Kunde, Gausepohl, & Heuer, 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013; Schwarz, Pfister, Wirth, & Kunde, 2018; Wirth, Pfister, Janczyk, & Kunde, 2015). In these situations, the anticipated resident and remote effects of the action are linked to different motor patterns based on the agent’s experience so when these are activated a motor conflict is elicited which is responsible for the slower and more error prone action generation. Nevertheless, despite these performance costs, humans can still perform actions with

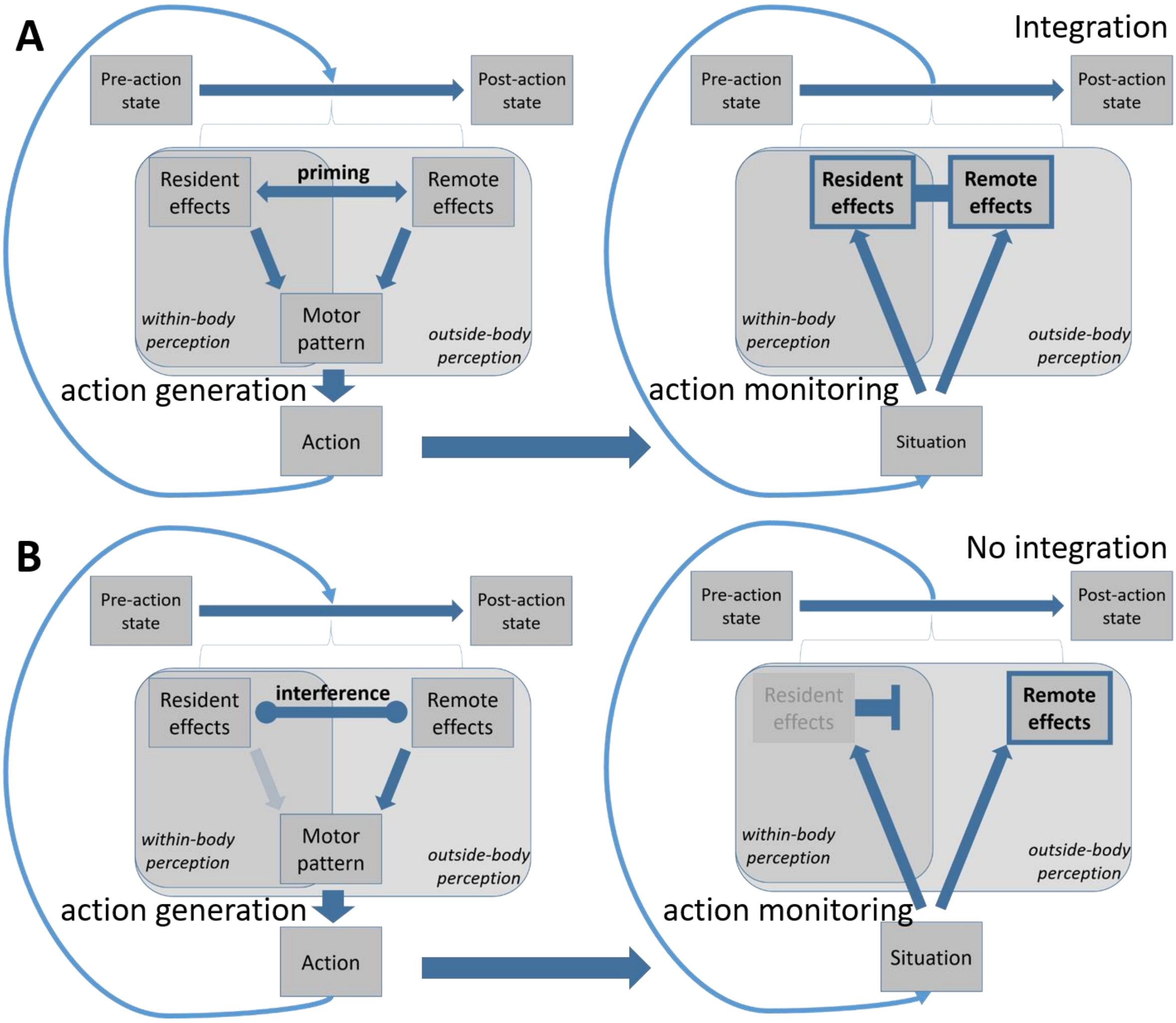

Figure 3. The interplay of resident and remote action effects both in action generation and in action monitoring (adapted from Liesner et al., 2021). **A**. The case of compatible combinations of resident and remote effects. **B**. The case of incompatible combinations of resident and remote effects.

foreseeably incompatible resident and remote effects and often do so with seemingly little difficulty, which indicates that the motor conflict caused by these effects can be resolved. Several studies investigating different forms of transformations of hand movements into movements of other objects have suggested that this resolution happens through a downregulation of resident action effects, a phenomenon which has been labelled as “haptic neglect” (Fourneret & Jeannerod, 1998; Heuer & Rapp, 2012; Knoblich & Kircher, 2004; Müsseler & Sutter, 2009; Sülzenbrück & Heuer, 2009). In most of these studies, participants were asked to move their hand in a certain way which also produced somewhat discrepant movements, mostly in form, extent, shape or timing, of another visual object. Participants often automatically and unconsciously adapted to these discrepancies to produce adapted visual feedback that matched their expectations in the given task. Furthermore, when asked to report this discrepancy in terms of its direction or size, participants were often highly unaware of these characteristics of the movement supporting the idea of the downregulation of resident action effects when these are in conflict with remote action effects (e.g., Fourneret & Jeannerod, 1998; Knoblich & Kircher, 2004; Müsseler & Sutter, 2009; see section *8.1. Experiment 5 - Introduction* for details). This downregulation of resident effect codes should then in turn also lead to a lower activation of the motor patterns linked to these effect codes so that one component of the interfering motor patterns is “ignored”. Action generation should then mainly be based on the anticipation of the remote action effects so that the performance of a goal-directed action is still enabled, though with performance costs, despite the initially conflicting activated motor patterns (Memelink & Hommel, 2013; Mocke et al., 2020; Pfister, 2019, see Figure 3B, left part).

In the case of an action that produces resident and remote effects that are compatible with the learned action-effect associations, there is no need for such haptic neglect since the anticipated action effects are linked to the same motor patterns so that there is no conflict present during action generation. On the contrary, since both kinds of anticipated effects of the action are linked to the same motor pattern, this motor pattern receives strong activation which should facilitate action generation compared to situations with incompatible effects (e.g., Crothers et al., 1999; Kunde, 2001; Kunde et al., 2007, 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013; Schwarz et al., 2018; Wirth et al., 2015) or when perceptual information from one of the action effects is absent or reduced (e.g., Brand et al., 2016; Elliott, 1988; Sivakumar, Quinian, Stubbs, & Culham, 2021; Woodworth, 1899). Furthermore, the fact that both resident and remote effects are linked to the same motor patterns through bidirectional links might also lead to mutual priming of the other effect respectively and thus a higher activation of both kinds of effect codes as well. Therefore, when monitoring one’s action and its outcomes the strong representation of both anticipated resident and remote effects might also lead to a strong representation of both kinds of actual action effects (Figure 3A). A strong representation of or attentional weight for the sensory signals from both action effects might then in turn lead to an integration of these multisensory signals (Debats, Ernst, & Heuer, 2017b; Ernst & Banks, 2002; Memelink & Hommel, 2013; Talsma et al., 2010). Thus, an integration of the remote effects with the resident effects of an action leading to experiences of agency and ownership over the source of the remote effects might occur with such compatible effects. The idea that the representational weight given to sensory signals from different modalities determines whether these signals are assumed to emerge from the same source and are therefore integrated, is very much compatible with a model of (body) ownership based on multisensory integration processes (Blanke, 2012; Blanke et al., 2015; Samad et al., 2015; Tsakiris, 2010, 2017; see section *3.1. The sense of (body) ownership*).

In the case of incompatible resident and remote effects of an action, the anticipated resident sensory effects have to be “neglected” or suppressed in order to generate the action in the first place. This suppression during action generation might however extend to monitoring the real sensory effects of the action as well so that the afferent sensory signals from resident effects might be suppressed as well. While the remote effects of the action might nevertheless still receive great attentional weight in this situation, the suppression of the resident effects, which can be construed as an “ignoring of the body”, prevents those remote effects to be integrated with resident effects resulting in a prevention of any agency or ownership experience (Figure 3B, right).

5. Overview

In the previous sections, I have developed an ideomotor action control based model explaining under which conditions actively controlling objects, which are not part of one's biological body, can lead to experiences of agency and ownership over these objects. In this dissertation, I will test various aspects of this model and provide empirical evidence for its claims.

In section *6. The interplay of predictive and postdictive components of experienced selfhood*, the influence of mutually compatible or incompatible resident and remote effects of an action on explicit experiences of agency and ownership will be tested. Furthermore, as an extension to Ebert & Wegner (2010), the differential role of predictable and thus anticipated remote action effects and unpredictable and thus non-anticipated remote action effects on the sense of agency and the sense of ownership will be investigated both in situations of compatible and incompatible action effects.

In section *7. Spatial action-effect binding depends on type of action-effect transformation*, the presented experiments will test how compatible or incompatible resident and remote effects influence the implicit sense of ownership for a controlled object. Additionally, Experiment 4 will shed light on the question whether incompatible action effects only reduce or actually eliminate ownership experiences for controlled body-external objects, and the possibility of explaining the findings through suppression of action effects will be discussed.

In section *8. Suppression of mutually incompatible proprioceptive and visual action effects in tool use*, the previously made speculations will then be tested by investigating the precision with which mutually incompatible resident and remote action effects are perceived by an agent. In addition to previous studies (Fourneret & Jeannerod, 1998; Heuer & Rapp, 2012; Knoblich & Kircher, 2004; Sülzenbrück & Heuer, 2009), the possibility of suppressing not only resident but also remote action effects will be tested and the influence of task characteristics on suppression will be investigated.

In section *9. Suppression of resident action effects which are incompatible to remote action effects during movement planning*, a further aspect of the suppression of mutually incompatible action effects will be tested. Namely, if this suppression does already occur purely based on the anticipation of incompatible action effects. Such an anticipatory suppression seems not only plausible but also necessary based on the discussed action control mechanisms which suggest that action conflict should already be present when planning movements with incompatible resident and remote effects (e.g., Crothers et al., 1999; Kunde, 2001; Müsseler et al., 2008; Pfister & Kunde, 2013; Schwarz et al., 2018; Wirth et al., 2015).

Finally, in section *10. Theoretical integration and synthesis*, I will discuss the findings from the reported experiments more generally and in an integrated manner and come back to the proposed model. Conclusions regarding the accuracy of the model are drawn and outlooks and implications are given for possible future directions based on the results and a further conceptualization of the model.

6. The interplay of predictive and postdictive components of experienced selfhood[2]

Objects that we affect by our body movements can be experienced as being controlled by (agency) and belonging to the own body (ownership). Such impressions of minimal selfhood arise when objects move as predicted prior to the action (predictive component). But they can also arise when otherwise unpredictable object movements turn out to be consistent with (e.g., spatially compatible to) preceding actions (postdictive component). Here we studied how the impact of postdictive components of inferred minimal selfhood in terms of action-object compatibility is shaped by different levels of predictability of these object movements. We found that compatibility between actions and object movements, and to a lesser extent predictability of object movements, affected reported agency while only compatibility affected reported ownership. Importantly, predictive and postdictive factors influenced these measures in an independent manner. We discuss these results against the background of models that assume multiple components of experienced minimal selfhood.

6.1. Introduction

When people alter objects by their own body movements they often tend to experience control for these object changes which has been labeled as sense of agency (Haggard & Tsakiris, 2009; Kalckert & Ehrsson, 2014a). Furthermore, people can to some extent perceive such objects as being part of their own body, even if these objects are non-corporeal and dissimilar to human body limbs as long as they move in accordance with the agent (ownership, Liepelt, Dolk, & Hommel, 2017; Ma & Hommel, 2013, 2015a, b; Zopf et al., 2018). For example, users of a tool typically experience control over that tool and such tools can become part of the body even up to the level of neural representation (Maravita & Iriki, 2004). Sense of agency and sense of body ownership are assumed to be two cornerstones of the so-called “minimal self”, that is “a consciousness of oneself as an immediate subject of experience, unextended in time” (Gallagher, 2000, p. 15). It is this minimal self, originating from the feeling of control over certain perceptual events and the feeling of inclusion of controlled objects to the instance exerting that control that we wanted to investigate in this study. This sets aside all aspects of the “narrative” self, thus the past and future in stories we and others tell about us.

How do such impressions of minimal selfhood arise? One important source of experienced sense of agency and sense of ownership is prediction. Humans predict or anticipate the perceptible effects of their actions, and such anticipation might in fact be a cause of body movements in the first place (Brown, Adams, Parees, Edwards, & Friston, 2013; Shin et al., 2010). When the actual action effects match those that were predicted, the impression of agency regarding these effects and a sense of ownership of the manipulated object can arise. There is ample evidence for this predictive component of the sense of agency and ownership (for a review cf. Haggard, 2017).

However, people can also have impressions of agency regarding events they did not predict and can perhaps even experience ownership for the involved objects then. For example, when an item drops from the shelf of a supermarket while just passing that shelf, a strong impression of agency for that event can arise, although that event was entirely unforeseen. As another example, amputees can vividly experience seen arm movements of another person as movements of their own phantom limb, although these movements are unpredictable for them (Ramachandran & Rogers-Ramachandran, 1996). Thus, there is likely also a postdictive component that influences the level of experienced selfhood. In other words, people judge "after the act", whether an event might be caused by that act or not (Synofzik, Vosgerau, & Newen, 2008b).

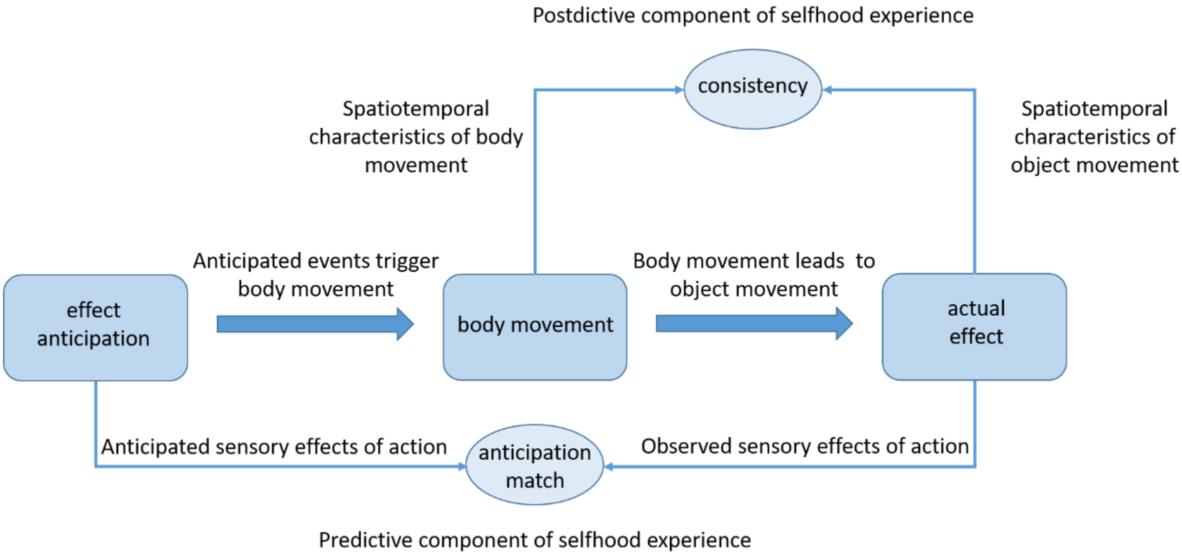

Figure 4. Predictive and postdictive components of experienced minimal selfhood. Anticipations of certain intended effects trigger body movements, which then trigger certain perceptual effects. Anticipated (predicted) effects are compared to actual effects, which, if matching, induce an impression of agency/ownership (predictive component). Moreover, actual effects are evaluated regarding their spatiotemporal consistency with body movements, which can also induce an impression of agency/ownership (postdictive component).

An important factor shaping the level of experienced selfhood due to such postdictive processes is action-event "consistency" (Wegner & Sparrow, 2004), that is whether action and event plausibly belong together based on general knowledge. To illustrate the role of consistency, consider a study by Ebert and Wegner (2010). Participants moved a joystick back or forth, and that movement triggered a back or forth movement of a picture on a screen. Participants showed higher degrees of agency in various measures for picture movements that were consistent (spatially compatible), rather than inconsistent (spatially incompatible) with the joystick movement. Importantly, the picture's movement was objectively unpredictable because for a given trial, it was unknown to the participants before their movement whether the picture would move consistently or inconsistently with the joystick, and thus this consistency influence must be based on postdictive processes. Figure 4 illustrates the described predictive and postdictive components of experienced minimal selfhood.

The present experiments studied in more detail the postdictive component as indexed by influences of action-effect consistency. We were interested to know how the influence of this postdictive component is shaped by the availability, or lack, of predictive components. Thus, we studied the joint influence of two factors on the sense of agency and the sense of ownership as proxies for the experience of minimal selfhood, namely action-effect consistency[3] (consistent or inconsistent) and action-effect predictability (predictable or unpredictable). Concretely, participants were asked to carry out a left or right manual action, which produced a spatially compatible or incompatible movement of an object on a screen. The movement direction of the object was either predictable or unpredictable.

Based on previous research it is hard to judge how predictability of action effects might influence the impact of action-effect consistency since current models usually assume experienced selfhood to be based on a weighting of various selfhood indicators (e.g., Chambon, Sidarus, & Haggard, 2014; Synofzik et al., 2008b), but they do not explain their precise interplay. A first possibility is that consistency and predictability affect experienced agency/ownership independently of each other. Thus consistency of an object movement might increase experienced agency/ownership so as predictability of that movement does, while these influences are additive to each other. Such an outcome would suggest that experienced agency/ownership is fueled by predictive and postdictive processes independently.

A second scenario is that the impact of postdictive components of experienced agency/ownership reduces, once predictability as another source of such selfhood comes in.

[3] One may construe action-effect consistency to be based on predictions as well, because pre-experimental experience suggests, that body movements normally produce spatially consistent feedback (e.g., a rightward hand movement produces the visual experience of a rightward moving hand). Viewed like that, action-effect consistency relates to predictions based on long-term experience, whereas our manipulation of action-effect predictability proper, relates to predictions based on short-term experience in the corresponding experimental session (for a discussion of this issue cf. Dogge et al., 2019; Wirth et al., 2018 and section *6.4. The interplay of predictive and postdictive components of experienced selfhood - General discussion)*.

This outcome is suggested by research showing that at least moderate levels of inconsistency between own body movements and produced object movements are barely noted, providing that objects move in an otherwise predictable manner (Fourneret & Jeannerod, 1998; Knoblich & Kircher, 2004; Müsseler & Sutter, 2009). In other words, people might rely on postdictive indicators to judge the origin of an action, if no prediction of action outcomes is possible. But once such prediction is possible, the weight of postdictive components is reduced. This would result in an interactive influence of predictability and consistency of agency/ownership measures. Our study aimed at manipulating these two components of experienced minimal selfhood independently of each other to investigate their contributions and possible interplay in the emergence of sense of agency and sense of ownership.

We also studied how our experimental manipulations impact performance as measured by reaction times. When the identity of an action effect is predictable, it could in principle already impact the time needed to generate that action, although the effect physically occurs only after action initiation. In fact, reaction times sometimes increase when actions foreseeably produce spatially incompatible action effects (e.g., Kunde et al., 2012; Pfister & Kunde, 2013; Müsseler et al., 2008; Müsseler & Skottke, 2011). This is explained by interference between anticipated body-related and anticipated body-external effects during action generation (response-effect compatibility, Kunde, 2001). If no anticipation about upcoming effects is possible no such influence should occur.

6.2. Experiment 1

Experiment 1 aimed at testing the joint influences of predictability and compatibility of object movements on experienced agency and ownership of the moved objects. Participants were asked to initiate as quickly as possible on an imperative stimulus a hand movement to the left or right. That hand movement started the movement of an object on a screen (i.e. a circular cursor). The movement direction of the object was either spatially compatible or spatially incompatible to the hand movement, and in different conditions that object movement was either predictable or not (cf. Figure 5). Once the object had started to move, it was under control of the participants, that is, moving the hand by a certain distance or in a certain speed moved the object to the same extent or speed into either the same or the opposite direction, depending on the action-object compatibility. This specific aspect of the procedure will be of relevance when discussing the results later. After each trial participants were asked about the experienced agency for that object movement, and to which extent they felt the object belonging to their body. On top of the predictability of the cursor movement and its compatibility to the hand movement, we additionally varied whether the hand movement direction was freely chosen (free choice trials) or prescribed by a specific color of the cursor (forced choice trials).

We expected to find higher ratings of agency and ownership with spatially compatible rather than incompatible object movements, and with predictable rather than unpredictable object movement directions, with a possible interaction between them. We also expected lower reaction times when hand movements triggered cursor movements which were foreseeably compatible rather than incompatible with the hand movement (e.g., Schwarz et al., 2018) whereas no such difference should occur, when cursor movement direction was unpredictable, because at the point where reaction time was measured, object movement direction was yet unknown to the participants.

6.2.1. Materials and methods

6.2.1.1. Ethics statement

The present study and all follow-up studies have been approved by the ethics committee of the institute for psychology of the University of Würzburg under the reference number GZEK 2018-33 and are all in line with the Declaration of Helsinki.

6.2.1.2. Participants

24 participants (16 female, eight male; 23 right-handed, one left-handed; M_{age} = 26.54, SD_{age} = 7.47, min_{age} = 19, max_{age} = 51) were tested in Experiment 1 and received either course credit or €8 per hour for their participation. All participants were recruited through an online platform

used by the University of Würzburg for this purpose and had to give their informed consent before their participation.

6.2.1.3. Apparatus and stimuli

The experiment was performed in a laboratory, which allowed for parallel testing of up to five participants. Stimuli were displayed on LCD monitors (24", BenQ XL 2411, BenQ) with a resolution of 1920 x 1080 pixels and a 100 Hz refresh rate. All stimuli were presented using E-Prime (version 3.0, https://www.pstnet.com/). All hardware and software was identical on all used computers and for all tested participants. Participants were seated approximately 60 cm in front of the screen with their left hand placed in front of the keyboard, which was in a central position directly in front of the screen, and their right hand placed on the computer mouse, which was located on the right-hand side from the participant's point of view in a middle position between the screen and the participant.

6.2.1.4. Procedure and task

At the beginning of each trial, participants saw a gray circle on a black background and two gray target boxes left and right of the circle on the screen. After a predefined delay of either 1500 ms or 2500 ms for half of the trials respectively, the circle was filled with a color indicating for the participants which action to perform. If the color of the circle changed to blue, participants had to move the mouse to the left, if the color changed to red, participants had to move the mouse to the right and if the color changed to green, participants were free to move the cursor to either of the two sides (color-response mapping was counterbalanced between participants for the stimuli which required a response to the left or right). Participants were instructed to respond to the color change as fast as possible and also to try to keep their right and left movements approximately in balance during the free choice trials. Upon response by mouse movement the circle moved simultaneously and visible to the participants behind one of two target boxes on the screen, either by moving in the same direction as the participant moved the mouse (compatible condition) or in the opposite direction of the mouse movement (incompatible condition, cf. Figure 5). Reaction times were measured as the time interval from the color change of the cursor until the mouse had been moved approximately 0.59 mm to either the left or right from the central starting position. Furthermore, 1/9 of the trials in every block were “deviant” trials in which the circle moved in a 45°, 135°, 225° or 315° angle from the starting point in the center of the screen. Participants had to react upon these deviant trials by pressing the space key within 500 ms after the movement offset to avoid an error message. The purpose of these deviant trials was that we wanted to make sure that participants did not solely focus on their hand movement and ignored the visual feedback of the circle. For later analyses however, these trials were excluded. After every trial, participants had to state on a 9 point Likert scale (Likert, 1932) how much they had the impression to control the circle (agency rating) and how much they had the impression that the circle was part of their body (ownership rating).

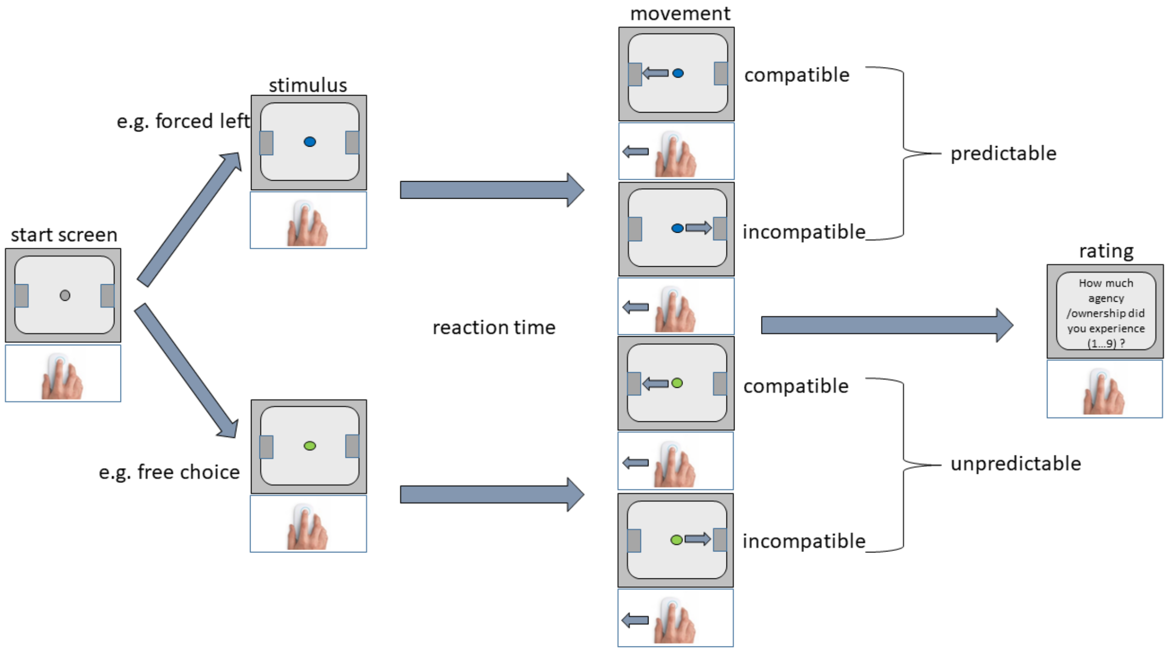

Figure 5. Schematic overview of (non-deviant) trials in Experiment 1. Participants were asked to move their hand to the left or right depending on the color of a cursor (or to freely choose where to move with one of the three colors). This triggered a movement of the cursor in either a spatially compatible or spatially incompatible direction, which in different conditions was either predictable or not. After the cursor movement, participants judged experienced agency and ownership regarding the cursor movement. For simplicity, in the figure only two out of three different kinds of stimuli are shown and the two displayed outcomes for forced left reactions are labelled as predictable while the two displayed outcomes for free choice reactions are labelled as unpredictable. Importantly though, all possible combinations of stimuli (3 colors), compatibility (2 levels) and predictability (2 levels) were presented to participants in the experiment so that also both free choice and forced choice trials could include either predictable or unpredictable action effects.

The experiment consisted of three types of blocks, with the order of type of block counterbalanced across participants: In two of the blocks, the circle always moved either only in the same direction as the mouse or only in the opposite direction, thus the circle movement was predictable for the participants. In the remaining block, the circle moved compatibly and incompatibly in 50% of the trials each in random order, thus the circle movement was unpredictable for the participants. Before the first presentation of each block, there was a short practice session for the respective response-effect mapping. Please note that there were no explicit instructions regarding the response-effect mapping, but participants learned the relationship between the direction of their hand movement and that of the cursor movement (or the fact that there was none) from experience. The predictable blocks included 24 free choice and forced choice trials each plus 6 deviant trials and were presented twice to every participant resulting in 108 trials overall each, while the unpredictable block included 48 free and forced choice trials each plus 8 deviant trials which were also presented twice resulting in a total of 208 trials with half of the trials representing compatible and the other half incompatible blocks. Thus, unpredictable blocks were twice as long as predictable blocks since they always included both compatible and incompatible trials while predictable blocks always included either only compatible or only incompatible trials. Counterbalanced over all conditions, half of the trials were preceded by a short (1500 ms) or a long (2500 ms) interstimulus interval (ISI) respectively. Overall, every participant thus completed 96 trials in each cell of compatibility x predictability combinations, excluding practice and deviation trials. The overall duration of the experimental session was approximately 45 min per participant.

6.2.1.5. Data preprocessing

We excluded all trials from analyses in which participants showed the wrong response to the stimulus because errors could only be made in forced choice trials and thus the manipulation of free choice and forced choice otherwise could have been confounded with possible effects related to these errors. Furthermore, we also excluded all deviant trials, all trials with missing data in either reaction times or ratings and all trials with reaction times < 150 ms (which has been suggested as a minimum time window for categorization processes, see e.g., Delorme, Rousselet, Macé, & Fabre-Thorpe, 2004; Rousselet, Fabre-Thorpe, & Thorpe, 2002) or > 1500 ms from analyses. The overall error rate was 9.30%.

6.2.2. Results[4]

All raw data and analysis scripts of Experiments 1 & 2 are available on the Open Science Framework (https://osf.io/wzdnk/).

