OWNING A BODY + MOVING A BODY = ME?

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OWNING A BODY + MOVING A BODY = ME?

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Editorial: Owning a Body + Moving a Body = Me?

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Editorial on the Research Topic

Owning a Body + Moving a Body = Me?

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Bodily self-consciousness involves awareness of being the embodied subject of our experience and of residing in and controlling a physical body. Such bodily self-awareness is ubiquitous and stands at the root of human nature (James, 1890). Indeed, sensing the body allows us to distinguish ourselves from the external world and shapes our identity. Currently, there is a wide consensus that the experience of our own body relies on at least two key neurocognitive components (Gallagher, 2000): the sense of agency (i.e., the feeling of authorship over one's own willed actions/thoughts) and the sense of body ownership (i.e., the sense that the physical body is experienced as mine). The sense of agency is thought to be rooted in efference copy mechanisms predicting the sensory consequences of the movements, and the resulting feedback (Haggard, 2008). In contrast, body ownership arises from the integration of body-related afferent signals (e.g., visual, somatic) that constantly reach our own body (Ehrsson, 2012; Kilteni et al., 2015).

Despite widespread agreement that a coherent experience of the bodily self emerges from the complex interplay between the sense of agency and the sense of body ownership, the character, and the form of this bond is not perfectly understood. Indeed, despite the increasing interest in the past years we do not conclusively know to which extent these two experiences interact, at both the behavioral and neural level. It is crucial to understand whether these agency related processes change actually the perceptual processes underlying the sense of ownership.

We have started to examine this relationship more closely, for example by using experimental manipulations of body ownership in healthy participants such as the rubber hand illusion (e.g., Kalckert and Ehrsson, 2012) or through investigating stroke-induced disorders of body awareness (e.g., Pia et al., 2016). This, in turn, has informed philosophical investigations on the bodily self and consciousness (De Vignemont, 2018; Wong, 2018). Our current research topic highlights the need to look at body ownership and sense of agency as a joint process in bodily self-awareness. Here we provide a brief overview of the contributions to the research topic, focusing on general themes that have emerged.

Amongst the non-original research articles, Gallagher defends the phenomenological nature of body ownership from deflationary and eliminativist critiques.

He argues that a phenomenological point of view sees ownership to be intrinsic to any experience and that pre-reflective self-awareness subserves ownership. In their meta-analysis of the neuroimaging literature (Zapparoli et al.) show that the three subcomponents of intentionality (i.e., content, timing, and the possibility of generating an action) are anatomically and functionally segregated within the human brain. Lastly, another paper reviews studies of disorders of the bodily self in schizophrenia. Klaver and Dijkerman propose that a weaker internal representation of one's own body can be considered a clinical subcomponent of schizophrenia. This, in turn, would render schizophrenic patients more susceptible to external stimulation.

Our original research articles make use of a variety of approaches, most notably, using virtual reality applications to manipulate perceptual input. Pritchard et al. for instance, implemented the rubber hand illusion paradigm using virtual reality. They investigate how incoming sensory signals affect ownership and agency. The data shows that the visual form, the plausibility, and the spatiotemporal integration of afferent input differentially affects ownership and agency. Similarly, another study (Ratcliffe and Newport) employs a virtual hand illusion paradigm which examines to what extent visual, spatial, and temporal properties of one's own hand affects action embodiment and body ownership. The authors show that visuomotor synchrony is sufficient to trigger agency, but not ownership, for which additional body-related visuospatial information is required. Harjunen et al. employ a virtual bimodal oddball task to study if vision of one's own body affects visuo-tactile interaction in endogenous spatial attention at different levels of visual and somatosensory processing. Results show that seeing one's own body affects cross-modal spatial attention and that this is reflected in early and late-sensory ERPs. Some other original research articles examine different pathological conditions, which affect the experience of one's own body. Rabellino et al. investigate whether traumatic experiences influence bodily perception. The authors administer the rubber hand illusion paradigm in individuals affected by Post Traumatic Stress Disorders (PTSD). The authors found that in PTSD there is a lower susceptibility to the illusion. Alfaro et al. present a rare case of alien hand syndrome in which a patient perceives her arm as having a "mind of its own." This condition prevented her from playing piano. In the light of the patient's brain damage, which includes the parietal lobe, the authors interpreted this abnormal motor control and anomalous self-body perception as a disruption of efferent outputs. Kanayama et al. examine neuroanatomical variations in relation to a self-report questionnaire measuring general experience of ownership and agency. Their voxel-based morphometry results show a negative correlation between ownership experience and insular gray matter volumes. Kashihara et al. examine the role of body ownership on the emergence of the observation inflation effect (OI)—a false memory phenomenon in which people falsely report having achieved an action when, in fact, they have only observed the action by another person. Indeed, their data shows that bodily self-consciousness has a key role in the emergence of such an effect.

One paper engaged in translational research (Raghavan et al.) attempt to exploit the current knowledge about the bodily self to treat disorders of the bodily self. The authors administered the Music Upper Limb Therapy-Integrated (MULT-I) to stroke patients, who exhibit a variety of symptoms related to the bodily self. They show that this intervention is effective in re-creating patients' sense of self because it allows for the integration of sensorimotor/emotional information and facilitates recovery across multiple domains of disability.

In summary, the present Research Topic suggests that body ownership and sense of agency do not arbitrarily co-occur in our experiences but, rather, can have a significant influence on each other and might even share some neuroanatomical and functional features. Future studies should continue to examine the complex relationship between ownership and agency in healthy as well as pathological conditions affecting bodily awareness. Finally, the development of next-generation prosthetic devices and virtual-reality applications may engender new approaches in neuroscience, rehabilitative medicine, and therapy.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Self-defense: Deflecting Deflationary and Eliminativist Critiques of the Sense of Ownership

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I defend a phenomenological account of the sense of ownership as part of a minimal sense of self from those critics who propose either a deflationary or eliminativist critique. Specifically, I block the deflationary critique by showing that in fact the phenomenological account is itself a deflationary account insofar as it takes the sense of ownership to be implicit or intrinsic to experience and bodily action. I address the eliminativist view by considering empirical evidence that supports the concept of pre-reflective self-awareness, which underpins the sense of ownership. Finally, I respond to claims that phenomenology does not offer a positive account of the sense of ownership by showing the role it plays in an enactivist (action-oriented) view of embodied cognition.

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INTRODUCTION

A growing army of theorists have struck out in attack mode against the notion of a pre-reflective, minimal sense of self or sense of ownership (e.g., Dainton, 2008, 2016; Bermúdez, 2011, in press; Prinz, 2012; Di Francesco et al., 2016; Garfield, 2016). To defend against such attacks I'll follow a divide and conquer strategy. Specifically, in this paper I take on the deflationary and eliminativist arguments advanced by Bermúdez, Dainton, and Di Francesco and colleagues.[1] My tactic will be to use a form of philosophical Jujitsu. That is, I'll use the power of the critics' own arguments against them by showing (1) that the pre-reflective sense of ownership is, on the phenomenological accounts that are criticized, intrinsic to experience, rather than some additional quality, and this is just what the deflationary account requires; (2) that the concept of a pre-reflective sense of ownership is consistent with the empirical evidence that the critics themselves cite; and (3) that a more positive account of the sense of ownership is to be found in the phenomenologically inspired enactivist (action-oriented) view of experience as always embodied and most often agentive.

The notion of the sense of ownership (SO) is a complex one. First, the phrase itself may be misleading. The term 'ownership' typically applies to the ownership of things, objects, or property and tends to signify a legal claim about such property. Clearly, one's body is not piece of property, except perhaps in a metaphorical sense. We are not in this kind of relationship of ownership to our own body. One can agree with Bermúdez on this point; he suggests that "ownership is a rather tenuous and metaphorical concept in this context. We do not own hands ...... in the way that we own personal property" (in press). Although there are contexts in which the concept

[1] I'll focus on the eliminativist views expressed in Bermúdez and defended by Di Francesco and colleagues. Prinz (2012) also offers what can be considered an eliminativist proposal – that there just is no experiential sense of self. Likewise, Garfield (2016, p. 73) claims, there is "nothing that it is like to have qualitative experience."

of legal ownership of one's body may be appropriate,[2] in the context that we are considering here, which involves a phenomenological conception, this would be a misunderstanding. In this context, however, we find the phrase 'sense of ownership' in use at least from the mid-1990s, for example in Martin (1995), who defines it as "the phenomenological quality that [a] body part appears to be part of one's body" (Martin, 1995, p. 269; see Martin, 1992). Moreover, this concept, if not this specific phrase, had been discussed by earlier philosophers, such as Husserl, and in the phenomenological psychiatry tradition following Jaspers. Rather than the term 'ownership,' however, phenomenologists tend to use the term *mineness* or the *experience of mineness* (see, e.g., Hopkins, 1993).

Importantly, SO or the sense of mineness, applies not only to one's body or one's body parts; it also applies to movement, action, and even to experience itself. I may have a sense that this is *my* action, or *my* thinking, or, most basically, *my* experience (Gallagher, 2000). Guillot's (2017) offers some clarification on this by distinguishing between three phenomena.

- **For-me-ness** – the awareness of the *experience* as I live through it
- **Me-ness** – a pre-reflective self-awareness that *I* am the one living through the experience
- **Mineness** – the sense that this is my experience (ownership), i.e., an awareness of the experience as my own.

Guillot argues that in non-pathological/normal experience we have all three.

> It is something about the experience, something intrinsic to it, that supports judgments [about the experience]. This I take to be at least a prima facie reason to think that we typically have experiential access to the experience, to ourselves, and to the fact that the experience is ours; or, in my terminology, that the phenomenal character of a normal experience includes for-me-ness, me-ness, and mineness (Guillot, 2017, p. 47).

I think it is quite possible to accept these distinctions as conceptual distinctions, without thinking that we actually experience such distinctions, or that these differences are experienced as such. On the phenomenological view, the experience is precisely the experience of mineness (ownership), which is an intrinsically relational experience, i.e., involving the relation between me (as experiencer) and the experience itself, rather than an experience of a relation. For-me-ness and me-ness are, accordingly, abstractions from mineness that I can make in reflective judgment.

Guillot also argues (following Billon, 2011) that in some pathological cases mineness (or the sense of ownership) goes missing. Without entering the various debates about depersonalization and schizophrenic delusions of control and thought insertion, however, there are two important points to take from the idea that SO is missing in such exceptional or pathological circumstances. First, it implies that SO is clearly not a necessary or essential aspect of all experience, but also, second, it implies that SO is present in everyday normal experience.

The phenomenological view is that SO/mineness is experienced in the pre-reflective (or non-reflective) self-awareness that is intrinsic in everyday (non-pathological, non-exceptional) conscious experience. It is experienced as this pre-reflective self-awareness and is nothing over and above this pre-reflective self-awareness (Gallagher and Zahavi, 2012, 2014). Nor does it require an extra or transitive act of self-awareness which takes experience as an object. Accordingly, it is also important to distinguish this first-order, pre-reflective SO from a retrospective (reflective) judgment about ownership (Vosgerau and Newen, 2007).

THE DEFLATIONARY ACCOUNT

Martin's (1995) use of the phrase 'sense of ownership' was meant to describe an experience of one's spatial boundaries. According to Martin, "when one feels a sensation, one thereby feels as if something is occurring within one's body" (p. 267). This is not a matter of explicit judgment, as if I were experiencing a free-floating sensation concerning which I needed to judge its spatial location as falling within my body boundaries. Rather, as Martin argues, the experience of location is an intrinsic feature of the sensation itself. This experience just is the SO for one's body as a whole, so that I have SO for particular body parts only as being parts of that whole body (Martin, 1995, pp. 277–278). In this regard, SO is not a quality in addition to other qualities of experience, but "already inherent within them" (p. 278). This is consistent with the phenomenological view: SO is an intrinsic aspect of proprioceptive and kinaesthetic experiences of bodily movement, and other bodily sensations.[3]

Bermúdez (2011, in press), however, in a critical discussion of SO, in contrast to Martin, rejects the idea that SO is a "special phenomenological relation" (Martin, 1995, p. 267), although he accepts the importance of "boundedness." He denies that there is a positive first-order (non-observational) phenomenology of ownership or feeling of 'mineness.' In contrast to what he calls an "inflationary" conception, which he attributes to phenomenologists like Merleau-Ponty (he also cites Gallagher, 2005; de Vignemont, 2007, 2013), he offers a deflationary account. "On a deflationary conception of ownership the sense of ownership consists, first, in certain facts about the phenomenology of bodily sensations and, second, in certain fairly obvious judgments about the body (which we can term judgments of ownership)" (Bermúdez, 2011, p. 162). His deflationary view is that an explicit experience of ownership

[2] Petchesky (1995) for example, traces the use of the concept of body ownership through a number of legal and historical contexts, and discusses a "shift in the early-modern European origins of ideas about owning one's body" which has less to do with property rights in an economic sense and more to do with claims about protecting "one's sexuality and personal security from arbitrary invasion" (p. 390). Also see, e.g., Pateman (1988) for use of this term in feminist discussions.

[3] de Vignemont (in press), suggests some qualifications to Martin's analysis by considering cases in which there is no SO for a bodily limb although sensations may register on that limb. In these cases, e.g., somatoparaphrenia and the case of IW, it is important to note that proprioception/kinaesthesia is missing (Gallagher and Cole, 1995; Vallar and Ronchi, 2009). Accordingly, for a more precise characterization of SO in terms of body boundaries, one should define such boundaries as proprioceptive.

only comes up when we turn our reflective attention to our bodily experience and attribute that experience to ourselves. This, I think, is the only way to make sense of his claim that "[w]hen we experience our bodies we experience them as our own ... there is a phenomenology of ownership" (Bermúdez, 2015, p. 38). I take this to mean that there is a second-order phenomenology of ownership derived from the judgment of ownership.[4] A second-order experience of ownership results as a product of this judgment, but it is not something that is there to begin with. "There are facts about the phenomenology of bodily awareness (about position sense, movement sense, and interoception) and there are judgments of ownership, but there is no additional feeling of ownership" (Bermúdez, 2011, p. 166).

Bermúdez thus comes close to the eliminativist view, since he rejects the idea that there is "a specific feeling of ownership – a qualitative 'feel' that one has in all and only those body parts that one experiences as one's own" (in press). According to Bermúdez (2011) SO is a philosophical fiction. Although one does experience a sense of body boundedness and connectedness, one does not experience, in addition, SO as a separate and independent feeling.

As we've seen, however, for the phenomenologists, to say that SO is an intrinsic aspect of proprioceptive and kinaesthetic experiences is to agree that it is not an additional or independent feeling, but rather, a sense "already inherent within" the phenomenology of bodily sensations. On the phenomenological view, and in contrast to Bermúdez, this intrinsic aspect is pre-reflective in the sense that one has this intrinsic experience of ownership without having to make a reflective judgment about ownership. This can be read in the deflationary way, so that the phenomenologists can agree that there is no additional feeling of ownership, or "perfectly determinate 'quale' associated with the feeling of myness" (Bermúdez, 2011, p. 165), independent of the proprioceptive and kinaesthetic sensations. In contrast to the eliminativist view, however, there is still an experiential SO. In fact, this implicit self-experience is precisely what makes first-person bodily (proprioceptive, kinaesthetic) awareness itself (i.e., prior to any judgment) a form of self-consciousness. It's what puts the 'proprio' in proprioception (Gallagher and Trigg, 2016).

Bermúdez doesn't want to deny, however, that we can have a proprioceptive and kinaesthetic awareness of bodily (and limb) posture and movement. This is clear in his (2015) discussion of an example from Anscombe (1962). Anscombe considers the meaning of the expression 'sensation of X' in the example of the sensation of going down in a lift. Does the phrase 'the sensation of going down in a lift' signify (1) the subjective feeling I have of an upward feeling in my stomach (the internal description or content of the sensation), or (2) the objective event of going down in a lift (the external accompaniment). Even if my focus of attention is on the objective event, that focus carries with it a non-reflective (non-observational) awareness of my phenomenal experience (the sensation content) which includes, implicitly, the sense that this is happening to *me*. This is a non-reflective self-awareness that, roughly, it is *my* stomach that is moving upward, or perhaps something more indeterminate, but nonetheless, an experience in or of *my* body. Bermúdez endorses the idea that such experiences give us a sense of boundedness and connectedness "from the inside." Throughout such proprioceptive experiences, however, there is a more or less integrated pattern of experience in which body awareness includes an intrinsic experience that it is *my* bodily experience. That's the *proprio* in proprioception.