6.2.2.1. Reaction times

Mean reaction times (RTs) we entered into a 2 x 2 x 2 repeated measures analysis of variance (ANOVA) with the factors compatibility (compatible vs. incompatible), predictability (predictable vs. unpredictable) and type of trial (forced choice vs. free choice). Reaction times were lower for compatible than for incompatible trials ($F(1, 23) = 8.51$, $p = .008$, $\eta_p^2 = .27$, $BF_{10} = 9.97$; $M_{compatible} = 581$ ms, $SD = 98$ ms; $M_{incompatible} = 606$ ms, $SD = 110$ ms). Moreover there was an interaction between compatibility and predictability ($F(1, 23) = 8.67$, $p = .007$, $\eta_p^2 = .27$, $BF_{10} = 7.31$), but no significant main effect of predictability ($F < 1$). RTs were significantly lower for predictably compatible than for predictably incompatible reaction times ($t(23) = 3.09$, $p = .003$, one-tailed, $d_z = .63$, $BF_{10} = 17.02$; $M_{compatible} = 570$ ms, $SD = 100$ ms; $M_{incompatible} = 620$ ms, $SD = 124$ ms), but almost identical in the unpredictable condition ($|t| < 1$, $d_z = .07$; $M_{compatible} = 591$ ms, $SD = 106$ ms; $M_{incompatible} = 593$ ms, $SD = 104$ ms; cf. Figure 6). Furthermore, RTs were lower for free choice as compared to forced choice trials ($F(1, 23) = 8.87$, $p = .007$, $\eta_p^2 = .28$, $BF_{10} = 556.54$; $M_{free} = 576$ ms, $SD = 96$ ms; $M_{forced} = 611$ ms, $SD = 115$ ms). Finally, the three-way interaction compatibility x predictability x type of trial ($F(1, 23) = 4.06$, $p = .056$, $\eta_p^2 = .150$, $BF_{10} = 0.41$) was marginally significant. This interaction reflected a larger compatibility

[4] In addition to test statistics and p-values from frequentist analyses, additional Bayes factors are reported for all experiments as well. This was done as an additional source of information for the reader and to increase consistency between the analyses of the different experiments since Bayes factors were also calculated and reported in the publication including Experiment 5 (Liesner & Kunde, 2020). Interpretations are still mainly based on frequentist analyses, however in the large majority of cases, frequentist and Bayesian analyses do not suggest different effects and interpretations anyway.

influence in forced choice as compared to free choice trials when compatibility was predictable, but no qualitative difference in the effects of compatibility and predictability for different types of trials (both simple effects of compatibility were still significant in the predictable condition when free and forced choice trials were analyzed separately, both *p*s < .015). The larger compatibility effect is likely due to the overall slightly higher RTs in forced choice trials as compared to free choice trials, as action-effect compatibility influences typically increase with RT (e.g., Wirth et al., 2015). The reduction of reaction times in free choice compared to forced choice trials has been reported before (e.g., Hinrichs & Suelzer, 1978; Kiesel et al., 2006). However, since this was not the focus of the present study, we will not touch these points in more detail here.

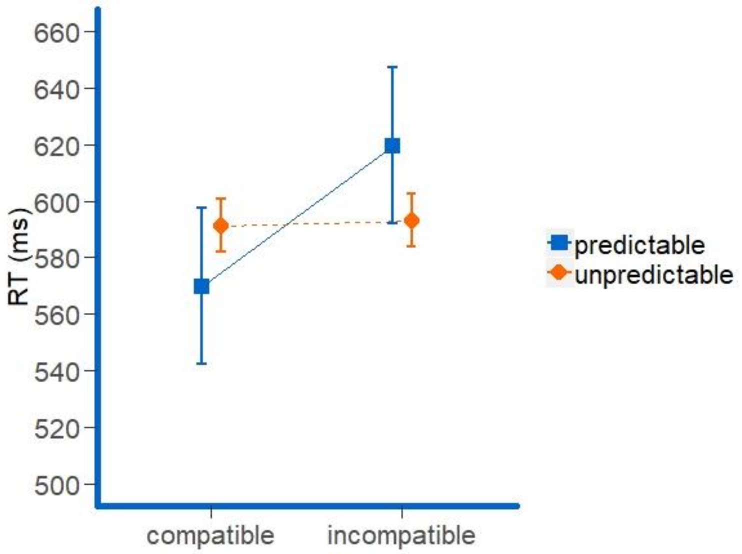

Figure 6. Mean reaction times as a function of action-effect compatibility and action-effect predictability in Experiment 1. Error bars represent 95% paired-difference confidence intervals (Pfister & Janczyk, 2013).

6.2.2.2. Ratings

The same ANOVA's for agency and ownership ratings revealed a main effect of compatibility for agency ($F(1, 23) = 17.84$, $p < .001$, $\eta_p^2 = .44$, $BF_{10} = 8.32 \times 10^{13}$) as well as for ownership ($F(1, 23) = 5.55$, $p = .027$, $\eta_p^2 = .19$, $BF_{10} = 6.45 \times 10^3$) indicating higher ratings for compatible than for incompatible trials (agency: $M_{compatible} = 6.51$, $SD = 2.17$; $M_{incompatible} = 4.27$, $SD = 2.21$; ownership: $M_{compatible} = 3.55$, $SD = 2.44$; $M_{incompatible} = 2.55$, $SD = 1.61$). Neither the main effect of predictability nor the predictability x compatibility interaction was significant (all *p*s > 0.1) even though both ratings were descriptively higher in the predictable than in the unpredictable condition (cf. Figure 7).

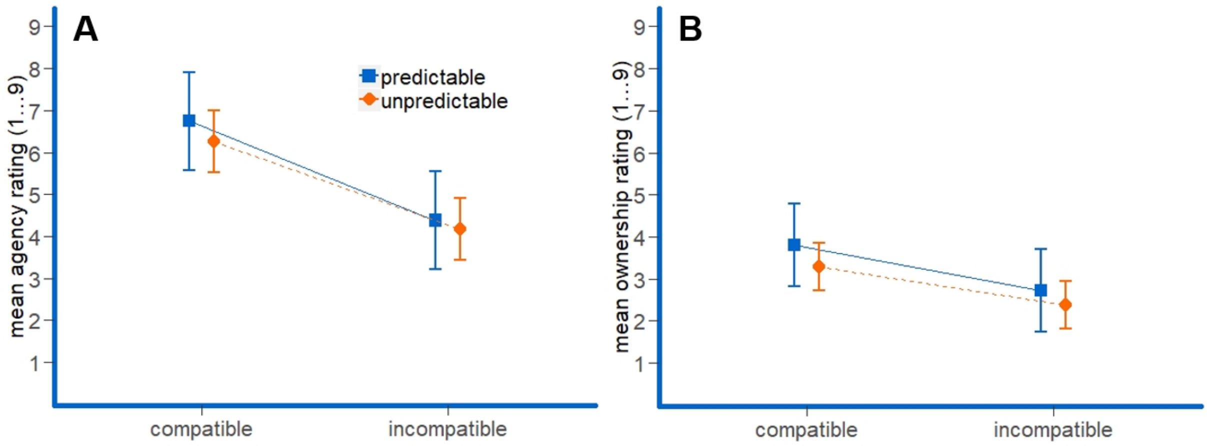

Figure 7. Mean agency (A) and ownership (B) ratings for Experiment 1 as a function of action-effect compatibility, and action-effect predictability. Error bars represent 95% paired-difference confidence intervals calculated separately for the predictable and unpredictable condition (Pfister & Janczyk, 2013).

6.2.3. Discussion

Experiment 1 revealed that experienced agency for an object movement and the feeling of ownership regarding this object are lower when that movement is inconsistent rather than consistent to the hand movement that triggered that object movement. However, experienced agency and ownership were essentially independent of whether the movement direction was predictable or unpredictable. This is a rather unexpected finding given the generally strong evidence for predictability on these measures in previous studies (Ma & Hommel, 2015a). One may argue that participants formed no prediction of cursor movements at all even in cases where this was possible. However, this is unlikely given the strong influence of predictable action-effect compatibility on RTs, which must be based on prediction of cursor movement, because at the point in time of RT offset, the cursor movement was only predictable but not yet perceptible. Also, as expected, this influence of predictions on RTs was represented both in a benefit through the prediction of compatible and in an interference through the prediction of incompatible object movements so that we assume that predictions were still made in both of these conditions. These results are in line with previous studies demonstrating an influence of response-effect compatibility on action generation (e.g., Kunde et al., 2012; Pfister & Kunde, 2013; Müsseler et al., 2008; Müsseler & Skottke, 2011; Schwarz et al., 2018).

A more tenable explanation for not observing an influence of predictability on our measures is that judgements of agency and ownership might rely on predictions other than that of object movement direction. This was possible because of the choice of the mouse as the response device, since the object on the screen always moved continuously with the participant's hand, once it had started to move. This might have led to the formation of "micro-predictions" after the movement had been initiated so that due to the matching of continuous movement of both the hand and the object on the screen participants updated predictions about the continuation of the movement, which then overshadowed the initial predictions regarding movement direction made before movement initiation. Such rapid updating of the predictions about the consequences of one's own motor actions in response to visual feedback has been shown before (e.g., Izawa & Shadmehr, 2011; Synofzik, Lindner, & Their, 2008a). Thus, an action-effect mapping is needed where initial predictions made during action generation cannot be overridden by predictions made while the response is transformed into an object movement. In Experiment 2, such an approach is implemented.

6.3. Experiment 2

Experiment 2 is identical to Experiment 1 except that here participants triggered object movements by pressing a key, instead of moving a mouse. However, the keypress had no impact on the object movement anymore *after* that keypress had been initiated. Thus the object movement direction was (in)consistent and (un)predictable only with respect to the location of the keypress. Because of the discrete nature of this response, an updating of predictions after response initiation due to perceived effects was not possible anymore in this experiment.

The lack of an influence of action-effect predictability on selfhood ratings casts some doubt on the credibility of these ratings, despite our explanations of the absence of this otherwise robust influence. Thus, Experiment 2 did not only serve to better disentangle predictive from postdictive components, but also to investigate whether our ratings were even sensitive for a manipulation of predictability.

6.3.1. Materials and methods

For brevity reasons we will mainly focus on the differences to Experiment 1 in this section.

6.3.1.1. Participants

24 participants (15 female, nine male; 19 right-handed, five left-handed; M_{age} = 27.33, SD_{age} = 10.96, min_{age} = 19, max_{age} = 67) were tested in Experiment 2 and received either course credit or €8 per hour for their participation. As in Experiment 1, all participants were recruited through the same online platform and again had to give their informed consent before their participation.

6.3.1.2. Apparatus and stimuli

The experimental setup was the same as in Experiment 1, except that, in this experiment, participants used the arrow keys of the keyboard instead of the mouse as response device. Therefore, the keyboard was placed right in front of the monitor with the arrow keys being vertically aligned with the center of the screen and the participants were asked to place the index and middle finger of their dominant hand on the right and left arrow keys.

6.3.1.3. Procedure and task

Procedure and task were exactly the same as in Experiment 1 except the different response device. After key presses the circle moved, again visible to the participants, with a constant speed of 12 pixels per frame resulting in a rash, yet clearly visible movement until it had fully disappeared behind one of the target boxes. There was a slight difference to Experiment 1 in the order of the blocks, though, because the unpredictable block was in Experiment 2 always either the first or the last block, but never inserted between the two predictable blocks. Whether it was presented before or after the predictable blocks was counterbalanced between participants. We used these orders to be able to identify possible effects that predictable or unpredictable action effects might have had on agency and ownership ratings when participants had not experienced the other predictability manipulation yet. Again, there were no explicit instructions regarding the predictability.

6.3.1.4. Data preprocessing

As in Experiment 1, we excluded all trials with missing data for either the reaction times or the ratings, all deviant trials and also all trials with reaction times < 150 ms or > 1500 ms and/or errors. The overall error rate was 4.56%.

6.3.2. Results

6.3.2.1. Reaction times

Mean reaction times (RTs) we entered into a 2 x 2 x 2 repeated measures ANOVA with the factors compatibility (compatible vs. incompatible), predictability (predictable vs. unpredictable) and type of trial (forced choice vs. free choice). There was neither a significant main effect of compatibility, nor a significant main effect of predictability nor a significant interaction between the two factors (all *p*s > .24). However, there was a marginally significant effect of type of trial ($F(1, 23) = 4.05$, $p = .056$, $\eta_p^2 = .15$, $BF_{10} = 27.59$), with slightly lower RTs in the free choice as compared to the forced choice condition, and a significant compatibility x type of trial interaction ($F(1, 23) = 5.18$, $p = .032$, $\eta_p^2 = .18$, $BF_{10} = 0.58$). Mean RTs of each condition and the size and significance (based on a paired *t*-test, one-tailed, with additional Bayes factors) of the compatibility effect in each predictability by trial type combination are listed in Table 1.

6.3.2.2. Ratings

The same 2 x 2 x 2 repeated measures ANOVA with the factors compatibility (compatible vs. incompatible), predictability (predictable vs. unpredictable) and type of trial (forced choice vs. free choice) was conducted for agency and ownership ratings respectively (cf. Figure 8).

Table 1. Means and standard deviations of reaction times in Experiment 2 for all predictability x compatibility x type of trial combinations.

		Compatibility		
		Compatible	Incompatible	Difference
Free choice	Predictable	572 ms (97 ms)	569 ms (107 ms)	−3 ms, p = .41, BF_{10} = 0.18
	Unpredictable	584 ms (104 ms)	576 ms (91 ms)	−8 ms, p = .39, BF_{10} = 0.39
Forced choice	Predictable	582 ms (126 ms)	604 ms (117 ms)	22 ms, p = .026*, BF_{10} = 2.45
	Unpredictable	607 ms (115 ms)	609 ms (123 ms)	2 ms, p = .13, BF_{10} = 0.22

Agency was rated higher in predictable than in unpredictable blocks (F(1, 23) = 6.56, p = .017, η_p^2 = .22, BF_{10} = 13.71; $M_{predictable}$ = 5.57, SD = 2.22; $M_{unpredictable}$ = 4.69, SD = 2.10), and in compatible than incompatible trials (F(1, 23) = 26.05, p < .001, η_p^2 = .53, BF_{10} = 3.13 x 10^{13}; $M_{compatible}$ = 6.23, SD = 2.09; $M_{incompatible}$ = 4.03, SD = 2.40), with no interaction between these factors (F < 1). The influence of compatibility was slightly stronger in forced choice than free choice trials (F(1, 23) = 5.37, p = .030, η_p^2 = .19, BF_{10} = 0.23 for the interaction of trial type x compatibility), while the influence of predictability was slightly stronger in free choice than in forced choice trials (F(1, 23) = 4.43, p = .047, η_p^2 = .16, BF_{10} = 0.22 for the interaction of trial type x predictability). The three-way interaction also reached significance, reflecting a slightly stronger modulating influence of trial type on compatibility in the unpredictable condition compared to the predicable condition (F(1, 23) = 6.86, p = .015, η_p^2 = .23, BF_{10} = 0.30). However, as shown in Figure 8, compatibility and predictability had clearly additive effects in both forced choice trials and free choice trials (both F's < 1 for the compatibility x predictability interaction in forced and free choice trials).

Ownership was marginally significantly higher with compatible than with incompatible trials (F(1, 23) = 3.86, p = .062, η_p^2 = .14, BF_{10} = 273.64; $M_{compatible}$ = 2.35, SD = 2.14; $M_{incompatible}$ = 1.88, SD = 1.69), but unaffected by predictability (F < 1) with also no interaction between these factors (F(1, 23) = 2.54, p = .12, η_p^2 = .10, BF_{01} = 2.01). Moreover, the influence of compatibility was stronger with forced choice than free choice trials (F(1, 23) = 6.61, p = .017, η_p^2 = .22, BF_{10} = 0.23), and this moderating influence of trial type was slightly stronger in unpredictable rather than predictable blocks (F(1, 23) = 4.70, p = .041, η_p^2 = .17, BF_{10} = 0.29).

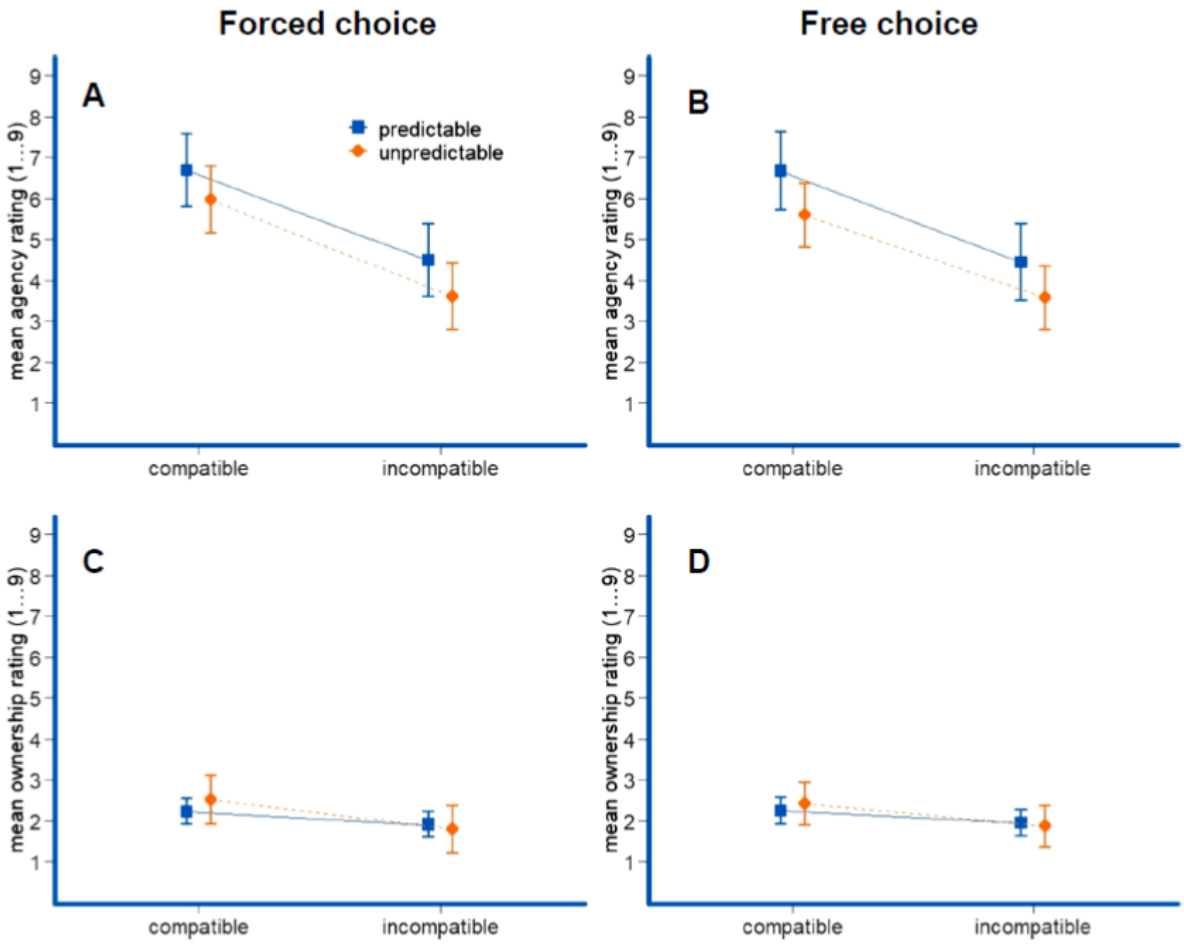

Figure 8. Mean agency (A and B) and ownership (C and D) ratings for forced choice (A and C) and free choice (B and D) trials in Experiment 2. Error bars represent 95% paired-difference confidence intervals calculated separately for the predictable and unpredictable condition (Pfister & Janczyk, 2013).

6.3.2.3. Between experiments analysis

To further investigate potential differences between the two experiments we analyzed the data from both experiments together in a 2 x 2 x 2 x 2 split-plot ANOVA with the three within subjects factors as stated in the previous analyses and the additional between subjects factor

Experiment (1 vs. 2). For brevity, we will not repeat effects already described in the previous analyses but focus on differences between experiments, thus effects that include the factor experiment.

For reaction times, compatibility had a stronger influence in Experiment 1 than Experiment 2 ($F(1, 46) = 4.60$, $p = .037$, $\eta_p^2 = .09$, $BF_{10} = 0.92$), and this compatibility effect tended to be stronger in the predictable condition of Experiment 1 as compared to all other conditions ($F(1, 46) = 3.38$, $p = .073$, $\eta_p^2 = .07$, $BF_{10} = 0.56$ for the three-way interaction compatibility x predictability x experiment). Neither for agency ratings nor for ownership ratings were there significant effects including the factor experiment (all *p*s > .08).

6.3.3. Discussion

Experiment 2 tested how postdictive influences of experienced minimal selfhood of object movements are affected by the predictability of these movements. The only (un)predictable aspect of the object movement was now movement direction, while other aspects such as movement speed or extent which were contingent on hand movements in Experiment 1 were now constant. Regarding agency we found both, indicators of postdictive influences on selfhood (higher experienced selfhood with action-effect consistency) and indicators of predictive influences (higher experienced selfhood with action-effect predictability), which were independent of each other. Thus, the influence of postdictive components is not modulated by the availability of predictive components. Regarding ownership, the ratings were generally low, and affected by action-effect consistency alone.

The fact that we found an influence of predictability on at least agency ratings in Experiment 2 also re-establishes confidence in these ratings and their sensitivity to predictive influences, which was somewhat doubtful after Experiment 1. This supports our assumption that the absence of an effect of predictability on selfhood ratings in Experiment 1 is due to other processes, like for example rapid prediction updating after movement onset (e.g., Izawa & Shadmehr, 2011; Synofzik et al., 2008a). This argument is supported by the observation that the level of experienced agency with predictable rather than unpredictable object movements in Experiment 2 resembles more those of Experiment 1 where predictable and unpredictable movements did not differ. This accords with our conjecture that the short exposure to predictable aspects of the object movement in Experiment 2, such as object movement speed while moving the computer mouse, replaced the lack of predictability of movement direction prior to action onset.

Noteworthy, despite the significant influence of predictability on agency in Experiment 2, we found no influence of predictability on ownership ratings in Experiment 2. We note though that overall level of reported ownership with the non-corporeal objects used here was generally low, suggesting a floor effect (e.g., Everitt, 2006). In other words, lack of predictability of object movements was unlikely to reduce the already low experienced ownership any further so that our results possibly underestimate the influence of predictive processes on ownership experiences.

Agency was slightly stronger affected by predictability of cursor movements in free rather than in forced choice trials. This accords with the general observation that action effects exert stronger influences in intention-based (free choice) rather than stimulus-based (forced choice) situations (e.g., Herwig & Waszak, 2012; Pfister, Kiesel, & Melcher, 2010; Waszak et al., 2005). However, in replicating Experiment 1, action effect consistency affected RTs less in free choice than forced choice trials (where no significant influence was observed in Experiment 2). As noted before, this might be due to the again significantly higher RT level of forced choice trials, which is known to increase such compatibility effects in RTs. Furthermore, also the influence of compatibility on agency was slightly larger in forced choice than in free choice trials so the precise influence of free and forced choice trials on the different components of experienced agency and how this relates to performance, which was not one of the main focusses of this study, still needs some further clarification through future research.

6.4. General discussion

The current study explored how predictive and postdictive factors jointly contribute to experienced agency over, and ownership of, non-corporeal objects, which are manipulated by the agent. The results can be summarized by saying that both predictive and postdictive components do contribute to experienced selfhood, but that postdictive components had a stronger influence. Our results thus support models that assume various sources of experienced selfhood (Chambon et al., 2014; Farrer, Valentin, & Hupé, 2013; Sidarus & Haggard, 2016; Synofzik et al., 2008b). Importantly, we found mainly independent influences of predictive and postdictive sources on experienced selfhood. Thus, the addition of action-effect predictability did not reduce the influence of action-effect consistency, if it had an influence at all.

However, future research is warranted to test the generality of this independency of postdictive and predictive components. For example, action effect consistency might get a higher weight for judging agency, if participants had never experienced predictability of such effects, or conversely, get a lower weight once predictability had been experienced before. Consider a plane pilot with strong predictions about the effects of his or her steering inputs. Regardless whether the pilot’s movements are transformed spatially consistently (such as when moving the yoke to the left and the plane turning to the left) or spatially neutral with respect to the input operation (such as when moving the yoke towards the pilot and the plane gaining height), the pilot will experience strong agency over the plane movements. Even the first encounter of an unpredicted movement of the machine though (e.g., due to a malfunction) may result in a breakdown of agency experience, be that movement spatially compatible to the input operation or not. By contrast, a novice without any predictions or expectations about the translation of steering inputs into plane movements might spontaneously gain the impression of agency on that same broken plane when the machine moves spatially compatibly rather than incompatibly to his or her input operations, even though it does not respond predictably at all.

Some hints for this speculation come from a more detailed analysis of Experiment 2. When looking at only the first half of trials it is possible to compare those participants who had only experienced predictable cursor movements with those who had only experienced unpredictable cursor movements up to this point of the experiment (basically a between participants manipulation of predictability). Though not significant, the influence of action-effect compatibility (the rating differences between incompatible and compatible trials) was considerably smaller for those participants who had only experienced predictable cursor movements as compared to those who had never experienced such predictability ($M_{predictable}$ = 2.38 (SD = 2.70) vs. $M_{unpredictable}$ = 2.88 (SD = 2.46), $t(22) = 0.47$, $p = .64$, two-tailed, $d = .19$, BF_{10} = 0.41 for agency; $M_{predictable}$ = 0.36 (SD = 1.18) vs. $M_{unpredictable}$ = 0.92 (SD = 2.04), $t(22) = 0.83$, $p = .42$, two-tailed, $d = .34$, BF_{10} = 0.48 for ownership). Thus, possibly the mere experience of predictability attenuates the weight given to compatibility at any later point in time[5]. This might explain why people who use tools that move in a perfectly predictable manner often feel about equal degrees of agency irrespective of whether that tool movement is spatially consistent or inconsistent to their hand movements (Knoblich & Kircher, 2004; Müsseler & Sutter, 2009).

While we have drawn here a picture of distinct components for perceived selfhood, one can think about a closer similarity of these two components. One way doing so was to consider that the influence of compatibility also reflects a kind of prediction, though a prediction based on knowledge acquired through lifelong experience prior to the experiment. Normally, perceptual feedback of motor output is compatible to that motor output. For example, moving the right hand produces visual feedback of that movement on the right side. Based on this experience, participants might still "predict" that body movements will more likely produce compatible visual effects, even when this was technically not so in the unpredictable conditions they faced here (for similar arguments, cf. Dogge, Custers, Gayet, Hoijtink, & Aarts, 2019; Wirth, Steinhauser, Janczyk, Steinhauser, & Kunde, 2018). In other words, the influence of compatibility might reflect long-term predictions, while the influence of predictability proper in our experiments might reflect short-term predictions. If construed that way, one can conclude

[5] This speculation is supported by another, methodically somewhat different experiment not reported here, in which action-effect predictability was varied between participants. This experiment revealed a significant interaction between compatibility and predictability for both agency ($F(1,30) = 11.91$, $p = .002$, $\eta_p^2 = .28$, $BF_{10} = 1.48 \times 10^6$) and ownership ($F(1, 30) = 8.69$, $p = .006$, $\eta_p^2 = .23$, $BF_{10} = 9.52 \times 10^4$) ratings, indicating stronger compatibility effects for participants for which the action-effect mapping was always unpredictable ($d_{Agency} = 1.91$, $d_{Ownership} = .98$) compared to those for which it was always predictable ($d_{Agency} = .83$, $d_{Ownership} = .55$).

that both long-term predictions and short-term predictions based on the present experimental context influenced sense of agency in our experiments.

A final word regarding the relationship of experienced agency and ownership is in order. Body ownership, as the unique feeling that one's body belongs to oneself (Gallagher, 2000), and agency, the feeling that one can control and cause perceivable actions in the world (e.g., Moore & Obhi, 2012; Haggard et al., 2002), together represent aspects of a minimal sense of self which is guided by sensorimotor processes (Tsakiris, 2010). It is therefore suggested that, even though not the same, there is reasonable overlap between these two concepts and that both concepts to some extent represent the integration of an event or object into the self (Synofzik, Vosgerau, & Newen, 2008c; Tsakiris et al., 2007). It is thus also not surprising that we could observe similar patterns of results for both measures despite differences. While we were interested in differences between conditions, rather than absolute values, it is fair to say that the level of experienced ownership for the manipulated objects was generally low, though in the range of similar settings where hand movements affect artificial objects (cf. Ma & Hommel, 2015a). As already touched in the discussion of Experiment 2, these generally low ratings for ownership might have also contributed to the absence of predictability effects on ownership. However, as Gallagher (2000) already mentioned in his introduction of the "minimal self", the prerequisites for experiencing a sense of ownership are probably higher and more complex than for experiencing a sense of agency since information from more sources (e.g., proprioceptive or tactile feedback) need to be integrated and match for a sense of ownership to emerge. One might thus also question to what extent such low reported explicit senses of ownership are actually comparable to the sense of ownership as it can be observed in, for example, the rubber hand illusion (Botvinick & Cohen, 1998) or other paradigms where there is a much larger feature overlap between the body and the incorporated object and where an integration of the object into the body of the agent seems much more likely (Hommel, Müsseler, Aschersleben, & Prinz, 2001) and has already been shown to be stronger (Kalckert et al., 2019a). Therefore, it remains to be clarified whether pure correlation between one's own movement and an object movement is sufficient to perceive this object as being part of one's self or body. One approach that might help to shed further light on this issue would be to investigate how more implicit measures of ownership, such as proprioceptive drift (Tsakiris & Haggard, 2005) are affected by the factors we investigated. This is something we aim to address in future research.

7. Spatial action-effect binding depends on type of action-effect transformation[6]

Spatial action-effect binding denotes the mutual attraction between the perceived position of an effector (e.g., one's own hand) and a distal object that is controlled by this effector. Such spatial binding can be construed as an implicit measure of sense of object ownership, thus the belonging of a controlled object to the own body. The current study investigated how different transformations of hand movements (resident action component) into movements of a visual object (remote action component) affect spatial action-effect binding, and thus implicit object ownership. In brief, participants had to bring a cursor on the computer screen into a predefined target position by moving their occluded hand on a tablet and had to estimate their final hand position. In Experiment 3, we found a significantly lower drift of the proprioceptive position of the hand towards the visual object when hand movements were transformed into laterally inverted cursor movements, rather than cursor movements in the same direction. Experiment 4 showed that this reduction reflected an elimination of spatial action-effect binding in the inverted condition. The results are discussed with respect to the prerequisites for an experience of ownership over artificial, non-corporeal objects. Our results show that predictability of an object movement alone is not a sufficient condition for ownership because, depending on the type of transformation, integration of the effector and a distal object can be fully abolished even under conditions of full controllability.

[6] The official citation that should be used in referencing this material is: Liesner, M., Kirsch, W., Pfister, R., & Kunde, W. (2020). Spatial action–effect binding depends on type of action–effect transformation. *Attention, Perception, & Psychophysics*, *82*(5), 2531–2543. https://doi.org/10.3758/s13414-020-02013-2. The following paragraphs may not exactly replicate the referenced article.

7.1. Introduction

Motor actions often aim at producing a change in the environment that does not occur in direct proximity of the effector, but rather at a more distant spatial location. This is especially the case when using a tool (e.g., when hitting a nail with a hammer or when moving a cursor with the computer mouse). Such (inter)actions give rise to a striking perceptual distortion: The perceived position of the effector is systematically shifted towards the location of the action's effect and vice versa, and such spatial binding has been documented in a range of studies.

For example, when a (nonvisible) hand movement produces a visual cursor movement with an angular deviation, the perceived position of the hand shifts towards the end position of the cursor, while the perceived end position of the cursor shifts towards the end position of the hand (Debats, Ernst, & Heuer, 2017a, b; Rand, Wang, Müsseler, & Heuer, 2013). Similarly, Kirsch, Pfister, and Kunde (2016) found the same mutual attraction effects when a spatial offset between uniformly, horizontally moving hand and cursor instead of an angular deviation was introduced.

The spatial binding effect has been explained as resulting from multisensory integration of sensory signals stemming from the action (especially proprioceptive and visual information) and sensory signals of the resulting effect (e.g., Kirsch et al., 2016). Indeed, similar spatial attraction effects have been observed in multisensory perception, suggesting that the currently most reliable sensory channel biases the localization of signals from other modalities (e.g., Alais & Burr, 2004). One striking example for this mechanism is the popular rubber-hand illusion (Botvinick & Cohen, 1998), in which the participant's real hand is occluded from vision while it is softly and synchronously stroked with an artificial hand that is positioned in the participant's view. Following synchronous stimulation, participants reliably report to "feel" the stroke no longer on their own hand, but rather on the rubber hand, and that when asked to localize their own hand, they tend to judge it closer to the rubber hand, a phenomenon now known as "proprioceptive drift" (Tsakiris & Haggard, 2005). This effect is often interpreted as an implicit proxy of experienced "ownership" (i.e., the feeling that the rubber hand is part of one's own self or body representation; Tsakiris, 2010).

Rubber hand illusions were also studied with an active version of the paradigm in which participants move their (occluded) real hand and observe an artificial entity to follow their movements (e.g., Dummer et al., 2009; Kalckert & Ehrsson, 2014a). Interestingly, several studies suggested that such procedures may induce feelings of ownership even for virtual entities that do not resemble the human body, given that the effects observed in these entities are controlled by the person and are temporally contingent to their own movements (e.g., simple geometrical objects; Ma & Hommel, 2015a; Sanchez-Vives et al., 2010; Zopf et al., 2018; but see Kalckert et al., 2019a). For example, for objects that move synchronously rather than asynchronously with the body, participants report larger embodiment or ownership, and show increased skin conductance in case of object threat.

The setup of these studies resembles experimental setups to study spatial action-effect binding. Here, participants are typically asked to carry out movements in a horizontal plane (e.g., on a digitizer tablet), which then cause object movements on either a vertically oriented screen or were projected onto the horizontal plane (e.g., Debats et al., 2017a, b; Kirsch et al., 2016; Liepelt et al., 2017; Rand & Heuer, 2013). Due to the high similarity of both types of experimental paradigms, it thus seems fair to assume that studies on active rubber-hand illusions and studies on spatial action–effect binding address similar processes.

Previous research suggests that a major driving force behind rubber-hand illusions and spatial action-effect binding is the detection of cross-correlations between sensory information from the manipulated object and sensory information from one's own hand (Debats et al., 2017a). Consequently, these effects diminish or even disappear when the object is no longer contingent on the body movements (Debats et al., 2017b; Debats & Heuer, 2018a; Kalckert & Ehrsson, 2014a; Kalckert et al., 2019b; Kirsch et al., 2016). Cross-correlations have typically been implemented in terms of high spatiotemporal similarity of (multimodal) sensory changes. However, for transformed movements, there are often situations in which hand movements trigger correlated events that are, however, spatially incompatible to the hand movement. This is the case, even in simple systems such as levers with one pivot point, in which hand movements in one direction (say, left) make the lever move in the opposite direction (say, right). In this situation, there is a high cross-correlation between sensory information resulting from the hand movement and sensory information relating to the lever movement, but the two movement trajectories are obviously in conflict. Studying spatial binding in this situation allows for drawing conclusions regarding the process that gives rise to perceptual distortions such as spatial action-effect binding: If the process underlying spatial binding mainly captures systematic covariation (i.e., unsigned cross-correlations), then spatial binding should also be apparent for transformed movements. If the process draws on direct spatial matching (i.e., signed cross-correlations), then spatial binding should not occur in the case of transformed movements.

We tested these hypotheses by coupling compatible or incompatible action effects to movements, which participants performed with a stylus on a digitizer tablet. That is, in the compatible condition, hand movements caused cursor movements in the same direction and of the same magnitude. In the incompatible condition, the cursor still moved to the same extent as the hand, but always in the opposite direction. Based on models of ownership it is difficult to judge whether a mismatch in the directions of hand and cursor movement results in less binding of the manipulated object and the hand (Tsakiris, 2010; Tsakiris et al., 2010). These models typically focus on a lack of predictability of vision and body-related stimulation (e.g., by reducing synchronicity of hand and object movements or corresponding stimulation). In the present study, in contrast, the predictability of hand and visual object movements remains the same, and only object movement direction is manipulated. Also, models of statistically optimal integration of proprioceptive and visual information make no clear prediction of whether spatial binding would occur at all in our conditions and whether it would vary with type of transformation (when controlled for all other kinematic characteristics). Typically, studies on optimal integration use setups with only marginal, and mostly unnoticeable, discrepancies between proprioceptive and visual information (e.g., Debats et al., 2017a, b; Kirsch et al., 2016). In contrast, in the current study, proprioceptive and visual information were clearly separated, rendering it uncertain whether integration of multimodal signals would occur at all. Previous studies showed some heterogeneous findings regarding the integration of more or less far apart sensory signals. Debats and Heuer (2020), for example, found that knowledge of spatial disparity of the sources of visual and proprioceptive feedback can reduce sensory integration, while Misceo, Jackson, and Perdue (2014) suggested that explicit knowledge about a common cause of the sensory signals did not increase integration. Furthermore, Rand and Rentsch (2016) showed that even with spatial disparities of up to 150° between an external cursor and the hand, integration of sensory signals can still occur in a way that the estimation of the actual hand location was biased towards the cursor. However, the aim of this latter study was actually to investigate adaptation effects to feedback rotations, so it remains unclear how or if this finding would generalize to other settings, and especially to the case of fully inverted action-effect relations.

As a second aim, we intended to further examine the similarity of rubber-hand illusions and spatial binding by introducing explicit ratings of sense of ownership (i.e., the feeling that the manipulated object belongs to one’s own body) to the study of spatial action-effect binding. That is, while studies on the rubber-hand illusions often included explicit measures of agency (i.e., the feeling of control over the object movement) and ownership alike (e.g., Kalckert & Ehrsson, 2014a), studies with more simple action effects have mainly focused on the former ratings. Such explicit ratings of agency were reported to be lower for spatially incompatible action-effect transformations than for spatially compatible ones (Ebert & Wegner, 2010; Experiments 1 & 2). Our goal was to replicate these findings for agency and to assess whether ratings of ownership, though perhaps relatively low for such artificial objects in the first place, would be affected by action-effect transformations in the same way as spatial binding. Finally, action-effect (in)compatibility is often found to affect performance as well (e.g., in terms of reaction times; e.g., Kunde, 2001; Kunde et al., 2012; Pfister & Kunde, 2013). Therefore, we also expected to find faster reactions when hand movements would produce spatially compatible rather than incompatible action effects.

7.2. Experiment 3

Experiment 3 targeted the influence of different action-effect transformations on spatial action-effect binding, reaction times, and explicit ratings of agency and ownership by employing a transformed mouse-cursor movement. In the most relevant conditions, participants were asked to move a cursor on a screen to a certain target position while hand and cursor movements were either spatially compatible or spatially incompatible to each other (cf. Figure 9). When cursor and hand were in the target position, participants were asked to judge the position of the cursor in one condition, and the position of the hand in another condition. Importantly, the positions of hand and cursor at the point of judgments were identical in both compatibility conditions. The only difference was whether these positions had been reached by a spatially compatible or spatially incompatible transformation of hand-to-cursor movement. We also added a baseline condition in which the cursor was always presented at the same position as the hand. This allowed us to control for possible general tendencies or biases in the spatial judgments. In a subset of trials, we further collected explicit measures of agency and ownership to compare them with the implicit measure of spatial action-effect binding.

Figure 9. The experimental setup used in both Experiment 3 and Experiment 4.

In addition to these judgments, we asked participants to begin each trial with an initial cursor movement to a left or right target box, depending on cursor color. This was meant to familiarize participants with the (in)compatibility of the movement transformation in the given trial and to reveal potential conflict between hand movement and cursor movement during action production, which should be reflected in overall increased response times with incompatible rather than compatible hand-cursor transformation (e.g., Kunde et al., 2012; Schwarz et al., 2018).

7.2.1. Material and methods

7.2.3.1. Ethics statement

The present experimental paradigm was approved by the ethics committee of the Institute for Psychology of the University of Würzburg under the reference number GZEK 2018-33. All procedures were in line with the Declaration of Helsinki.

7.2.1.2. Participants

39 participants were tested in Experiment 3 and received either course credit or €10 per hour. Participants were recruited through an online platform used by the University of Würzburg and gave informed consent prior to the experiment. Visual inspection of the data suggested that three participants had obviously misunderstood the task, because their spatial judgments were consistently much closer to the not-to-be-judged position (hand vs. cursor) than the position they were meant to judge. These participants were excluded from analyses so that the final sample contained 36 participants (27 female, nine male; all right-handed; M_{age} = 27.81 years, SD_{age} = 9.26 years, min_{age} = 19 years, max_{age} = 65 years).

The sample consisted of two subgroups, one of which had to judge the position of the cursor upon reaching the final position, whereas the other group had to judge the position of the hand, or, more precisely, the stylus in their hand. Assuming an effect size of d_z = .77 as observed for the smaller effect on cursor judgment in Kirsch et al. (2016), a power analysis suggested a sample size of 16 participants for a power of .8. To keep order of conditions and stimulus-response mappings counterbalanced between all participants, we thus decided to test 18 participants per judgment condition.

7.2.1.3. Apparatus and stimuli

Figure 9 shows a photograph of the experimental apparatus. The setup consisted of a graphics tablet (Intuous 4 XL, Wacom, Kazo, Saitama, Japan), which was horizontally fixated on a table and placed under an additional board to prevent vision of the tablet, a digitizing stylus to operate the tablet, a 22'' LCD monitor to present stimuli and ratings, and a keyboard placed on top of the occluding board. The experimental procedures were programmed using E-Prime (Version 2.0, https://www.pstnet.com/). The tablet and the occluding board were placed at the edge of the table, while the monitor was placed in a central position behind the tablet and board (around 46.2 cm from the front edge of the table). Furthermore, two additional plastic bars were attached to the upper part of the tablet, forming a rail for the digitizing stylus to prevent participants from moving the stylus in the direction of the y-axis of the tablet. This rail was placed as close to the top of the tablet as possible to minimize the actual physical distance between the stylus on the tablet and the stimuli presented on the monitor. The height of the monitor was adjusted so that the bottom of the screen was approximately at the same level as the occluding board to ensure that visual features of the monitor (e.g., buttons or letters printed on its frame) could not serve as supporting landmarks for the spatial judgments, and the boundaries of the active surface of the tablet were set so that they resembled the left and right boundaries of the screen. One pixel of the monitor was approximately 0.47 x 0.47 mm^2 in size. Finally, the keyboard was placed on top of the occluding board. Participants were seated in front of the setup with their left arm laying on the occluding board, allowing them to use the keyboard, and their right arm placed on the tablet with the digitizing stylus in their hand. They could freely adjust the height of the chair and its proximity to the table to make sure that participants were sitting in a position from which they could properly perform all parts of the experiment. All participants used the right hand to move the stylus on the digitizing tablet.

7.2.1.4. Procedure and task

Each trial included the following steps for the participants. First, participants had to move the cursor (a little green dot, approximately 1.40 mm in diameter) on a gray horizontal line on the screen until the center of the screen was reached, as marked by another yellow dot, equal in size. Reaching the screen center made two target boxes appear approximately 86 mm to the left and right of the center position. After a predefined delay of either 1000 ms or 2000 ms (in 50% of all trials each and counterbalanced over all conditions), an auditory signal (50 ms, 2000 Hz) was played, and the cursor changed its color to either blue or orange, which indicated whether the cursor had to be moved into the left or right target box (color-response mapping was counterbalanced between participants). Participants were instructed to respond to the color change as fast as possible. When the correct target box was reached with the cursor, it turned gray to provide feedback to the participant of successful completion of this task. When participants moved the cursor to the wrong side or showed no reaction within 1500 ms after stimulus onset, an error message was shown, and the trial was repeated. In all conditions and also in all conditions including reaction-time tasks in Experiment 4, reaction times were measured as the time interval from stimulus onset until the stylus had been moved 1.7 mm either to the left or the right. After another delay of 1000 ms, both target boxes disappeared, and the participants' task was to move the cursor on the horizontal line until it turned red at one out of six predefined positions, and then maintain this position. These positions were spread out on the entire horizontal line and could be more lateral than the target boxes that had to be reached for in the first reaction-time task. Thus, the final movement of the hand towards the estimation position could be both a movement towards the center of the tablet or further towards its sides. By doing so, there was an equal number of hand movements towards the cursor or away from it in both the additive and inverted mapping. After pressing a button on the stylus, both the cursor and the horizontal line disappeared, and after a delay of 1000 ms, a red vertical line (about 17 mm long) appeared at the top of the screen about 110 mm above the previous height of the horizontal line and with a displacement from the to-be-judged position (cursor vs. hand) of 17 mm to the left or right varying randomly. The final task of the participants was to adjust the vertical line by pressing the left and right arrow keys with their left hand so that the line would “point” down on either the position where the cursor had just disappeared or the position where they perceived the tip of the stylus in their hand to be. Whether the stylus position or the cursor position had to be judged was manipulated between participants so that half of the participants always judged the cursor position and the other half always judged the stylus position. Importantly, during the whole process of the spatial judgment, participants had to maintain the stylus and cursor at the same position, or an error message was shown and the trial was repeated. Additionally, every 12 trials, participants had to state on a 9-point Likert scale (without anchor or label values; Likert, 1932) how much they had the impression to control the cursor (agency rating) and how much they had the impression that the cursor was part of their body (ownership rating).

The experiment consisted of three types of blocks, which alternated the mapping with which the stylus movements were translated into cursor movements on the screen. The order of blocks was counterbalanced across participants. In blocks with direct mapping, the horizontal cursor position always exactly reflected the position of the stylus (i.e., their x coordinates were equal). In blocks with inverted mapping, the horizontal cursor always reflected a centrally mirrored position of the stylus in the plane. Thus, a movement of the stylus to the left or right from the center of the tablet always resulted in a movement of the cursor to the same extent in the opposite direction from the central position (see Figure 10). Finally, in blocks with additive mapping, the cursor always moved in the same direction as the stylus, like in the direct mapping, but there was always a certain, constant offset either to the left or to the right between the cursor and the stylus in every trial. There were six different kinds of offset, which were chosen in such a way that the final distance between stylus and cursor when reaching the position for the spatial judgment was always identical to the difference in the inverted mapping when the cursor had to be brought to the same position (see Figure 10).

Each block consisted of 48 trials, with every combination of all manipulated factors (judgment position: six levels; required response left/right in reaction-time task: two levels; ISI: two levels; offset of vertical line for judgment left/right: two levels) presented once. Order of blocks was counterbalanced across participants, and before every block, there were 12 practice trials so that participants could get used to the stylus-cursor mappings. Overall, participants thus completed 180 trials plus possible repetition trials due to mistakes. Per participant, the experimental session took approximately 60-75 minutes.

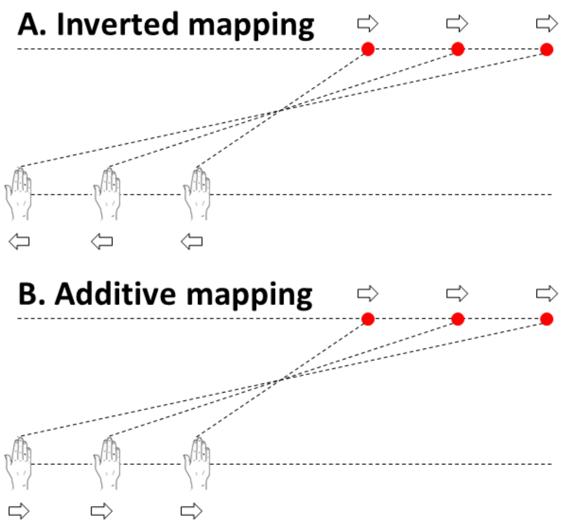

Figure 10. Action-effect mappings and final positions of hand and cursor during judgments in the two main conditions of Experiments 3 & 4. Hand movements were either transformed to yield inverted cursor movements (A) or they were displayed with an additive horizontal offset (B). Arrows indicate the direction of the movement of hand and cursor. In the inverted condition, the cursor always moved in the opposite direction than the hand while it moved in the same direction in the additive condition. The offsets between hand and cursor in the additive condition were chosen in a way that the end point of hand and cursor always resembled those in the inverted condition. Thus, there were three different offset sizes either to the left or to the right in the additive mapping so that the end positions of both hand and cursor would always exactly reflect those in the inverted mapping, where the cursor behaved mirror-symmetrically to the hand. Experiment 3 further included a baseline condition with direct mapping of hand and cursor position, whereas Experiment 4 introduced two additional control conditions in which the participants did not control the cursor.

7.2.1.5. Data preprocessing

We excluded all practice trials and all trials with any kind of errors that were replaced by repetitions of that exact same trial. For every judgment of cursor or stylus position, we computed the estimation error by calculating the difference between the estimated position and the actual position. Thus, negative values for estimation errors represent a judgment that is more to the left than the actual position, and positive values for estimation errors represent a judgment that is more to the right than the actual position.

7.2.2. Results

All raw data and analysis scripts of Experiments 3 & 4 are available on the Open Science Framework (osf.io/tgd95/).

7.2.2.1. Spatial binding

Median estimation errors were analyzed separately for cursor and stylus judgments. We calculated separate 3 x 6 repeated-measures (RM) analyses of variance (ANOVAs), with the factors mapping (additive, inverted, direct) and final stylus or cursor position during judgment (six levels) for both kinds of judgments, respectively. In cases of violation of the sphericity assumption, Greenhouse-Geisser-corrected *p* values and the correction factor ε are reported (Greenhouse & Geisser, 1959), accompanied by uncorrected degrees of freedom.

Figure 11 shows means of median estimation errors for stylus judgments. There was no significant main effect of mapping ($F(2, 34) = 1.17$, $p = .31$, $\varepsilon = .76$, $\eta_p^2 = .06$, $BF_{01} = 11.17$); however, both the main effect of stylus position ($F(5, 85) = 18.48$, $p < .001$, $\varepsilon = .25$, $\eta_p^2 = .52$, $BF_{10} = 2.77 \times 10^{18}$) and the interaction between the two factors ($F(10, 170) = 23.74$, $p < .001$, $\varepsilon = .37$, $\eta_p^2 = .58$, $BF_{10} = 2.06 \times 10^{12}$) were significant. To unravel this interaction, we first assessed possible general biases towards the left or the right or for certain stylus positions by testing the median estimation errors for the direct mapping against zero, which revealed no judgment errors different from zero for any hand position (all *p*s > .67, two-tailed). To analyze the differences between the additive and inverted mapping, we computed separate linear regressions for every participant for each of the two mappings, with the difference in horizontal direction between stylus and cursor during judgment as predictor and estimation error as criterion. We then compared the slopes for the regressions for both mappings (Lorch & Myers, 1990), which revealed a significantly more negative slope for the additive than for the inverted condition ($M_{\beta\ additive} = -.68$, $SD = .29$; $M_{\beta\ inverted} = -.45$, $SD = .42$; $t(17) = 3.29$, $p = .002$, one-tailed, $d_z = .77$, $BF_{10} = 21.26$). This suggests that the attraction of the judged stylus position towards the cursor is stronger in the additive than in the inverted condition, both when the hand with the stylus is to the left of the cursor (negative difference between stylus and cursor, positive values for estimation error) and when it is to the right of the cursor (positive difference between stylus and cursor, negative values for estimation error). Please note that while the second, six-level factor in the analysis was the actual stylus position on the tablet during judgments, in Figure 11 the distance between the stylus (or the hand holding it) and the cursor are plotted on the x-axis to represent the relationship between hand-cursor distance and estimation error. Therefore, the direct condition is only represented by a single dot in Figure 11, as the distance between cursor and stylus/hand was always zero in this condition.

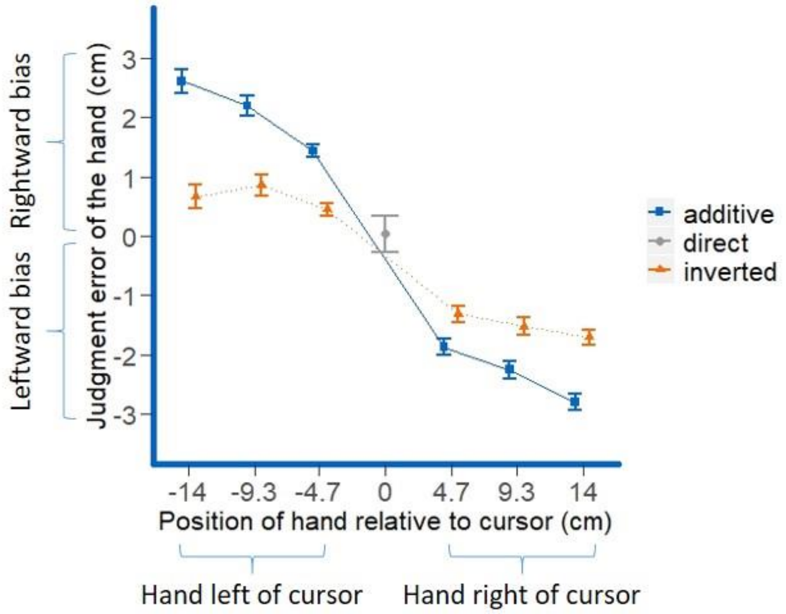

Figure 11. Mean estimation errors for all three mappings and all final stylus and hand positions in Experiment 3. Note that in the direct condition, the cursor was always right above the hand, and so the difference between the hand and cursor coordinate was always zero. Negative values for the relative cursor position indicate that the final cursor position is to the right of the hand and positive values for the relative cursor position indicate that the final cursor position is to the left of the hand. Positive values for the judgment error indicate judgment errors of the hand to the right and negative values for the judgment error indicate judgment errors of the hand to the left. Error bars for the additive and inverted conditions represent 95% confidence intervals of paired differences between the two conditions (Pfister & Janczyk, 2013) and for the direct condition they represent the standard error of the mean. Please note that the actual relative cursor/hand positions were equidistant with an increase of 4.658 cm between cursor and hand for each position further away from the center of the tablet. Due to rounding, this equidistance is not reflected exactly in the figure.

The same 3 x 6 RM ANOVA for cursor judgments (now the second six-level factor representing the final cursor position) did not reveal any significant effects (all *p*s > .065).

Additionally, we also performed exploratory analyses for nonlinear (i.e., quadratic and cubic) regression components. However, neither the quadratic nor the cubic regression coefficients significantly improved the fit for any of the two relevant conditions, though there were reasonable descriptive cubic influences in both conditions (both βs > .30, both ps < .18). However, these coefficients also did not differ between conditions.

7.2.2.2. Agency/ownership ratings

Mean agency and ownership ratings were entered into a 3 x 2 split-plot ANOVA, with the within-subjects factor mapping (additive, direct, inverted) and the between-subjects factor judgment type (cursor vs. stylus). We found a significant main effect of mapping for agency ratings ($F(2, 68) = 4.66$, $p = .016$, $\varepsilon = .89$, $\eta_p^2 = .12$, $BF_{10} = 3.50$). Experienced agency was higher for the direct ($M = 6.79$, $SD = 1.93$) than for the inverted ($M = 6.08$, $SD = 1.89$; $t(35) = 3.09$, $p = .002$, one-tailed, $d_z = .51$, $BF_{10} = 18.90$), and the additive mapping ($M = 6.40$, $SD = 1.78$; $t(35) = 1.99$, $p = .027$, one-tailed, $d_z = .33$, $BF_{10} = 2.01$) while there was no difference between the latter two ($t(35) = 1.22$, $p = .11$, one-tailed, $d_z = .20$, $BF_{01} = 1.60$). The main effect of mapping for experienced ownership did not reach significance ($F(2, 68) = 1.37$, $p = .26$, $\varepsilon = .91$, $\eta_p^2 = .04$, $BF_{01} = 3.89$), and neither did all other effects for both kinds of ratings (all Fs < 1; see Table 2).

Table 2. Means (and standard deviations) of ratings in Experiment 3 for all mappings.

		Mapping		
		Direct	Additive	Inverted
Rating type	Sense of agency	6.79 (1.93)	6.40 (1.78)	6.08 (1.89)
	Sense of ownership	3.91 (1.95)	3.71 (2.18)	3.55 (2.10)

7.2.2.3. Reaction times

Mean reaction times (RTs) were entered into a 3 x 2 x 2 split-plot ANOVA, with the within-subjects factors mapping (additive, direct, inverted) and required response (left or right), and the between-subjects factor judgment type (cursor or stylus).

We found a significant main effect of mapping ($F(2, 68) = 15.16$, $p < .001$, $\varepsilon = .86$, $\eta_p^2 = .31$, $BF_{10} = 7.47 \times 10^5$) which was modulated by a significant interaction between mapping and judgment type, ($F(2, 68) = 5.10$, $p = .012$, $\eta_p^2 = .13$, $BF_{10} = 29.92$) so we analyzed the RTs of the different mappings separately for the two judgment conditions. For the cursor judgment condition, RTs were slower for the inverted (M = 739 ms, SD = 127 ms) than for the direct (M = 657 ms, SD = 120 ms; $t(17) = 5.41$, $p < .001$, one-tailed, $d_z = 1.28$, $BF_{10} = 1.11 \times 10^3$) and additive mapping ($M$ = 658 ms, SD = 110 ms; $t(17) = 4.34$, $p < .001$, one-tailed, $d_z = 1.02$, BF_{10} = 150.84) while there was no difference between the latter two ($|t| < 1$). For the stylus judgment condition, there were no significant differences in RTs for the three mappings (all ps > .068, one-tailed; see Table 3). None of the remaining effects was significant (all ps > .25).

Table 3. Means (and standard deviations) of reaction times in Experiment 3 for all combinations of mapping and judgment type.

		Mapping		
		Direct	Additive	Inverted
Judgment condition	Cursor	657 ms (120 ms)	658 ms (110 ms)	739 ms (127 ms)
	Stylus	701 ms (147 ms)	690 ms (164 ms)	717 ms (163 ms)

7.2.3. Discussion

In Experiment 3, we investigated how different kinds of action-effect transformations affect reaction times in a forced-choice task, explicit ratings of agency and ownership, and, most importantly, spatial binding between the participant's hand used to control an object and the object itself. We observed that proprioceptive drift of the felt hand position towards the cursor was larger in the additive condition where hand movements and object movements were spatially compatible than in the inverted condition where they were incompatible. Thus, there is a stronger integration of body and controlled object in the case where body and controlled object move into the same direction as when they move into different directions. Importantly, these observations can be explained neither by different distances between hand and cursor nor by different levels of covariation or contingency between hand and cursor movement, which were both identical in the additive and inverted condition. Moreover, they cannot be explained by differences in the final movement direction towards or away from the cursor just before the spatial judgments had to be made.

Interestingly, the pattern of results for the explicit agency and ownership ratings did not mirror the results of the spatial judgments, since agency ratings did not differ between the additive and inverted conditions, and both of these ratings were lower than the ones for the direct condition. Additionally, there were no differences at all between the ownership ratings for different conditions. These results add to previous studies which showed diverging patterns of results for explicit and implicit measures of agency (such as temporal binding; Buehner, 2012; Kirsch et al., 2019; Majchrowicz & Wierzchoń, 2018; Moore et al., 2009; Schwarz et al., 2019; Suzuki et al., 2019) and extend these findings to the spatial domain and measures of ownership as well.