It's not clear what this kind of awareness could be, other than a pre-reflective awareness that is built into (not something separate and distinct from) the structure of precisely the experience I have of my body or of a sensation that is located in my body. This idea is consistent with both the phenomenological view, and the deflationary account offered by Martin. This is also what Dokic (2003) claims in an account that Bermúdez identifies as deflationary. "Bodily experience gives us a *sense of ownership*. . .. The very idea of *feeling* a pain in a limb which does not seem to be ours is difficult to frame, perhaps unintelligible" (Dokic, 2003, p. 325).

THE SENSE OF SELF IN THE PHENOMENAL BACKGROUND

Dainton (2008), in his discussion of what he terms the "isolation thesis," i.e., the idea that there could be just one isolated bodily sensation, e.g., of pain, takes issue with the phenomenological concept of pre-reflective self-awareness. Typically, in contrast to the isolation thesis, when I experience some sensation I experience it "against the backdrop of various other forms of consciousness: a range of bodily experience, tactile sensations, visual and auditory experience, intentional or willed bodily movements, conscious thinking ... [etc.]" (2008, pp. 239–240). This backdrop of experience, to which we are not attending when we attend to the pain, he calls the 'phenomenal background.' This background consists of two regions – a worldly region where I experience, e.g., in exteroception, the sights and sounds around me, and an "inner" region, an elusive set of bodily experiences, thoughts, memories, and so on. He suggests that this inner aspect of the phenomenal background contributes to (and perhaps constitutes) "the feeling of what it is typically like to be *me* (or *you*)' (p. 240). This inner background may be relatively stable, as Dainton suggests, but it does not consist of a particular kind of sensation or feeling. Specifically, he argues, it does not consist of a pre-reflective self-awareness or sense of mineness or ownership.

> I can see no reason to take this stability as indicative of a single special type of experience, something over and above the changing stream of thought, perception, volition, emotion, memory, bodily sensation, and so on (p. 240).

He argues that if we subtract all of these various experiences, there would be nothing of experience left; therefore, there is nothing over and above just these experiences – no extra or

[4]See Alsmith (2015). Also, de Vignemont (in press) attempts to clarify this by distinguishing between a 'feeling of myness' understood as a first-order experience, which she associates with the inflationary account; and a sense of ownership as a second-order phenomenology, which Bermúdez associates with the deflationary account. I am not distinguishing between a sense of mineness and a sense of ownership – I treat both phrases as signifying a first-order aspects of experience distinguishable from the judgment of ownership.

additional experience that we would identify as the experience of mineness. Rather, he suggests, the "ambient 'sense of self'" is something like the product of all of these experiences. This phenomenal background is always something of which we are co-conscious, but always something precisely in the background, and of which we are not *explicitly* aware. It's this ubiquitous presence of the phenomenal background – this ambient sense of self – that makes it impossible to imagine an "ownerless" isolated pain sensation.

Dainton takes this argument to undermine the phenomenological claim that there is a particular form of self-consciousness, of the minimal or 'non-reflexive' variety, that always accompanies experience. Zahavi, whom Dainton quotes, defends this sort of phenomenological claim.

> One commonality [shared by all experiences] is the quality of *mineness*, the fact that experiences are characterized by first-person givenness. That is, the experience is given [i.e., experienced] (at least tacitly) as *my* experience, as an experience *I* am undergoing or living through. . .. Phenomenal consciousness must be interpreted precisely as entailing a minimal or thin form of self-awareness. On this account, any experience that lacks self-awareness is non-conscious (Zahavi, 2005, p. 16; cited in Dainton, 2008, p. 242).

Dainton pushes back against this claim. "There is certainly no obvious need to posit a quality of *mineness* to explain how it is that we are always aware of our own experiences" (2008, p. 242). Rather, Dainton holds that experiences are intrinsically conscious and as such they "automatically contribute to the overall character of their subject's consciousness," without any "further assistance" by an additional quality of mineness. The phenomenologists may be right that I, as experiencing subject, am not usually in doubt about who the subject of my experience is, and again Dainton cites Zahavi: "Whether a certain experience is experienced as mine or not, however, depends not on something apart from the experience, but precisely on the givenness of the experience" (2005, p. 124). But then Dainton goes on to ask: "do we need *mineness* to explain whether an experience is experienced as mine?" (2008, p. 242). It's not that Dainton doubts that one's experience is something that one is aware of living through – it's just that he doubts that we need the additional experience of mineness to make it so. Rather, the sense of self is given by the phenomenal background.[5]

Two things follow from Dainton's analysis.[6] "First, we can account for the phenomenology of *mineness* without positing any primitive 'ownership' quality" (p. 243). And second, a reductionist view of our sense of self is possible – that is, "our sense of self is not the product of a single simple form of experience, but rather the joint product of several different sorts of (quite ordinary) experiences" (p. 243).

If we accept Dainton's argument, then there does exist a sense of mineness or SO, but it is not a special or additional quality, or a primitive pre-reflective self-awareness added to the phenomenal background. Does this actually constitute an argument against the phenomenological concept of sense of mineness or ownership? It's difficult to see how it would count against the phenomenological conception since the phenomenologists, including Zahavi, describe the sense of mineness as an *intrinsic* aspect of experience, not as something extra that is added, or an additional quality that one experiences in addition to experiencing pain, or bodily sensations, or thinking, etc. To repeat Dainton's quotation from Zahavi: "Whether a certain experience is experienced as mine or not, however, depends not on something apart from the experience, but precisely on the givenness of the experience" (2005, p. 124). As Zahavi most recently put it:

> the what-it-is-likeness of phenomenal states is properly speaking a what-it-is-like-for-me-ness. On this view, experiential processes are *intrinsically* conscious and hence self-revealing. They are characterized by an *inherent* reflexive (not reflective) or pre-reflective self-consciousness in the weak sense that they are like something for the subject, i.e., in virtue of their mere existence, they are phenomenally manifest to the subject of those experiences (Zahavi, in press; emphasis altered).

Likewise, Gallagher and Zahavi (2014) emphasize the intrinsic or inherent nature of pre-reflective self-awareness.

> Experience happens for the experiencing subject in an immediate way and as part of this immediacy, it is implicitly marked as *my* experience. . .. [P]re-reflective self-consciousness is pre-reflective in the sense that (1) it is an awareness we have before we do any reflecting on our experience; (2) it is an implicit and first-order awareness. . .. The mineness in question is not a quality like being scarlet, sour or soft. It doesn't refer to a specific experiential content, to a specific what; nor does it refer to the diachronic or synchronic sum of such content, or to some other relation that might obtain between the contents in question. Rather, it refers to the distinct givenness or the how it feels of experience. . .. That pre-reflective self-awareness is implicit, then, means that I am not confronted with a thematic or explicit awareness of the experience as belonging to myself. Rather we are dealing with a non-observational self-acquaintance.

'Intrinsic' means that it is built into the structure of such experiences,[7] not something added on. That it is an intrinsic aspect of the phenomenal background is not something that phenomenologists would disagree with. It is not clear, however, that one should regard it as the "product" of the experiences that make up the phenomenal background, as Dainton suggests, since that way of putting it actually implies that it is something in addition to those experiences. As I understand it, however,

[5]I note that for Dainton, the sense of self is being equated with mineness or the sense of ownership. As one reviewer pointed out, these are at least conceptually distinct, in that a sense of self could be defined as a very basic form of self-consciousness (e.g., sensitivity to self-specific information) without a sense of ownership. What Dainton denies is that the sense of self or mineness is something separate from the phenomenal background.

[6]I leave aside the specifics of his argument about the isolation thesis – he does think that it is difficult to rule out the idea that we might be able to experience an "isolated and *phenomenologically ownerless*" sensation, i.e., that the phenomenal background might in fact go missing.

[7]That it is built into the structure of experience is explained by Husserl, and the phenomenologists who follow him, in terms of the temporal structure of experience – the retentional-protentional structure that characterizes all of our typical experiences. It would take us too far a field to sketch this analysis, but see Gallagher (1998) for more detail.

that is not Dainton's intended claim, and in this respect (*pace* his critique) he is in agreement with the phenomenological conception of the sense of ownership.

Accordingly, for both Dainton and Bermúdez, the force of their arguments against the phenomenological conception of the SO as a form of pre-reflective self-awareness intrinsic to experience can be turned around and redirected to show that in fact the phenomenological conception is precisely the conception that they need in order to make sense out of their own views, at lease if we take them to be defending deflationary views.

THE ELIMINATIVIST ACCOUNT

I suggest that a similar philosophical Jujitsu can also be used against the more sustained critique offered by Di Francesco et al. (2016). They argue (citing Schear, 2009) that by using a contrastive strategy we can find states of consciousness that *prima facie* lack any kind of self-consciousness. Specifically, they cite experiences involved in meditative trance and high-level athletic performance.

> In these kinds of mental states, we are completely immersed in a certain task and forgetful, so to speak, of ourselves. We are one and the same thing with a certain thing or task. However, this strategy is not available to Gallagher and Zahavi, since it implies that there are conscious but non-self-conscious states, whereas, according to these authors and their followers, mineness is a *necessary* ingredient of consciousness (2016, p. 79).

First, let me block the thrust of their point about meditative trance. Perhaps it's an open question, but it is not at all clear how one can report on that state of consciousness if in fact at the time of that experience one is not, at least, pre-reflectively aware that one is in that state of consciousness. And if it is a retrospective report, it implies that there was some minimal self-awareness present, and that the subject registered the experience as his or her own; otherwise, it's not clear how or why he or she would be reporting it. Indeed, according to MacKenzie (2008), reflexivist or self-illumination (*svaprakāśa*) theories in classical Indian philosophy defend the idea that if a state is conscious, it is simultaneously consciousness of both the object of consciousness and the conscious state itself. In this respect, it is like Hume's famous claim not to be able to find a self among his experiences. But the fact that he looks among *his own* experiences, rather than anyone else's (and it could not be otherwise), and reports it as such ("whenever I enter into what I call *myself*"), suggests that there is some kind of implicit self-awareness that these are *his* experiences. In any case, in regard to the claim about meditative trance, it's not clear what the evidence is.

Second, the evidence against Di Francesco and colleagues, claim may be clearer with respect to high-level athletic performance, since there are studies that show that in such flow-like performance there still is some kind of pre-reflective self-awareness involved [e.g., Christensen et al., 2016; likewise, in dance (Legrand, 2007; Montero, 2012, 2016) and in flow-like states during musical performance (Høffding, 2015; Salice et al., 2017)]. Furthermore, as we noted with respect to pathological experience, if Di Francesco and colleagues were right about meditative trance and exceptional performance, the implication is that these experiences, at the very least, would be exceptions to the rule that everyday (non-exceptional) consciousness actually does involve an implicit pre-reflective self-awareness. The exceptions contrast to the more general fact of the matter – otherwise they would not be so exceptional. Yet, this is clearly not what Di Francesco and colleagues intend. Indeed, they suggest there is "an extreme difficulty" in finding mineness in experience, in contrast to the phenomenological claim that it would be difficult (if not impossible) to find instances in which experience was without a sense of mineness. Since they do indicate that this is an empirical issue,[8] the best way to address this conflict of intuitions would be to cite empirical evidence. Di Francesco and colleagues, however, question some of that evidence.

For example, they reject the idea that studies of neonate imitation can offer any evidence that young infants have a pre-reflective sense of mineness. They consider any such appeal to involve an adultist interpretation of infant experience.[9] Despite being fans of both contrastive strategies and operationalizing phenomena, however, they ignore the precise operational definition of neonate imitation that Meltzoff and Moore (1977) adopt, namely differential imitation. Instead, they accept the account given by Jones (2009), which ignores the operational definition and treats tongue protrusion as simple arousal. The point for Di Francesco and colleagues is that if neonate imitation were just arousal, then there would be no proprioceptive awareness necessary – and so, no SO. The operational definition of neonate imitation adopted by Meltzoff and Moore, however, is not the production of one gesture more often than an unrelated one (as Keven and Akins, 2016, suggest). Rather, they, and the majority of neonate imitation studies, operationalize imitation as "the greater frequency of a gesture in response to the same gesture than in response to other gestures" (Vincini et al., in press, 2017). The operational definition entails reference to a plurality of gestures exhibiting a comparative increase. As Meltzoff and Moore were well aware, this is a crucial point since if only one gesture is matched, then arousal would be the most plausible explanation; the operational definition of differential imitation was meant to exclude the arousal explanation. This makes it an empirical question: is there evidence for differential imitation? A recent study by Coulon et al. (2013), for example,

[8] Di Francesco and colleagues also indicate that no one is making a transcendental claim in this regard. They go on, however, to suggest that the claim made by phenomenologists may be *a priori* (2016, p. 79) or "heavily dependent on *a priori* assumptions" which they associate with transcendental phenomenology (p. 78). To suggest that the phenomenologists' claim is *a priori*, however, is to misconstrue the nature of phenomenology. Phenomenology is an appeal to experience if it is anything at all. To be clear, one should distinguish between an *a priori* claim (i.e., a claim that is not based on experience) and a claim about an *a priori* aspect of experience. Thus, when a phenomenologist claims that it is only in consultation with *one's own* experience that one can identify an implicit SO, this implies, on the strongest interpretation, that such a thing is possible only because we, as human experiencers, have experiences that are *a priori* our own. Whether this strong claim is true or not, this is not an argument based on *a priori* assumptions; it's based on an appeal to experience.

[9] Di Francesco and colleagues rightly suggest that there are two forms of adultism (or what they call 'adultocentrism'): the excluding kind (the infant is not like an adult), or the projecting kind (the infant is like an adult) (2016, p. 82). It's not clear that they avoid the excluding form of adultism themselves since they make a lot of claims about precisely what infants are lacking in their experience (see, e.g., p. 85).

provides evidence for differential imitation. A more recent study, Oostenbroek et al. (2016), fails to provide evidence for differential imitation, but that may be because they employed highly conservative criteria. If this question remains unsettled in the literature, then the jury is still out, and Di Francesco and colleagues cannot simply help themselves to their preferred account.

In regard to the question of pre-reflective proprioceptive self-awareness, the relevant aspect of what Meltzoff and Moore showed was that that the infant's imitation improved with practice, implying that the infant was able to discriminate between its own facial gesture and the gesture it saw on the other's face. This was regarded as evidence for a basic, proprioceptive-based distinction between self and non-self in newborns (see, e.g., Bermuúdez, 1996; Gallagher, 1996).[10] But if Di Francesco and colleagues are not happy with the evidence from neonatal imitation, that is not the only place one can find evidence for this basic distinction. One can find it in turn-taking in proto-conversation, and differential kinematic responses to self versus non-self (Reddy, 2008). Even the fetus can discriminate the difference between being moved and moving itself (Glass, 2005). The differentiation is also built into touch, so that the sensory-motor system of the infant can register the difference between someone else's hand touching its face (eliciting the rooting reflex) and it's own hand touching its face (no rooting reflex) (Rochat and Hespos, 1997). Even prior to birth the physiological requisites for proprioception are in place (Humphrey, 1964; Van der Meer et al., 1995).

This kind of evidence is, of course, open to interpretation. On the one hand, Di Francesco and colleagues might argue that all of this differentiation between self and non-self is really non-conscious. Whether or not that is the case for the late-term fetus, however, it's not clear why conscious discrimination in the infant would need to wait until 4–5 months, as Di Francesco and colleagues suggest. Indeed, Di Francesco and colleagues they cite Bermúdez's view on this: "Somatic proprioception and the structure of exteroceptive perceptual experience can be a source of non-conceptual first-person contents from the very beginning of life" (Bermuúdez, 1998, p. 163; cited by Di Francesco et al., 2016, p. 72). If the structure of perception contains propriospecific information, for example, as the boundary of the visual field that originates in the embodied perspective of the agent, that just is the basis for the inbuilt structure of pre-reflective self-awareness. As Di Francesco and colleagues note, on this ecological view, "affordances, visual kinestesis and bodily invariants all carry self-specifying information" which is "precociously available to the child" (p. 83).