It should be noted that despite the strong binding effect that we found for stylus judgments, we found no drift of the cursor judgments towards the hand. Previous studies suggested that the visual drift is often substantially smaller than the proprioceptive drift and that it might also be more restricted regarding the conditions under which it occurs (Debats et al., 2017b; Debats & Heuer, 2018a, b; Kirsch et al., 2016; Rand & Heuer, 2013). One possibility for why we did not find significant effects of visual drift towards the cursor in Experiment 3 could be that the final cursor position was very salient because participants carefully had to search for this position and the judgment task was thus rather easy. Another possible reason is that the visual drift was too weak to be detected under the present conditions.

Finally, we found the expected impeding influence of the inverted action-effect transformation on reaction times in the condition where the cursor position had to be judged, but only a trend in the expected direction in the stylus judgment condition. Conceivably, the blocked manipulation of the judgment type led participants to devote less attention to the cursor in stylus judgment blocks. Moreover, they might have recoded the imperative stimuli in the response-time task in terms of required hand movements rather than of required cursor movements. The less attention is devoted to cursor movements, the less likely is inversion of hand and cursor movement to affect action generation (see Ansorge, 2002, for similar observations). Note, though, that we obtained a compatibility influence on RTs in stylus judgment conditions of Experiment 4, allowing for the possibility that the lack of the compatibility effect might be a Type II error (see below).

7.3. Experiment 4

Experiment 3 revealed reduced spatial binding for spatially incompatible as compared with spatially compatible action-effect transformations. This result, however, leaves open whether and to what extent an integration of cursor and hand occurred in the incompatible condition. Kirsch et al. (2016), for instance, observed that in the absence of control over an object there can still be a tendency towards this object when estimating the hand position. Such an effect can have several origins, which, however, are not related to perceptual action-effect binding. For example, it could be that because of the generally larger uncertainty related to proprioceptive than to visual feedback, the cursor might have served as an anchor for the judgment of the stylus position. Consider, for example, a situation in which you walk into your dark living room at night, and you are to locate pieces of furniture with the only available visual information being a light from your TV, in one corner of the room. Even though unrelated to the furniture you wish to locate, it is likely that you will use this light as an orientation point for your estimation, which might also lead you to estimate the piece of furniture as being closer to that light than it actually is. Thus, to assess the extent of integration in the incompatible condition, it would be important to contrast it with a condition without any control over the object to be able to distinguish between such fully perceptual biases in spatial judgments and biases due to the action-effect transformation. This was done in Experiment 4.

There were two main differences between Experiment 3 and Experiment 4. First, we decided to drop the condition where participants had to judge the cursor. So all participants of Experiment 4 had to judge the final stylus position. Second, and more importantly, we added two additional baseline conditions in which participants did not control a visual object, because it was stationary and thus not affected by stylus movements at all.

7.3.1. Materials and methods

For brevity, we will only focus on the differences to Experiment 1 here.

7.3.1.1. Participants

18 new participants (eleven female, seven male; all right-handed; M_{age} = 26.72, SD_{age} = 6.61, min_{age} = 20, max_{age} = 51) were tested in Experiment 4 and received either course credit or €10 per hour for their participation. All participants were recruited through the same online platform as in Experiment 3 and again had to give their informed consent before participating.

7.3.1.2. Apparatus and stimuli

All hardware, software, and additional equipment were the same as in Experiment 3.

7.3.1.3. Procedure and task

As stated above, no cursor judgments had to be made in this experiment, but all participants judged the stylus position. Experiment 4 was split into two parts, the order of which was counterbalanced between participants. The first part was essentially the same as in Experiment 3, except that all three blocks were shortened to 24 trials. Furthermore, the practice blocks before each of the blocks were also shortened to six trials.

The second part of Experiment 4 introduced two baseline conditions to the paradigm. Therefore, the reaction-time task was dropped in this block, and only the gray horizontal line and a red dot were presented at one of the six judgment positions in every trial. Importantly, however, this dot was stationary and under no control of the participant. The participants' task was then to slowly move the stylus on the digitizer tablet (without visual feedback on the screen) until a short beep (50 ms, 2000 Hz) indicated that the final position was reached, which had to be maintained. Subsequently, participants judged the position of the stylus as in Experiment 3. There were two blocks within this part of the experiment, which we will shortly describe in the following. In the direct baseline condition, the stylus always had to be moved so that its position on the x-axis of the tablet would correspond to the horizontal position of the dot on the screen, like in the direct mapping condition. In the additive-inverted (AI) baseline condition, the stylus had to be moved to the same position where the stylus would be needed to be moved in the original additive and inverted mapping conditions. In both blocks, the participants were not informed about the target position of the stylus before they had reached it. Thus, despite the elimination of control over the dot in the baseline conditions and it essentially being unrelated to the participants' task, the spatial relations between cursor and stylus were identical to the inverted and additive conditions. Each baseline block consisted of 24 trials, while there were no practice trials for the baseline blocks. Overall, participants thus completed 138 trials, including practice trials, which took approximately 60-75 minutes.

7.3.2. Results

7.3.2.1. Spatial judgments

Median estimation errors were analyzed using a 5 x 6 RM ANOVA, with the factors mapping (direct vs. inverted vs. additive vs. AI baseline vs. direct baseline) and stylus position during judgment. There was no significant main effect of mapping (F < 1); however, there was a significant main effect of stylus position ($F(5, 85) = 22.70$, $p < .001$, $\varepsilon = .28$, $\eta_p^2 = .57$, $BF_{10} = 2.18 \times 10^{20}$) and most importantly also a significant interaction between the two factors ($F(20, 340) = 13.06$, $p < .001$, $\eta_p^2 = .43$, $BF_{10} = 1.76 \times 10^{17}$). To unravel this interaction, we first assessed possible general biases towards the left or the right or for certain stylus positions by testing the median estimation errors for the direct mapping and the direct baseline condition against zero, which revealed no judgment errors different from zero for one of the mappings at any hand position (all ps > .30, two-tailed). To analyze the differences between the remaining conditions, we computed separate linear regressions for every participant for the additive, inverted and AI baseline condition, with the horizontal difference between stylus and cursor during judgment as predictor and estimation error as criterion. We then compared the slopes for the regressions for the three mappings which revealed a significantly more negative slope for the additive condition ($M_{\beta\ additive} = -.70$, $SD = .27$) than for the inverted ($M_{\beta\ inverted} = -.32$, $SD = .42$; $t(17) = 5.57$, $p < .001$, one-tailed, $d_z = 1.31$, $BF_{10} = 1.49 \times 10^3$) and the AI baseline condition ($M_{\beta\ AI\ baseline}$ = −.35, *SD* = .39; $t(17) = 5.14$, $p < .001$, one-tailed, $d_z = 1.21$, BF_{10} = 676.27), while there was no difference between the latter two ($|t| < 1$; see Figure 12). As in Figure 11, please note that the second, six-level factor in the analysis was the stylus position on the tablet during judgments, while the x-axis of Figure 12 shows the distance between the stylus (or the hand holding it) and the cursor to represent the relationship between hand-cursor distance and estimation error. Therefore, the direct condition and the direct baseline conditions are also only represented by single dots in Figure 12; the horizontal distance between cursor and stylus/hand was always zero in these conditions.

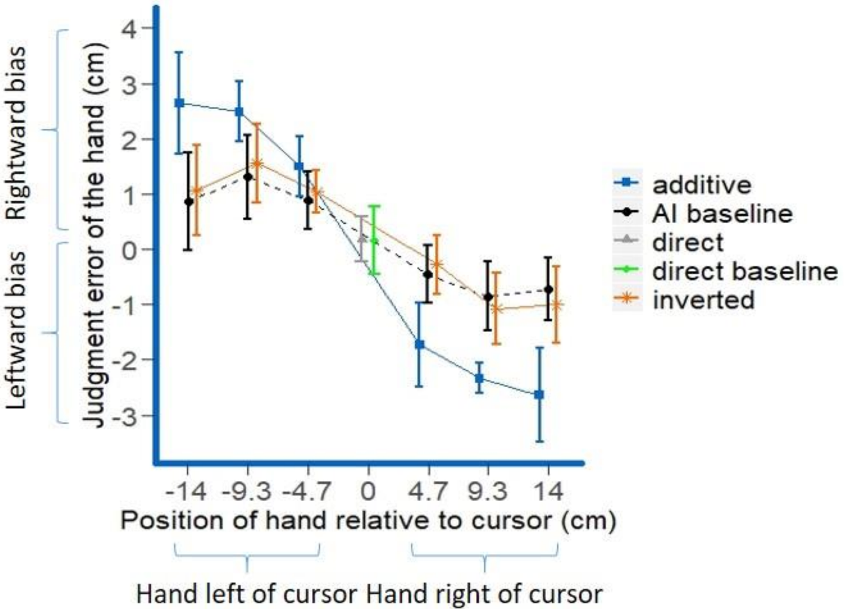

Figure 12. Mean estimation errors for all five mappings and all final stylus and hand positions in Experiment 4. In the direct condition and the direct baseline condition, the cursor was always right above the hand, and so the difference between the hand and cursor coordinate was always zero. Negative values for the relative cursor position indicate that the final cursor position is to the right of the hand and positive values for the relative cursor position indicate that the final cursor position is to the left of the hand. Positive values for the judgment error indicate judgment errors of the hand to the right, and negative values for the judgment error indicate judgment errors of the hand to the left. Error bars for the additive, inverted, and AI baseline conditions represent within-subjects confidence intervals calculated separately for each final stylus and hand position (Loftus & Masson, 1994), error bars for the direct condition and the direct baseline conditions represent standard errors of the mean. Again, actual relative cursor/hand positions were equidistant with an increase of 4.658 cm between cursor and hand for each position further away from the center of the tablet.

Again, we also tested for possible nonlinear influences and found that adding a cubic component led to significantly better predictions of the criterion in the additive condition (β = .40, $\Delta R^2 = .022$, $p = .044$), but not in the other two conditions (both *p*s > .24). However, again, none of the nonlinear parameters significantly differed from each other when comparing single regression coefficients between conditions (all *p*s > .17).

7.3.2.2. Ratings

Ratings were analyzed by pairwise t tests comparing agency and ownership ratings separately for the three mappings direct, inverted, and additive. Since there was no cursor in the baseline conditions, but just a stationary dot, we thus also did not assess any agency and ownership measures in the baseline condition. Experienced agency was lower for the inverted (M = 6.39, SD = 2.34) than for the direct (M = 7.15, SD = 2.17; $t(17) = 2.65$, $p = .008$, one-tailed, $d_z = .62$, $BF_{10} = 6.80$) and the additive mapping (M = 7.19, SD = 1.96; $t(17) = 1.99$, $p = .009$, one-tailed, $d_z = .62$, $BF_{10} = 6.58$) while there was no difference between the latter two ($|t| < 1$). The same pattern of results was observed for experienced ownership ($M_{direct} = 4.42$, SD = 2.73, $M_{inverted} = 3.29$, SD = 2.15, $M_{additive} = 4.24$, SD = 2.64); direct versus inverted: $t(17) = 2.65$, $p = .018$, one-tailed, $d_z = .54$, $BF_{10} = 3.62$; additive versus inverted: $t(17) = 1.93$, $p = .035$, one-tailed, $d_z = .45$, $BF_{10} = 2.13$; direct vs. additive: $|t| < 1$ (Table 4).

Table 4. Means (and standard deviations) of ratings in Experiment 4 for all mappings.

		Mapping		
		Direct	Additive	Inverted
Rating type	Sense of agency	7.15 (2.17)	7.19 (1.96)	6.39 (2.34)
	Sense of ownership	4.42 (2.73)	4.24 (2.64)	3.29 (2.15)

7.3.2.3. Reaction times

Reaction times were analyzed by means of a 3 x 2 RM ANOVA with the factors mapping (direct, inverted, additive) and required response (left or right). Since there was no reaction times task in the baseline blocks, these were also not included in the analysis. We found a significant main effect of mapping ($F(2, 34) = 10.26$, $p = .001$, $\varepsilon = .82$, $\eta_p^2 = .38$, $BF_{10} = 3.49 \times 10^3$). RTs were slower for the inverted (M = 708 ms, SD = 93 ms) than for the direct (M = 632 ms, SD = 76ms; $t(17) = 3.88$, $p < .001$, one-tailed, $d_z = .92$, $BF_{10} = 64.21$) and additive mapping (M = 638 ms, SD = 81 ms; $p = .002$, one-tailed, $d_z = .77$, $BF_{10} = 20.03$) while there was no difference between the latter two (|*t*| < 1). Neither the main effect of required response nor the interaction between the two factors reached significance (both *p*s > .055; Table 5).

Table 5. Means (and standard deviations) of reaction times in Experiment 4 for all mappings.

	Mapping	
Direct	Additive	Inverted
632 ms (76 ms)	638 ms (81 ms)	708 ms (93 ms)

7.3.3. Discussion

Experiment 4 replicated the findings of Experiment 3 regarding the difference in proprioceptive drift towards the cursor between the additive and the inverted condition. Crucially, we found no difference in proprioceptive drift between the inverted condition and a baseline condition with identical physical distances between hand and cursor. This outcome suggests that there was indeed no binding for the spatially incompatible action-effect transformations and that the remaining proprioceptive drift reflects action-unrelated mechanisms, and is possibly due to the previously mentioned anchor effect. Another explanation for the differences in proprioceptive drift between conditions could be that people are used to integrate representations of their hand and a mouse cursor on a computer screen due to pre-experimental experience with correlated hand and cursor movements. Construed that way, there might be a "default" coupling of hand and cursor based on long-term experience, while the additional short-term experiences from the correlations of hand and cursor movements made in the experiment are modulating this general integration tendency (for similar arguments, cf. Debats & Heuer, 2018a; Dogge et al., 2019: Wirth et al., 2018). If the long-term and short-term experiences overlap like in the additive condition, this would then lead to a stronger integration, while contradicting long-term and short-term experiences in the inverted condition should lead to a decrease in this default coupling.

Interestingly, we observed a different pattern for the explicit ratings in Experiment 4 than we observed in Experiment 3. While in Experiment 3 explicit ratings of ownership for the cursor were essentially unaffected by the different mappings and explicit agency ratings were higher in the direct condition than in both other conditions, in Experiment 4 the inverted condition yielded significantly lower ratings for both agency and ownership. This inconsistency might be due to different reliabilities of the estimations of mean values for the ratings in different conditions because the number of trials in which ratings had to be given was reduced from four to two per condition in Experiment 4 (in both experiments, ratings had to be given every 12 trials).

Furthermore, we found significant reaction-time effects in Experiment 4, which had not been significant in the stylus judgment condition in Experiment 3. Given the generally strong influence that spatially incompatible action-effect transformations usually have on action generation with the type of continuous movements we used here (e.g., Kunde et al., 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011), we believe these results of Experiment 3 might have reflected a statistical Type II error.

7.4. General discussion

The present study investigated how the integration of a non-corporeal object in terms of spatial binding is shaped by the way that the individual’s movements are transformed into movements of the object. There has been an increasing interest in this field of research in the past years, and multiple studies could show that objects, which are under full control of an individual, tend to lead to a mutual attraction of the perceived location of the object and the effective hand of the individual (Debats et al., 2017a; Debats & Heuer, 2018a; Kirsch et al., 2016; Rand & Heuer, 2013). These biases are reduced when the magnitude of control and thus cross-correlation of sensory signals decreases. For example, Debats et al. (2017a) observed less binding for curved cursor movements than for straight cursor movements when hand movements were straight. The results from the present study extend this research for several reasons. First, they demonstrate that spatial action-effect binding can be completely eliminated in situations of full and immediate control over an object when the movement direction of the object is reversed to the movement direction of the effector. Thus, controllability of an object is a necessary, but not a sufficient condition for such binding. The interesting question, however, is why an inverted movement transformation should eliminate integration of a distal controlled object and the effector controlling that object, or speaking in sensory terms, lead to less attraction of visual and proprioceptive signals.

Second, we held all other kinematic characteristics of the cursor and hand movements equal between the additive and inverted condition, except the movement direction itself: actual physical distance at judgment positions and thus “usability” of the cursor position for hand position judgments, equal gain of hand and cursor movement, controllability of cursor, and whether the hand was moving towards or away from the cursor before the spatial judgments did not differ between the two conditions. Previous studies that observed reduced mutual attraction of spatial hand and cursor judgments with increasing mismatch between hand and object movements did not control for all of these confounds (e.g., Debats et al., 2017a; Rand & Rentsch, 2016). It might be possible, though, that differences in binding resulted from different exposure times to the hand and cursor movements in the different conditions. We cannot ultimately rule out this possibility, as we did not record the time it took to complete trials. Informal observation of participants’ behavior during testing provided at least no obvious cue for differences in this respect.

Third, Debats et al. (2017a) speculated that decreases in spatial binding with discrepancies in visual and proprioceptive feedback could be related to the experience of agency. We were able to test this assumption, at least on a correlational basis, in the present study and found inconsistent results regarding the explicit ratings of agency and ownership. Thus, it has to remain unclear whether and/or to what extent the conscious experience of these conditions might have influenced the extent to which body-related and body-external signals were integrated in the present study.

Ideomotor models of human action control (e.g., Hommel, 2013; James, 1890/1981; Koch et al., 2004; Shin et al., 2010; Waszak et al., 2012) provide another view on our findings and possibly also on previous findings (e.g., Debats et al., 2017a; Rand & Rentsch, 2016) that found reduced multisensory integration, or reduced integration of a body effector and an external object. Ideomotor theory states that action-effect incompatibility leads to a conflict between the representation of the action's resident effect (the body movement) and its remote effect (the object movement). In order to carry out an action, representations of the effects of an action need to be activated, which then in turn activate the appropriate motor commands. Since both, representations of body movements and of visual effects of these movements, can be used to perform actions (Pfister, 2019), humans could strategically suppress some conflicting representations to reduce conflict (e.g., Heuer & Rapp, 2012; Wirth, Pfister, Brandes, & Kunde, 2016). This mechanism could thus be another possible explanation for the absence of action-effect binding in the inverted condition. In particular, the strong conflict between hand and cursor movement during movement might have prompted the participants to suppress the irrelevant cursor position when judging the stylus position. Support for this assumption also stems from our findings that reaction times were significantly slower in the inverted (incompatible) condition than in the additive (compatible) condition, which reflects this conflict during movement planning. Whether and to what extent this conflict is still present at later stages of the movement and during the spatial judgments is something we aim to address in future research. Nevertheless, we believe that the ability of our paradigm to show such conflict and how it possibly relates to the elimination of spatial binding through suppression of conflicting sensory signals is a valuable extension to the field.

While we focused our analyses on linear relationships, the figures and exploratory analyses suggested a contribution of nonlinear components. Linear relations are typically assumed as a kind of default in studies on spatial binding and multisensory integration (Debats & Heuer, 2018a, b, 2020; Kirsch et al., 2016; Rand & Heuer, 2013; Rand & Rentsch, 2016; Rand et al., 2013). Nonlinear relations suggest a kind of breakdown of integration with sufficiently large distances of hand and cursor. While the linear component captures the main variance and thus our underlying research question (with nonlinear aspects not consistently improving the fit significantly), it would certainly be interesting to study in more detail the shape of the drift curve under various conditions.

In past research, proprioceptive drift has generally been interpreted as a marker for an (implicit) sense of ownership over remote objects, thus the feeling how much a body-external object tends to be integrated into one's own body (Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2012). While originally observed and studied in the rubber hand illusion, proprioceptive drift has by now been reported to emerge with other non-corporeal objects as well (e.g., Armel & Ramachandran, 2003; Ma & Hommel, 2015). One could argue that the actual incorporation of an arbitrary object into the body seems unlikely and should not be compared with the proprioceptive drift observed with a rubber hand or virtual hand, which seems more "realistic" to be actually experienced as belonging to one's own body because it actually resembles the anatomy of the human hand (Guterstam et al., 2013; Kalckert et al., 2019a). However, given the increasing number of studies showing proprioceptive drift also for anatomically nonplausible objects, it seems tenable to assume that artificial, non-corporeal objects can at least lead to a shift of the body representation towards these objects since this is essentially what proprioceptive drift measures.

Whether or to what extent the subjective experience of agency and ownership for the cursor were also affected similarly by the different kinds of movement transformations is questionable, though. In fact, we found little evidence that ownership ratings were affected by the different kinds of movement transformations at all. It has to be noted, though, that overall explicit ownership ratings were very low, so it is questionable if or to what extent these reflect actual, conscious experiences of ownership of the cursor, regardless of possible differences or lack of differences between conditions (see also Kalckert et al., 2019a, for similar arguments).

However, and especially against this background, the inconsistencies between the implicit binding measure and the explicit ratings are an interesting finding that add up to an increasing number of studies showing that implicit measures of agency and ownership, such as temporal or spatial binding, might be related to explicit sense of agency and ownership to a lesser extent than previously thought (Buehner, 2012; Kirsch et al., 2019; Majchrowicz & Wierzchoń, 2018; Moore et al., 2009; Schwarz et al., 2019; Suzuki et al., 2019). While we cannot rule out possible methodological reasons for our inconsistent findings, disentangling the relationship between explicit agency and ownership experiences and different binding measures further could be an interesting question for future research.

7.5. Conclusions

Spatial action-object binding, an indication of implicit object ownership, can be obtained with actively controlled non-corporeal objects that show little, if any, similarity to the human body. However, immediate control over an object is not sufficient to induce implicit ownership. If the object moves into a direction that is in conflict to the movement of the controlling effector, then no spatial binding occurs, possibly due to suppression of conflicting visual representations.

8. Suppression of mutually incompatible proprioceptive and visual action effects in tool use[7]

Movements of a tool typically diverge from the movements of the hand manipulating that tool, such as when operating a pivotal lever where tool and hand move in opposite directions. Previous studies suggest that humans are often unaware of the position or movements of their effective body part (mostly the hand) in such situations. It has been suggested that this might be due to a "haptic neglect" of bodily sensations to decrease the interference of representations of body and tool movements. However, in principle this interference could also be decreased by neglecting sensations regarding the tool and focusing instead on body movements. While in most tool use situations the tool-related action effects are task-relevant and thus suppression of body-related rather than tool-related sensations is more beneficial for successful goal achievement, we manipulated this task-relevance in a controlled experiment. The results showed that visual, tool-related effect representations can be suppressed just as proprioceptive, body-related ones in situations where effect representations interfere, given that task-relevance of body-related effects is increased relative to tool-related ones.

[7] Copyright © 2020 by Marvin Liesner and Wilfried Kunde. The official citation that should be used in referencing this material is Liesner, M., & Kunde, W. (2020). Suppression of mutually incompatible proprioceptive and visual action effects in tool use. *Plos One*, *15*(11), e0242327. https://doi.org/10.1371/journal.pone.0242327. The following paragraphs may not exactly replicate the referenced article. No further reproduction or distribution is permitted without written permission from the authors.

8.1. Introduction

When we move our body, we typically do so for a reason. More precisely, we move to change what we perceive in a specific way. Sometimes such intended perceptual changes relate to the body itself. For example, when exercising or pantomiming, a person may just aim to move the body in a certain way, and observe her- or himself doing so. In most cases, though, humans aim to change the environment beyond their own body, such as when transporting an object from one place to another, or opening a door that was closed a moment before.

Body movements typically come with various perceptual changes for obvious reasons. All body-external changes are produced by some body movement, which inevitably goes along with some body-related perceptual changes as well. For example, when transporting an object from one place to another the actor not only perceives the movement of the object itself but he or she also sees and feels the movement of the corresponding effector bringing this object movement about. William James termed these inevitable perceptual changes “resident” effects of body movements (James, 1890/1981). Second, many of our body movements consistently produce changes in the environment, even when actors might not specifically aim to produce such body-external changes. For example, exercising in the sunlight naturally produces a corresponding movement of the shadow of the moving body, although the movement of the shadow was not the reason for moving. James called these body-external perceptual consequences “remote” movement effects (James, 1890/1981). It should be noted that other authors sometimes use different labels for these effects such as, for example, “body-related” vs. “body-external”, “proximal” vs. “distal” or “internal” vs. “external” with sometimes slightly different meanings and connotations. We chose here to stick with William James’ terminology because it reflects the crucial difference between the effects we studied here: namely, effects “residing” in or on the biological body and effects, which are “remote” and thus detached from the biological body.

Given the variety of perceptual changes that come with any given body movement, the question arises which of these changes should be mentally represented and attended to when it comes to generate and monitor such movements (representational weight; Pfister, 2019;

Prinz, 1998; Waszak et al., 2012). At first glance, there is no obvious reason to take into account and attend at all a certain resident effect when aiming at a certain remote effect, or conversely, to take into account and attend a certain remote effect when just aiming at a certain resident effect. Not attending, or “neglecting”, currently task-irrelevant movement effects, might be particularly important when remote and resident effects are mutually inconsistent to each other. For example, when you turn your computer mouse upside down and try to move the cursor from left to right, it is best to focus on this intended remote effect and to neglect that the hand has to move, and of course feels doing so, from right to left. Not “neglecting” the spatially inconsistent movement of the hand in such a situation can in fact create all kinds of performance costs (Janczyk, Skirde, Weigelt, & Kunde, 2009; Kunde, 2001; Kunde et al., 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013; Experiments 1-4).

There is evidence for “haptic neglect” (Heuer & Rapp, 2012) in case of such inconsistencies between resident and remote movement effects (Fourneret & Jeannerod, 1998; Knoblich & Kircher, 2004; Müsseler & Sutter, 2009; Sülzenbrück & Heuer, 2009). In one study (Müsseler & Sutter, 2009), participants had to trace a dot performing circle movements on a screen with a cursor by moving their hand which was occluded from vision on a plane tablet in front of the screen. Crucially, the participants’ hand movements were not transformed into identical movements of the cursor. Instead, to produce circular cursor movements elliptic hand movements with either horizontal or vertical deviations from the “standard” circle were required. After every trial, participants had to indicate whether they believed they had drawn horizontal or vertical ellipses. The results showed that even with large deviations (with x-y ratios between 1:1.29 and 1:1.86 depending on conditions), participants could not reliably judge the orientation of the ellipses anymore. Moreover, haptic neglect seems to actually facilitate performance when there are spatial inconsistencies between proprioceptive and visual movement consequences.

Another instance where this occurs is mirror drawing, where participants have to copy a drawing but can only see a mirror image of their hand. Here a felt movement of the hand to the right produces a visual image of the hand moving to the left. Interestingly both, participants with permanently removed body perception (i.e., deafferented patients; Lajoie et al., 1992) or transiently reduced body perception (because of rTMS over somatosensory cortex; Balslev et al., 2004), outperform neurotypical participants. Of course, it is unlikely that resident effects are ignored completely when performing a tool task given their high biological importance. For example, a person operating a tool should still notice when his or her hand is approaching a hot stove or bumping into another object. Indeed, it could be shown that despite focusing attention on the effective end of a tool, some attention still remains on the body part controlling the tool (Collins, Schicke, & Röder, 2008). Furthermore, the previously mentioned performance costs when resident and remote effects are inconsistent (Janczyk et al., 2009; Kunde, 2001; Kunde et al., 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013, Experiments 1-4) could not occur if people would always engage in "full" haptic neglect.

Nevertheless, there is accumulating evidence for haptic neglect when producing remote object movements that are spatially incompatible to movements of an operating body effector while the possibility of the opposite mechanism, an attenuation of conflicting remote object movements and conversely a focus of attention on the resident action effects has sparsely been considered so far. We are aware of two studies doing so. In one study (Janczyk, Pfister, & Kunde, 2012) participants were asked to move their occluded hand to the left or right, which then foreseeably produced a movement of a cursor on a screen in either the same or the opposite direction. The response time increase for generating hand movements, which produced opposite rather than same movements of the cursor were reduced, though not abolished when participants were asked to ignore rather than attend to the cursor movement. This finding suggests some instruction-based control over the degree of processing remote movement effects in the course of generating a movement prior to actual movement execution though it also shows that even when asked to ignore visual action effects, these must still be attended to some degree.

Another study suggests that increased task-relevance of resident effects (and decreased importance of the remote effects) prompts attenuation of processing visual information after movement execution (Experiments 3 & 4). In this study, participants had to estimate the position of their visually occluded hand after performing hand movements that were transformed into either spatially compatible or spatially incompatible cursor movements on a screen. The usual finding in such paradigms is that spatial judgments of body effector and external object are biased towards each other suggesting an integration of the two to a certain degree ("spatial binding", e.g., Kirsch et al., 2016). The results of this study showed an absence of this spatial binding effect when hand movements were transformed into spatially incompatible cursor movements, which accords with the idea that the representation of the visual, remote action component (the cursor) was given less weight in the incompatible conditions when participants were asked about their proprioceptive, resident effects.

To summarize, it has frequently been shown that incompatibility, for example in movement direction, of a controlled object and the effective body part controlling that object leads to performance deficits because of the conflicting associated effect codes (Kunde, 2001; Kunde et al., 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013; Experiments 1-4). The idea of neglecting or suppressing one of the two conflicting components to reduce these difficulties seems a plausible assumption. Previous research has mainly argued in favor of a haptic neglect of the resident effects in such situations and a coding of one's actions mainly through remote codes. Such haptic neglect renders position estimates of body effectors less accurate and biased towards the position of a controlled remote object (Fourneret & Jeannerod, 1998; Heuer & Rapp, 2012; Knoblich & Kircher, 2004; Müsseler & Sutter, 2009). Haptic neglect appears functional in most tool-use tasks because it relates to a component of movement feedback that is of limited task relevance and thus it might be the "default" state when dealing with a spatially discrepant tool. Thus, it seems plausible that when operating a tool to produce a certain remote effect, which also produces an incompatible resident effect, one might focus one's attention mainly on the remote effect to decrease the impact of conflicting sensory information and of divided attention. Recent research suggests though, that an increase of the relevance of resident action effects might lead to a reversal of this imbalance in perceptual precision (Experiments 3 & 4). This raises the question whether it is the nature of resident action effects per se or their reduced task-relevance that renders it subject to such neglect.