Although Di Francesco and colleagues don't reject these ecological claims, they do reject the idea that such experience could be taken as evidence for pre-reflective self-awareness. Why? I think we get to the real punch of their view here. They reject ecological experience as a form of pre-reflective self-awareness in younger infants because those younger infants do not yet have a more advanced objective experience of their body as a whole. First, they claim that ecological self-awareness is awareness of "single parts of the body, not of the body taken as a whole" (p. 84). Yet ecological self-awareness may very well be awareness that I am moving through the environment, for example, by walking or running, or that I am sitting or standing still. It's not at all clear that such awareness is focused on one or several body parts rather than the entire body.

Second, they claim that "when a baby, say, 6 or 8 months old perceives, say, her hand, she perceives it *as an object among others*, not as *part* of her body" (p. 84); to perceive it as part of her body she would have to be able to represent her body as a whole, which is not yet possible, according to Di Francesco and colleagues. But isn't this move already blocked by our previous considerations? Although it may be clear that the child can indeed take an objective view of her hand, and in this regard does not have immunity to error with regard to identifying her hand as *her* hand, it should also be clear from the evidence cited above, and from the very nature of proprioception and kinaesthesis, the child often and usually does have an agentive, first-person experience of her hand as her own – as the one she is actively moving, for example (Gallagher, 2015). Phenomenologists refer to this as the body-as-subject (e.g., Legrand, 2007) or the body-as-agent (the *Leib*), which is associated with body-schematic processes, in contrast to body image, the body-as-object, or the objective perception of one's body (Gallagher, 2005). On any account of SO that involves agentive body-schematic processes rather than body image, the role of the body-as-object can only be secondary or accessory (see, e.g., de Vignemont, 2007, in press). I'll come back to this point in the final section.

Di Francesco and colleagues claim, then, is that before an agent can have a sense of her own body-as-subject – before she is able to sense that her whole body is moving as she crawls around or starts to walk – she must have developed a body image for her whole body. She apparently just doesn't have a sense that this hand is her hand until a point in development when she has a developed body image for her whole body. Thus, "we can say that the newborn, like the infant at 6 months or 1 year of age, produces a rich subjectivity, but being immersed in it, cannot objectify it" (p. 85). Likewise for pain: the infant experiences pain, but does not objectify herself as being in pain. For the infant to be able to experience pain as *her own* pain, or her movement as *her own* movement, or her body (or body part) as *her own* body, she requires a developed, objective bodily self-consciousness which comes, according to Di Francesco and colleagues at around 18 months with mirror self-recognition when the child is able to form a body image of herself as a entire object and associate this with herself as a subject – "the active source of the representation" of herself (p. 85).

[10] To be clear, in seeking empirical evidence for SO, as in many experiments and discussions the focus usually shifts to the sense of body ownership or SO for movement or action – this is *my* hand or this is *my* body, this is *my* movement – and this involves proprioception and kinaesthesia. It is specifically the implicit reflexive (or ecological, or auto- or self-awareness) character of proprioception (giving me information about or awareness of myself) that is at stake here, rather than the intentional or sensory content of the experience. As one reviewer notes, "the mineness-feature is constant across sensory experiences irrespective of the content." In tactile experience, for example, I might touch different objects, X, Y, and Z, but the touching experience is always mine because of its proprioceptive nature. If X turns out to be my body (in the case of self-touch) proprioception is doubled (and, as Martin, 1995 suggests, body ownership is tied to body boundary, which is also proprioceptively defined). See Merleau-Ponty's (2012) concept of 'reversibility,' discussed in the final section.

Di Francesco and colleagues claim here is largely definitional. That is, they define self-consciousness precisely as an explicit *objective* view of "the whole body of the organism [objectively] *experienced as one's own body*" (p. 85), and nothing less. On the one hand, of course, if we accept this as the exclusive definition of self-consciousness, then nothing like a pre-reflective self-awareness exists, full stop. On the other hand, to say that there may be a developed perspective where one is able to make an objective judgment about bodily ownership, is not to show that self-specifying proprioceptive/kinaesthetic information does not provide a pre-reflective sense of ownership for one's experience, one's body, and/or one's action. A more developed higher-order (conceptual and objective) form of self-consciousness remains consistent with the existence of a pre-reflective sense of ownership. Indeed, on some accounts, one requires just such a proprioceptive sense of one's own body to be able to recognize it in the mirror. To opt for a purely higher-order conception of self-consciousness is just to endorse a definition that, as Rochat and Zahavi (2011, p. 206) put it, has "dramatic implications . . . for our ascription of an experiential life to infants," and opens a larger set of questions, for example, about social cognition, than can be explored here. In this respect, if opting for a more objective conception of self-consciousness was meant to be a knockout blow to the concept of a pre-reflective SO, Di Francesco and colleagues are unable to land their strongest punch.

ACTION-ORIENTED OWNERSHIP

Di Francesco and colleagues suggest that phenomenologists fail to offer a positive account of pre-reflective SO, and that it is "characterized only negatively" and without reference to the capacities or processes of self-consciousness (2016, pp. 86–87). One might also think that a deflationary account, that takes SO to be nothing over and above experience itself, will not give us a positive account of this phenomenon. In this final section I want to argue that phenomenologically inspired enactivist approaches to experience and action, specifically involving the agentive body (or the body-in-action), do provide a positive account of SO in terms of the capacities and processes of self-consciousness.

One concern directly related to action is about reliability and precision. In this regard, it is important to note that *bodily* awareness, i.e., awareness not just of the body (body awareness), but awareness of the world that includes pre-reflective self-awareness of my active moving body, following the ecological view, is multimodal (see, e.g., Gallagher, 2005; Tsakiris, 2016). There is good reason for this. Proprioceptive awareness of one's body is attenuated and not overly precise. The attenuation would be a "flaw" (de Vignemont, 2014, p. 998), however, only if one assumed that proprioception was supposed to deliver precise awareness of the objective body. Proprioception, or any other bodily sense, however, never functions just by itself (Dainton is right about this), and reliability should be measured in terms of the whole system and its integrated functioning. Moreover, we should consider questions about reliability and precision in pragmatic (action-oriented) terms rather than in epistemic terms. In this case, proprioception, functioning along with other modalities (touch, vision, interoception, etc.), provides a pragmatic bodily awareness related primarily to the subject's action possibilities. The fact that, as Vignemont notes, it does not give me a precise sense of my bodily posture, or shape, or boundaries as I am lying in bed or am not moving, in contrast to when I am moving, is not a problem since accuracy in such circumstances is not that important. Even in regard to action, I do not always need precision information about body boundary or limb location, and, as I've suggested elsewhere (Gallagher, in press), we get enough precision when we need it *via* the mix of senses, and pragmatic estimates are good enough in most cases. Indeed, if we take precision to mean objective position sense, this is not something we need for most of our actions.

The enactivist point in this is that bodily experience, in the form of proprioception, kinaesthesia, interoception, etc. is action-oriented. In the same way that perception is enactive, that is, oriented to the possibilities or affordances for action and for responding to others, the proprioceptive-kinaesthetic, pre-reflective SO contributes to how the body attunes to what it can do. Proprioception, as position sense, i.e., as a positive sense of where my limbs are (and the *mineness* of those limbs being an implicit but still positive experience), is not simply the registration of where my limbs are for the sake of knowing where my limbs are, as if it were solving an epistemological or theoretical problem. Rather, it addresses a pragmatic problem: if I want to pick up a hammer, I don't first of all have to go looking for my hands – they are already ready to go.

In typical, everyday experience, SO readily integrates with a sense of agency (SA) and in most cases SA and SO are experientially indistinct, a fact that is consistent with the deflationist account of SO and with an embodied enactivist conception of SA (see Tsakiris et al., 2007; Gallagher, 2012, 2013; Buhrmann and Di Paolo, 2015). Langland-Hassan (2008), for example, suggests that the phenomenology of agency is "one that is embedded in all first order sensory and proprioceptive phenomenology as diachronic, action-sensitive patterns of information; it does not stand apart from them as an inscrutable emotion" (p. 392). Again, this is fully consistent with the phenomenological view.

Not only does SO play a role in everyday pragmatic actions, it also serves communicative actions and social interactions. This is not a topic that I will develop in detail here (see Gallagher, 2005, 2017), but I want to at least give some indication of what this role is. de Vignemont (2007) suggests that you experience SO for your hand when another person touches it, in a way that you do not feel SO for the touching hand. In this regard, Merleau-Ponty's well-known example of one hand touching another, as an example of what he calls 'reversiblility,' can help to show that there is a potential for action (something action-oriented) in the experience of my hand being touched, and not just an experience of bodily location.

Merleau-Ponty's example is first of all about my own two hands. If I use my right hand to touch my left hand, there is the immediate possibility of a reversibility – that my right hand touching can immediately become the touched; and my left hand touched can immediately become the touching. If the touching-touched is in some objective sense simultaneous, in terms of our single-minded attention it is not; it involves a dynamic sequential reversibility, not unlike the reversing of the Necker cube in vision, but one that can be easily done at will (Merleau-Ponty, 1968, p. 141). My attention can go back and forth between touching and being touched, attempting to capture a structure that is pre-reflectively already established at the sensory level. Each hand, whether touching or being touched holds a relation to action, something actualized in the case of touching, but only potential in the case of being touched. Even as my one hand is touched, it holds a certain power for touching which could reverse the action[11].

This is the case whether it is my own hand touching my other hand, or, as in Vignemont's example, someone else's hand touching mine. Indeed, Merleau-Ponty suggests that something similar manifests itself in social interaction: "when touching the hand of another, would I not touch in it the same power to espouse the things that I have touched in my own?... [T]he handshake too is reversible; I can feel myself touched as well and at the same time as touching" (1968, pp. 141–142). I suggest that these very basic, embodied contingencies, which Merleau-Ponty associates with the phenomenon of 'intercorporeity' (2012, pp. 190–191; Gallagher, 2016), play a positive role in communicative turn taking as well (Reddy, 2008). In the sensation of being touched there is, along with a sense of location and boundary, and the implicit SO that comes along with this, a sense of agency to the extent that I have control over the reversibility – in effect, to the extent that I can immediately turn the being touched into an act of touching. This sense of agency, tied to my potentiality for action and interaction, just to the extent that it is *my* hand that is involved, is integrated with SO.

Given that the whole body can move and can touch or be touched, this applies not just to hands. Likewise, this is not just about proprioception. A pain in my leg can define what I can and cannot do, and can diminish my sense of agency or potential for action in the world. Interoceptive aspects of hunger or fatigue may do the same. Proprioception, however, is important not only for registering the location or position sense of my body. Proprioception also plays a role in motor control, and without proprioception we lose control over our body, and this can diminish SA as well as SO[12].

[11] Gallese and Sinigaglia (2010), in their extensive of the empirical research, rightly associate this with the concept of motor intentionality. They claim that this sense of potentiality for action is more primitive and a necessary condition for both SO and SA. A more deflated account would suggest that as an aspect of bodily experience it is intrinsically integrated with SO and SA, part of what Merleau-Ponty (1964) would call a 'form' or gestalt structure of the minimal self.

[12] We see this in the case of IW who, when he first was unable to control his bodily movement felt alienated from his body (Cole, 1995).

There is one final point to be made in regard to a positive action-related characterization of SO. The principle experimental paradigm for studying a bodily sense of ownership is the Rubber Hand Illusion (RHI) (Botvinick and Cohen, 1998). It turns out, however, that SO's agentive function does not play a clear role in the experience of the RHI. Although we can be tricked into experiencing the rubber hand as our own, if the illusion is maintained, the rubber hand seemingly plays no role in action preparation; ownership seemingly serves no agentive function. Vignemont, however, proposes an alternative agentive role for SO that does persist through the RHI, namely, a self-defense role that retains the connection between SO and body schematic processes, and does not reduce SO to a pure body image phenomenon. Rather than focus on the goal-directed instrumental movements (pointing and grasping) that are tested (albeit infrequently) in the RHI, she suggests that there is a "different range of movements . . . worth exploring, namely defensive movements" (in press).

> [I]t has been repeatedly shown that participants react [defensively] when the rubber hand is threatened, but only when they report it as their own after synchronous stroking, and the strength of their reaction is correlated with their ownership rating in questionnaires (Ehrsson et al., 2007).

Vignemont thus suggests that SO has "a specific agentive mark in the context of self-protection." One might think that this function is even more evolutionarily basic than SO's function in instrumental and communicative actions. It's clear, however, that the sense of ownership, described as a pre-reflective bodily self-awareness, can play important and positive agentive roles in action, communication, and self-defense – and this idea is not something that we should give up without a fight.

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The What, the When, and the Whether of Intentional Action in the Brain: A Meta-Analytical Review

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In their attempt to define discrete subcomponents of intentionality, Brass and Haggard (2008) proposed their *What, When, and Whether model* (*www-model*) which postulates that the content, the timing and the possibility of generating an action can be partially independent both at the cognitive level and at the level of their neural implementation. The original proposal was based on a limited number of studies, which were reviewed with a discursive approach. To assess whether the model stands in front of the more recently published data, we performed a systematic review of the literature with a meta-analytic method based on a hierarchical clustering (HC) algorithm. We identified 15 PET/fMRI studies well-suited for this quest. HC revealed the existence of a rostro-caudal gradient within the medial prefrontal cortex, with the more anterior regions (the anterior cingulum) involved in more abstract decisions of whether to execute an action and the more posterior ones (the middle cingulum or the SMA) recruited in specifying the content and the timing components of actions. However, in contrast with the original *www*-model, this dissociation involves also brain regions well outside the median wall of the frontal lobe, in a component specific manner: the supramarginal gyrus for the *what* component, the pallidum and the thalamus for the *when* component, the putamen and the insula for the *whether* component. We then calculated co-activation maps on the three component-specific *www* clusters of the medial wall of the frontal/limbic lobe: to this end, we used the activation likelihood approach that we applied on the imaging studies on action contained in the BrainMap.org database. This analysis confirmed the main findings of the HC analyses. However, the BrainMap.org data analyses also showed that the aforementioned segregations are generated by paradigms in which subjects act in response to conditional stimuli rather than while driven by their own intentions. We conclude that the available data confirm that the neural underpinnings of intentionality can be fractionated in discrete components that are partially independent. We also suggest that intentionality manifests itself in discrete components through the boosting of general purpose action-related regions specialized for different aspects of action selection and inhibition.

Keywords: intentional action, motor control, fMRI, PET, meta-analysis

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INTRODUCTION

Motor control has been the object of interest of many disciplines, including psychology, cognitive neuroscience, and, since the earliest days, philosophy, particularly when the object of enquiry are the conscious aspects of motor control and intentionality (Jeannerod, 1997; Frith et al., 2000; Haggard, 2008).

A comprehensive model that differentiates the various stages of movement production is not available: even articulated models of motor control (see for example Frith et al., 2000) remain underspecified, especially when considering the intentional components and their neural implementation.

In an earlier attempt to provide a model of the brain bases of intentionality, Jahanshahi (1998) argued that, in principle, it should be possible to characterize intentional actions in at least three main components: the content (*what* component), the timing (*when* component) and the possibility of being executed or inhibited (*whether* component). However, in reviewing the then available neuroimaging literature, they concluded that there was no sufficient evidence that such components are represented in discrete brain circuits. In their unitary brain model of intentionality, they proposed a "system" for intentional actions located in the pre-frontal cortex, anterior cingulate cortex, and supplementary motor area (SMA), with subcortical inputs coming from the striatum and through the thalamus: in their views, these systems are responsible for the all three features of intentional action (Jahanshahi, 1998).

Ten years later, Brass and Haggard (2008) re-assessed the early insights of Jahanshahi (1998) and, taking advantage of a larger set of imaging data, proposed that a "What, When, and Whether" model (*www-model*)[1] of intentional action is justified also on anatomical grounds. The original *www-model* was based on a set of experiments that we review here briefly together with more recent observations.

"*What*" Component

The *What* component has been mostly investigated by using fMRI procedures similar to the "Free selection paradigm" (Lau et al., 2004b), in which two experimental conditions are compared: a condition in which responses are externally determined by a cue and a condition in which the participants have to choose freely between different motor responses. Typically, the *What* component has been related with the activation of the fronto-medial cortex at the level of the rostral cingulate zone (Deiber et al., 1991; Frith et al., 1991; Hyder et al., 1997; Lau et al., 2004a,b; Mueller et al., 2007; Krieghoff et al., 2009), the SMA (Lau H. C. et al., 2006; van Eimeren et al., 2006) and pre-SMA (Deiber et al., 1991; Lau et al., 2004a,b; Brass and Haggard, 2007).

"*When*" Component

The timing component of intentional actions has been investigated by using the paradigm of Libet (Libet et al., 1983). For example, Lau et al. (2004a) associated the judgment of the onset of the intention to move with activation of the pre-SMA (Lau et al., 2004a). Libet' s paradigm has a number of limitations (see for example Trevena and Miller, 2002; Lau H. et al., 2006; Miller et al., 2011), first and foremost, of being meta-cognitive in nature and perhaps not terribly well-suited to fMRI given the temporal resolution of the technique and the time scale of the neurophysiological events seen with EEG during the paradigm.

The *When* component has been explored also by Jahanshahi et al. (1995) and Jenkins et al. (2000) who compared self-initiated extensions of the index finger with fingers' extensions triggered by pacing tones at unpredictable intervals: they found an activation of the dorsolateral prefrontal cortex specifically for the self-paced condition (Jahanshahi et al., 1995; Jenkins et al., 2000).

Finally, in an early and solitary attempt to dissociate the anatomical bases of the *What* and the *When* components in the same experiment, Hoffstaedter et al. (2013) manipulated the content and the timing of the motor responses of their participants. They found activations of the SMA, the insula, the globus pallidus, and the anterior putamen in relation to the free selection of the action's timing and the activation of the pre-SMA and the dorsal premotor cortex in relation to the free selection of the actions' content (Hoffstaedter et al., 2013).

"*Whether*" Component

The absence of a motor response as the result of the choice of action inhibition has partly hindered the study of the intentional inhibition processes with an explicit experimental task. The Libet' s task has been the main paradigm used to investigate voluntary inhibition. Using fMRI, Brass and Haggard have shown that an area of the dorsal and rostral fronto-medial cortex is more active when participants intentionally inhibit a response rather than when they complete the same action (Brass and Haggard, 2007). In any event, the voluntary inhibition of actions has been recently studied also with novel tasks like in the case of the *marble task* (Kühn et al., 2009; Schel et al., 2014) or the motivation driven *pain avoidance paradigm* of Lynn et al. (2016). These experiments showed that intentional inhibition rely on a neural network that includes parietal and lateral prefrontal cortex bilaterally (Kühn et al., 2009; Schel et al., 2014) and the pre-SMA (Schel et al., 2014; Lynn et al., 2016).

Aims of the Study

After the initial proposal of the *www-model*, some new ground has been covered with new explicit experiments to justify a formal assessment of the model, this time with explicit meta-analytical techniques.

Abbreviations: AAL, Automatic Anatomical Labeling; ALE, Activation likelihood estimation; CSTC, Cortico-striato-thalamo-cortical; EEG, Electroencephalography; fMRI, Functional magnetic resonance imaging; FDR, False Discovery Rate; HC, Hierarchical clustering; MNI, Montreal Neurological Institute; OCD, Obsessive-Compulsive Disorder; OCTD, Obsessive-Compulsive Tic Disorder; PD, Parkinson's Disease; PET, Positron emission tomography; Pre-SMA Pre Supplementary motor area; WWW MODEL, What, When and Whether model; SMA, Supplementary motor area.

[1] In their words, the model comprises "a component related to the decision about which action to execute (what component), a component that is related to the decision about when to execute an action (when component), and finally the decision about whether to execute an action or not (whether component)."

Is the segregation of different components of the *www-model* justified by the new evidence? If so, does it involve specific portions of the medial wall of the frontal lobe and of the cingulate gyrus? Further, does the mapping of the discrete components involve other brain regions in a specific manner? Again, if so, is it possible, with all the needed caution, to infer from these additional regions on the nature of the subcomponents of intentionality postulated by the original model?

Further, are the regions involved in intentionality anatomically specific or do they simply contribute to this aspect of behavior while being also involved in conditional aspects of action selection?

These were all lingering questions on the *www-model* that we tried to address in the present study. To this end, we first used hierarchical clustering (HC) to identify component specific clusters. As the reader will see, the specific literature available is barely sufficient to make statistical inferences on the significance of the clusters identified. However, after the initial hierarchical clustering procedure, we interrogated the vast BrainMap.org database and generated co-activation maps based on the main component-specific medial wall clusters of the frontal lobe. This permitted the desired statistical assessment of the anatomical dissociations initially identified by hierarchical clustering.

MATERIALS AND METHODS

Data Collection and Preparation

Our meta-analysis was based on neuroimaging articles investigating the neurofunctional correlates of intentional action using PET or fMRI in adult subjects.

Candidate studies were selected through the PubMed database (http://www.ncbi.nlm.nih.gov/pubmed/). The search keys were: "Intentional action & fMRI" and "Intentional action & PET." These queries returned 27 neuroimaging articles investigating the neurofunctional correlates of intentional actions. We included only studies that did satisfy the following inclusion criteria: (1) sample population composed of normal adult subjects; (2) imaging technique: PET or fMRI; (3) data reported using stereotactic coordinates; (4) comparison between intentional actions and stimulus-driven actions. As a consequence of these inclusion criteria, 12 studies were excluded from the analysis. Among the 15 studies that satisfied our inclusion criteria, 6 studies investigated the *What* component, 3 studies the *When* component, and 4 studies the *Whether* component. Finally, 2 studies investigated both the *What* and the *When* components. These studies were then classified on the basis of the examined component (see Supplementary Table 1).

For the suitable studies, in the meta-analysis we used data derived from (i) within group *simple effects* and (ii) interaction effects. The simple effects were: "Intention driven trials" and "Stimulus driven trials." The interaction effects[2] were "Intention driven trials > Stimulus driven trials" and vice versa. As there were no sufficient local maxima for the contrasts designed to identify the stimulus driven acts, these were not analyzed any further.

To summarize, the data selection led us to analyse 150 stereotactic activation loci, *71* peaks associated with the *What* component, *42* peaks with the When component and *37* peaks with the Whether component of intentional actions.

Classification of the Raw Data Prior to Clustering Analyses

For each activation peak, we recorded all relevant information about the statistical comparison that generated it, the nature of the experimental task and the investigated component.

We therefore determined a list of classification criteria to characterize each peak of activation included in the dataset:

- t-values or z-scores;
- Sample size;
- Average age of the subjects;
- Stereotactic template (MNI or Tailarach and Tournoux template);
- Whole brain or region-of-interest analysis;
- Scanning Technique (PET or fMRI);
- Statistical thresholds and nature of the correction for multiple comparisons.

In order to combine the data coming from studies based on different stereotactic spaces, the stereotactic coordinates of studies in which activation peaks were reported in terms of the Talairach and Tournoux (1988) atlas were transformed into the MNI (Montreal Neurological Institute) stereotactic space using Matthew Brett's procedure as implemented in the software GingerAle (www.brainmap.org).

Clustering Procedure

We first performed a component specific hierarchical clustering analyses (HC) of the activation peaks: the analysis allowed us to extract the principal clusters of regional effects from the database (Cattinelli et al., 2013) for each www component.

Hierarchical clustering was performed by using functions implemented in MATLAB 2016a. After computation of squared Euclidean distances between each pair of the input data, clusters with minimal dissimilarity were recursively merged using Ward's (1963) criterion which minimizes total intra-cluster variance after each merging step. As described in Cattinelli et al. (2013) and Crepaldi et al. (2013), "*this procedure results in a tree, whose leaves represent singletons (i.e., clusters formed of a single activation peak), and whose root represents one large cluster including all the activation peaks submitted to the algorithm. Each level of the tree reports the clusters created by the algorithm at a specific processing step, as it progresses from individual activation peaks at the lowest level to the all-inclusive final cluster at the top of the tree.*" The procedure was continued until the average standard deviation around the cluster centroids of the individual peaks, in the *x*, *y*, and *z* directions, remained below 5.0 mm. This measure roughly mimics the spatial resolution of fMRI studies. As hierarchical clustering may be sensitive to the order in which the individual data are processed, and may generate alternative clustering trees when integers are used (Morgan and

[2]Because second level fMRI analyses imply the use of contrast images generated, at the very least, by comparison with an implicit baseline, comparisons of experimental conditions end up being interaction effects.

Ray, 1995), an optimal clustering solution was identified by accepting the solution with maximized the between cluster error sum of squares (see for example Cattinelli et al., 2013). The mean coordinates of each cluster included in the final set were then passed as an input to a MATLAB script to automatically label the anatomical correspondence of the stereotactic coordinates of the centroids of each cluster. This procedure implied a query of the Automatic Anatomical Labeling (AAL) template available in the MRIcron visualization Software (Rorden and Brett, 2000). The initial automatic anatomical assignations were then double-checked by the authors with direct visual inspection on the AAL template and, if needed, the corresponding volumetric MRI scan template Ch2Bet released with the MRIcron software.

Given the number of peaks available for each analysis, relevant clusters at this stage were identified on the basis of the numerosity of the peaks in each cluster. Clusters were further considered if they contained a number of coordinates greater than the median of the distribution for each analysis and, in any event, with no <3 coordinates.

Activation Likelihood Analyses

To assess to what extent the functional segregations identified by the HC analyses could be replicated on a much larger dataset of studies on action, we interrogated the BrainMap.org database to generate co-activation maps for the *What*, *When,* and *Whether* patterns using the Activation Likelihood Estimate approach (Turkeltaub et al., 2002; Eickhoff et al., 2012). Co-activation maps are essentially estimates of the probability that local effects, expressed as triplets of stereotactic coordinates, co-occur in a data-set together with the activation of a seed reference region. The advantage of the ALE approach is that the statistical significance of the clusters identified is assessed using formal statistical thresholding. In this case, three separate co-activation maps were calculated using as seeds the three specific clusters identified in the medial wall of the frontal/limbic lobe, as they were also postulated in the original www-model. The interrogation of the BrainMap.org database was performed by using a 10 mm wide 3D region of interest defined around the centroid of each cluster (the coordinates are indicated in bold font in **Table 1**).

We interrogated all the studies that in the database are classified with the key-word "*action*" and "*activation.*"

The aim of these analyses was three-fold: (1) on the one hand we wanted to test the hypothesis that co-activation maps generated starting from the three main clusters of the medial wall of the frontal lobe and of the cingulate cortex can produce similarly segregated results as in the specific hierarchical clustering, once the three maps were formally compared (2) further, we wanted to test the hypothesis on whether the brain regions outside the frontal lobe would co-vary with the original seeds in a similar manner (3) by analyzing the composition of the BrainMap.org data-base experiments, that contributed to the identification of medial-wall clusters, we wanted to learn to what extent these could be associated, even if loosely, to intentional action and its subcomponents at the center of our quest.

As an initial step, three separate co-activation maps were calculated for each of the three seed clusters identified by the HC procedure. Subsequently, each co-activation map was compared with the other two lumped together.

Furthermore, once a component specific cluster was identified in the BrainMap.org database, we explored its composition as far as the generative paradigms was concerned. We paid particular attention to the relative contribution of go/no-go paradigms as these are closer to aspects of motor control entailed by the intentional/conditional dichotomy, particularly for the whether component.

TABLE 1 | Hierarchical clustering analysis.

Brain regions (BA)	MNI coordinates									
	Left hemisphere					Right hemisphere				
	Cluster ID	*x*	*y*	*z*	*K*	Cluster ID	*x*	*y*	*z*	*K*
A. WHAT COMPONENT										
Frontal_Inf_Tri (46)*	12	−35	33	27	6					
Frontal_Mid (46)*						8	36	32	34	9
Cingulum_Mid (24)						**4**	**4**	**20**	**38**	**10**
SupraMarginal (40)*						18	47	−42	45	6
B. WHEN COMPONENT										
Frontal_Inf_Oper*	13	−45	13	5	3					
Rolandic_Oper*						11	45	7	10	3
Frontal_Mid (46)*						16	35	39	31	4
Supp_Motor_Area (6)						**9**	**5**	**−3**	**62**	**4**
Parietal_Inf (40)						6	46	−43	47	5
Angular*						5	34	−51	37	3
Pallidum*	12	−20	5	−2	3	10	21	5	1	3
C. WHETHER COMPONENT										
Frontal_Inf_Orb (47)	15	−40	32	−4	5					
Cingulum_Ant (11)						16	12	37	2	3
Cingulum_Mid (24)	**17**	**−1**	**29**	**35**	**3**					
Insula*						13	40	21	0	5
Thalamus	4	−1	−20	7	3					
Putamen	14	−26	5	−6	3					

*In BOLD the stereotactic coordinates used as centroids for subsequent the co-activation maps analyses using the Activation Likelihood Estimate technique. *Regions shown also by the co-activation maps analyses for each centroid. K = number of peaks in the cluster.*

RESULTS

Hierarchical Clustering

For the ***what*** component the data clustered in the right middle cingulum, the right frontal middle gyrus, the right supramarginal gyrus and the left inferior triangular frontal gyrus (see **Table 1A** and **Figure 1A**).

For the ***when*** component we found clusters in the right SMA, the right frontal middle gyrus, in the right inferior parietal lobule, in the right rolandic operculum, in the left inferior opercular frontal gyrus and in the lenticular nucleus bilaterally (see **Table 1B** and **Figure 1B**).

Finally, for the ***whether*** component, specific clusters were seen at the level of the right anterior and the left middle cingulum, the left inferior orbital frontal gyrus, the right insula and subcortical

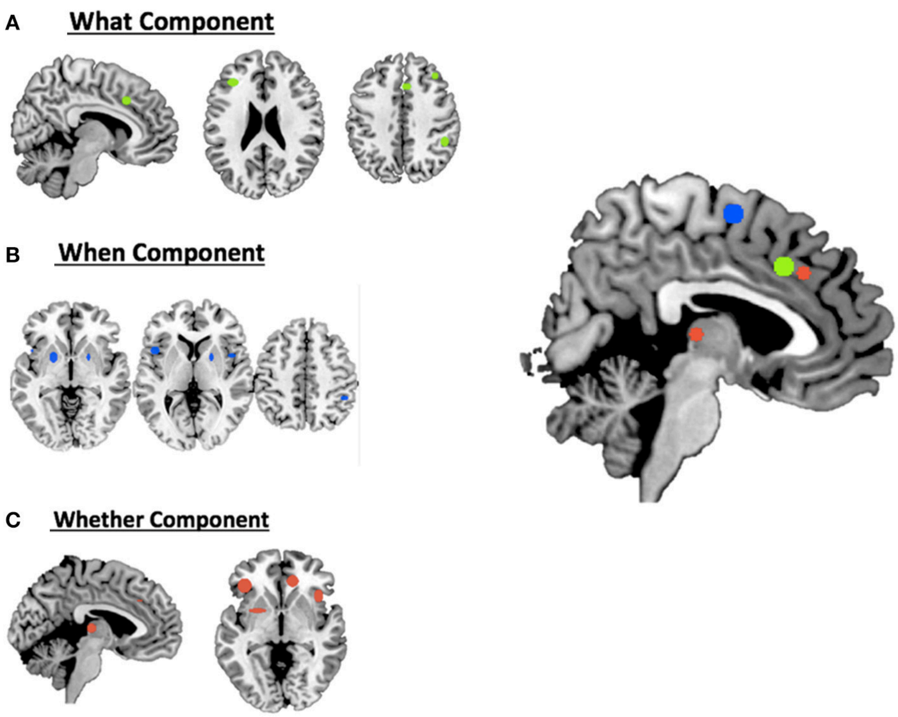

FIGURE 1 | Hierarchical clustering analysis results for (A) the what component; **(B)** the when component; **(C)** the whether component and a summary of all the components on the medial view of the brain.

structures, such as the thalamus and the putamen (see **Table 1C** and **Figure 1C**).