Both approaches suggest that when performing an action, which produces mutually incompatible resident and remote effects, one of these effects might be suppressed or attended to less and the other one might be enhanced or attended to more to reduce the conflict emerging from the anticipation and observation of these interfering action effects. Previous studies have suggested that resident effects are the ones that might be more prone to be suppressed in such situations (Fourneret & Jeannerod, 1998; Knoblich & Kircher, 2004; Müsseler & Sutter, 2009; Sülzenbrück & Heuer, 2009). Possible reasons for this are, for example, that such haptic neglect helps to maintain a feeling of control over the tool and flexibly adapt to new situations (Müsseler & Sutter, 2009) or that the saliency of the visual, remote effects might make a coding and attending of actions through remote effects more likely than through resident effects (Janczyk, Yamaguchi, Proctor, & Pfister, 2015). Furthermore, it has been shown that visual feedback plays an important role when learning visuomotor transformations, thus stressing the importance of remote effects when they are spatially discrepant to resident effects (Sülzenbrück, 2012). These findings might suggest a general bias towards perceiving remote effects relatively unaltered and neglecting resident effects whenever they are interfering. However, one factor which has never been investigated in a controlled fashion to our knowledge, though its importance has been noticed (e.g., Müsseler & Sutter, 2009), is the factor of task relevance of the remote effects in situations commonly studied. When operating a remote tool (e.g., when putting a nail in a wall with a hammer), the effects on that tool are obviously more relevant for achieving the task than the resident effects on the body so they should obviously also be in the focus of attention of the acting individual. Distinguishing these factors might seem artificial since tools are almost always used to achieve a certain distal effect, which is thus task-relevant. However, other examples (e.g., the shadow example from the beginning) show that the relevance of resident and remote effects can indeed vary in other real-world contexts. Additionally this differentiation would give interesting insights into motor planning processes.

With this study, we aimed to show that both, remote action effects and resident effects can be equally neglected to overcome potential interference between them. Specifically, we manipulated the compatibility between resident and remote effects and their task-relevance independently (for details see *8.2.1.4. Procedure and task*). We expected that the precision of sensory information decreases with decreasing task-relevance of the respective effect component. This decrease of perceptual accuracy would indicate the “neglect” of the respectively less relevant effect component, i.e. a shift of attention away from this component. This would be an economic way of processing only the more relevant perceptual information to a larger extent given the observed division of attention between resident and remote effects in past research (Collins et al., 2008; Janczyk et al., 2012; Song & Bédard, 2013). More importantly, we expected the decline of perceptual precision for the less relevant effect component to be more pronounced when resident and remote effects were incompatible because the contradiction of visual and proprioceptive effects should boost the necessity for this representational weighting mechanism. This would support the idea that neglect of one effect component, preferably the less relevant one, is involved in resolving interference between conflicting remote and resident effect components.

8.2. Experiment 5

8.2.1. Materials and methods

8.2.1.1. Ethics statement

The project was approved by the ethics committee of the Institute for Psychology of the University of Würzburg under the reference number GZEK 2018-33. All procedures were in line with the Declaration of Helsinki.

8.2.1.2. Participants

30 participants were tested and received €20 for their participation. The number of participants was limited by laboratory capacities. Participants were recruited through an online platform used by the University of Würzburg and gave informed consent prior to the experiment. Due

to the relatively long testing sessions (~ 120-135 minutes), four participants decided to cancel the testing before completion. Another two participants had to be excluded due to technical malfunctioning so that the final sample of participants consisted of 24 participants (all right-handed; 18 female, six male; M_{age} = 25.67, SD_{age} = 4.43, min_{age} = 20, max_{age} = 33). All participants had normal or corrected to normal sight and did not report any relevant medical conditions.

8.2.1.3. Apparatus and stimuli

The experimental set-up is depicted in Figure 13. The apparatus consisted of a graphics tablet (Intuous 4 XL, Wacom, Kazo, Saitama, Japan) which was horizontally fixated on a table and an iron construction around the tablet holding a semi-silvered mirror approximately 26.9 cm above the tablet and a 24" LCD screen facing down on the mirror approximately 48.4 cm above the tablet. Furthermore, the computer keyboard was placed left of the construction. The experimental procedures were programmed using E-Prime (version 2.0, https://www.pstnet.com/). Because the monitor was slightly larger than the graphics tablet, the projection area of the monitor was adjusted so that it resembled the measures of the tablet to ensure that the screen image was projected onto the mirror which gave the impression for participants that a screen of just the same size and dimensions as the tablet was mounted above the tablet. One pixel was approximately 0.25 x 0.25 mm^2 in size. Participants were seated in front of the construction and were instructed to lean their forehead against the upper part of the construction facing down at the mirror. Additional black cardboard prevented vision of the computer screen. Participants placed their right hand between the tablet and the mirror and were able to operate the tablet with a digitizing stylus. They were instructed to place their left hand left of the construction so that they were able to operate the keyboard with it. Because vision of the keyboard was hindered due to the set-up, all relevant keys for the experiment (arrow keys, space bar, return key) had little soft markers attached to them so that they could be easily identified without vision. To ensure that participants could not see their hand on the tablet through the mirror, all testing was carried out in a darkened room.

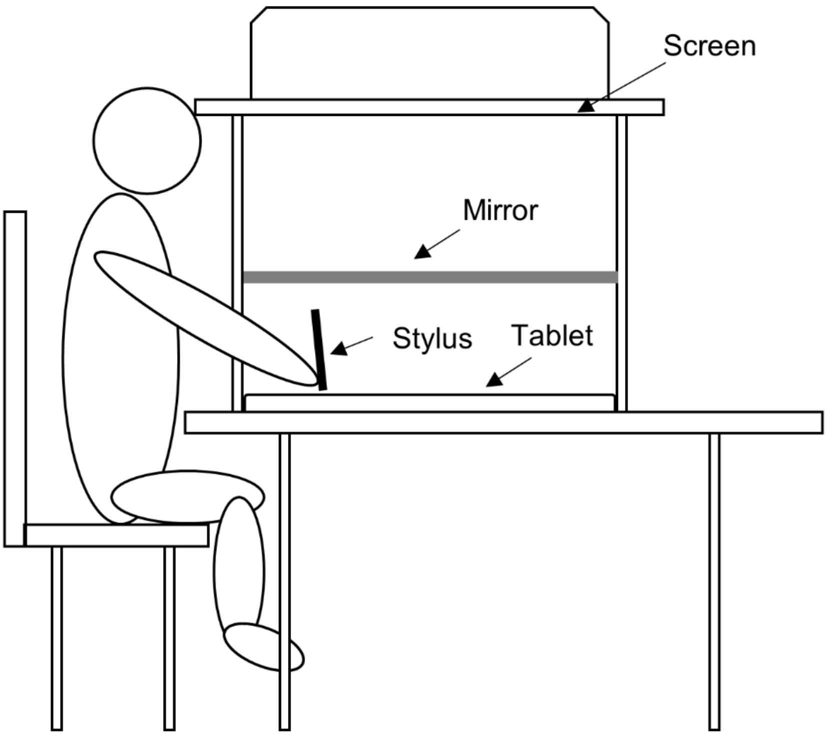

Figure 13. Experimental set-up as used in Experiment 5.

8.2.1.4. Procedure and task

Each trial included the following steps for the participants (also depicted in Figure 14). First, participants had to move a red cursor (a dot approximately 0.5 mm in diameter) controlled with the stylus to the center of the screen, which was marked by another green dot equal in size. After a short random delay (1000 ms or 2000 ms, counterbalanced across all conditions), a beep tone (50 ms, 2000 Hz) was played as a start signal and the green dot started moving in one out of four directions (up, right, down, left) chosen randomly in a straight line of a length chosen randomly within a range of 12.5-37.5 mm with a constant speed of 0.5 mm per frame. After this distance was covered by the dot, the experiment generated another random segment in one out of the four directions and within the same range. This procedure was repeated until a number of segments between 5 and 15 was reached. Again, also number of segments was determined on a random basis within this range in every trial. This procedure resulted in the green dot moving on the screen continuously taking several 90˚ or 180˚ turns for about 30 s per trial. Throughout the whole dot movement phase, the participants' task was to follow the green dot as accurately as possible with the cursor by moving the stylus on the tablet. If the distance (measured as Euclidean distance) between the green dot and the cursor exceeded 10 mm, an error message was shown and the trial was repeated. During the last segment of every trial, another short tone (50 ms, 500 Hz) indicated that the trial was about to end after this segment.

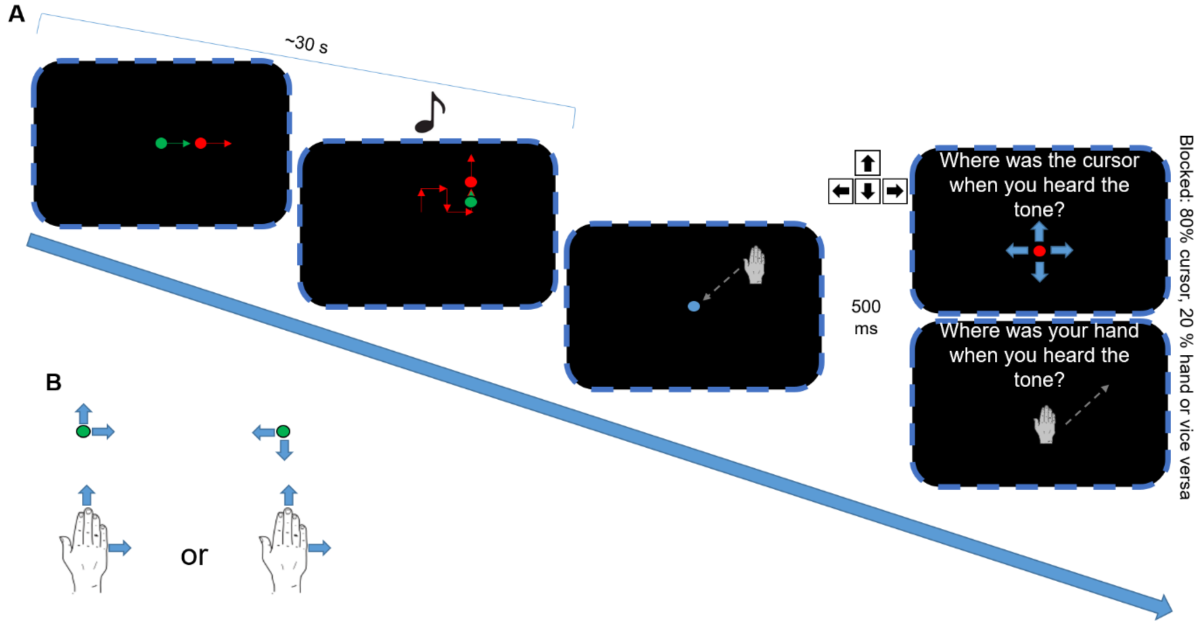

Figure 14. (A) Trial structure of Experiment 5. Please note that the depicted hand was not visible to the participants since it was placed beneath the projection area as shown in Figure 13. (B) Hand-cursor movement transformations in the compatible (left) and incompatible (right) conditions.

After the last segment had ended, both the green dot and the red cursor disappeared and participants had to move the stylus back to the center of the tablet as marked by a blue dot. After the center had been approached and an additional delay of 500 ms, the second, judgment phase of the trial started in which participants were asked to estimate either the position of the red cursor or the position of the stylus at the moment when the second tone occurred which had signaled the end of the trial. In cursor judgment trials, the red cursor appeared on the screen again and it had to be moved to the estimated position by the participants by using the arrow keys of the keyboard with their left hand and confirming their judgment with the return key. In stylus judgment trials, no cursor was shown but the participants were simply asked to move the stylus back to the estimated position and confirm their judgment by pressing a key on the stylus. After one of the two judgments had been made, the next trial started.

The experiment was split into four blocks, which differed in the way the participants' movements of the stylus were transformed into movements of the cursor and in the ratio of stylus judgment and cursor judgment trials (see Table 6). In *compatible* blocks, the cursor always moved in the same direction as the participant moved their hand, thus a movement of the hand to the left caused a cursor movement to the left, an upwards hand movement caused an upwards cursor movement etc. In *incompatible* blocks, the direction of cursor movements was always inverted both in the x and in the y direction compared to the hand movements. Thus, a hand movement to the left caused a cursor movement to the right, an upwards hand movement caused a downwards cursor movement etc.. Furthermore, the blocks differed in terms of the frequency of cursor and stylus judgments. In *mainly proprioceptive* blocks, 80% of the judgments that had to be made were stylus judgments and only 20% were cursor judgments whereas in *mainly visual* blocks this proportion was the other way round. Please note that the order of judgments in a given block was still randomized so that only the ratio, but not the sequence of certain judgments could be predicted. Additionally, there were no explicit instructions for the participants regarding the judgment ratios. The manipulations of compatibility and judgment ratio were combined leading to the blocks *compatible x mainly proprioceptive*, *compatible x mainly visual*, *incompatible x mainly proprioceptive* and *incompatible x mainly visual* (see Table 6). Participants always either completed both compatible or both incompatible blocks first before experiencing the second movement transformation and furthermore underwent short practice blocks (8 trials) before both the compatible and incompatible half of the experiment. In these practice blocks, the percentage of cursor judgments and hand judgments was 50% each. Whether participants first performed the compatible or incompatible blocks and order of judgment ratio blocks within the compatible and incompatible blocks was counterbalanced between participants.

Furthermore, we varied the time point of the occurrence of the tone signalizing the end of the trial. The tone could occur either when the cursor was still 2.25-2.5 mm away from the end of the last segment (we will refer to that from now on as *very late*), when it was 4.75-5 mm away from the end of the last segment (*late*), when it was 7.25-7.5 mm away from the end of the last segment (*early*) or when it was 9.75-10 mm away from the end of the last segment (*very early*). We varied this time point to prevent participants from developing strategies for their judgments, which they could possibly do if the continuation of the movement after the tone occurred had always been of the same length. In combination with the variable start delay of either 1000 ms or 2000 ms which was counterbalanced over all other conditions, participants thus performed 40 trials per block leading to a total number of 176 trials including practice blocks and plus potential additional trials to replace error trials. Within blocks, trials were randomized.

Table 6. Blocks used in Experiment 5 combining the manipulations of hand-cursor transformation and judgment proportion.

Hand-cursor transformation	Judgment proportion
Compatible	80% cursor, 20% hand
Compatible	20% cursor, 80% hand
Incompatible	80% cursor, 20% hand
Incompatible	20% cursor, 80% hand

Participants always underwent either both compatible or both incompatible trials before experiencing the second transformations. Order of transformations and order of blocks within transformations were counterbalanced.

8.2.1.5. Data preprocessing

We excluded all practice trials and trials in which participants deviated more than 10 mm at any time, measured as Euclidian distance, from the green dot they had to track with the cursor. For every trial, we calculated the absolute error of the judgments as the Euclidian distance between the actual position of the to-be-judged entity (i.e., the cursor or the stylus) at the moment of sound occurrence and its estimated position by the participant.

8.2.2 Results

All raw data and analysis scripts of Experiment 5 are available on the Open Science Framework (osf.io/kmbe3/).

Median absolute errors were entered into a 2 x 2 x 2 x 4 repeated measures analysis of variance (RM ANOVA) with the factors judgment modality (proprioceptive vs. visual), compatibility (compatible vs. incompatible), judgment frequency (high vs. low) and time point of tone (very late vs. late vs. early vs. very early). Furthermore, exploratory Bayes Factors were estimated for all reported main effects and interactions. As expected, absolute errors were larger for the incompatible than for the compatible movement transformation ($M_{incompatible}$ = 34.81 mm, $SD_{incompatible}$ = 23.25 mm; $M_{compatible}$ = 20.08 mm, $SD_{compatible}$ = 8.92 mm; $F(1, 23) = 18.80$, $p = .001$, $\eta_p^2 = .37$; $BF_{10} = 1.27 \times 10^{13}$) and for the less frequently judged modality than for the more frequently judged one (M_{low} = 31.69 mm, SD_{low} = 17.82 mm; M_{high} = 23.20 mm, SD_{high} = 11.85 mm; $F(1, 23) = 28.81$, $p < .001$, $\eta_p^2 = .56$; $BF_{10} = 2.93 \times 10^3$).

These effects were further modulated by the significant two-way interactions compatibility x judgment modality ($F(1, 23) = 8.93$, $p = .007$, $\eta_p^2 = .28$; $BF_{10} = 4.38 \times 10^{11}$) and compatibility x frequency ($F(1, 23) = 4.94$, $p = .036$, $\eta_p^2 = .18$; $BF_{10} = 0.91$) although for the latter one the Bayes factor suggested inconclusive evidence. Follow-up t-tests for the compatibility x judgment modality interaction indicated that the difference between absolute errors in the compatible and incompatible condition was only significant for proprioceptive but not for visual judgments ($M_{compatible\ x\ visual}$ = 22.16 mm, $SD_{compatible\ x\ visual}$ = 12.55 mm; $M_{incompatible\ x\ visual}$ = 24.11 mm, $SD_{incompatible\ x\ visual}$ = 10.82 mm; $|t|_{visual} < 1$; $M_{compatible\ x\ proprioceptive}$ = 17.92 mm, $SD_{compatible\ x\ proprioceptive}$ = 6.70 mm; $M_{incompatible\ x\ proprioceptive}$ = 45.52 mm, $SD_{incompatible\ x\ proprioceptive}$ = 42.55 mm; $t_{proprioceptive}(23) = 3.48$, $p = .002$, one-tailed, $d_z = .71$, adjusted for multiple testing). More importantly, the compatibility x frequency interaction indicated that the observed frequency effect was larger in the incompatible than in the compatible condition ($M_{high\ x\ compatible}$ = 17.59 mm, $SD_{high\ x\ compatible}$ = 8.10 mm; $M_{low\ x\ compatible}$ = 22.57 mm, $SD_{low\ x\ compatible}$ = 10.42 mm; $M_{high\ x\ incompatible}$ = 28.81 mm, $SD_{high\ x\ incompatible}$ = 18.47 mm; $M_{low\ x\ incompatible}$ = 40.82 mm, $SD_{low\ x\ incompatible}$ = 29.07 mm; see Figure 15), though the frequency effects were significant in both compatibility conditions (both *t*s > 4.05, both *p*s < .001, one-tailed, adjusted for multiple testing). This effect was not further modulated by the three-way interaction compatibility x frequency x judgment modality ($F(1, 23) = 1.20$, $p = .29$, $\eta_p^2 = .050$; $BF_{01} = 3.88$) suggesting that this pattern was independent of the to-be-judged entity. Thus, the results suggest that in the case of incompatible hand and cursor movements, the judgment error is specifically increased for the less frequently judged modality, regardless of whether this is the visual or proprioceptive modality (Figure 16). Neither the main effects of judgment modality and time point of tone nor any other interactions reached significance (all *p*s > .059).

Due to the relatively low number of trials for estimating the median values for some of the cells (especially in the low frequency condition), we also conducted an analysis based on

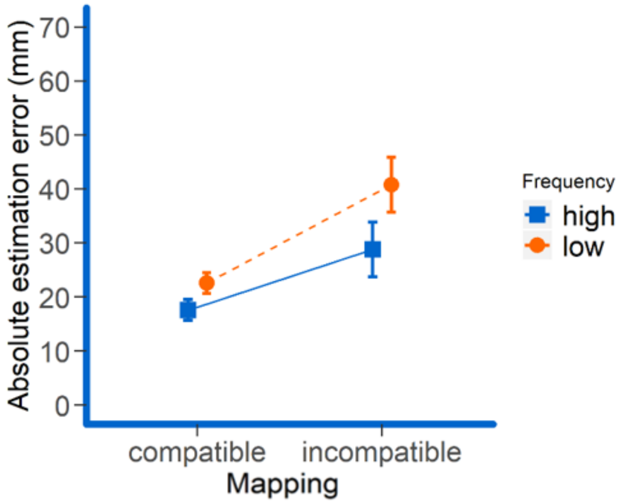

Figure 15. Mean absolute errors in Experiment 5 as a function of compatibility and frequency of the judgment. Error bars represent 95% paired-difference confidence intervals (Pfister & Janczyk, 2013).

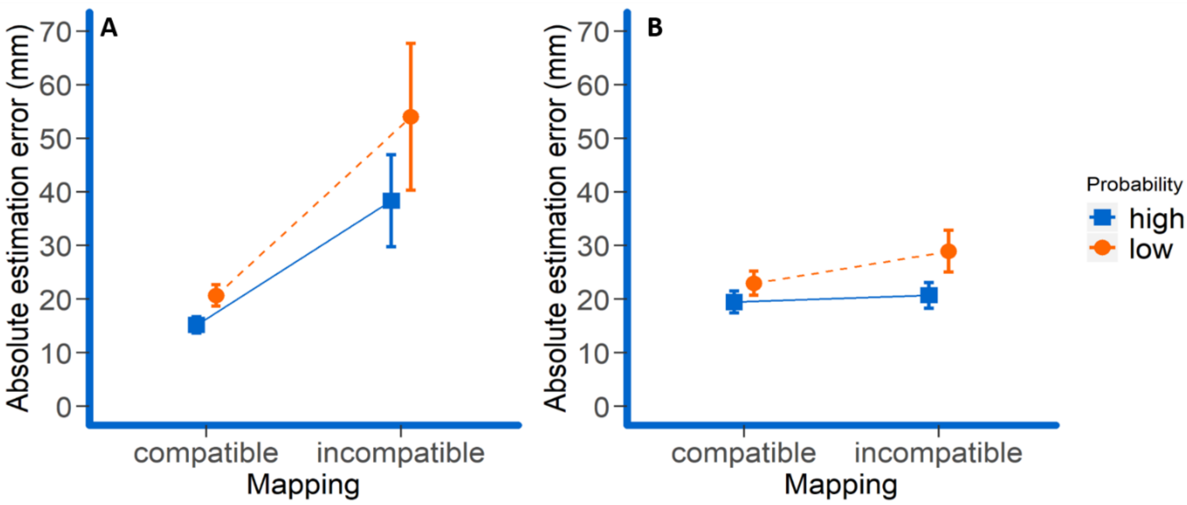

Figure 16. Mean absolute errors in Experiment 5 as a function of compatibility and frequency of the judgment split up for stylus judgments (A) and cursor judgments (B). Error bars represent 95% paired-difference confidence intervals (Pfister & Janczyk, 2013).

linear mixed models (LMMs) which does not require the aggregation over trials like the RM ANOVA. The results largely confirmed those of the ANOVA with the only difference that the main effect of judgment modality reached significance in the LMM analysis (t = 10.46, p < .001). Most importantly though, the fit of the main effects model was improved significantly by adding the two-way interaction of compatibility x frequency ($\chi^2(1)$ = 5.91, p = .015) and the fit of the two-way interaction model was not improved further by adding the three-way interaction of compatibility x frequency x modality ($\chi^2(2)$ = 3.06, p = .22). This shows that the observed results were not due to properties of particular analysis methods.

As an example, Figure 17 shows the judgment data of a typical participant.

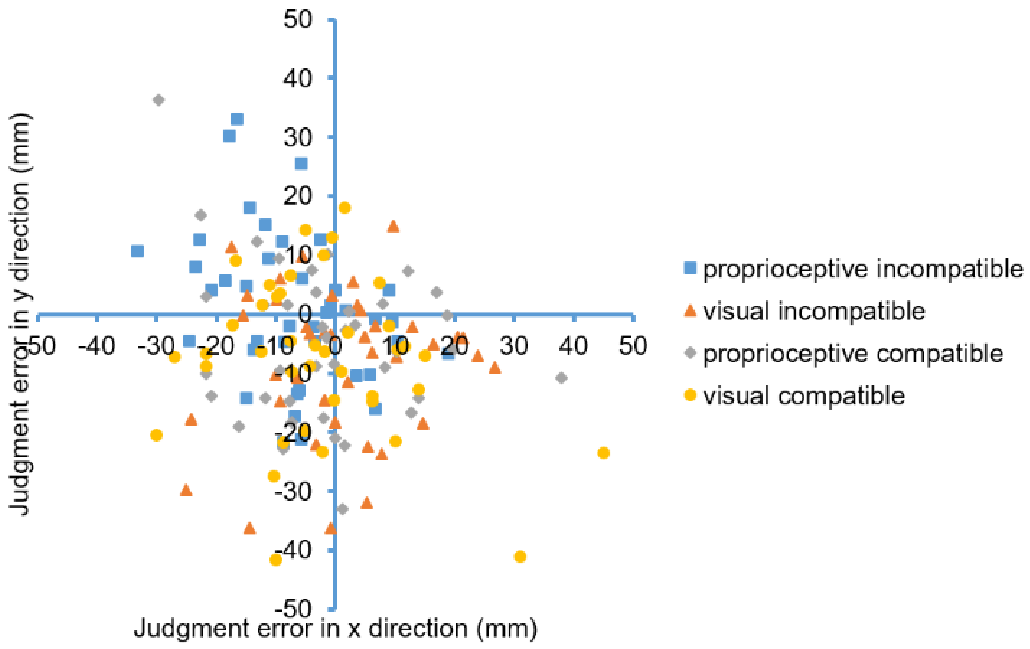

Figure 17. Example data for Experiment 5 from one participant (participant 9) showing the deviation from the to-be-judged position in x and y direction. Target and judgment positions for all trials were remapped to the upper left quadrant of the screen so that data points in the right and lower half of the figure represent judgment errors towards the center and data points in the left and upper half of the figure represent judgment errors towards the sides.

8.2.2.1. Exploratory analyses

To assess whether our paradigm is able to trigger a default haptic neglect without making one of the two action components more or less task-relevant, we calculated an additional 2 x 2 RM ANOVA on median absolute errors in the practice trials with the factors judgment modality (proprioceptive vs. visual) and compatibility (compatible vs. incompatible).[8] We found significant main effects of both factors (modality: $F(1, 23) = 7.10$, $p = .014$, $\eta_p^2 = .27$, $BF_{10} = 23.48$; compatibilty: $F(1, 23) = 17.98$, $p < .001$, $\eta_p^2 = .44$, $BF_{10} = 397.06$), but more importantly also a significant interaction between the two ($F(1, 23) = 13.05$, $p = .001$, $\eta_p^2 = .36$, $BF_{10} = 1.59 \times 10^3$). Follow-up t-tests revealed that this was due to significantly less precise proprioceptive judgments in the incompatible compared to the compatible condition ($M_{compatible\ x\ proprioceptive} = 22.46$ mm, $SD_{compatible\ x\ proprioceptive} = 8.74$ mm; $M_{incompatible\ x\ proprioceptive} = 57.88$ mm, $SD_{incompatible\ x\ proprioceptive} = 40.58$ mm; $t(23) = 4.86$, $p < .001$, $d_z = .99$), but that there was no such effect in visual judgments ($M_{compatible\ x\ visual} = 23.71$ mm, $SD_{compatible\ x\ visual} = 12.59$ mm; $M_{incompatible\ x\ visual} = 26.53$ mm, $SD_{incompatible\ x\ visual} = 25.38$ mm; $|t| < 1$). Furthermore, proprioceptive judgments were only less precise than visual ones in the incompatible ($t(23) = 3.23$, $p = .004$, $d_z = .67$), but not in the compatible condition ($|t| < 1$).

8.3. Discussion

In this experiment, we investigated how the task-relevance of resident and remote action effects (as manipulated by probability of probing) and level of interference (as manipulated by mutual (in)compatibility between them) impacts the precision with which these action effects are perceived. We found that perceptual precision was generally lower for the effects that were less likely probed, and when resident and remote effects were incompatible to each other. This suggests that people are generally sensitive to task demands when it comes to shift attention to either resident effects of their actions or effects located in a remote, controlled object. Most notably, the drop of judgment accuracy was particularly pronounced for less relevant, incompatible action effect components.[9] This suggests that “neglect” of task-irrelevant effect components might be involved to overcome interference that would otherwise occur by

[8] We did not include the factor time point here because it did not reveal any significant effects in the previous analysis.
[9] The corresponding interaction was significant in the ANOVA and the linear mixed model analyses, while the Bayes analysis yielded inconclusive evidence for this interaction. So a higher-powered study of this effect is certainly desirable.

attending to these effect components. Importantly, this occurred both when the cursor position was less likely to be probed indicating the neglect of interfering visual information when proprioceptive judgments were more likely, and when the stylus judgment was less likely to be probed indicating the neglect of interfering proprioceptive information (i.e., *haptic neglect*) when visual judgments were more likely (Figures 15 & 16).

Previous studies on tool use have argued that visual attention is focused on the effective end of the tool rather than the person's body movements (Collins et al., 2008; Müsseler & Sutter, 2009; Sülzenbrück & Heuer, 2009). The present study however showed that this mechanism is shaped by the relevance of the resident sensations while performing a tool task. Heuer & Rapp (2012) have suggested that interference between action effect components is reduced by neglecting proprioceptive information. Here we showed that not only proprioceptive but also remote information can be suppressed to reduce conflict. It is thus not the particular nature of proprioceptive action effects that makes them subject of such suppression. Instead, this happens because of their irrelevance in tasks where remote effects, such as movements of a tool, are the goal of the action (Fourneret & Jeannerod, 1998; Knoblich & Kircher, 2004; Müsseler & Sutter, 2009). In line with previous work (Heuer & Rapp, 2012; Müsseler & Sutter, 2009), our exploratory analyses also showed that without the upweighting of proprioceptive information through increased relevance of resident signals these are more likely to be ignored or suppressed than remote visual information about the tool when the information from these sources is contradictory.[10] In line with these exploratory analyses, we also found no general compatibility effect in precision judgments for the visual condition in absence of further manipulations of task-relevance. Both observations suggest that there is no "vision neglect" under normal tool use conditions, which makes sense given the inherent importance of the tool and its effects for achieving one's goal when using a tool

[10] One might wonder why the absolute errors were larger with a 50% chance of being probed in the practice blocks than in the 20% chance condition in the experimental blocks. This is most likely due to practice effects with the judgment task. However, this inflation in the practice trials should not affect the critical comparisons.