Co-activation Maps

The BrainMap.org search for co-activations on the *What, When,* and *Whether* clusters of the medial frontal lobe wall (based on the centroids in bold in **Table 1**) retrieved 1,201 foci from 56 statistical comparisons for the *What* cluster, 1,488 foci from 73 statistical comparisons for the *When* cluster, and 614 foci from 24 statistical comparisons for the *Whether* component.

Figure 2 illustrates the co-activation maps calculated around the original clusters used as seeds for the interrogation of the BrainMap.org database (statistical threshold $p < 0.05$ FDR corrected).

It should be noted that when seen as simple effects (e.g., the co-activation map generated by the ***what*** seed alone) most of the regions implicated by the HC analysis were also identified by the co-activation maps analysis (regions indicated with the symbol * in **Table 1**). Their relative segregation and embedding is illustrated in **Figure 2**.

Each individual map was then compared with a combination of the other two maps: for example, the ***What*** map vs. ***When*** & ***Whether*** ones combined, and so forth. For these comparisons, a more lenient $p < 0.005$ uncorrected threshold (cluster size threshold 300 mm^3) was used.

These analyses led to identification of regions that genuinely dissociate on the basis of their co-activation with the seeds used.

As illustrated in **Figure 3B** and summarized in **Tables 2A–C**, the comparative co-activation maps analysis confirms the functional dissociation along the medial wall of the frontal lobe, in a caudo-rostral direction, into a *what, when, and whether* components. Together with these brain regions, there were co-segregations of component-specific regions, particularly for the lenticular nuclei for the *when* component (see **Figures 3A,B** for a comparison between the two analyses).

We also assessed whether the foci that contributed to the segregation of the component specific clusters of the median wall of the frontal lobe were associated with specific tasks. **Tables 3A–C** describes the nature of the tasks behind the regional effects. First, it should be noted that these did not contain foci from the studies that were entered in the present meta-analysis. Second, after an initial qualitative scrutiny, we compared the relative prevalence of go/no-go paradigms vs. other kind of paradigms.

We then performed three Chi-squared pairwise comparisons between component specific cluster compositions to find that the relative prevalence of go/no-go data was significantly greater for the **whether** and **what** clusters in comparison with the data that generated the **when** cluster (see **Table 3**).

DISCUSSION

Contrary to previous anatomically "unitary" models of willed action (Jahanshahi, 1998), Brass and Haggard (2008) proposed the existence of a distributed meso-frontal system, responsible

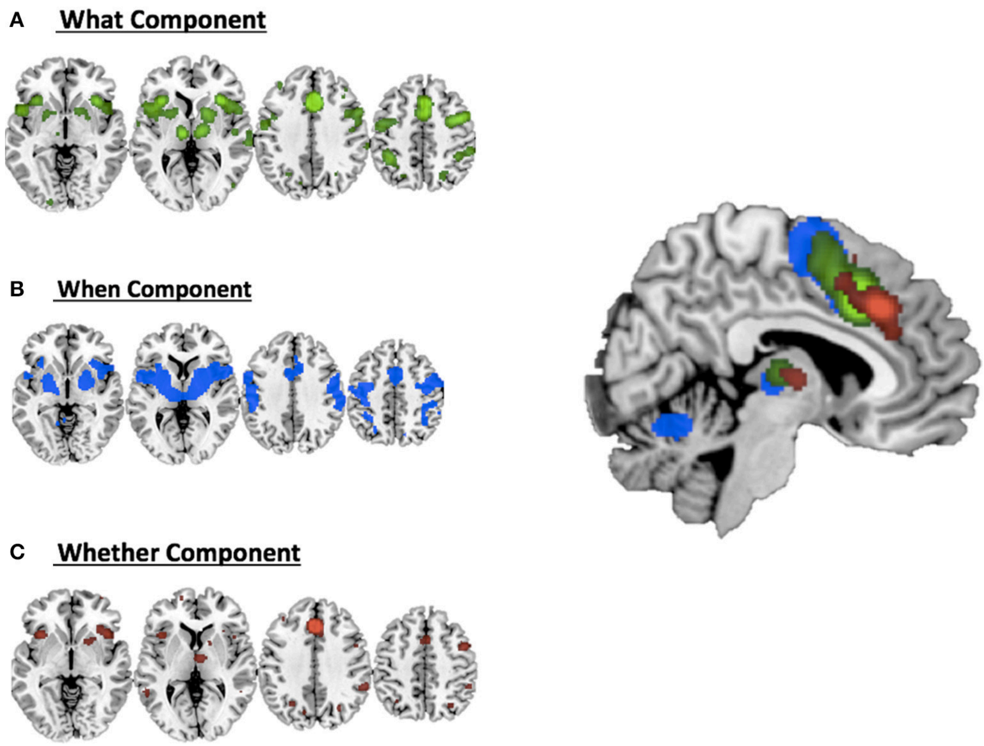

FIGURE 2 | Co-activations maps calculated with ALE for (A) the what component; **(B)** the when component; **(C)** the whether component and a summary of all the components on the medial view of the brain.

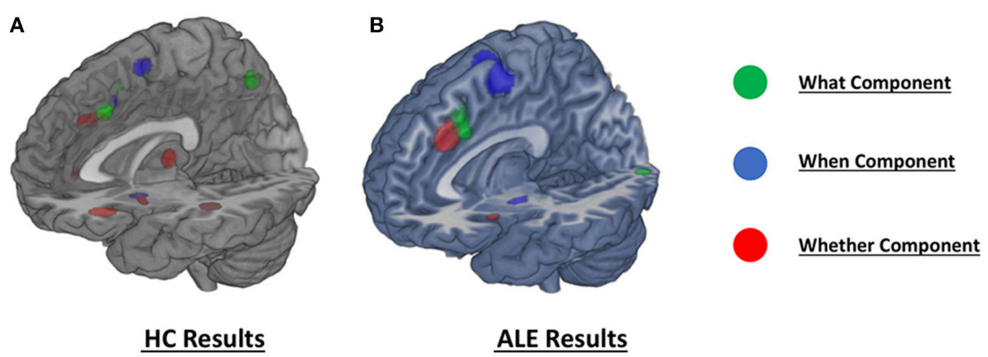

FIGURE 3 | Comparison of the dissociation between components assessed with (A) hierarchical clustering analysis results and **(B)** ALE co-activation maps.

for discrete aspects of intentionality, encoding what to do, when to do it or whether or not to do it. However, in both the cited models, the authors based their conclusions on a qualitative analysis of the available PET/fMRI literature, characterized by a number of different experimental approaches.

The current meta-analytic study was conducted in order to further test these alternative neurocognitive models of intentional action, by formally exploring, as quantitatively as possible, the available literature. The results of our combination of hierarchical clustering and ALE meta-analytical procedures expands the initial model of Brass and Haggard (2008) showing that (1) a segregation of intention specific regions is possible even though the regions involved go beyond the mesial wall of the frontal lobe; (2) the regions involved coincide with brain areas that are active also for conditional (non-intentional) motor behaviors. This latter finding suggests that intentionality manifests itself in discrete components through the boosting of general purpose action-related regions specialized for different aspects of action selection and inhibition.

A Multi-Component Neural Model of Intentionality

Our results partially confirm the assumption of Brass and Haggard's model (2008), suggesting the existence

TABLE 2 | Co-activation maps analyses.

Brain regions (BA)	MNI coordinates									
	Left hemisphere					Right hemisphere				
	Cluster ID	mm^3	*x*	*y*	*z*	Cluster ID	mm^3	*x*	*y*	*z*
A. WHAT COMPONENT										
Frontal_Inf_Tri	2	856	−39.3	14	27.7					
Frontal_Inf_Oper (44)	2	856	−42	10	30					
Frontal_Mid_R (6)						3	416	32	4	50
Cingulum_Mid_R (24)						1	4760	3.7	18.5	40.3
Precentral_R (6)						3	416	34	−2	42
Insula_R						5	304	36	24	4
Temporal_Pole_Sup_L	6	200	−48	12	−2					
Calcarine_L (18)	4	304	−17	−97	−4					
B. WHEN COMPONENT										
Frontal_Inf_Oper (44)	7	816	−56	7	16					
			−62	8	18					
Frontal_Mid (8)	9	232	−32	−10	58					
Frontal_Sup (6)						4	7432	32	−10	66
Supp_Motor_Area						1	7432	4.2	−4.2	61.8
Precentral_gyrus (6)						8	424	63	6	18
Precentral gyrus (4)	13	56	−40	−24	62	4	7432	38	−16	58
						4	2952	55.5	−21.5	32.9
Postcentral gyrus (3)	11	168	−43	−36	61	4	2952	58	−16	38
	6	920	−42	−22.7	42.7					
			−42	−24	38					
Precuneus						5	1232	16.2	−50.8	−25.6
Cerebellum_6	12	136	−34	−62	−20	4	7432	40	−10	54
Cerebellum_Crus1	10	216	−22	−66	−30					
Putamen						2	4008	31.7	−1.2	7.1
Pallidum	3	3216	−23.6	−10.4	1.9	2	2952	22	−4	0
Thalamus	3	3216	−10	−26	10					
C. WHETHER COMPONENT										
Rolandic_Oper (44)	10	80	−46	24	18					
Cingulum_Mid (24)	1	3368	−1	29.2	34.6					
Precentral (6)						6	128	44	8	46
Insula	3	288	−36	14	−2	5	136	44	20	−8
Parietal_Inf	9	96	−34	−60	44					
Temporal_Mid (21)	2	456	−60	−48	4					
	7	120	−56	−54	6					
Putamen						4	136	20	12	−8
Thalamus L/R	2	456	0	−9	4	2	456	0	−9	4
Caudate	8	120	−10	6	18					
		120	−14	6	18					

A, What > (When and Whether) from seed at $x = 4$; $y = 20$; $z = 38$.
B, When > (What and Whether) from seed at $x = 5$; $y = -3$; $z = 62$.
C, Whether > (What and When) from seed at $x = -1$; $y = 29$; $z = 35$.

of a rostro-caudal gradient within the medial prefrontal cortex, with the more anterior regions involved in more abstract decisions of whether to execute an action and the more posterior ones recruited in specifying the content and, yet more dorsally, the timing components of actions.

For example, for the decision about which action to perform (*what* component) the data clustered at the level of the right middle cingulum; the middle cingulum has been previously associated to conflict processing and conflict monitoring (Botvinick et al., 2004; Carter and van Veen, 2007) and it could contribute to the specific resolution of an

TABLE 3 | Composition analysis of the medial frontal wall clusters isolated by the comparative co-activation maps analyses performed on the BrainMap.org dataset.

	Go/No-Go	Other	Chi Squared value	*P*-value
A				
What	17	39		
vs.			10.6	0.001
When	6	67		
B				
Whether	9	14		
vs.			12.86	0.0004
When	6	67		
C				
Whether	9	14		
vs.			0.57	0.451
What	17	39		

The table reports the comparison of the proportion of regional effects derived from go/no-go paradigms and all other paradigms within each of the three clusters from the medial wall of the frontal/limbic lobe.
A, Chi-Squared Test—What vs. When.
B, Chi-Squared Test—Whether vs. When.
C, Chi-Squared Test—Whether vs. What.

internal conflict about which action to execute among different alternatives.

For what concerns the decision about the timing of the action, we found a cluster in the right SMA; this region has been previously explicitly linked to the timing or to the intentional initiation of a movement (Cunnington et al., 2003; Debaere et al., 2003). The association between the SMA and timing of intentional action is supported by recent studies on Parkinson's disease (PD). PD is characterized by difficulties in implementing intentional behaviors, but this impairment is reduced in the presence of an external salient cue, such as, for example, a fire (Jahanshahi, 1998); for this reason, it has been widely hypothesized that PD patients have a malfunctioning of the internal timing of action (Brass and Haggard, 2008). In PD patients, the SMA has abnormal connectivity with the thalamus, especially during the OFF-medication phase (Michely et al., 2015).

Finally, the studies investigating the intentional decision about whether or not to act converged in a cluster at the level of the right cingulum in its anterior portion, a region more anterior than the ones involved in the other two components. This finding confirms that the intentional inhibition of an action involves separate neural structures fleshing out the concept that deciding whether to act or not is separable from other aspects of intentionality.

Going beyond the Frontal Mesial Cortex

In contrast with the original www-model, the dissociations for the different components involved also brain regions well outside the median wall of the frontal lobe, in a component specific manner.

For example, for the *what* component the data clustered at the level of the right supramarginal gyrus, a finding confirmed by the co-activation maps analysis. The involvement of the parietal lobule in the decision about which action to execute should not be a surprise: the inferior parietal lobules are in fact critical nodes for the representation of actions and intentions to act according to previous findings (Tunik et al., 2007). Recently, Gallivan et al. (2011) showed that intentions for specific movements could be predicted by the spatial activity patterns in these areas. Moreover, direct electrical stimulation of the right inferior parietal lobule induces a strong intention to move; at relatively high stimulation intensities (∼8 mA) patients may even feel an illusory sense of movement (Desmurget et al., 2009). Thus, in the context of intentional action, the parietal lobule seems to contribute to movement intention and motor awareness with specific reference to specific body parts.

For what concerns the internal timing of the action, a specific cluster was found in the frontal operculum, a structure previously associated with the synchronization of voluntary hand movements to an auditory rhythm (Thaut, 2003). It is also telling the involvement of the motor component of the lenticular nuclei bilaterally: these are of course part of a cortico-subcortical-cortical network that regulates motor behavior (Graybiel, 1998) and that is dysfunctional in movement disorders (see review in Crittenden and Graybiel, 2011).

Finally, for the *whether* component, our data clustered also at the level of the right anterior insula; anterior insula activations have been reported in various studies on response inhibition (Wager et al., 2005). Moreover, there is evidence indicating that anterior insula is associated with concentration and "cognitive effort" (Allen et al., 2007): if so, its involvement in this class of tasks, may represent the strain to decide whether to do or not to do something after this has already been planned.

We found two more clusters associated with the whether component, at the level of the thalamus and the putamen; the thalamus, and the basal ganglia in general, are known to play a crucial role in action selection (Humphries and Gurney, 2002; Humphries et al., 2006). The specific involvement of such structures in the intentional inhibition of actions is supported by their abnormal functioning in Gilles de la Tourette Syndrome, a movement disorder characterized by the presence of unwanted movements that patients are not usually able to inhibit (see review in Zapparoli et al., 2015): this neurological disease is most likely associated with aberrant activity in the basal ganglia and with functional changes in the cortico-striato-thalamo-cortical (CSTC) circuits (see Mink, 2006; Leckman et al., 2010; Felling and Singer, 2011; Ganos et al., 2013). A malfunction of the same circuitry has been described also in the obsessive-compulsive disorder (OCD, see for example Bandelow et al., 2016). The spectrum of OCD symptoms is too broad to be readily accommodated by malfunctions of the www-neural circuitry alone. However, as much as complex motor tics can be very similar to motor compulsions (Worbe et al., 2010), OCD symptoms are frequently observed in patients with Gilles de la Tourette Syndrome. Considerations about their frequent comorbidity suggest that the co-occurrence of the two syndromes may in fact represent a specific clinical entity, the recently defined Obsessive-Compulsive Tic Disorder (OCTD; see Dell'Osso et al., 2017): this may comprise the "malfunctioning" of the neural systems associated with the *whether* component of intentionality, explaining the difficulty of these patients to inhibit their compulsive/ticking behaviors.

The Functional Neural Correlates of Intentional Action and of Action in General

The issue of whether the anatomy of intentional action, and its subcomponents, involves brain regions generally responsible for action was assessed by the co-activation maps analyses. This analysis confirmed the segregation of the clusters along the medial wall and the additional regions seen for the *www* components by our hierarchical clustering analysis. It also confirmed by far and large the extension of component specific regions outside the medial wall of the frontal/limbic lobe.

A composition analysis of the paradigms that contributed to each of the three clusters of the medial wall of the frontal/limbic lobe[3] revealed, as one could expect, first and foremost the extreme heterogeneity of the paradigms that were retrieved with the only constraint of the key-words "action" and "activation" and "normal subjects" (see the Supplementary Table 2). Having identified the relative proportion of go/no-go paradigms behind each cluster, the *what* and the *whether* ones proved to have a significant larger proportion of such paradigms. Although some aspects of these findings are open to discussion, it is a matter of little surprise to observe that the *whether* component of intentionality maps into a cluster that contains a fair proportion of go/no-go paradigms in a general database of experiments on action.

However, the analysis of the paradigms that contributed the raw data for co-activation maps were far from being associated with intentional action experiments only. In fact, at the time of this writing (February 2017), as strange as it might seem[4], the BrainMap.org database did not contain the 15 studies that were submitted to our hierarchical clustering analysis on the studies on intention. This fortuitous feature was instrumental to our analyses as we were guaranteed that the hierarchical clustering and the co-activation maps analyses were independent, adding validity to our inferences.

In returning to the crucial matter of our contention here, the fact that the medial wall seeds, on which the co-activation maps analyses were based, segregate in an identical manner to what is revealed by the hierarchical clustering performed on "intentional" experiments, suggests that the specificity of intentionality and its subcomponents cannot be sought *phrenologically* in terms of minute segregated regions exclusively involved in intentionality; on the other hand, the same observation suggests that the *what, when, and whether* segregation for action most likely exists beyond the concept of intentionality.

However, it cannot be denied that the presence of an intentional stance during the paradigms meta-analyzed here induced stronger activity in these regions in a component specific manner. This suggests, on the one hand, that intentionality is expressed in these *www* action regions at some microscopical level, perhaps thanks to the boosting effect of some ascending modulatory attentional pathways for tasks in which subjects have to decide how and whether to act by themselves, rather than in reaction to a conditional stimulus. Another possibility is that the relative weights of the connections between the regions involved in the different aspects of intentionality change during intentional action, something that needs to be explored with effective connectivity techniques and that goes beyond the potentials of meta-analyses based on data generated by univariate analyses.

[3]These were the *what, when* and *whether* clusters defined on the BrainMap.org database using as seeds the centroids of the clusters of the hierarchical clustering analysis,

[4]The BrainMap.org database, as large as it is, has contents that are dependent on the input of a distributed set of users. At the time of writing, it contained data from 3066 papers with 118308 regional effects and 15155 statistical comparisons.

CONCLUSION AND FUTURE DIRECTIONS

After this meta-analytic review, it is clear that further studies are needed to assess the functional anatomical foundations of the *www-model* of intentionality, in order to overcome the methodological limitations of previous attempts. In particular, we are much in need of novel fMRI experiments in which the sub-components of intentionality, postulated by the above mentioned neurocognitive models, are assessed with an uniform procedure in the same group of subjects. The advantages of a uniform procedure are obvious: significant differences between the intentional tasks in the different conditions should not be confounded by factors (e.g., different populations; different tasks; different scanning protocols) that may hamper the possibility of firm assignations of specific functional anatomical patterns to subcomponents of intentionality. Another unexplored issue is the characterization of intentional actions in conditions in which content, timing and the very decision on whether to act or not are explicitly and jointly manipulated. Furthermore, it remains to be discovered how general-purpose action brain regions become more active when intentionality is operating. This will clearly require analytical approaches that go beyond univariate analyses of the fMRI data. Clearly, one such ambitious model should have some predictive value for pathologies in which a disorder of intentionality and its specific components is expected. Brass and Haggard (2008) speculated about candidate pathologies that may entail a specific disorder of intentionality (e.g., the *when* component in Parkinson's disease). These specific associations also remain to be demonstrated convincingly. However, in spite of all these unsolved issues, we believe that the available literature contains sufficient evidence to think that the *www-model* of intentionality might be a useful starting framework for future investigations.

AUTHOR CONTRIBUTIONS

LZ, SS, and EP reviewed the data for the meta-analyses, performed the analyses, and drafted the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fnhum.2017.00238/full#supplementary-material

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REVIEW
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Bodily Experience in Schizophrenia: Factors Underlying a Disturbed Sense of Body Ownership

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Emerging evidence is now challenging the view that patients diagnosed with schizophrenia experience a selective deficit in their sense of agency. Additional disturbances seem to exist in their sense of body ownership. However, the factors underlying this disturbance in body ownership remain elusive. Knowledge of these factors, and increased understanding of how body ownership is related to other abnormalities seen in schizophrenia, could ultimately advance development of new treatments. Research on body ownership in schizophrenia has mainly been investigated with the rubber hand illusion (RHI). Schizophrenia patients show higher susceptibility to the RHI, which may be explained by a stronger reliance on multisensory information over weaker stored body representations. This review shows that a coherent sense of body ownership arises from the integration of both bottom-up sensory processes and higher order, top-down bodily- and perceptual representations. Multisensory integration, temporal binding, anticipation, intention and efferent signals all partly modulate the complex experience of body ownership. Specifically, we propose that patients with schizophrenia have weaker stored body representations, and rely to a greater extent on external stimuli, such as visual information, due to imprecise or highly variable internal predictions. Moreover, the reduced sense of agency in schizophrenia may additionally contribute to the disturbed sense of body ownership, as evidence from healthy participants suggests that agency and body ownership are interrelated. *Vice versa*, a reduced sense of body ownership may also contribute to a reduced sense of agency. Future studies should explicitly target the precise relationship between the two in schizophrenia.

Keywords: body ownership, self-agency, schizophrenia, multisensory integration, body representations, internal predictions, temporal binding

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INTRODUCTION

Schizophrenia is described as a psychiatric disorder in which there is loss of coherence in the minimal sense of self (Nelson et al., 2014). From a phenomenological perspective, three layers in the sense of self are distinguished (Sass and Parnas, 2003). At the first and most basic level, there is an implicit and unconscious awareness of oneself as an origin of experience, as a medium for relating to the world, referred to the "minimal self" or *ipseity*. Secondly, a more explicit or reflective awareness of the self exists as a constant subject of experience and action. Finally, the "social" or "narrative self" refers to personal characteristics such as habits, social identity and history, and often involves reflective, metacognitive processes (Nelson et al., 2014). These different levels of self-experience are interconnected and cannot be observed in isolation from each other.

Different authors have stated that the most basic level of self-experience, *ipseity*, is rooted in the bodily experience (e.g., Merleau-Ponty, 1945; Piaget, 1954). The sense of one's own body is variously termed "corporeal awareness", "bodily self-consciousness", or "embodiment", and is described as an implicit form of knowledge that is both non-conceptual and somatic (Kant and Smith, 2003). Embodiment specifically is defined as *"the perception that one's sense of self is localized within one's bodily borders"* (Arzy et al., 2006). Some authors have proposed that this embodiment is a necessary prerequisite for other kinds of self-experience (e.g., Kant and Smith, 2003). According to the phenomenological approach, the coherence between the diverse symptoms in schizophrenia can only be understood if their shared bodily roots are taken into account (de Haan and Fuchs, 2010).

The embodied sense of self is a complex phenomenon that consists of different components, including body ownership and the sense of agency over actions. In this review, we adopt a broad definition of body ownership conceived by Tsakiris et al. (2007) as *"the special perceptual status of one's own body, which makes bodily sensations seem unique to oneself"*. In healthy people, a sense of body ownership is continuously present and they therefore experience body ownership not only when performing intended actions, but also when resting and during passive movement. The sense of agency, on the other hand, is the perception that one is the initiator of one's actions. The observation that people with schizophrenia often misattribute their own actions to someone or something else, or deny intending their actions, has led to the prevailing idea that there is a selective impairment in their sense of agency, while body ownership is thought to be intact.

This prevalent view, in which patients with schizophrenia have a disturbed sense of agency but a normal sense of body ownership, has caused research to focus on motor control processes. To date, only few studies have specifically examined body ownership in schizophrenia, mainly with the use of the rubber hand illusion (RHI) paradigm, first described by Botvinick and Cohen (1998). During this illusion, the participant's hand is hidden from view whilst a rubber model hand is placed in front of him. The experimenter simultaneously strokes the rubber hand and the participant's hidden hand with two brushes. This produces an illusory sensation of ownership over the rubber hand and a shift in perceived hand location toward the fake hand (Botvinick and Cohen, 1998).

This RHI is generally experienced more intensely in people with schizophrenia (Peled et al., 2000, 2003; Thakkar et al., 2011; Germine et al., 2013). This finding challenges the idea that people with schizophrenia have a selective deficit in sense of agency. Additional disturbances in the sense of body ownership seem to exist. However, the underlying factors contributing to a disturbed sense of body ownership in schizophrenia are not clear. We will therefore review current evidence, and examine which factors contribute to a disturbed sense of body ownership in people diagnosed with schizophrenia. Specific studies and experiments that have contributed to an increased understanding of bodily experience will be highlighted. Finally, the connection between agency and ownership will be investigated. A summary of the possible factors underlying a disturbed sense of body ownership in schizophrenia is included in **Table 1**. Knowledge on how body ownership is related to other types of self-experience and psychosis-proneness can help increase our understanding of factors that lead to psychosis development and could ultimately advance development of new treatments.

MULTISENSORY INTEGRATION

Multisensory integration involves the processing of sensory input from various modalities and the resolution of possible conflicts in order to represent the body and the world coherently. Body ownership specifically is thought to result from the integration of visual and proprioceptive signals (Giummarra et al., 2008). The RHI depends on an interaction between sensory inputs from three different modalities, namely vision, touch, and proprioception. In this paradigm, a distorted sense of body ownership can be elicited by inducing a sensory conflict. Seeing the tactile stimulation on the rubber hand, while simultaneously feeling this on one's own hand, results in a visual capture of the tactile sensation which subsequently causes a feeling of relocalization of one's own hand towards the location of the rubber hand. This is termed "proprioceptive drift" and is thought to result from the dominance of vision over proprioception (Botvinick and Cohen, 1998). Using a psychometric approach with principal component analysis, Longo et al. (2008) found four dissociable components of the RHI experience, namely embodiment of the rubber hand, loss of the own hand, movement, and affect. Embodiment could in turn be separated into the three tightly interacting components of agency, ownership and location. Ownership specifically correlated with proprioceptive drift (Longo et al., 2008). This is in line with results obtained by Holmes et al. (2006), who found that proprioceptive bias correlated to questionnaire items investigating specifically ownership, but not other types of questions (Holmes et al., 2006).

Strength of the RHI has traditionally been measured in three ways, namely with the use of introspective questionnaires, proprioceptive drift and skin conductance response elicited by threatening or injuring the rubber hand. Statements on a questionnaire cannot be used to quantify the illusion in absolute terms, but should rather be used to measure differences between conditions. Indirect measurement may allow bypassing problems that are inherent to quantification of subjective experience such as suggestion, variability due to beliefs and top-down influences (Rohde et al., 2011). Proprioceptive drift has been reported to correlate with the subjective feeling of ownership over the rubber hand (e.g., Botvinick and Cohen, 1998; Longo et al., 2008; Lopez et al., 2010). This drift has been widely used as a proxy for the subjective feeling of ownership. However, recent studies indicate that a dissociation between subjective ratings and drift exists (e.g., Shimada et al., 2009; Rohde et al., 2011; Romano et al., 2015). This dissociation implies that conclusions about the experience of ownership cannot be drawn from measuring proprioceptive drift alone. There is more or less a consensus in the field that objective measures such as proprioceptive drift or skin conductance response should be combined with subjective ratings (Rohde et al., 2011; Kalckert and Ehrsson, 2012; Asai, 2015).

Originally, Botvinick and Cohen (1998) proposed a bottom-up explanation of the RHI which suggests that synchronized tactile and visual stimulation are needed for the illusion to occur, since the illusion was not elicited with the use of asynchronous stimulation (Botvinick and Cohen, 1998; Ehrsson et al., 2004). However, intermodal matching of tactile and visual information does not seem sufficient to generate an experience of body ownership. Most studies use a rubber hand that visually corresponds to a human hand in shape, color and texture. If synchronous multisensory stimulation is the single factor causing body ownership, then it should be possible to induce ownership over objects that do not visually resemble a limb. Studies show that the illusion is not elicited when a neutral object such as a wooden plank is used instead of a rubber hand (Haggard, 2005; Holmes et al., 2006; Haans et al., 2008; Tsakiris et al., 2008, 2010b). Armel and Ramachandran (2003) report that a sense of ownership can be elicited over a table to some extent, but significantly less than over a rubber hand as measured by intensity ratings and skin conductance response (Armel and Ramachandran, 2003). Instead, a (partial) visual match between the object and the subject's hand is usually needed for body ownership over the artificial hand. Also, the sense of body ownership is diminished when the rubber hand is of a different laterality or is placed in an incongruent anatomical posture in relation to the subject's own hand (Pavani et al., 2000; Tsakiris et al., 2005; Costantini and Haggard, 2007). Apart from visual and postural congruence, spatial proximity (<30 cm) is another necessary condition for the illusion to occur (Lloyd, 2007).

When active control over objects is involved, however, people may experience some sense of ownership over non-corporeal objects. Ma and Hommel (2015) designed a virtual reality set-up, in which people could actively manipulate movement, size and color of either a virtual balloon or square. Participants reported a sense of ownership over the virtual effectors to some extent. The finding that people can experience ownership over non-corporeal objects would provide support for bottom-up approaches of self-representation (Botvinick and Cohen, 1998). Integration of temporally and spatially congruent multisensory signals would then be sufficient to induce the illusion of body ownership. However, the results of Ma and Hommel (2015) should be interpreted with caution, since participants reported low ownership ratings. Moreover, the ownership illusion was more convincing when the virtual effectors seemed to be connected to the participant's body, suggesting that Gestalt principles influence self-perception. These Gestalt principles indicate that connectedness, governed by the laws of proximity and continuity, is central to perceiving unity (Ellis, 1999). Studies by Newport and Preston (2010) and Tieri et al. (2015) indeed show that virtually detaching the hand or finger in virtual reality, thereby disrupting continuity, abolishes body ownership of the proxy hand completely (Newport and Preston, 2010; Tieri et al., 2015).

These studies suggest that integration of visual, tactile, and proprioceptive information mediates ownership of single limbs. Petkova and Ehrsson (2008) investigated how ownership of individual body parts translates into the experience of owning a whole body. They used a "'body-swap'" illusion, in which people experienced a virtual body to be their own through visuo-tactile stimulation. Their findings suggest that the experience of owning an entire body is produced by neuronal populations that integrate multisensory information across body segments (Petkova and Ehrsson, 2008). In a following study, Petkova et al. (2011) found that the first person visual perspective poses a fundamental constraint on the full-body illusion. This supports the proposed model that the sense of body ownership relies on mechanisms for multisensory integration operating in body-part-centered reference frames (Ehrsson et al., 2004; Makin et al., 2008; Petkova and Ehrsson, 2008).

Patients with schizophrenia have been shown to experience the RHI more strongly (Peled et al., 2003) and faster (Peled et al., 2000) compared to healthy controls, as indicated by self-report questionnaires. These results have generally been explained as a decreased sense of body ownership, or less distinct self-other perception in schizophrenia due to deficits in multisensory integration. However, these studies used introspective reports (questionnaires) for both diagnosing schizophrenia and strength of the illusion, and the results could therefore merely reflect a response bias. Also, the study conducted by Peled et al. (2000) lacked a control condition. A possible general tendency to endorse bodily sensations in people with schizophrenia can therefore not be excluded.