(Heuer & Rapp, 2012; Müsseler & Sutter, 2009). As laid out before, to invert this tendency proprioceptive information needs to become more task relevant.

Our findings thus suggest that despite a "default" tendency to neglect incompatible proprioceptive instead of visual information the mechanisms related to the processing of resident and remote effects still seem to be more similar than previous studies on tool use suggested. This is well in line with theoretical notions that humans should be very flexible in their way of representing actions either through anticipation and feedback from resident or remote action effects (Pfister, 2019; Prinz, 1998). There might be a more general mechanism underlying these observations, related to the processing of spatially incompatible sensory information of different modalities in general, independent of the stage of movement, or possibly of movements at all. We will come back to this possibility at a later point. To what extent participants are actually aware of these seemingly strategical suppression mechanisms is certainly something to be determined in future research.

As outlined above, the neglect of the less relevant action effects in a given block and the modulation of this through (in)compatibility of resident and remote effects was independent of the judgment modality, thus whether visual or proprioceptive estimates had to be made. Additionally though, we also found no significant differences between absolute estimation errors of the two judgment modalities in the experimental blocks which is surprising given the common finding that people are usually much better in judging visual compared to proprioceptive positions (Debats et al., 2017b; Debats & Heuer, 2018a; Kirsch et al., 2016; Rand & Heuer, 2013, 2019), though we did find a significant effect of this factor in the exploratory single-trial analyses. However, this might be due to the significant crossed judgment modality x compatibility interaction which indicated not only a compatibility effect for the proprioceptive judgments, but also that these were both less precise than visual judgments in the incompatible condition, while being more precise than visual judgments in the compatible condition. Conceivably, the surprisingly precise proprioceptive judgments in the compatible condition resulted from moving the stylus back to where it had been during the occurrence of the tone. Thus, participants could have tried to move back from the center position to the estimated position in more or less the same trajectory in which they moved from the end position of the tracking task to the center position. We tried to circumvent this by introducing a delay before indicating the judgment modality and by varying the time point of the tone; however, it could still be that this experimental characteristic might have led to an advantage for the proprioceptive judgments, which was not available in the visual judgments. Another possible factor might have been that despite the disappearance of the cursor, the neutral center position of the cursor after every trial and the delay before judgments, the location of the visual information might have been more accurately remembered than the location of proprioceptive information (Jones & Henriques, 2010). Consequently, the stylus judgments might have been supported by additional visual information to a greater extent than the cursor judgments were supported by additional proprioceptive information.

Furthermore, in compatible trials cursor and hand were always right on top of each other throughout the tracking phase while this was not the case in incompatible trials. Thus, besides the (in)compatibility of the movement directions of hand and cursor, there was also an additional spatial discrepancy in the incompatible condition between them which might have additionally contributed to the distribution of attention between hand and cursor. As a result, the possible additional support of the proprioceptive judgments through visual information in the compatible conditions might have led to an underestimation of both the overall level and the compatibility effect of proprioceptive estimation errors. Nevertheless, such biases would have not affected the previously discussed main findings. On the contrary, that incompatibility affected uncertainty about proprioceptive sensations stronger than uncertainty about visual sensations, renders the suppression of conflicting visual signals of low task relevance even more remarkable.

An important point that should still receive some attention here is our manipulation of task-relevance through the frequency of probing a specific modality in the judgment task. While the relevance of the sensory modalities for the judgment task is obviously manipulated by this, the relevance of especially visual information during the tracking task might be more difficult to manipulate. The processing of the visual information from the cursor is essential in the tracking task since the task cannot be fulfilled based on proprioceptive information alone. Therefore, one might expect that participants should perform the two tasks as if they were independent of each other and there should be no carryover between the two tasks. However, this would render the judgment task impossible to do above chance performance, because the sensory information (visual or proprioceptive) necessary for the position judgment was only available during the tracking task and thus had to be attended and encoded during this task already for the subsequent judgment. Thus, if participants were to adapt to the different movement transformation mappings and the proportion of cursor or hand judgments, they necessarily had to process this sensory input differently already during the tracking task, which then showed up in the subsequent judgement task.

While it might seem contradictory, that especially visual information could already be suppressed during the tracking task, a way to solve this is to think of neglect of sensory information less in absolute or discrete ways, but rather as a continuous distribution of attentional resources between different sensory modalities (Hommel, 2009; Hommel et al., 2001; Memelink & Hommel, 2013; Pfister, 2019; Prinz, 1998). Participants certainly could not completely neglect visual information in the less relevant condition because it was still necessary for the tracking task, nevertheless they might have already shifted away some attention from the visual information compared to the high relevance condition but leaving still enough to perform the tracking task. Thus, the manipulation of task relevance might still also have an effect on the degree to which visual information is already neglected in the tracking task, though the impact of the manipulation might have been smaller here than for the proprioceptive information. This might also explain the smaller visual effects in general and the tendency towards neglecting proprioceptive rather than visual information during practice trials and when leaving out the relevance manipulation. Possibly, this imbalance could be reduced if one chose a stronger manipulation of relevance of resident or remote effects already in the tracking task, like for example by making the tracking task dependent on haptic instead of visual guidance. However, this would have essentially undermined the purpose of this study to investigate perception of resident and remote effects under different movement transformations in tool use since tool use is characterized by manipulating an external object, in this case, a cursor. Thus, making the goal of the tracking task directly related to the resident effect itself would lead to a conceptually different situation. There might still be other ways to manipulate the relevance of resident and remote effects and at the same time maintain the nature of the tool use task, which might be worth to be tested in future research, however we believe to have provided one possible way to do so.

Discrepant sensory input of different modalities might be processed to different degrees without active movements. Therefore, an experiment similar to ours where locations of mutually (in)compatible visual and tactile stimulations have to be judged with varying probabilities might reveal similar results, without actively producing that input. Still, tool-use is a real world example where such a situation is inevitably created, while it needs to be studied further whether the active production and passive encounter of such discrepancy matters. Ideomotor theory (James, 1890/1981; Pfister, 2019; Shin et al., 2010; Waszak et al., 2012) suggests that it would matter, as mutually incompatible sensory effects of motor patterns create a problem for producing these motor patterns in the first place, which adds a reason to suppress one of the two components already during action generation.

An additional point that we shortly want to touch is a possible relationship between the two tasks and specifically whether differential performance on the tracking task might have influenced performance on the judgment task. While we did not have tracking data to control for this possibility, such possible influences could, if at all, only affect the main effect of compatibility in the judgment task. Since our main results however rest on more complex interactions with this factor, additional mechanisms, presumably the ones we suggested, have to be at play for these. Actually, since we suggest that these mechanisms are already present during the tracking task, they might also be the reason for possible performance differences in the tracking task

Furthermore, also the manipulation of time point of the tone that indicated the to-be-judged position of either hand or cursor should still receive some attention here. While the main reason for varying this time point was to prevent predictability of the to-be-judged position based on the movement endpoint, in principle this manipulation could have also had an influence on the absolute estimation error so that it could have made judgments for example more inaccurate, the earlier before the end of the movement it occurred and thus the more time had passed between the tone and the judgment. However, we did not find such an effect, either because the spatial judgments were insensitive to this manipulation or because the time points were chosen too close together.

8.4. Conclusions

Controlling an external object through one's own body movements can lead to discrepancies (e.g. spatial) between the body effector and the controlled object. Previous research has suggested that the conflict emerging from this can be overcome or reduced by focusing one's attention on the effects in the object and attending away from one's body. Implementing a paradigm, which manipulated the relevance of the object on the one hand and of the body on the other hand during the task showed that this attentional focus can also be reversed so that the body instead of the object is attended.

9. Suppression of resident action effects which are incompatible to remote action effects during movement planning

Previous studies have demonstrated that sensory information from a body effector is suppressed or neglected during the movement of this body effector, a phenomenon called "tactile gating". This seems to be especially the case when controlling the movements of another object with these body movements and when these body and object movements diverge from each other. It has been suggested that the reason for this "haptic neglect" is that the diverging ("incompatible") body and object movements cannot be attended to simultaneously and also should not be to prevent a motor conflict during such actions and thus to assure that the action can still be performed with relative ease. According to ideomotor theory, humans generate goal-directed actions by anticipating the sensory effects of these actions which means that they should also anticipate the diverging visual and proprioceptive effects from diverging body and object movements. The aim of the current experiment was to assess whether this anticipation of motor conflict would lead to a downregulation of resident sensory effects from the body effector already before movement onset. The results suggested that such a downregulation indeed takes place as tactile stimuli on the to-be-moved hand were perceived as significantly weaker when the planned body and object movement were incompatible than when they were compatible. We suggest that such anticipatory downregulation of resident action effects that conflict with remote action effects is a necessary mechanism for human agents to generate actions with such incompatible action effects in the first place.

9.1. Introduction

As laid out above, controlling body-external objects, such as for example when using tools, can lead to situations in which visual effects of the action stemming from the tool and proprioceptive or tactile effects of the action stemming from one's own body interfere in their spatiotemporal dimensions. In Experiments 1-4, we could show that this decreases or even eliminates the otherwise often experienced and robust effect that a voluntarily controlled object is perceived as being part of oneself in terms of a sense of agency and a sense of ownership (e.g., Dummer et al., 2009; Haggard & Tsakiris, 2009; Kalckert & Ehrsson, 2012, 2014a; Kirsch et al., 2016; Liepelt et al., 2017; Ma & Hommel, 2013, 2015a, b; Maravita et al., 2002; Sanchez-Vives et al., 2010; Weser et al., 2017; Zopf et al., 2018). The model we presented (see section *4.3. A model accounting for and explaining the limitations of extending the self through action*) explains these findings by suggesting that the conflict generated by incompatible action effects leads to the suppression of one of the two action effects (Heuer & Rapp, 2012) so that they cannot be integrated anymore. Experiment 5 provided a first test of this hypothesis and demonstrated that with an incompatible hand-to-object movement transformation, the (spatial) information about one of the two action components was less accessible than the other and compared to a compatible transformation, which supports the idea of suppression of one of the incompatible action effects. However, there are a few limitations to this experiment concerning the implications that can be drawn from it regarding the proposed model.

First, the measure used in Experiment 5 was a rather indirect measure of the processing strength of resident and remote action effects since it was not directly related to the perceived intensity of resident and remote effects, but rather just captured the amount of attended information that participants had over the endpoint of the resident and remote effects. While attention might likely still play a role in the proposed model and Experiment 5 might have thus captured one aspect of the proposed mechanism, a direct demonstration of an actual downweighting of incompatible sensory action effects still remains missing.

Second, the paradigms of Experiment 1-4 and of Experiment 5 differed substantially. The required actions in Experiments 1-4 were only one-dimensional while they were two-dimensional and also inverted in both dimensions in the incompatible condition in Experiment 5 making the latter task considerably more complex and more difficult for participants. Additionally, also the form and duration of the actions differed largely between the different paradigms: In Experiments 1-4, participants had to produce speeded and very short (often ~20 ms) responses which also did not require high precision when hitting the target box. The focus in these Experiments was thus clearly on action generation and there was no need to adjust and/or carefully monitor the produced action effects to fulfill the task requirements. In Experiment 5 however, participants carefully had to track the visual effects of their actions on the screen since they had to follow the “leading” dot without great deviation from it. Furthermore, the required movements took much longer (often around ~30 s) and participants had to produce continuous movements and constantly monitor both their resident and remote action effects to fulfill the needs of the task. Admittedly, the second phase of the trials in Experiment 3 and 4 also required longer and more continuous movements, since participants had to search for the required cursor position. Nevertheless, these movements were still essentially self-paced and participants were not in danger to produce errors (and thus to repeat a given trial) when their movements were not precise enough or when they did not monitor their action effects closely for a moment. The task requirements and the actions produced by participants in Experiments 1-4 and in Experiment 5 thus clearly differed from each other. Given that these different paradigms also provide support for different aspects and predictions of the proposed model, it would considerably strengthen the argument of the suggested causal role of action effect suppression for the elimination of selfhood experiences if these effects could also be demonstrated with more similar paradigms. The current Experiment 6 thus aimed at demonstrating the suppression of incompatible resident action effects in a paradigm similar to the one in Experiments 1-4.

Third and finally, there is another relevant aspect of the action effect suppression as conceptualized in the presented model that is not captured in Experiment 5. Importantly the ideomotor-based model assumes that in the case of incompatible resident and remote action effects, a conflict already occurs due to the anticipation of the mutually incompatible resident and remote effects when generating and before initiating the action (e.g., Crothers et al., 1999; Kunde, 2001; Kunde et al., 2007, 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013; Schwarz et al., 2018; Wirth et al., 2015). Therefore, to solve this conflict, suppression of one of the incompatible action effects should already be present before movement onset to be able to generate the action in the first place. In Experiment 5 however, participants were asked to judge the location of either their hand or the manipulated object at the end of the action so the "suppression" measured in this experiment was most likely present during the action. While the proposed model does not speak against an extended suppression of incompatible action effects during the action, in fact it might even be beneficial to maintain control over the manipulated object with continuous movements, the demonstration of such suppression already before movement onset and during movement planning might provide even stronger support for the suggested model.

Experiment 6 aimed at overcoming these limitations by testing the tactile sensitivity on participants' hands during the preparation of hand lateral movements which led to spatially (in)compatible movements of a cursor (for details see *9.2.1.4. Procedure and task*). It is a well-known phenomenon in the action-perception literature that preparing and performing voluntary movements modulates the tactile sensitivity on the moving body effector. For example, there have been various studies which have reported a decreased tactile sensitivity on a body effector already shortly before starting to move which extends to movement execution (e.g., Arikan, Voudouris, Voudouri-Gertz, Sommer, & Fiehler, 2021; Buckingham, Carey, Colino, deGrosbois, & Binsted, 2010; Colino & Binsted, 2016; Colino, Buckingham, Cheng, van Donkelaar, & Binsted, 2014; Voss, Ingram, Wolpert, & Haggard, 2008), an effect that has been labelled as "tactile gating". In contrast, also increases in tactile sensitivity before or during moving have been reported (e.g., Juravle & Deubel, 2009) while again another line of studies has revealed differential effects on suppression and enhancement of tactile signals before and during movement (e.g., Juravle, Deubel, Tan, & Spence, 2010; Voudouris & Fiehler, 2017, 2021). When taking a closer look at these seemingly contradictory results, it seems that tactile enhancement and suppression are not only influenced by the time point during the action preparation and performance interval, but also by the specific kind of action and the role of the tactile signals during the task as well. For example, it has been shown that tactile sensitivity is enhanced when participants had to respond to the tactile stimuli delivered to the to-be-moved body effector and thus had to attend these stimuli (Juravle & Deubel, 2009) or during the performance of exploratory actions (Juravle, McGlone, & Spence, 2013). Furthermore, Voudouris & Fiehler (2021) recently demonstrated that tactile gating on the moving hand was present during movement planning and early and late stages of a reaching movement, but that it was absent approximately halfway throughout the movement. Interestingly, this “release” from gating coincided with the time point of maximum movement speed which led the authors to conclude that tactile suppression would mainly be present when tactile information is of less relevance for the agent while its absence or even tactile enhancement could be observed in situations when tactile information is highly relevant for the agent. It thus seems that agents seem to be relatively flexible regarding their sensitivity for tactile events, depending on the specific task demands (Voudouris & Fiehler, 2017).

To our knowledge, there is no study which has previously investigated the influence of the (in)compatibility of resident and remote action effects on the tactile sensitivity on the body effector producing this action. However, the previously discussed findings on tactile suppression and tactile enhancement clearly demonstrate that experimental manipulations of the relevance of tactile sensations and therefore also of resident action effects shape tactile sensitivity during actions. This opens up the question whether the (in)compatibility between resident and remote action effects might similarly influence (anticipatory) tactile suppression on the to-be-moved body effector. As demonstrated in Experiment 5, when confronted with incompatible resident and remote action effects, human agents have to “decide” which of the conflicting action effects to attend to and which to suppress and this “decision” is mainly driven by the task relevance of the particular action effects. Furthermore, Experiment 5 also showed that without any objective determinant of such relevance, resident effects are the ones that tend to be suppressed with mutually incompatible action effects. It thus seems plausible that tactile gating as a more direct measure of resident effect suppression might also be observable with incompatible resident and remote action effect combinations. Experiment 6 aimed to test this assumption.

Specifically, it was expected that tactile sensitivity should be lower on the active hand when planning a hand movement that led to a spatially incompatible object movement compared to a spatially compatible object movement. Previous studies on tactile gating with other tasks had only identified a relatively narrow time window for anticipatory tactile gating of approximately 100 ms before movement onset (e.g., Buckingham et al., 2010; Voss et al., 2008). However, it is unclear whether this would also account for tactile gating in the current context since action planning with incompatible resident and remote action effects has been shown to take substantially longer than without conflicting action effects (Crothers et al., 1999; Kunde, 2001; Kunde et al., 2007, 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013; Schwarz et al., 2018; Wirth et al., 2015; Experiments 1-4). Given the crucial role that the suggested model assumes for tactile gating in generating actions with incompatible effects, an extended anticipatory gating effect might thus also be plausible in this context. Additionally, the results from Experiment 5 suggest that there might also be an extension of the tactile suppression into the movement or post-movement phase since the kind of suppression measured in Experiment 5 was essentially based at the end of the movement. Whether there should also be any tactile suppression, anticipatory, during or after movement, in the compatible condition to a smaller degree or no suppression at all or even tactile enhancement remains unclear based on the existing literature and the suggested model.

9.2. Experiment 6

9.2.1. Materials and methods

9.2.1.1 Ethics statement

The project was approved by the ethics committee of the Institute for Psychology of the University of Würzburg under the reference number GZEK 2018-33. All procedures were in line with the Declaration of Helsinki.

9.2.1.2 Participants

44 participants were tested in Experiment 6 and received €10 per hour for their participation. For various reasons (see section *9.2.1.5 Data* preprocessing) a number of participants had to be excluded so that the final dataset consisted of 29 participants (M_{Age} = 23.79, SD_{Age} = 3.10, min_{Age} = 19, max_{Age} = 32; 23 female, six male; 28 right-handed, one left-handed). None of the participants reported any medical conditions which might have been of relevance for the experiment. All participants had normal or corrected-to-normal sight.

9.2.1.3. Apparatus and stimuli

Participants were tested one person at a time. Stimuli were displayed on LCD monitors (24", BenQ XL 2411, BenQ) with a resolution of 1920 x 1080 pixels and a 100 Hz refresh rate. All stimuli were presented using E-Prime (version 2.0, https://www.pstnet.com/). Participants were seated approximately 70 cm in front of the monitor and could freely choose a comfortable sitting position. They operated the computer mouse with their right hand, which was placed in a "natural" position right of and in front of the screen, and were instructed to place the left hand in a central position in front of the keyboard. Additionally, participants had vibrotactile stimulators attached to both backs of their hands at positions right below the knuckles of their middle fingers. The stimulators were approximately 1.8 cm in diameter and were attached to the skin using adhesive rings. The stimulators were driven by a TactAmp Amplifier (Dancer Design, St. Helens, Merseyside, United Kingdom) which translated audio signals from the soundcard of the computer into vibratory movements of the magnetic cores of the stimulators. The audio signals were produced using the open source software Audacity (version 2.1.1, https://www.audacity.de/) and were designed to produce vibratory stimuli of 50 ms and a frequency of 250 Hz in 14 different intensities. The intensities were measured as peak-to-peak displacement of the stimulators and were approximately 3.33 μm, 6.67 μm, 10 μm, 13.33 μm, 16.67 μm, 20 μm, 23.33 μm, 26.67 μm, 30 μm, 33.33 μm, 36.67 μm, 40 μm, 43.33 μm and 46.67 μm. Please note that for individual participants the displacements might differ slightly due to different physical properties of an individual participant's skin.

9.2.1.4. Procedure and task

The experiment was split into two sessions of 60-75 minutes each, which were performed by participants on two consecutive days. Upon arrival, participants had to give written informed consent about the procedure of the experiment before the stimulators were attached to their hands and the experiment was started.

The trial procedure was similar to Experiments 1 and 2. At the beginning of each trial participants first saw a gray circle in the center of the screen and two gray square boxes on the left and right side of the screen. After a predefined delay of either 1500 or 2500 ms the circle changed its color to either green or blue which indicated that participants had to move the circle either into the left or right target box. Stimulus-response mapping was counterbalanced between participants. Participants controlled the circle through movements of the mouse with their right hand. As in the previous experiments, the transformation of hand movements into circle movements was manipulated: In the compatible condition, the circle always moved in the same direction as the hand while it always moved in the opposite direction in the incompatible condition. Participants underwent the compatible and incompatible conditions on separate days, the order of which was counterbalanced between participants. After the circle had changed its color, participants were asked to withhold their response and to observe a counter in the middle of the circle counting up from 1 to 4 in a rhythm of 500 ms. Participants were asked to mentally count along and try to provide their response as accurately as possible with the occurrence of the “4” (“Timed Response Paradigm”; Favilla, Gordon, Hening, & Ghez, 1990). Responses had to be as accurate as $\pm$200 ms around the onset of the “4” to be counted as correct.

In addition to the response task, participants also received vibrotactile stimulations on both hands either 50, 100, 150, 200, 250 or 300 ms before the onset of the “4”. The intensity of the stimulation on both hands differed both within and across trials. One of the stimulations always had an intensity of either 20 or 30 µm as a “reference” intensity while the other stimulation could have any of the 14 intensities. This way the difference in intensity between the stimulation on both hands could have 17 different magnitudes: -26.67 μm, -23.33 μm, -20 μm, -16.67 μm, -13.33 μm, -10 μm, -6.67 μm, -3.33 μm, 0 μm, 3.33 μm, 6.67 μm, 10 μm, 13.33 μm, 16.67 μm, 20 μm, 23.33 μm and 26.67 μm (negative values depict a stronger stimulation on the left, inactive hand while positive values depict a stronger stimulation on the right, active hand). After the movement had been completed in a given trial, participants were asked to rate whether the stimulation on the right or left hand felt stronger. Participants indicated their judgment by pressing either the left or the right arrow key on the keyboard with their left hand and were furthermore instructed to press the "0" key in case they did not feel a stimulation on any of their hands, which could happen in rare cases of technical malfunction. After participants had given their judgment, the next trial started.

Each participant completed 672 trials both in the compatible and in the incompatible session (14 stimulation intensities x 2 reference intensities x 2 reference sides x 2 required responses x 6 stimulation times). Furthermore, in half of all trials and randomized over all conditions, stimulus onset was preceded by a short (1500 ms) or a long (2500 ms) inter trial interval.

9.2.1.5 Data preprocessing

All trials in which any kind of error was produced were excluded from analyses. This included (i) trials in which participants showed the wrong response to the stimulus, (ii) trials in which participants failed to respond within the time window defined by the counter, (iii) trials in which participants failed to produce a response at all, and (iv) trials in which participants indicated that they did not feel a stimulation on either of their hands.

For all trials, the difference between movement onset and stimulation onset was calculated and trials were classified into the following categories: stimulation more than 300 ms before movement onset, stimulation between 200 and 300 ms before movement onset, stimulation between 100 and 200 ms before movement onset, stimulation less than 100 ms before movement onset and stimulation after movement onset. Subsequently, for every participant, every combination of time point category and compatibility and every difference in stimulation intensity on the two hands, probabilities were calculated that the stimulation on the right, active hand was judged as stronger than the one on the left, inactive hand. Based on these probabilities individual points of subjective equality were calculated for every participant and combination of the factors compatibility and time point category using maximum likelihood estimation with the R package “quickpsy” (Linares & López-Moliner, 2016; R Core Team, 2019). A (more) positive or larger point of subjective equality would in this context represent a decrease in the perceived strength of the tactile stimulation on the right, active hand while a (more) negative or smaller point of subjective equality would represent an increase in the perceived strength.

Besides the exclusion of single trials as explained above, datasets of some participants had to be excluded completely or the following reasons: 2 participants quit the experiment before completion. 2 participants each produced either too many error trials or indicated that they did not perceive any stimulation at all in too many trials for the maximum likelihood method to estimate reliable points of subjective equality still. 7 participants did not show any stable tendency to respond to physically relatively stronger stimuli with stronger intensity judgments accordingly and 2 participants pressed the same button during the judgment phase irrespective of the tactile stimulation intensity.

9.2.2. Results

Points of subjective equality were entered into a 2 x 5 repeated measures analysis of variance with the factors compatibility (compatible vs. incompatible) and time point category (stimulation more than 300 ms before movement onset vs. stimulation between 201 and 300 ms before movement onset vs. stimulation between 101 and 200 ms before movement onset vs. stimulation less than 100 ms before movement onset vs. stimulation after movement onset). The analysis revealed a marginally significant main effect of compatibility ($F(1, 28) = 3.45$, $p = .074$, $\eta_p^2 = .11$, $BF_{10} = 2.43$) with larger points of subjective equality in the incompatible than in the compatible condition ($M_{incompatible} = 3.33$ µm, $SD_{incompatible} = 5.70$ µm; $M_{compatible} = 1.09$ µm, $SD_{compatible} = 5.40$ µm; see Figure 18), a significant main effect of time point category ($F(1, 28)$

= 33.91, $p < .001$, $\varepsilon = .72$, $\eta_p^2 = .54$, $BF_{10} = 3.80 \times 10^{13}$) and no significant interaction between the two factors ($F < 1$).

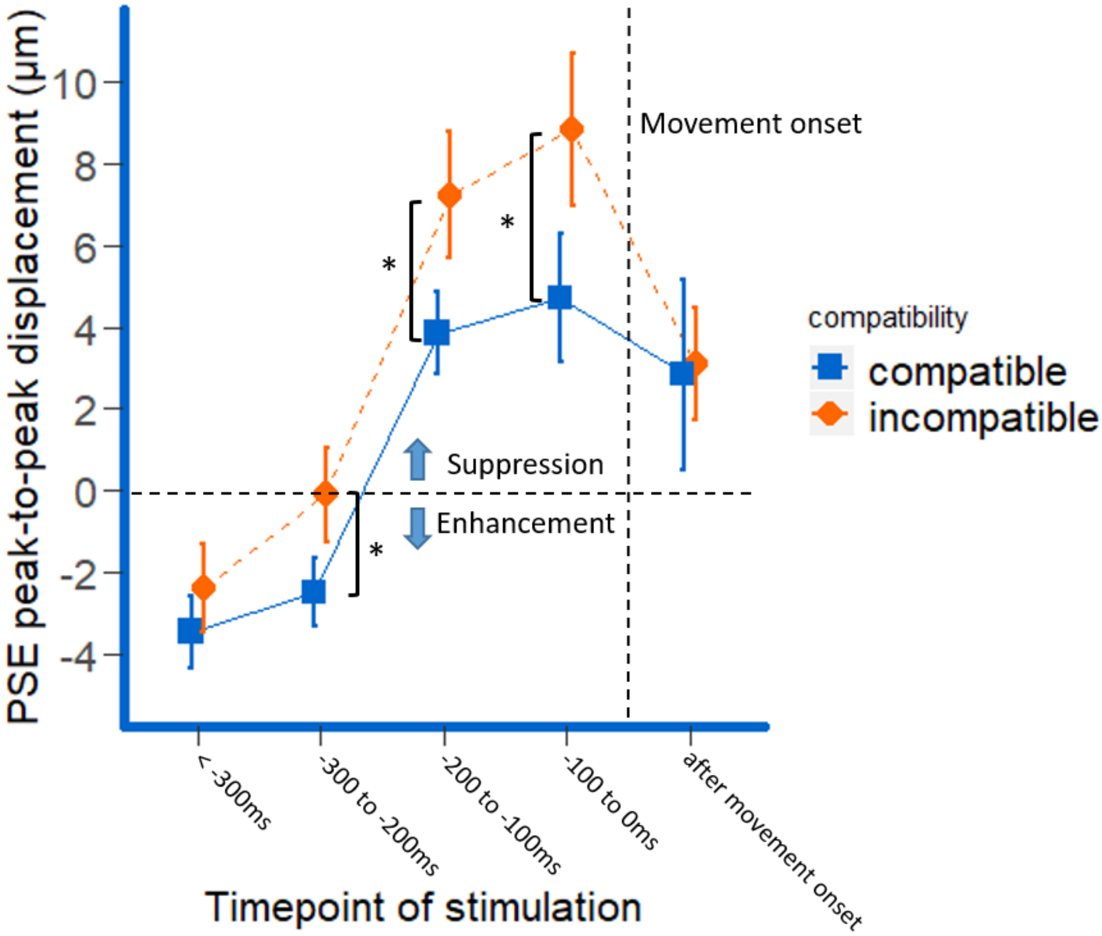

Figure 18. Temporal development of points of subjective equality measured with tactile stimuli on the right, active hand as test stimuli and tactile stimuli on the left, inactive hand as reference stimuli. The depicted values represent means ± standard errors of the mean. Positive values represent tactile suppression on the right, active hand while negative values represent tactile enhancement. Significant compatibility effects are marked within the figure.