In another study, Thakkar et al. (2011) investigated the RHI in schizophrenic patients compared to healthy controls with the use of both subjective (questionnaire) and objective (proprioceptive drift, autonomic response) measurements. Experience of the RHI was stronger during synchronous stimulation in both healthy controls and patients, indicated by both self-report and proprioceptive drift. Moreover, people with schizophrenia reported a stronger RHI than controls. In regard to the objective measures, Thakkar et al. (2011) found a larger proprioceptive drift in patients, but only with synchronous stimulation. This may indicate that proprioceptive drift and introspective reports represent distinct aspects of the illusion or that one of the measures does not adequately capture strength of experiencing the RHI (see Holmes et al., 2006; Shimada et al., 2009; Rohde et al., 2011; Romano et al., 2015). Another finding of the study is that temperature dropped in the stimulated hand during right hand stimulation whereas it increased in the unstimulated hand. Altogether, the authors conclude embodiment of the RHI to be stronger in schizophrenic patients than in healthy controls, in agreement with previous investigations (Peled et al., 2000, 2003). Psychosis-like symptoms in otherwise healthy individuals were correlated to greater illusion susceptibility/strength of body ownership in the RHI

TABLE 1 | The different factors possibly underlying a disturbed sense of body ownership in schizophrenia.

Factor		Literature
Multisensory integration	A stronger effect of visual information overriding weaker multisensory integration.	Peled et al. (2000, 2003), Asai et al. (2011), Thakkar et al. (2011) and Germine et al. (2013)
Temporal and intentional binding	A "longer" window of temporal binding, in which events that happen further away in time are experienced as co-occurring.	Elvevåg et al. (2003), Franck et al. (2005), Foucher et al. (2007) and Graham et al. (2014)
Predictive mechanisms and anticipation	More variable predictive mechanisms resulting in a higher reliance on external information such as vision.	Ross et al. (2000), Voss et al. (2010), Lalanne et al. (2012) and Ferri et al. (2014)
Efferent motor signals	Aberrant efferent signals possibly leading to a more flexible sense of body ownership and higher interference of external information on the self.	Malenka et al. (1982), Frith and Done (1989), Daprati et al. (1997), Blakemore et al. (2000, 2002), Shergill et al. (2005) and Synofzik et al. (2010)
Self-agency	Agency and ownership are dissociable components of self-experience, but they do seem to interact. The disturbed sense of agency may therefore contribute to a disturbed sense of ownership in schizophrenia.	Tsakiris et al. (2006, 2010a), Longo et al. (2008), Waters and Badcock (2010), Kalckert and Ehrsson (2012, 2014), Asai (2015), Louzolo et al. (2015), and Garbarini et al. (2016)

Only research specifically targeted at schizophrenia patients is included except for self agency, in which also evidence from healthy individuals is taken into account.

with synchronous stimulation in a study conducted by Germine et al. (2013).

The RHI is thought to arise from multisensory (visual and tactile) information overruling stored body representations (Tsakiris, 2010). Following this, stronger experience of the illusion could either result from increased multisensory integration, a stronger reliance on visual cues overriding proprioceptive information, or weaker pre-existing body representations. Previous research demonstrates that being prone to psychosis is related to a decrease in multisensory integration, as opposed to an increase (e.g., Asai et al., 2011; Germine et al., 2013). This makes increased visual-tactile integration a less likely explanation for the abovementioned findings. Rather, this can be interpreted for support of the hypothesis of weaker stored body or somatosensory representations. Previous studies have indeed already indicated that cognitive and perceptual deficits in schizophrenia are due to inadequate coupling of sensory information to pre-existing representations and environmental context, the details of which are beyond the scope of this review (but see: Schneider et al., 2002; Fletcher and Frith, 2009). Higher susceptibility to the illusion may therefore be due to a stronger reliance on multisensory information over potentially weaker stored body representations.

In conclusion, these studies indicate that simultaneous intermodal stimulation is necessary, but not sufficient for a sense of ownership to occur in the RHI. Spatial proximity, visual resemblance and postural correspondence are also important in eliciting a sense of body-ownership. When active manipulation is involved however, these prerequisites are attenuated, suggesting that a sense of agency may be important for a sense of body ownership to occur. This provides some support for the hypothesis of Short and Ward (2009), who postulate that ownership can be experienced over any object, irrespective of visual appearance, if predictable action outcomes follow the intentions of the agent (Short and Ward, 2009). In the absence of direct control, however, other factors, such as visual resemblance, spatial proximity and postural correspondence may become more important. With respect to schizophrenia, studies with the RHI suggest an enhanced illusion. While multisensory integration seems to be impaired in schizophrenia, this is likely to result in a reduced rather than increased RHI. Therefore, factors other than bottom-up multisensory processes, such as a weakened stored body representation, may contribute to a disturbed sense of body ownership.

TEMPORAL AND INTENTIONAL BINDING

Multisensory integration is generally seen as a crucial component in coherent bodily self-experience and sense of body ownership. As discussed above, disturbances in sensory processing that involve multisensory integration have been shown to exist in people with schizophrenia. However, other factors seem to play a role. Recent studies have investigated the temporal factors important for multisensory integration, with a focus on the "temporal binding window", which is defined as the timespan within which stimuli from different modalities are perceptually bound. These studies have demonstrated that the window of temporal binding is distorted in various neurodevelopmental disorders, such as autism, dyslexia and schizophrenia. For example, Graham et al. (2014) investigated body ownership in schizophrenia patients divided into three groups, namely patients with current, past, and no history of passivity symptoms. They used a projected-hand illusion, in which a live video image of the participant's hand is projected onto a video screen, with the real hand and the image of the hand being separated by 15 cm. Two delay conditions were present in the illusion; *synchronous* (<10 ms video delay) and *asynchronous* (an additional imposed 500 ms delay) feedback. A remarkable finding is that patients in the subgroup with current passivity symptoms did not show the typical reduction in body illusion with asynchronous feedback (with a 500 ms delay in visual feedback) as opposed to the synchronous condition. So, the clinical subgroup with passivity symptoms continued to experience ownership over the projected hand during asynchronous stimulation, whereas the other subgroups did not retain the sense of ownership in this condition (Graham et al., 2014). This may suggest that the window of temporal binding, which provides connections between the self and external stimuli, is "wider" in patients with current passivity symptoms. Consequently, they experience stimuli that are further apart in time, as co-occurring. However, this effect has not been replicated and more research into this particular factor is warranted.

Other evidence in support of this increased window of temporal binding is found in studies that report an impairment in time perception in people with schizophrenia (Elvevåg et al., 2003; Franck et al., 2005). Patients with passivity symptoms have been shown to exhibit aberrant cognitive and motor timing. Particularly, these studies have shown that these people perceive events as happening closer in time than they actually occurred (Blakemore et al., 2000; Foucher et al., 2007). This links to a related psychological phenomenon called "intentional binding". Research conducted by Haggard et al. (2002) shows that, when a voluntary action is followed by an expected sensory consequence, a psychological binding effect causes events to be perceived closer in time, which contributes towards a sense of self-agency and self-recognition. This intentional binding effect involves the subjective perception that cause and effect are drawn together in perceived time (Haggard et al., 2002). Subjective, intentional experience of actions contributes to the inference of self-recognition (Haggard et al., 2002; Haggard, 2005; Engbert and Wohlschläger, 2007). Outcome expectations, sensory feedback and causal beliefs all partly influence binding (reviewed by Moore and Obhi, 2012).

Another phenomenon that is linked to the sense of agency is sensory attenuation, in which the sensory consequences of self-produced action are attenuated compared to externally generated events (Blakemore et al., 2000; Shergill et al., 2005). Both temporal binding and sensory attenuation can be modulated by cognitive expectations about either the outcome or source of an action (Moore et al., 2009; Desantis et al., 2011; Gentsch and Schütz-Bosbach, 2011). When expectations about the outcome of an action are induced in an experiment through showing the action outcome before the actual action performance, stronger temporal binding (Moore et al., 2009) and stronger sensory attenuation (Gentsch and Schütz-Bosbach, 2011) are reported. In an extensive review, van der Weiden et al. (2015) show that individuals diagnosed with schizophrenia have impairments in both motor prediction and cognitive processes (such as biased expectation of actions), which may lead to over-attribution of agency (see van der Weiden et al., 2015). In addition, research conducted by Renes et al. (2013) shows that, when the outcome of an action is implicitly primed, healthy people experience an increased sense of agency over actions, whereas schizophrenic patients do not (Renes et al., 2013).

The finding that the temporal binding window in schizophrenia is altered has important implications. Precision of internal timing is a crucial element in a variety of processes, including self-recognition and sensory–motor awareness (Haggard et al., 2003). Accurate temporal and intentional binding is important in forming causal mental relationships. This binding effect is thought to be modulated by top-down processes associated with motor intentions, and subjective experience of anticipated actions can therefore have distal effects on sensory-motor perception. Expectation of actions may thus also be involved bodily experience and ownership, but the precise role of anticipatory mechanisms still needs to be clarified.

PREDICTIVE MECHANISMS AND ANTICIPATION

As discussed above, expectation of actions may also play an important role in bodily experience. Additional evidence for this comes from a study conducted by Ferri et al. (2014), who created an edited version of the RHI in which they aimed to measure illusion susceptibility in the absence of the multisensory integration that occurs with the experience of touch. In this experiment, participants were instructed to observe the hand of the experimenter approaching, without touching, either a rubber hand or a piece of wood placed on a table in front of them. In healthy participants, expectation of touch due to the sight of a hand approaching the rubber hand is sufficient to elicit ownership over the rubber hand. Schizophrenia patients, however, reported a much lower sense of ownership over the rubber hand compared to healthy controls. Apparently, the mere expectation of touch is not sufficient for patients to experience the illusion. A possible explanation is that people with schizophrenia anticipate touch in a different way than healthy subjects do, or have a deficit in their predictive mechanisms of action (Ferri et al. (2014).

Voss et al. (2010) recorded subjective time estimates of a self-initiated voluntary action (a key press) followed by a sensory effect (a tone). When the voluntary action had a high probability of causing a tone, healthy volunteers showed a predictive shift of the perceptual estimate of the action towards the tone, whereas schizophrenia patients did not show this effect. This indicates that patients may lack a predictive component of action awareness. The deficit in predicting the relationship between action and effect was correlated with severity of positive psychotic symptoms, specifically delusions and hallucinations. Furthermore, individuals with schizophrenia showed an exaggerated retrospective binding between action and tone (Voss et al., 2010). Other studies also show impaired anticipation of the position of a moving stimulus in schizophrenia with smooth pursuit eye movements (e.g., Ross et al., 2000). Additionally, research on the *Simon effect*, the finding that manual responses are faster and more accurate when the stimulus appears on the same side as the responding hand (Simon and Wolf, 1963), also suggests that predictive mechanisms are dysfunctional in patients (Lalanne et al., 2012).

EFFERENT MOTOR SIGNALS

In the static RHI only tactile, visual and proprioceptive information are involved in evoking the feeling of ownership. During passive movement, information from skin receptors, muscle spindles, joint receptors and visual feedback provide additional kinesthetic information (Edin and Johansson, 1995; Proske and Gandevia, 2012). In active movement, this information is accompanied by efferent information from voluntary motor commands and the sensory predictions they produce (Bays and Wolpert, 2007). This is described in the "forward model" (Frith et al., 2000), which proposes that the sensory consequences of self-produced actions are predicted using internal information, such as efference copies of a motor command (Bell, 2001). By comparing the internal prediction with the sensory afference, one can differentiate between externally caused events and self-produced actions. In case of a match between the different sources of information, the salience of sensory information is diminished, and the afference is interpreted as the result of a self-produced action. When there is mismatch, the action is interpreted as being externally caused (Synofzik et al., 2008). Attenuation of self-produced stimulation occurs in healthy controls and psychotic patients without passivity symptoms or auditory hallucinations. By contrast, self-generated stimulation is not attenuated relative to externally produced stimulation in patients with passivity symptoms and/or auditory hallucinations (Blakemore et al., 2002; Shergill et al., 2005). This would support the proposal that such symptoms are associated with a deficit in the forward mechanism that normally predicts and cancels out self-produced actions.

During active movements, when efference information is involved, recognition of a body part or action is enhanced in healthy individuals (Daprati et al., 1997; Farrer et al., 2003; MacDonald and Paus, 2003; Tsakiris et al., 2005; Nahab et al., 2011). The importance of efferent signals and proprioception in self-recognition was investigated by Haggard (2005) with a self-recognition experiment in which healthy participants saw either their own hand or the experiment's through video feedback, while their hand was passively moved either by the participants own left hand (active movement) or by the experimenter (passive movement). Participants were asked to judge whether the hand was their own. During passive movement, with only proprioceptive information available, self-recognition was at chance level. With the added efferent information available, when the participant actively made his own hand move, performance in the self-recognition task significantly increased, indicating that efferent information enhanced self-recognition in this task. Shimada et al. (2009) showed that threshold for the detection of mismatches (such as delayed visual feedback) is indeed lower during passive movement, suggesting improved discrimination ability when efferent information is available. According to the authors, these results mean that efferent signals give more important cues for self-recognition than just proprioception.

Synofzik et al. (2010) examined whether lower performance of schizophrenic patients in action attribution tasks is due to inaccurate predictions about the sensory consequences of self-produced action. Participants were asked to perform pointing movements in a virtual-reality setup in which the visual feedback of movements was rotated. Patients noticed the visual rotation at a higher rotation angle compared to controls, and the size of this angle was correlated to delusions of influence reported in these patients. In a second experiment, participants had to estimate their pointing direction in the presence of rotated video feedback. Estimates done by patients were more influenced by the feedback rotation and showed higher variability compared to controls. Moreover, during trials without visual feedback, in which estimates are completely dependent on internal action-related signals, the variability in estimates was likewise increased. These findings support the suggestion that the "comparator mechanism", which relates internal and external cues (Frith, 2012), is impaired in schizophrenia due to elevated variation in internal predictions about the sensory consequences of action. Importantly, aside from greater variability in internal predictions, external information about self-produced actions (in this case visual feedback) influenced self-agency judgments to a greater extent in patients. The weighting of internal and external cues with respect to self-action may depend on the reliability of internal predictions (Synofzik et al., 2010). Imprecise or unreliable internal predictions may cause patients to depend more strongly on external information on self-action such as vision. This is in line with previous research showing that schizophrenia patients with delusions of control fail to make rapid error corrections based on awareness of discrepancies between intended and predicted limb positions (Malenka et al., 1982; Frith and Done, 1989), even though they have no difficulty correcting errors based on visual feedback about limb position (Frith and Done, 1989). This suggests that individuals with schizophrenia are deficient in their ability to monitor ongoing motor behavior on the basis of internal, self-generated cues (Daprati et al., 1997; Blakemore et al., 2000, 2002).

Although studies on self-recognition have contributed to our understanding of self-experience, these paradigms can provide only indirect evidence for the role of sensory and efferent cues in body ownership. The participant's body-part is objectified as it is presented as an external object, for example projected on a screen (Tsakiris, 2010). The participant is asked to judge whether the action or body part belongs to the self. These experiments therefore involve explicit judgments rather than the feeling of body ownership and agency (see also Synofzik et al., 2008). Experimentation with the feeling of body-ownership becomes possible when multisensory stimulation is used to alter the experience of the body. The experience of ownership of a body (part) can then be present in one condition, and absent in another, as in the RHI (Tsakiris, 2010).

Tsakiris et al. (2006) studied the importance of efferent signals in an adjusted version of the RHI in which the participants performed both passive and active finger movements. With passive movement, the feeling of ownership was specifically localized to the moved finger. When actively moving a finger, however, ownership expanded over the whole hand. This suggests that efferent motor signals can integrate limbs into a wider awareness of the body. The authors argue that efferent motor signals enhance self-recognition by facilitating a "global subjective awareness" of body parts. A purely proprioceptive sense of body-ownership is local and fragmented, but the motor sense of agency seems to integrate different body parts into a coherent, global awareness of the body (Tsakiris et al., 2006).