To investigate further whether the marginally significant effect of compatibility could represent an actual difference between points of subjective equality for compatible and incompatible situations, follow-up t-tests were calculated comparing the points of subjective equality between these conditions for the different time points each (see Figure 18). Points of subjective equality were larger in the incompatible than in the compatible condition for the time point categories of 1 to 100 ms before movement onset ($M_{difference}$ = 4.11 µm, $SD_{difference}$ = 10.95 µm, $t(28) = 2.02$, $p = .027$, one-tailed, $d_z = .86$, $BF_{10} = 2.25$), 101 to 200 ms before movement onset ($M_{difference}$ = 3.39 µm, $SD_{difference}$ = 7.99 µm, $t(28) = 2.29$, $p = .015$, one-tailed, $d_z = .42$, $BF_{10} = 3.58$) and 201 to 300 ms before movement onset ($M_{difference}$ = 2.39 µm, $SD_{difference}$ = 6.39 µm, $t(28) = 2.02$, $p = .027$, one-tailed, $d_z = .37$, $BF_{10} = 2.22$). There were no such significant compatibility effects in the time point categories of more than 300 ms before movement onset ($M_{difference}$ = 1.05 µm, $SD_{difference}$ = 7.11 µm, |*t*| <1) and after movement onset ($M_{difference}$ = -.26 µm, $SD_{difference}$ = 16.10 µm, |*t*| <1).

To disentangle the main effect of time point category, follow-up t-tests were calculated between the mean points of subjective equality for each time point category. Due to the highly significant main effect of time point category and the interaction time point category x compatibility being far from significant, mean values for each time point category were aggregated over compatible and incompatible conditions. Except for the comparisons between the category from 1 to 100 ms vs. from 101 to 200 ms before movement onset ($M_{difference}$ = 1.22 µm, $SD_{difference}$ = 4.47 µm, *t*(28) = 1.48, *p* = .15, two-tailed, d_z = .27, BF_{01} = 1.91), mean points of subjective equality for all time point categories significantly differed from each other (all |*t*|s > 2.09, all *p*s < .046, all d_zs > .38). In general, for the time point categories before movement onset, points of subjective equality increased the later the stimulation was delivered, while the magnitude of points of subjective equality for the category after movement onset was between those for the category from 101 to 200 ms and from 201 to 300 ms.

Finally, to test for individual sensory suppression or enhancement effects in the different time point categories, one sample t-tests were calculated for each time point category x compatibility combination and the points of subjective equality were tested against 0 (see Figure 19). For the incompatible condition, this revealed points of subjective equality that were significantly larger than 0 for the after movement onset (*M* = 3.10 µm, *SD* = 7.32 µm, *t*(28) = 2.28, *p* = .030, two-tailed, BF_{10} = 1.81), 1 to 100 ms before movement onset (*M* = 8.83 µm, *SD* = 10.05 µm, *t*(28) = 4.73, *p* < .001, two-tailed, BF_{10} = 428.40) and 101 to 200 ms before movement onset categories (*M* = 7.24 µm, *SD* = 8.27 µm, *t*(28) = 4.71, *p* < .001, two-tailed, BF_{10} = 415.54), a point of subjective equality that was significantly smaller than 0 for the category of more than 300 ms before movement onset (*M* = -2.42 µm, *SD* = 5.77 µm, *t*(28) = 2.26, *p* = .032, two-tailed, BF_{10} = 1.73) and a point of subjective equality that was not significantly different from 0 in the 201 to 300 ms before movement onset category (*M* = -0.11 µm, *SD* = 6.18 µm, |*t*| <1). For the compatible condition, points of subjective equality were significantly larger than 0 in the 1 to 100 ms before movement onset (*M* = 4.72 µm, *SD* = 8.49 µm, *t*(28) = 2.99, *p* = .006, two-tailed, BF_{10} = 7.35) and 101 to 200 ms before movement onset categories (*M* = 3.86 µm, *SD* = 5.34 µm, *t*(28) = 3.89, *p* = .001, two-tailed, BF_{10} = 55.41), significantly smaller than 0 in the category of 201 to 300 ms before movement onset (*M* = -2.50 µm, *SD* = 4.54 µm, *t*(28) = 2.97, *p* = .006, two-tailed, BF_{10} = 6.93) and more than 300 ms before movement onset (*M* = -3.46 µm, *SD* = 4.77 µm, *t*(28) = 3.91, *p* = .001, two-tailed, BF_{10} = 58.24) and not significantly different from 0 in the after movement onset category (*M* = 2.85 µm, *SD* = 12.55 µm, *t*(28) = 1.22, *p* = .23, two-tailed, BF_{01} = 2.58).

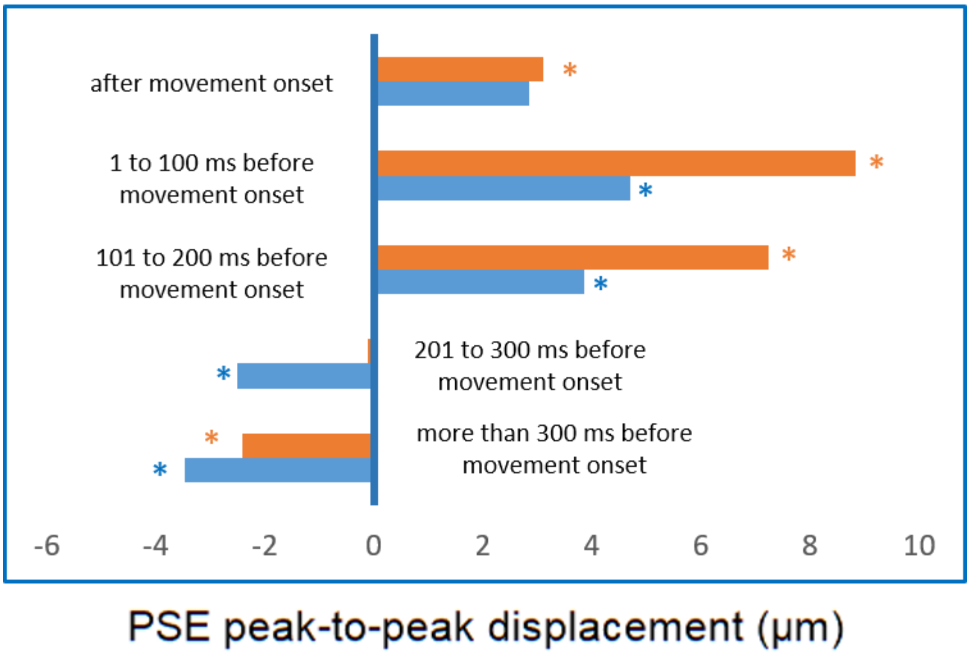

Figure 19. Points of subjective equality calculated separately for all compatibility x time point category combinations. Points of subjective equality that are significantly different from 0 (two-tailed) are marked. Orange bars depict the incompatible condition and blue bars depict the compatible condition.

9.3. Discussion

The aim of Experiment 6 was twofold: First, we wanted to replicate the findings of Experiment 5 demonstrating the downregulation of resident action effects that are in conflict with accompanying remote action effects and extend these findings by demonstrating actual tactile suppression in these situations in a more direct manner. Second, we wanted to demonstrate that this suppression does already occur during movement planning based on the anticipation of the to-be-produced action effects. The results of Experiment 6 support both of these hypotheses. As expected we found that tactile stimuli were suppressed to a significantly higher degree on the moving hand when the hand movement resulted in a spatially incompatible remote action effect than when it resulted in a spatially compatible remote action effect. This effect was present from approximately 300 ms before movement onset on which supports the idea of anticipatory haptic neglect (Heuer & Rapp, 2012) when preparing actions with incompatible resident and remote action effects.

Ideomotor theory suggests that human agents produce their actions by anticipating the sensory effects of the to-be-produced action, a claim that has by now gained strong empirical support (e.g., Elsner & Hommel, 2001; Hommel, 2013; James, 1890/1981; Koch et al., 2004; Kunde, 2001; Shin et al., 2010; Waszak et al., 2012). For this purpose, it does not matter what the modality of these anticipated effects is or if they are resident or remote (Mocke et al., 2020; Pfister, 2019; Experiment 5). However, once resident and remote effect combinations become incompatible, i.e. the currently anticipated effects are usually linked to different actions based on typically learned links, the matter becomes different. In this situation, the system has to select one of the incompatible, conflicting action effects to anticipate and thus base the action anticipation upon, and in turn suppress the other anticipated action effect. We believe that the increased points of subjective equality for stimulations on the active hand with incompatible compared to compatible action effects reflects such suppression of the anticipated resident effects in the case of incompatibility.

One point that should receive some more elaborate discussion is the specific temporal pattern of the observed tactile suppression effect. In the present Experiment 6, we found evidence for relative anticipatory sensory suppression of tactile stimuli delivered to the actively moving hand or incompatible compared to compatible actions from approximately 300 ms before movement onset on. However, even though in the category from 201 to 300 ms before movement onset, we found significantly larger points of subjective equality in the incompatible than in the compatible conditions, the point of subjective equality in the former condition was actually statistically indistinguishable from 0. The significant difference between the incompatible and compatible condition in this category was thus due to the significantly negative point of subjective equality in the compatible condition, demonstrating an enhancement in tactile sensitivity in the compatible condition with more than 200 ms prior to movement onset. While we will still discuss these results and its implications at a later point, we can for now constitute that haptic neglect, measured as tactile suppression on the active hand when producing incompatible resident and remote effects, was present from 200 ms before movement onset on in Experiment 6. This is a slightly larger time window than the one which previous studies have suggested for the tactile gating effect that often only found gating effects within the last 100 ms before movement onset (e.g., Buckingham et al., 2010; Voss et al., 2008). However, previous studies have usually also investigated gating or suppression effects for simpler actions than we investigated here which often only included simple reaching or grasping movements or button presses (Arikan et al., 2021; Buckingham et al., 2010; Colino et al., 2014; Juravle et al., 2010; Voss et al., 2008; Voudouris & Fiehler, 2017, 2021) but no production of an additional remote effect like the action our participants had to produce. There is ample evidence suggesting that the production of not only incompatible compared to compatible (e.g., Crothers et al., 1999; Kunde, 2001; Kunde et al., 2007, 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013; Schwarz et al., 2018; Wirth et al., 2015; Experiments 1-4), but also of in general more complex compared to less complex actions takes more time (Canic & Franks, 1989; Klapp & Erwin, 1976; van Mier & Hulstijn, 1993). It thus would not be implausible or surprising if also the effects that this extended action preparation process has on perception would be temporally extended as well.

A more surprising finding of Experiment 6 might however be the absence of a difference between the compatible and incompatible condition in the suppression strength after movement onset. While the main aim of this experiment was to investigate anticipatory tactile suppression, the results of Experiment 5 revealed a downregulation of incompatible resident effects after and most likely also during action execution suggesting that haptic neglect might also extend to movement execution in Experiment 6. However, we only found a general tactile gating effect for the after movement onset category (though only descriptive in the compatible condition), but no specific haptic neglect in the incompatible condition which is contradictory to the results of Experiment 5. The reason for these diverging patterns of results might however lay in the different task characteristics of Experiments 5 & 6. In Experiment 5, the task required continuous monitoring of action effects throughout the whole movement phase which might likely have led to a more or less constant need to downregulate one of the incompatible action effects to suppress the otherwise occurring conflict in motor control. In Experiment 6 however, participants could produce very short and fast movements which also did not require much monitoring anymore once they had been initiated since participants also did not have to stop within the target boxes, but only had to move the cursor beyond a certain point to complete a given trial. Therefore the motor conflict was most likely only present during movement planning in Experiment 6, but not anymore during or after the (very short) movement. This conjecture based on the task characteristics of the different experiments is also in line with a recent study by Voudouris & Fiehler (2021) who demonstrated that tactile gating effects were negatively correlated with movement speed. Specifically they found that tactile sensitivity on a hand performing a reaching movement was decreased at early and late stages during the reaching movement when the hand was moving relatively slowly, but that gating disappeared almost completely during the time of maximum movement speed halfway through the movement. Given the strong differences in movement speed of participants between Experiments 5 & 6, the results by Voudouris & Fiehler (2021) could thus provide an additional explanation for the absence of haptic neglect in Experiment 6 compared to Experiment 5 and the low general tactile gating after movement onset in Experiment 6.

Even though the main aim of Experiment 6 was to study tactile suppression in situations of compatible and incompatible action effect situations, the present results also demonstrated tactile enhancement in some of the experimental conditions. Specifically, the results suggested that tactile stimulations were experienced as significantly stronger on the active hand compared to the inactive hand more than 200 ms prior to movement onset in the compatible condition and more than 300 ms prior to movement onset in the incompatible condition. It is not uncommon to observe both tactile suppression and tactile enhancement effects in the same experiment as the occurrence of suppression and enhancement depend on multiple factors such as the time point and location of the stimulation and the specific action or movement to be performed (e.g., Juravle et al., 2010; Juravle, Heed, Spence, & Röder, 2016; Voudouris & Fiehler, 2017, 2021; see Juravle, Binsted, & Spence, 2017, for a review). It seems that, perhaps not surprisingly, the “decision” by the system whether to suppress or enhance sensory information is dependent on the relevance of the tactile information at a given location, at a given point in time and under the given task characteristics. Against this background it is interesting that we could observe tactile enhancement both in the compatible and in the incompatible condition before tactile suppression was present in the movement planning phase. Due to the nature of the Timed Response Paradigm (Favilla et al., 1990), participants had to withhold their response after the presentation of the visual stimuli until the counter indicated that participants should perform their response. Given the relatively long time interval between stimulus onset and go signal (2 s), participants should have selected their response way before the tactile stimulation was delivered (Pashler, 1994; Sigman & Dehaene, 2008). Therefore, it seems likely that participants withheld the prepared response for most of the time while observing the counter before actually generating the motor response to respond with the go signal. The actual motor conflict generated by the anticipated incompatible resident and remote action effects might thus also only be present after this period of withholding the response and during actual motor preparation which could explain the onset of tactile suppression and gating effects approximately 200 to 300 ms before movement onset. The suggestion that this time interval and the perceptual effects observed during it are indeed linked to motor generation processes is also supported by the finding that this time interval approximately coincides with previously observed reaction times for fully pre-planned movements (Rosenbaum, 1980). While the onset of these effects can thus be explained by the onset of motor generation, we can only speculate about the reasons for tactile enhancement during the period while the motor response was still withheld. Given that previous studies have found tactile enhancement especially in situations of increased relevance of tactile information for the agent and the action (Juravle et al., 2017; Voudouris & Fiehler, 2021), it might be that tactile enhancement during response withholding in the current experiment might have been due to an increased alertness for sensory signals on the to-be-moved body effector that could have indicated the need to adjust the selected response.

Another point that we briefly want to discuss is the fact that we did not only find (anticipatory) tactile suppression effects in the incompatible condition of Experiment 6, but also to a smaller extent in the compatible condition. The suggested model of active self-generation (see section *4.3. A model accounting for and explaining the limitations of extending the self through action*) does not suggest that suppression of action effects should also occur in the case of compatibility. Neither did we observe such effects in Experiment 5, though the measure of Experiment 5 and essentially its lack of a baseline condition would have also made it difficult if not impossible to detect such general suppression effects. The results of Experiment 6 are however not at odds with these previous findings and the suggested model since they essentially suggest that there are two different, additive sources of tactile suppression taking place simultaneously. One of these is the suggested effect of the suppression of anticipated resident action effects which are in conflict with anticipated remote action effects that is manifested in the significant differences in points of subjective equality between compatible and incompatible conditions. On top of this there also seems to be a general effect of tactile gating (Arikan et al., 2021; Buckingham et al., 2010; Colino & Binsted, 2016; Colino et al., 2014; Voss et al., 2008) during motor generation and (partially) during or after motor execution which is present both in the compatible and in the incompatible condition.

Finally, the current experiment also has some limitations which should also receive some attention still. First, the critical main effect of compatibility in the repeated measures ANOVA on points of subjective equality was only marginally significant and rather small. However, the simple effects analyses revealed significant compatibility effects for at least some time point categories and essentially for the theoretically most relevant ones where we had also expected compatibility effects. The absence of significant compatibility effects in the other time point categories might have thus led to a decrease of the overall main effect of compatibility thus resulting in the only marginally significant result. Though it is odd to observe an insignificant interaction effect as well in this situation where some simple effects show significant differences and others do not, such situations can occur in cases of limited statistical power. Given the relatively small size of the observed effects and the complexity of the 2 x 5 design it is likely that the experiment was indeed relatively low-powered. A second, related limitation of Experiment 6 is the relatively high drop-out rate of participants. This was most likely due to the relatively challenging task of providing an accurately timed response while at the same time attending to the tactile stimuli in order to give valid judgments of their perceived intensity. Indeed the number of participants showing stereotypical response patterns or response patterns that were completely unrelated to the physical stimulus intensity in addition to the participants who decided to quit the experiment early, suggest that a relatively high number of participants seemingly “gave up” on performing the task properly.

9.4. Conclusions

Controlling a body-external object that moves in a spatially discrepant way compared to the body effector controlling that object has been shown to lead to “haptic neglect”, a downregulation of the perceived sensory signals on the body effector (Fourneret & Jeanneord, 1998; Heuer & Rapp, 2012; Knoblich & Kircher, 2004; Müsseler & Sutter, 2009; Sülzenbrück & Heuer, 2009; Experiment 5). Experiment 6 showed that this effect is also already present before movement onset based on the anticipation of the to-be-produced action effects. Such anticipatory haptic neglect most likely serves to solve otherwise occurring motor conflict when producing spatially discrepant body and object movements and might thus be a necessary precondition for the production of such movements.

10. Theoretical integration and synthesis

10.1. Empirical summary

In the previously reported experiments, I investigated how combinations of mutually compatible or incompatible resident and remote action effects affect the perception of these action effects and how this determines whether or to what extent a controlled body-external object becomes integrated into the agent's self in terms of agency and ownership experiences.

In Experiment 1, subjective levels of agency and, to a lesser extent, ownership were higher when remote effects were compatible with body movements and thus with resident effects than when they were incompatible. Similarly, reaction times indicated a performance benefit when resident and remote effects were predictably compatible and performance costs when they were predictably incompatible. Predictability of the compatibility or incompatibility however did not have an influence on the sense of agency or the sense of ownership, possibly because of the use of continuous actions, which allowed the formation of predictions while already moving.

Experiment 2 replicated the findings of Experiment 1 regarding the influence of compatibility on the sense of agency and ownership. Using discrete actions, which prevented the formation of predictions while moving, also predictability now had an independent influence on the sense of agency, but not on the sense of ownership. In contrast to Experiment 1, predictable compatibility only affected reaction times under forced choice conditions.

In Experiment 3, I demonstrated that proprioceptive drift of the body effector towards a controlled object, which can be construed an implicit measure for the sense of ownership for this object, was larger with compatible than with incompatible resident and remote effects. This effect was reflected by explicit agency ratings, though explicit ownership ratings did not differ for compatible or incompatible effects. Reaction times were again faster in the compatible than in the incompatible condition, though this effect was not significant in all conditions.

Experiment 4 showed that the previously observed reduced proprioceptive drift towards the controlled object under incompatible conditions reflected a full elimination of ownership experience by adding an additional baseline condition with no control over the same object.

This effect was reflected in both kinds of ratings, which were also lower in the incompatible than in the compatible condition. Furthermore, also reaction times showed the same compatibility effect.

In Experiment 5, I showed that incompatibility between resident and remote effects of an action leads to less precise representations of these effects after and most likely also during the action. The results demonstrate that both resident and remote effects can be flexibly suppressed by an agent when confronted with an incompatible combination of the two and that the “decision” which of the two gets suppressed is determined by the importance of the sensory information from the specific modality in a given situation.

Experiment 6 demonstrated the suppression of resident action effects which are incompatible with remote action effects in a more direct way than the indirect measure in Experiment 5. Furthermore, I also showed in Experiment 6 that suppression of resident action effects with incompatible accompanying remote effects already happens during movement planning based on the anticipation of action effects before any efferent activity is executed. The experiment provides evidence for the occurrence of this effect from approximately 200 ms before movement onset on.

10.2. Linking action control with the sense of agency and the sense of ownership

According to ideomotor theory, planning and executing goal-directed, voluntary actions requires the anticipation of the intended sensory effects of this action and thus crucially depends on knowledge about which sensory effects an action typically produces (Elsner & Hommel, 2001; Hommel, 2013; James, 1890/1981; Koch et al., 2004; Kunde, 2001; Shin et al., 2010; Waszak et al., 2012). Similarly, also selfhood experiences, such as the sense of agency and the sense of ownership, depend on the matching of one’s own actions, resident and remote sensory effects (Armel & Ramachandran, 2003; Blanke, 2012; Blanke et al., 2015; Botvinick & Cohen, 1998; Ma & Hommel, 2015a; Samad et al., 2015; Tsakiris, 2010, 2017). The model I proposed suggests that when performing an action, the representational strengths of both anticipated and actually perceived sensory effects varies depending on the compatibility of resident and remote action effects based on previous experiences (see section *4.3. A model accounting for and explaining the limitations of extending the self through action*). As others and I demonstrated, human agents tend to suppress incoming sensory information from the body effector, i.e. the resident effects of an action, when these are incompatible with the visual information about the movements of a controlled object, i.e. the remote effects of an action (Fourneret & Jeannerod, 1998; Knoblich & Kircher, 2004; Heuer & Rapp, 2012; Müsseler & Sutter, 2009; Sülzenbrück & Heuer, 2009; Experiments 5 & 6). While this seems to be a useful and even necessary strategy to be able to perform movements with such incompatible resident and remote effects in the first place, the results presented in Experiments 1-4 clearly demonstrate that this strategy comes at the cost of reducing or even eliminating agency and ownership experiences for incompatible action effects. If there is no incompatibility between resident and remote effects of an action, there is also no need to suppress any of these. Without suppression, remote effects that are accompanied by contingent resident effects are easily integrated into the agent's self in terms of agency and ownership as suggested by bottom-up approaches (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Ma & Hommel, 2015a).

As demonstrated by Experiments 5 & 6, suppression of incompatible action effects can occur prior to, during and after action execution suggesting that both the anticipation and the monitoring of mutually incompatible action effects can trigger these suppression effects. In Experiment 6 we mainly observed anticipatory suppression of incompatible action effects supporting the claim that such suppression is a necessary correlate of generating actions with incompatible resident and remote effects. In contrast, Experiment 5 demonstrated extended suppression during and after the performance of longer periods of continuous control over an external object which moved incompatibly to the participants' movements, which must be at least partially based on the monitoring of action effects. It is exactly this effect monitoring which I suggest to be the underlying factor behind active agency and ownership experiences as laid out in section 4*.3. A model accounting for and explaining the limitations of extending the self through action* (see also Figure 3, right part). While the initial suppression of resident effects that are incompatible with remote effects thus serves to produce actions in the first place, its continuation during the action because of effect observation is likely the reason for the elimination of active ownership.

Further support for the suggested model and the "double-edged sword" of suppression of resident effects regarding action control and selfhood experiences comes from the previously mentioned deafferented patients (e.g., Cole & Paillard, 1995; Gallagher & Cole, 1995; Lajoie et al., 1992; Renault et al., 2018; Taub, 1976). Deafferented patients are due to their loss of proprioceptive and tactile sensations basically in a constant state of haptic neglect. While these patients do not show the typical performance drops in tasks with incompatible resident and remote effects compared to tasks with compatible effects such as in mirror drawing that neurotypical participants show, they also have a drastically altered self-perception (Cole & Paillard, 1995; Gallagher & Cole, 1995; Renault et al., 2018). In self-reports of these patients, one of them, for example, described a feeling of "floating" without a body just after the onset of his condition while another patient perceives her body rather as a "tool" than as a body which is actually owned by her (Cole & Paillard, 1995, see section *3.1. The sense of (body) ownership*).

While the empirical findings presented here are greatly in line with the predictions derived from the model I presented at the beginning, some of the results from the reported experiments provide additional insights, which should be discussed with regard to the applicability of the model. One of these results is the finding from Experiment 2 that compatibility of resident and remote effects had an influence on the sense of agency, regardless of whether the remote effects of the action were predictable. This is in contrast to previous notions that have emphasized the role of a match between intended and observed perceptual changes following one's efferent activity and thus objective controllability of the perceptual changes (Carruthers, 2012; Gallagher, 2000; Haggard, 2017; Haggard & Chambon, 2012; Ma & Hommel, 2015a; Verschoor & Hommel, 2017; Wegner, 2017; Zaadnoordijk et al., 2019). According to these comparator-based points of view, there should be no difference between the sense of agency of remote effects which are unpredictably compatible or unpredictably incompatible with the resident effects since the effects do not match a sensory prediction in either case. Furthermore, because of the lack of a prediction, sense of agency should also be low or completely absent in both cases according to comparator models. This is however in stark contrast to the results of Experiment 2, which show high levels of agency for compatible action effects and significant differences between compatible and incompatible effects. The results also pose a challenge to the model presented here though. Without anticipation of compatibility or incompatibility between resident and remote effects, neither facilitation nor conflict can occur during action generation so also no representational weighting of the effects should occur which should lead to no differential effects regarding the integration of resident and remote effects. This absence of both facilitation and conflict is very clearly reflected in the intermediate level of reaction times for actions with unpredictable remote effects, regardless of their compatibility. However, even in the absence of conflict between resident and remote effects during action generation, their incompatibility is most likely still recognized during action monitoring (Figure 3B, right) and one of the conflicting action effects might therefore still be suppressed based on this observed incompatibility. The results of previous experiments (e.g., Ebert & Wegner, 2010; Ramachandran & Rogers-Ramachandran, 1996) mirror the results from Experiment 1 and 2 in demonstrating that even for unpredicted (and essentially uncontrolled) action effects, one can readily experience feelings of agency and possibly even ownership based on the “consistency” (Wegner & Sparrow, 2004) between resident and remote action effects. However, that humans can seemingly experience agency and ownership for unpredicted action effects, simply based on monitoring their overlap with concurrent resident effects, is not to say that predictability of action effects has no role at all for selfhood experiences. In contrast, Experiment 2 clearly demonstrated that predictability of action effects also had a significant influence on the sense of agency[11]. Furthermore, the effects that predicted action effects had on action generation in Experiments 1 & 6 as well as

[11] There was no significant influence of predictability on the sense of ownership in Experiment 2. However, as explained above (section *6.3.3. Discussion*), this was likely due to a floor effect (Everitt, 2006) given the generally very low ownership ratings.

in previous studies (e.g., Crothers et al., 1999; Kunde, 2001; Kunde et al., 2007, 2012; Müsseler et al., 2008; Müsseler & Skottke, 2011; Pfister & Kunde, 2013; Schwarz et al., 2018; Wirth et al., 2015) show that the prediction, or anticipation, of specific action effects has clear influences on the action-perception complex.

Additionally, it might also be that the engagement in voluntary actions but the absence of any predictability of possible remote action effects makes the agent very alert and sensitive for any possible action-contingent sensory changes in the environment. Action-concurrent afferent signals might thus be seen as potential effects of one's own action and are therefore tested for their consistency with resident action effects which would be in line with bottom-up approaches of the minimal self (e.g., Ma & Hommel, 2015a, b; Verschoor & Hommel, 2017). It might thus be that participants in the unpredictable conditions of Experiments 1 & 2 still predicted (or better: expected) that their actions would trigger some remote action effect, even though they were not able to predict the specific nature of this effect. This could explain why the cursor movements were attended to at all and thus had an influence on the sense of agency and the sense of ownership in the absence of any specific sensory predictions. While to this point only speculative, this idea is supported by various studies showing that children who still need to develop a robust self-model are highly sensitive to sensorimotor contingencies and strongly base their judgments of agency and ownership on these contingencies (Bahrick and Watson, 1985; Zmyj, Jank, Schütz-Bosbach, & Daum, 2011; Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013; Filippetti, Lloyd-Fox, Longo, Farroni, & Johnson, 2015). It might thus be that, especially in novel situations, also adults might attend any motor-correlated sensory effects very closely to detect agency and ownership cues. This explanation is not mutually exclusive to the model I presented previously, but could rather help to explain how and why the previously mentioned mechanisms also come to play in the absence of sensory predictions.

In summary, the independence of predictability and compatibility effects on selfhood measures in Experiments 1 & 2 speaks for a comparison of both anticipated and actually perceived resident and remote action effects, which both have an additive influence on agency and ownership experiences. This is supported by the findings of Experiments 5 & 6 which show that also the suppression of incompatible action effects can occur both based on predictions and based on the monitoring of incompatibility. Admittedly, a direct test if the observed suppression mechanisms also causally account for the observed selfhood experiences still remains necessary for future empirical work due to the practical challenges and the complexity that such an experiment would bring about. Nevertheless, I believe that the present experiments provide strong support for a causal link between these two effects and thus also for the suggested model.

10.3. Limitations of the active self account

Recent bottom-up approaches of active self-construction have argued that a self-experience is actively generated by the observations of afferent sensory signals which are intended and thus controlled by an individual (e.g., Ma & Hommel, 2015a; Verschoor & Hommel, 2017). This essentially assumes that any object, which a person controls through voluntary actions, should also become part of oneself in terms of experiences of agency and ownership. However, the present results suggest that this is clearly not the case as I have demonstrated that (i) active control is not sufficient for experiences of agency and ownership and (ii) experiences of agency and ownership can differ from each other in the same situation. In the following, I will elaborate on these two limitations in more detail.

10.3.1. The insufficiency of active control for selfhood experience

If controllability of afferent sensory signals was the only determinant of whether the source of these sensory signals is perceived as being part of the self, essentially any object that falls into the visual field should be regarded as being part of the self, given the controllability of visual input through oculomotor activity (Liesner & Kunde, 2021). However, this is clearly not the way we experience ourselves and the world around us. As pointed out in the introduction, the self-experience of a person is closely linked to the perception of their body (Gallagher, 2000). Therefore, any perceptual changes in the environment that might be integrated into the self must essentially be accompanied by concurrent perceptual changes in the body itself, i.e. by resident effects. This is essentially also the original idea of the active rubber hand illusion (e.g., Dummer et al., 2009; Kalckert & Ehrsson, 2012, 2014a, 2017; Ma & Hommel, 2013, 2015b; Pfister et al., 2021; Sanchez-Vives et al., 2010) and implemented in its various modifications (e.g., Kirsch et al., 2016; Ma & Hommel, 2015a; Weser et al., 2017; Slater et al., 2010; Zopf et al., 2018) since in all these situations, the active generation of efferent activity also produces resident effects that provide the agent with feedback about the current limb positions. However, as Experiments 1-4 as well as previous studies (Ebert & Wegner, 2010; Farrer et al., 2003) have demonstrated, the coincidence of simultaneous resident and remote action effects is not sufficient for a self-experience either. Instead, the observed remote action effects must be compatible with resident action effects in their spatiotemporal dynamics and must be linked with the same motor patterns based on previously learned action-effect contingencies. Only if this prerequisite is fulfilled, the system ascribes both the resident and remote effects to the same common cause (i.e., the action) and integrates them so that the source of the remote effects is experienced as part of one's (minimal) self (Blanke, 2012; Blanke et al., 2015; Samad et al., 2015; Tsakiris, 2010, 2017).

Given that remote effects that are compatible or incompatible to the accompanying resident effects do not need to differ regarding the information they provide to the agent about the current state of the action or limb positions, these findings are far from trivial and provide new insights into an important mechanism shaping minimal self-experiences. In Experiments 3 & 4, the final distance between hand and cursor was identical in the additive and inverted condition so that sensory information from hand and cursor were essentially equally "helpful" to estimate the position of each other in these situations. Furthermore, in both conditions, resident and remote effects were perfectly synchronous and controllable. These characteristics of (in)compatibility differ from previously identified variables that disrupt experiences of agency or ownership such as increasing distances between body effectors and external objects (Lloyd, 2007; Kalckert et al., 2019b) or delays and asynchronies between resident and remote sensory effects (Botvinick & Cohen, 1998; Dummer et al., 2009; Ehrsson et al., 2004; Kalckert &

Ehrsson, 2012, 2014a; Ma & Hommel, 2013, 2015a, b; Tsakiris & Haggard, 2005). Such spatial or temporal discrepancies objectively decrease the plausibility that resident and remote effects might stem from the same common cause; however, they cannot explain the present findings. Additionally, also most previous studies on multisensory integration, which have already demonstrated decreased integration of spatially discrepant resident and remote action effects (e.g., Debats et al., 2017b; Debats & Heuer, 2018a, b, 2020; Rand & Heuer, 2013, 2019; Rand & Rentsch, 2016; Rand et al., 2013), cannot explain the findings I presented here. While these studies already demonstrated that spatial discrepancy between a body effector and a controlled visual object can lead to differential effects regarding the integration of visual and proprioceptive signals, the differential effects in these studies were essentially driven by actual differences in physical distances between body effector and visual object. Thus, unlike in Experiments 3 & 4, the informative value of hand and object position for each other varied in these studies. There is one study that poses a notable exception to this (Debats et al., 2017a). However, while in this study, the final position of hand and cursor differed equally between conditions, like in Experiments 3 & 4, the complexity of the relationship between hand and cursor movement and of the movements themselves differed in this study. In the conditions in which Debats et al. (2017a) found reduced integration of tactile and visual signals, the straight hand movements of participants were transformed into curved cursor movements. While it is unclear whether the reduced integration in this study was due to this specific aspect of the transformation or due to the discrepancy between hand and cursor during the transformation, in Experiments 3 & 4 the complexity of movement transformations was held constant so it cannot account for the previously discussed results.

The data I presented in this dissertation thus provide empirical evidence for a further limiting mechanism of how actively controlled body-external objects can become integrated into what one calls the "self": The combination of resident and remote effects of an action must sufficiently overlap in their dimensional characteristics with previous experiences about typical effect combinations in order for voluntarily controlled objects to become integrated into the self.

10.3.2. Differentiating between the sense of agency, the sense of ownership and different aspects of the two

While originally seen as two related but different aspects of the minimal self (Gallagher, 2000), the sense of agency and the sense of ownership have lately been regarded as widely equivalent by sensorimotor approaches of the self (e.g., Ma & Hommel, 2015a; Verschoor & Hommel, 2017). The experiments I presented here step into a line of other empirical findings that suggest a differentiation of these concepts (Jeannerod, 2003; Kalckert & Ehrsson, 2012; Riemer et al., 2013; Tsakiris et al., 2006, 2007).

Regarding explicit measures of subjective sense of agency and sense of ownership, the results clearly demonstrate that experiences of agency were more strongly affected by the implemented manipulations and that levels of experienced agency were also generally higher than those of ownership. This is not surprising given the use of highly body-dissimilar stimuli and previous findings that the sense of ownership decreases the less similar to the biological body an object is (Guterstam et al., 2013; Kalckert et al., 2019a; Tsakiris et al., 2010). Given this low overall level of experienced ownership, the often weak or absent effects of (in)compatibility of resident and remote effects on explicit ratings of ownership might also be due to a floor effect (Everitt, 2006). Sense of agency however has been shown to be more easily elicited also by relatively arbitrary effects in past research, provided that these effects were sufficiently contingent on a person’s control (e.g., Chambon et al., 2014; Chambon, Wenke, Fleming, Prinz, & Haggard, 2013; Farrer & Frith, 2002; Sperduti, Delaveau, Fossati, & Nadel, 2011).

Regarding the measure of proprioceptive drift in Experiments 3 & 4 though, the results show that an implicit sense of ownership can still emerge with compatibly controlled body-dissimilar stimuli, which is in line with previous findings (e.g., Armel & Ramachandran, 2003; Ma & Hommel, 2015a). It remains an open question for future research whether this implicit sense of ownership is comparable to the sense of ownership assessed with implicit measures for body-similar objects like virtual or fake hands (Kalckert et al., 2019a; Liesner et al., 2021). However, as the measure of proprioceptive drift in essence indicates the degree of misjudgment of a body part toward a body-external object, it must represent an integration of the two at least to a certain degree.

Actually, some researchers have suggested that a sense of ownership, especially an explicit one, cannot be experienced for body-dissimilar objects at all (Guterstam et al., 2013; Kalckert et al., 2019a; Tsakiris et al., 2010; Tsakiris & Haggard, 2005). It has been suggested that this is due to top-down influences of a fixed body-model against which all incoming sensory information is tested (Tsakiris, 2010; Tsakiris, Constantini, & Haggard, 2008). The present results as well as the findings of other studies (e.g., Fan, Coppi, & Ehrsson, 2021; Ma & Hommel, 2015a, b; Maravita et al., 2002; Kirsch et al., 2016; Weser et al., 2017) are however in contrast to this as they clearly show that various forms of a sense of body ownership can also be experienced with non-corporeal objects or in unnatural settings. However, these findings do not speak against top-down influences on the sense of ownership in general, but they only suggest that these top-down influences might be less deterministic in that they do not influence the presence or absence of a sense of ownership in an absolute manner, but rather influence the intensity of the ownership experience. In line with this, several studies that have identified a sense of ownership both for corporeal and non-corporeal objects, have often found this sense to be more pronounced with the former than with the latter (e.g., Liepelt et al., 2017; Ma & Hommel, 2015b; Zopf et al., 2018). However, recent theoretical approaches have suggested that bottom-up and top-down models of the sense of ownership might be less incompatible than previously thought and that both kinds of mechanisms contribute to the formation of ownership experiences (e.g., Ehrsson & Chancel, 2019; Liesner et al., 2021; Samad et al., 2015). The present experiments and the model I presented here step into this line by demonstrating the importance of bottom-up sensorimotor contingencies for an experience of agency and ownership, but also revealing some clear limitations regarding the kind of sensorimotor contingencies which are able to elicit these sensations. It seems plausible that for the experience of a sense of ownership for body-external objects, multiple cues and information from different sources are integrated to an overall “likelihood” that a perceived sensation stems from one’s body (Chancel, Hasenack, & Ehrsson, 2021; Kilteni, Maselli, Kording, & Slater, 2015; Maselli & Slater, 2013; Samad et al., 2015; Slater et al., 2010). Once this likelihood then exceeds a certain threshold a sense of ownership of some form might be experienced. Corporeality might likely be one source of information for this process and for corporeal objects the likelihood that these are seen as part of one's body might be higher by default. This could also explain why non-corporeal objects are usually only experienced as "owned" by the own body when there are additional ownership cues such as controllability of the objects (i.e. agency) while for corporeal objects ownership experiences can often also arise under passive stimulation conditions (e.g., Kirsch et al., 2016; Liepelt et al., 2017; Ma & Hommel, 2015b; Zopf et al., 2018).

The results I presented here thus suggest a need to differentiate between the sense of agency and the sense of ownership, though they also show that the two are clearly related and partially dependent on each other. While the sense of agency and the sense of ownership generally seem to be affected similarly by the relationship between resident and remote action effects, the sense of ownership is obviously more difficult to elicit for body-dissimilar objects (Guterstam et al., 2013; Kalckert et al., 2019a; Tsakiris et al., 2010). Moreover, while the sense of ownership for body-dissimilar objects depends on voluntary actions manipulating these objects (Kirsch et al., 2016; Ma & Hommel, 2015a, b; Maravita et al., 2002; Weser et al., 2017), the explicit experience of this control does not seem to be essential for an implicit sense of ownership to arise. Experiment 3 showed no differences in explicit agency experiences for compatible and incompatible remote effects, though the proprioceptive drift towards the two differed significantly. While I did not use implicit measures of the sense of agency such as temporal (or "intentional") binding (e.g., Cao et al., 2020; Cravo, Claessens, & Baldo, 2009; Engbert & Wohlschläger, 2007; Haggard, 2017; Haggard et al., 2002) in the present experiments, it might be that these could have revealed an even tighter relationship between the sense of agency and ownership for controlled body-dissimilar objects. This might be an interesting avenue for future research, especially against the background of accumulating evidence demonstrating the non-redundancy of explicit and implicit measures of the sense of agency and the sense of ownership (Buehner, 2012; Kirsch et al., 2019; Majchrowicz & Wierzchoń, 2018; Moore et al., 2009; Schwarz et al., 2019; Suzuki et al., 2019).

10.4. Future directions and open questions

10.4.1. Suppression of resident effects or shifting of attentional resources between resident and remote effects?

Besides providing empirical evidence for the suppression of resident effects that interfere with incompatible remote effects of the same action, Experiment 5 also demonstrated that this effect is not constrained to resident effects, but that also incompatible remote effects can be suppressed. While I argued that the “decision” which of the incompatible action effects is suppressed is driven by their relevance for the given task, the idea that both effects follow the same mechanisms is very much compatible with the common ideomotor notion that humans can flexibly decide which effects they want to base their actions upon (e.g., Memelink & Hommel, 2013; Mocke et al., 2020; Pfister, 2019). However, these findings also open up questions about the precise nature of this suppression, its effect on the non-suppressed effects and the interplay between suppressed and non-suppressed effects.

The suppression hypothesis states that suppression of incompatible action effects happens to resolve the interference triggered by the conflicting motor patterns linked to the incompatible action effects so that one of the motor links is no longer activated. However, the active suppression of one action effect seems to be a rather disadvantageous mechanism for an agent to engage in since it is resource consuming while at the same time hindering rather than supporting action-relevant perception. Attentional pool-of-resources theories (Kahneman, 1973) however propose a different point of view on how resident and remote action effects might be processed. According to this account, humans possess a limited amount of attentional resources, which they can flexibly divide between different tasks or sources of information. Under this framework, incompatible effects of one source might not simply be suppressed per se, but this “suppression” might be better understood as a downregulation of attentional resources to the effects from this source while the effects of the other conflicting source might then receive this additional attentional resource instead. This alternative conceptualization does not make any alternative predictions regarding the action effects which are processed to a lesser degree in response to incompatibility since, instead of an active suppression of these effects, it simply assumes an “attending away” from these effects (Liesner et al., 2021). For the non-suppressed or non-neglected action effects, the attentional approach would however predict that these should be processed stronger correspondingly, which would presumably be advantageous for the agent given that the action is generated and represented through these effects. Importantly, for actions with compatible resident and remote effects, the attentional resources account does not differ from the previously presented model in any respect. In compatible situations, there is no conflict between resident and remote action effects and therefore both effect components can be easily attended to. The shared attention on both resident and remote effects should therefore lead to a strong representation of both of these and thus facilitate integration of them in terms of sense of agency and sense of ownership (see section *4.3. A model accounting for and explaining the limitations of extending the self through action*). Indeed, previous research on action-perception interaction, has demonstrated that most, if not all, effects of action planning and action performance on perception are mediated by changes in attention (e.g., Cañal-Bruland, Zhu, van der Kamp, & Masters, 2011; Gray, 2013; Gray & Cañal-Bruland, 2015; Kirsch, Heitling, & Kunde, 2018; Kirsch, Kitzmann, & Kunde, 2021).

Regarding the issue whether the non-integration of mutually incompatible resident and remote action effects is due to pure suppression of resident effects or shifts of attentional resources between resident and remote effects, also the question of equivalence of resident and remote effect representations arises. As explained above, according to ideomotor theory, resident and remote effect codes are equally linked to motor patterns and can equally be used to activate the associated motor patterns (e.g., Memelink & Hommel, 2013; Mocke et al., 2020; Pfister, 2019). The results of Experiment 5 point in the same direction by demonstrating that both incompatible resident and remote action effects can be equally suppressed (or ignored), supporting the claim that the underlying mechanisms regarding the processing of resident and remote effects do not differ qualitatively. However, the exploratory analyses of Experiment 5 (see section 8.2.2.1) also showed that without an external manipulation of relevance of either resident or remote action effects, resident effects seem to be the ones that are more likely to be suppressed in situations of mutual incompatibility. I have previously argued that this would be an adaptive strategy in most situations since when manipulating external objects, the effects produced on, in or with these external objects are usually the very reason for acting. If one could achieve the same effect with one's body only, one would not need the external object (Liesner & Kunde, 2021). While this bias to neglect bodily information thus seems justified, it is nevertheless surprising that a human agent would neglect this information so easily given its necessity for survival. However, the downregulation approach can solve this contradiction as it seems more easily still since it does not exclude the possibility that some of the agent's attention still remains on the body (see also Collins et al., 2008, for empirical support for this claim).

Interestingly, a similar idea regarding the competition of multisensory stimuli for limited attentional resources has recently been put forward as a new explanation for the phenomenon of "sensory attenuation" (Horváth, 2015). Sensory attenuation describes the finding that self-produced sensory action effects are perceived as less intense than physically identical sensory stimuli that are not produced by the agent himself, which is also reflected in reduced event-related sensory potentials for self-produced effects (e.g., Brown et al., 2013; Desantis et al., 2012; Hughes, Desantis, & Waszak, 2013; Voss et al., 2008). Similarly, it has been shown that event-related potentials as response to unattended compared to attended stimuli are attenuated as well (e.g., Hillyard, Hink, Schwent, & Picton, 1973; Ozaki et al., 2004; Saupe, Widmann, Trujillo-Barreto, & Schröger, 2013). Horváth (2015) suggested that these two effects might be related and that the self-generation of a sensory effect in the environment inevitably produces other (resident) effects as well that might bind a substantial amount of attentional resources, which are then no longer available for the monitoring of other (remote) sensory effects. While direct evidence for this role of attention for the findings on sensory attenuation yet remains to be demonstrated, the mechanism suggested by Horváth (2015) fits very well with the currently presented model on the determinants of the integration of resident and remote action effects. This supports the previously made point that the integration or suppression of action effects might indeed be due to different allocations of attentional resources between compatible or incompatible resident and remote action effects.

The proposed explanation of downregulation of incompatible effects through a shift of attentional resources could be an interesting topic to investigate in future research. To directly test this idea against the concept of "pure" suppression of one incompatible action effect, one could design an experiment in which stimuli related to both resident and remote components of incompatible actions have to be detected. When introducing a manipulation of effect relevance (for example as in Experiment 5), the stimulus detection related to the less relevant action effect should deteriorate. However, if the attentional shift hypothesis is true, this should lead to an improved detection of stimuli for the more relevant component or even a negative correlation between the two detection rates. It is important to note that this attentional shift however most likely does not happen in an all-or-nothing manner. As suggested by Experiment 5 and in previous studies (e.g., Collins et al., 2008), while the attentional focus usually lies on either the biological body or on the (effective part of the) controlled object, also the suppressed or neglected component of the action seems to be processed at least to some degree still. However, the specific interplay of the processing of compatible and incompatible resident and remote effects and their potential influence on agency and ownership experiences is still unclear and could thus be a fruitful ground for future research.

To test the attentional shift hypothesis, the paradigm of Experiment 6 could be used and in addition to the tactile stimuli presented before also visual stimuli related to the controlled cursor could be used. Participants could then be asked to report whether one or both of these stimuli have been present in a given compatible or incompatible trial. Additionally, also eye-tracking could be used to gain some insights into the perceptual mechanisms that are at work when performing actions with different kinds of action effects as eye movements can give information about overt attention orientation processes (Posner, 1980, 2016). Interestingly, in a recent EEG study, Huber-Huber, Steininger, Grüner, & Ansorge (2021) showed neural evidence that saccades to a visual target do not only direct attention to that target, but that they also enhance the sensory processing and representation of these targets. This finding suggests that saccadic shifts of overt attention might closely represent the assumed mechanisms taking place when monitoring different action effects. Eye tracking could thus be used as an additional measure to test the suggested model and to corroborate the findings on detection and integration of different action effects.

10.4.2. Developmental trajectory of action control, the sense of agency and the sense of ownership

Knowing which sensory effects are typically produced by an action, how to achieve a certain intended sensory effect through a voluntary action and whether observed sensory effects might stem from the same action crucially depend on an agent's sensorimotor experience (e.g., Fabbri-Destro & Rizzolatti, 2008; Hommel et al., 2001; Liesner et al., 2021; Meltzoff, 2007; Piaget, 1936/1963; Verschoor & Hommel, 2017). Humans thus do not possess innate links between motor patterns and the sensory effects these produce (Greenwald, 1970; Hommel & Elsner, 2009; James, 1890/1981), but have to learn these associations based on exploration and observation of the perceived effects, a mechanism which is often referred to as "motor babbling" in children (e.g., Paulus et al., 2012). As explained above, also incompatibility between different effects of an action is therefore based on experience with the sensory effects, which are typically produced by an action or which typically occur together, and on the violations of these associations. It would therefore be interesting to investigate how different levels of sensorimotor experience might influence both ideomotor action control mechanisms on the one hand, but also the sense of agency and the sense of ownership on the other hand. Children of different age groups might give interesting insights into these questions.

When investigating the sense of agency in children, it is often observed that children tend to overestimate their own agency for external events and attribute events to themselves that objectively were not caused by them and that this bias decreases with increasing age (e.g., Metcalfe, Eich, & Castel, 2010; van Elk, Rutjens, & van der Pligt, 2015). Similar observations have been made in multisensory illusion studies with children such as rubber hand illusion studies where children up to ten years often show a tendency to “overintegrate” sensory signals of different modalities (Cowie, Sterling, & Bremner, 2016; Gori, Del Viva, Sandini, & Burr, 2008; Nava, Föcker, & Gori, 2020). While adults, for example, usually only show partial integration of proprioceptive and visual information in the rubber hand illusion in terms of proprioceptive drift suggesting an optimal integration of multisensory signals (Ernst & Banks, 2002), children often seem to completely shift estimations of one modality towards the other. It thus seems that young children up to a certain age are very liberal when it comes to integrating external events into their self in terms of agency or ownership and that a more stable and restricted self-representation such as the internal body model suggested by Tsakiris and colleagues (Tsakiris, 2010; Tsakiris et al., 2008) is only established throughout development. Without such an elaborated model and consequently without strong top-down influences on the formation of agency and ownership experiences, the reliance on bottom-up cues, such as contingencies from different sensory modalities, to judge whether an effect in the environment was caused by oneself or might even represent a part of one’s body presumably increases. Further evidence for this point stems from studies, which have shown that children sometimes experience the rubber hand illusion already before stroking onset (Nava, Bolognini, & Turati, 2017) and that it is less vulnerable to asynchronous stroking in children (Cowie, Makin, & Bremner, 2013).

Regarding action control, previous studies have demonstrated that children up to eight years have severe problems when performing actions that produce incompatible resident and remote effects that exceed those of adults or sometimes are not able to perform these actions in a goal-directed manner at all (Beisert & Daum, 2021; Contreras-Vidal, Bo, Boudreau, & Clark, 2005). In combination with the findings reported above about agency and ownership experiences in young children, these results fit remarkably well with the mechanistic model of the active self I presented in this dissertation. As children should have less experience with typical action-effect combinations, they might not detect the interference emerging from incompatible action effects and might consequently also not engage strategies to cope with this interference (Liesner et al., 2021). They might thus not downregulate effect codes and sensory signals from incompatible resident and remote action effects, which could explain the increased difficulties when performing actions producing such effects (Beisert & Daum, 2021; Contreras-Vidal et al., 2005). On the other hand, the missing downregulation could however also explain children's relatively unselective integration of remote effects into the self in terms of agency and ownership since their representation of both resident and remote action effects should be strong for any action, regardless of the relationship between these effects.

To test the explanations for these results given by the presented model as well as its further predictions, one could test children from different age groups with the paradigms from the presented experiments. Specifically, the model would predict that performance costs due to incompatible resident and remote effects should decrease through childhood until it should stabilize at the level that is also observed in adults. Furthermore, younger children should experience agency and ownership equally for remote effects that are compatible and incompatible with resident effects and a differentiation between selfhood experiences for these situations should emerge and gradually increase with decreasing performance costs. Finally, also the downregulation of incompatible action effects, as for example seen in haptic neglect (Heuer & Rapp, 2012), should increase throughout childhood with increasing differences in selfhood experiences.

10.4.3. Implications for the design of virtual reality applications

Even though the experiments I described in this dissertation were mainly motivated by fundamental research questions, some implications for more applied settings can also be drawn from it. For example, a growing field for which the present results might be of relevance is the design and use of virtual (VR) or augmented reality (AR) scenarios. VR and AR applications are nowadays used in a wide range of different fields including, among many others, the treatment of mental health problems (e.g., Gonçalves, Pedrozo, Coutinho, Figueira, & Ventura, 2012), education and training in various work fields (e.g., Seymour et al., 2002), controlling robots or tools (e.g., Pérez, Diez, Usamentiaga, & García, 2019), the entertainment industry and psychological research (e.g., Slater et al., 2010). What these applications typically have in common is that the use of virtual reality instead of non-virtual settings facilitates the performance of tasks in a given situation or enables the users to experience situations that they would otherwise not be able to experience in vivo. However, in order for these effects to actually take place it is necessary that humans perceive the virtual reality setting as sufficiently realistic and controllable. This thus implies that users of virtual reality need to experience agency for the actions and the effects they produce in the virtual environment and, especially when it comes to the control of virtual objects such as, for example, avatars, also need to experience ownership.

Previous research has already identified various factors influencing the sense of agency and the sense of ownership in virtual reality scenarios such as the similarity between the real body and the controlled virtual object (Ma & Hommel, 2015b; Pritchard, Zopf, Polito, Kaplan, & Williams, 2016; Zopf et al., 2018), the synchrony between real and virtual objects (Ma & Hommel, 2013, 2015a; Pritchard et al., 2016) and the spatial distance between them (Aoyagi et al., 2021). The current experiments extend these findings by demonstrating that also the relationship between the movement trajectories of the real body and the virtual object and the resident and remote effects triggered by them plays a larger role than suggested by previous studies. Additionally, this relationship also influences the performance of humans when controlling external (real or virtual) objects with actions usually being facilitated and less error-prone the more similar body and object movements are (Kunde, 2001; Kunde et al., 2007, 2012; Müsseler & Skottke, 2011; Wirth et al., 2015; Experiments 1 & 3). This shows that taking into account the movement trajectories of both the body and the controlled objects in virtual reality does not only play a role for subjective user experience but also for the quality of the action outcomes when using virtual reality. This might be especially of relevance when using virtual reality in training settings for real-word situations or when using virtual reality as an interface to control and interact with real-world objects such as robots or tools. Overall, the present experiments thus suggest, in line with and in extension to previous studies (Aoyagi et al., 2021; Ma & Hommel, 2013, 2015a, b; Pritchard et al., 2016; Zopf et al., 2018), that virtual reality applications should strive for an as large as possible overlap between the movements and the body effector of the user on the one hand and the triggered movements and controlled objects in virtual reality on the other hand.

11. Final conclusions

I started off this dissertation by posing the question how we know that we have a “self” and introduced the framework by Gallagher (2000) suggesting that the answer to this question lies at how we know that we have a body and how we know that we are the one causing an action. Multisensory illusions, like for example the rubber hand illusion (e.g., Botvinick & Cohen, 1998), however suggest that we are relatively easily fooled regarding what is part of our body or which events we control in our environment. This has led some researchers to the conclusion that the minimal self in terms of a sense of agency and ownership is constructed in a strict bottom-up fashion so that all perceived parts of the environment, which are actively controlled by a person’s actions, become part of the self (e.g., Ma & Hommel, 2015a; Verschoor & Hommel, 2017). In the presented experiments, I investigated the restrictions to this approach by testing agency and ownership experiences for different kinds of actions and action effects.

The results presented here demonstrate that actively controlling body-external objects, such as for example tools, is not sufficient to experience these objects as belonging to the self since a sufficient dimensional overlap in the characteristics of resident and remote effects is necessary for this experience. Specifically, the resident and remote effects of an action must be linked to the same motor patterns based on long-term experiences for integration of an external object into the self to occur. If they are not, one of these action effects is suppressed which facilitates action generation but also prevents integration of resident and remote effects. This shows that controlled body-external objects as the origins of remote action effects are not integrated into the self unselectively, but that they have to be accompanied by resident effects that, based on learning experience, are highly likely to stem from the same action. While previous work has already pointed out the pivotal role of perceiving one’s body and thus of resident effects for minimal self-experiences (e.g., Gallagher, 2000; Liesner & Kunde, 2021), the current work does not only identify the specific characteristics of resident and remote effects that need to overlap so that an external object can be integrated into the self, but also provides a mechanistic explanation for this process.

We thus know that we have a self through the perception of bodily sensory signals from our own voluntary actions. If we perceive concurrent sensory signals from a body-external object with these bodily sensory signals and if, and only if, these concurrent sensory signals have been associated in the past with the same motor patterns that typically produce them, then also these body-external objects can be perceived as part of one's self.

12. References

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13. List of figures and tables

14. Anteile von (Ko-)Autoren an dem kumulativen Teil der Dissertation

Liesner, M., Kirsch, W., & Kunde, W. (2020). The interplay of predictive and postdictive components of experienced selfhood. *Consciousness and Cognition*, *77*, 102850. https://doi.org/10.1016/j.concog.2019.102850.

- Marvin Liesner: Konzeptualisierung, Vorbereitung und Durchführung der Experimente; Analyse und Interpretation der Daten; Schreiben des originalen und revidierten Manuskripts; Korrespondenz während des Review- und Produktionsprozesses

Datum, Ort	Unterschrift

- Wladimir Kirsch: Konzeptualisierung, Vorbereitung und Durchführung unpublizierter Pilotstudie; Feedback zu originalem und revidiertem Manuskript

Datum, Ort	Unterschrift

- Wilfried Kunde: Konzeptualisierung der Experimente; Bereitstellung finanzieller und technischer Ressourcen; Projektleitung; Feedback zu originalem und revidiertem Manuskript

Datum, Ort	Unterschrift

Liesner, M., Kirsch, W., Pfister, R., & Kunde, W. (2020). Spatial action–effect binding depends on type of action–effect transformation. *Attention, Perception, & Psychophysics*, *82*(5), 2531–2543. https://doi.org/10.3758/s13414-020-02013-2.

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Datum, Ort	Unterschrift

- Wladimir Kirsch: Feedback zu originalem und revidiertem Manuskript

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- Roland Pfister: Feedback zu originalem und revidiertem Manuskript

Datum, Ort	Unterschrift

- Wilfried Kunde: Konzeptualisierung der Experimente; Bereitstellung finanzieller und technischer Ressourcen; Projektleitung; Feedback zu originalem und revidiertem Manuskript

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Liesner, M., & Kunde, W. (2020). Suppression of mutually incompatible proprioceptive and visual action effects in tool use. *Plos One*, *15*(11), e0242327. https://doi.org/10.1371/journal.pone.0242327.

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Mit ihren Unterschriften bestätigen alle an den Publikationen beteiligten Koautoren einvernehmlich, dass sie die genannten Anteile an den jeweiligen Publikationen geleistet haben.

15. Affidavit

Ich bestätige hiermit, dass ich die vorgelegte Dissertationsschrift „I control it, but does it mean it is part of me? How the relationship between body movements and controlled object movements influences the sense of agency and the sense of ownership“ selbstständig angefertigt und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

Ich bestätige, dass ich die Gelegenheit zum Promotionsvorhaben nicht kommerziell vermittelt bekommen und keine Person oder Organisation eingeschaltet habe, die gegen Entgelt Betreuer bzw. Betreuerinnen für die Anfertigung von Dissertationen sucht.

Ich bestätige, dass ich die Regeln der Universität Würzburg über gute wissenschaftliche Praxis eingehalten habe.

Ich bestätige, dass die vorgelegte Dissertation bisher bei keinem Prüfungsverfahren eingereicht wurde; sie ist nicht identisch mit einer früher abgefassten wissenschaftlichen Arbeit, z. B. einer Magister-, Diplom-, Master, Bachelor- oder Zulassungsarbeit.

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