In line with this, other studies have recently tried to examine whether added signals from passive and active movement are as important as visuo-tactile cues for developing a sense of body ownership. Most of these studies compared the strength of experiencing the RHI as elicited by active movements, passive movements, or visuo-tactile stimulation. Conflicting results have emerged from this research. Some studies indicate that movement enhances body ownership (Tsakiris et al., 2006; Dummer et al., 2009), some report no differences between movement and no-movement conditions (Kalckert and Ehrsson, 2014) and another study suggest that movement decreases ownership (Walsh et al., 2011). A recent study by Riemer et al. (2013) found no difference in the subjective strength of the ownership illusion when induced by active movements or visuotactile stimulation. However, the study by Riemer et al. (2013) found that the proprioceptive drift was stronger for the actively moving RHI compared to the classical version. Kalckert and Ehrsson (2012) reported higher subjective ownership ratings during active movements compared to passive movements (Kalckert and Ehrsson, 2012).

An interesting finding of the study conducted by Kalckert and Ehrsson (2014) was that, despite differences in available sensory and motor information between the three induction types, a very similar illusion was elicited. No differences were found along the passive movement, active movement and visuo-tactile stimulation conditions. This suggests that the RHI does not depend on specific types of sensory signals. Rather, the spatiotemporal relationship of the available signals seems to be important (Ehrsson, 2012). More evidence emerges from a study conducted Walsh et al. (2011), who used a moving RHI and anaesthetized the finger with lidocaine, thereby eliminating somatosensory information from the superficial skin. Nevertheless, in this situation with only proprioceptive and visual information available, participants experienced the illusion of ownership (Walsh et al., 2011). It seems that a match between any two independent sources of sensory information such as visual and tactile information or correlated sensorimotor signals can elicit the illusion. This explanation emphasizes bottom-up mechanisms in the illusion, but does not exclude top-down influences, which may pose *a priori* constraints on the types of objects can become part of one's own body or may modulate the experience of ownership (Tsakiris et al., 2010a; Petkova et al., 2011). Moreover, Kalckert and Ehrsson (2014) found that active movements did not increase strength of the illusion, which does not support the proposal that efferent signals from voluntary motor commands are important for experiencing ownership (Kalckert and Ehrsson, 2014).

In order to understand how an enduring absence of movement-related signals affects body ownership, Burin et al. (2015) administered the classical RHI to a group of healthy participants and to a group of neurological patients affected by left upper limb hemiplegia without proprioceptive or tactile deficits. Their results show that patients experienced a stronger illusory effect when their left (affected) hand was stimulated, but the illusion was absent when the right (unaffected) hand was stimulated. This indicates that individuals with hemiplegia have a weaker/more flexible sense of body ownership for the affected hand, but an enhanced/more rigid one for the healthy hand (Burin et al., 2015). A prolonged absence of efferent signals may thus induce a more flexible sense of body ownership.

Overall, at present there is no consensus on the extent to which efferent signals contribute to the sense of body ownership. The discrepancy in the results obtained in above mentioned studies may be partly due to differences in the setups (model hand and projected hand), types movements that are used (full hand movements and finger movements) and the measures for illusion strength. Some studies only used proprioceptive drift (Tsakiris et al., 2006; Kammers et al., 2009) others only questionnaires (Dummer et al., 2009; Longo and Haggard, 2009) or a combination of measures but obtained discrepant results (Kalckert and Ehrsson, 2012; Riemer et al., 2013). It is therefore not clear to what extent efferent signals could contribute to the change in body ownership observed in schizophrenia. Self-recognition paradigms have shown us that individuals with schizophrenia exhibit elevated variation in internal predictions about the sensory consequences of action. Individuals with schizophrenia are deficient in their ability to monitor ongoing motor behavior on the basis of internal, self-generated cues (Blakemore et al., 2000, 2002). Moreover, external information about self-produced actions (in this case visual feedback) influences self-agency judgments to a greater extent in schizophrenia patients (Synofzik et al., 2010). These studies presented the participant's body-part as an external object, for example projected on a screen (Tsakiris, 2010). It would be interesting to investigate the contribution of efferent signals to ownership experience specifically with the use of the moving RHI in schizophrenia.

THE RELATIONSHIP BETWEEN SELF-AGENCY AND BODY OWNERSHIP

For a long time, it was thought that patients with schizophrenia have a selective deficit in their sense of agency, whilst their sense of body ownership would be intact. This links to the idea that sense of agency and body-ownership are completely distinct phenomena, without any shared component (Longo et al., 2008). The model that stems from this view is termed the "independence model" (Tsakiris et al., 2010a). However, several lines of evidence now indicate that there could be a relationship between the sense of agency and body ownership. This idea is reflected in the "additive model", in which the experience of self- agency consists of the sense of body-ownership, plus the added possible sense of voluntary control over actions (Longo and Haggard, 2009; Tsakiris et al., 2010a). In this view, the sense of agency and body ownership are strongly related to each other, and sense of agency is rooted in body ownership. Other relationships between agency and ownership are also possible, in which agency and ownership are dissociable components of bodily experience but do interact. Agency is not a necessary condition for body ownership as a sense of ownership over a rubber hand can be elicited without movement, but perceived non-agency may prevent ownership (Newport et al., 2010) while perceived agency may enhance the sense of body ownership (Tsakiris et al., 2006).

In an experiment utilizing functional magnetic resonance imaging (fMRI), Tsakiris et al. (2010a) investigated this relationship between the sense of body ownership and agency. They influenced the sense of body ownership by showing either real-time or delayed visual feedback of movement, whereas agency was manipulated through voluntary and passive movement. As shown before, synchronous visual feedback can cause body parts and bodily events to be attributed to oneself. Thus, the condition producing body-ownership would follow from passive movement with synchronous visual feedback, and the condition with active movement and synchronous visual feedback would result in a sense of agency. The additive model predicts that the fMRI shows common activation in areas in both the conditions that produce agency and body-ownership. Secondly, there should also be additional activation of area(s) for the condition producing agency. The independence model, on the other hand, predicts that the brain contains different networks for sense of body ownership and agency. Therefore, there should be no common activation in conditions inducing agency and ownership and distinct activations should be shown in the agency condition that are not seen in the other conditions. Also, specific activation should be seen in the condition of ownership that is absent from the agency condition.

Interestingly, the results of the introspective data (questionnaire) showed support of the additive model. Subjects described significantly more feelings of agency in the AS (active synchronous) condition, which causes a sense of agency, compared to the three remaining conditions. Moreover, participants reported stronger sense of body-ownership in the AS condition compared to the passive synchronous (body ownership) condition. This indicates that agency enhances the sense of body ownership. The fMRI data, on the other hand, showed support for the independence model. There was no common activation in brain areas in the condition producing both agency and body ownership. Also, both body-ownership and agency showed different and exclusive activation of brain areas, which provides evidence that different neural networks underlie these experiences. Tsakiris et al. (2010a) postulate that the discrepancy between neural activation and questionnaire data indicates that conscious experience and brain activity cannot be mapped one-to-one. Alternatively, this result may reveal a limitation of introspective data.

In an earlier study, Marcel (2003) differentiated between attribution of an action to one's self, and attribution of the *intention* of the action to one's self. For example, patients with an anarchic hand report the distinct sense of their involuntary movements as being their own, but they do not experience intending these movements. They do not have a feeling of agency, whilst they continue to experience body ownership (Marcel, 2003). Also, recognizing actions as one's own requires an explicit judgment, contrary to the experience of an action as being one's own. Introspective data may not properly distinguish the difference between ownership of intentional action and ownership of more general bodily actions and sensations (Tsakiris et al., 2010a). The reverse dissociation, in which people retain a sense of agency, but not body ownership, is harder to envisage. As Tsakiris et al. (2010a) point out, however, this can be seen in anosognosia patients with hemiplegia who also have somatoparaphrenic delusions. When a patient looks at her arm she would report that the arm belongs to another person. Nevertheless, the patient denies paralysis and describes that she is able to move her arm voluntarily, which indicates awareness of self-agency (Fotopoulou et al., 2008). This may indicate a double dissociation between agency and ownership.

On the other hand, there is also evidence to suggest that the sense self-agency and body ownership are interacting and overlapping rather than modular and discrete (Legrand, 2006; Synofzik et al., 2008). Action processes that contribute to a sense of agency depend on processes involved in body ownership, such as multisensory integration and internal body representations (Waters and Badcock, 2010). Lower performance on attribution tasks in people with schizophrenia have often been brought up as evidence for a selective dysfunction in sense of agency (Franck et al., 2001). It has been argued, however, that performance on these tasks, in which subjects have to judge whether a movement belongs to oneself based on visual feedback, requires "*an implicit knowledge of one's body as a sensory object that is moving (i.e., a sense of body ownership)*" (Waters and Badcock, 2010). This means that attribution errors may partly be caused by a distortion in sense of body ownership. Moreover, deficits in integrating visual and somatosensory signals from limbs have been shown to affect the ability to judge self-action (Bulot et al., 2007).

Kalckert and Ehrsson (2012) used a version of the RHI in which they systematically varied the relative timing of the finger movements (synchronous vs. asynchronous), the mode of movement (active vs. passive), and the position of the model hand (anatomically congruent vs. incongruent positions). Their results indicate that voluntary finger movements elicit a robust illusion of owning the rubber hand. Asynchrony eliminated both ownership and agency, passive movements selectively eliminated the sense of agency, and incongruent positioning diminished ownership but not agency. These findings provide evidence for a double dissociation of ownership and agency. However, the authors also note that the sense of agency was stronger when the hand was perceived to be part of the participant's body, and in this condition a significant correlation between agency and ownership was found. A later study by Kalckert and Ehrsson (2014) reported that questionnaire ratings of ownership and agency were correlated across individuals, even in the passive versions of the illusion (passive movement and visuo-tactile). This result suggests that ownership modulates agency and produces a weak tendency for agency even in the absence of intentions and voluntary motor commands (Kalckert and Ehrsson, 2014).

Garbarini et al. (2016) showed that people with schizophrenia exhibit a greater interference of visual information about the movements of another person on their sense of agency. The authors administered two versions of a manual drawing task to 20 schizophrenic patients and 20 age-matched healthy controls. In the bimanual version, participants had to draw lines with one hand and circles with the other. In the modified version, participants were instructed to draw lines while observing the examiner drawing circles from a first person perspective. In the bimanual version, patients and controls showed a comparable interference effect. In the observation version, however, schizophrenics showed a significantly greater interference the examiners' hand drawing circles on their own hand drawing lines. This effect was significantly correlated to the strength of the positive symptoms (hallucinations and delusions) and to the sense of agency that was reported during the task. These findings suggest that an altered sense of agency can induce changes in the motor system. However, there was no correlation between motor performance and feeling of ownership over the experimenter's hand (Garbarini et al., 2016).

Louzolo et al. (2015) used the version of the RHI that is based on finger movements rather than tactile stimulation (Kalckert and Ehrsson, 2012, 2014) to investigate the relationship between delusion-proneness and sense of agency. Individuals with a high delusion-proneness score gave equally strong agency ratings in active and passive conditions, suggesting that they experienced both conditions as self-produced (Louzolo et al., 2015). This may imply that delusion-prone individuals experience agency in the absence of motor intentions possibly due to increased reliance on external sensory signals, in this case vision. This was also reflected in the ownership scores. These results are in line with the idea that motor prediction is weakened (Blakemore et al., 2000; Blakemore and Frith, 2003; Shergill et al., 2005; Teufel et al., 2010) whereas external cues become more salient (Synofzik et al., 2010; Voss et al., 2010) in delusion-prone individuals. Hypersalient processing of both agency and ownership cues might be related to failures of self-recognition in schizophrenia (Waters and Badcock, 2010).

To summarize, the relationship between agency and ownership remains elusive. A double dissociation between the sense of agency and body ownership may exist, but more research on this subject in schizophrenia is warranted. Rather, phenomenological studies indicate that patients have distortions in the sense of self beyond only action awareness, extending over a broad area of self-experience, including the sense of body ownership. Previous studies with healthy participants and neurological patients suggest that agency and body ownership are dissociable to some extent, but also interact with agency affecting ownership and *vice versa*. Studies indicate that agency and ownership are dissociable elements of self-experience. However, evidence from healthy individuals also suggests that the sense of agency and ownership interact. The disturbed sense of agency in schizophrenia may therefore contribute to a disturbed sense of body ownership. Further experimental studies are necessary to disentangle agency and body ownership related problems in schizophrenia.

CONCLUSION

In this article, we have reviewed the various sources of information that may contribute to a coherent sense of body ownership. It is thought that bodily experience is the result of a complex integration of both bottom-up sensory processes and higher order, top-down bodily and perceptual representations. Bodily experience involves the integration of multisensory information. Ownership is enhanced by visual capture of proprioceptive information on limb position. In order to infer body ownership, people with schizophrenia rely to a greater extent on external stimuli, such as visual information, that override weaker stored body representations. In addition, the temporal and intentional binding window seem to be altered in people with schizophrenia. This effect of temporal binding is thought to be modulated by top-down processes associated with motor intentions. Moreover, predictive, re-afferent information on the spatial position of body parts is related to increased sense of agency and ownership (Giummarra et al., 2008). We have also discussed evidence for a disturbance in predictive mechanisms that normally allow for anticipation of upcoming events.

The evidence presented in this review indicates that people with schizophrenia have higher variability in internal predictions about the sensory consequences of action. Importantly, aside from internal predictions, additional external information about self-produced actions influences self-agency judgments to a greater extent. The weighting of internal and external cues with respect to self-action may depend on the reliability of internal predictions (Synofzik et al., 2010). Imprecise or unreliable internal predictions might cause patients to depend more strongly on external information on self-action such as vision. People with schizophrenia and individuals with elevated psychosis-prone characteristics (Teufel et al., 2010), show reduced susceptibility to perceptual illusions, a phenomenon driven by prior expectations (reviewed in Notredame et al., 2014). The abnormalities in low-level processing that are observed in schizophrenia may indicate imprecise prior beliefs (Denève and Jardri, 2016). A possible mechanism could involve the capacity of higher-order areas to predict the state of lower level representations (sensory, motor, or cognitive). This is described in the predictive coding framework (Friston and Kiebel, 2009). The Bayesian model of schizophrenia proposes that stronger aberrant signals may contribute to even more imprecise expectations which may influence belief formation, which eventually results in delusions (Fletcher and Frith, 2009; Denève and Jardri, 2016). Imprecise or weaker predictions may result in increased salience of external cues due to a lack of suppression of the input signals. Alternatively, aberrant or hypersalient input signals may prevent establishment of stable low-level predictions (Schmack et al., 2013). Further examinations into the interaction between higher order cognitive processes and sensory-motor processes could prove to be crucial for understanding abnormal self-experience in schizophrenia. In an extensive review, van der Weiden et al. (2015) show that individuals diagnosed with schizophrenia have impairments in both motor prediction and cognitive processes, such as biased expectation of actions (van der Weiden et al., 2015).

We have provided arguments against the prevailing idea that people with schizophrenia have a selective deficit in the sense of agency. Even though concepts of agency and ownership can be dissociated to some extent, there is also evidence to suggest that the sense of agency and body ownership are interconnected. Evidence for this in healthy participants comes from a study conducted by Tsakiris et al. (2006). During active finger movement, the RHI extended to the whole hand. A purely proprioceptive sense of body-ownership is local and fragmented, but the motor sense of agency integrates different body parts into a coherent, global awareness of the body (Tsakiris et al., 2006). Other studies in healthy participants indicate that people are more likely to experience an external object as part of their body when they have active control over the object. Agency and ownership seem to be dissociable yet interacting, but there is no consensus on this topic yet.

In summary, studies so far show that individuals with schizophrenia have a disturbed sense of body ownership. This review discussed several factors that may contribute. They include deficits in multisensory integration, a weaker stored representation of the body, differences in temporal binding as well as impairments in predicting sensory consequences of efferent motor signals. The latter is particularly relevant for the reduced sense of agency in schizophrenia patients. While agency has been considered to be separate from the sense of body ownership, recent studies with healthy participants suggest that they are linked and that an enhanced sense of agency increases feelings of body ownership. The reduced sense of agency in schizophrenic patients may therefore be one of the contributing factors with regards to the disturbed sense of body ownership. Vice versa, a reduced sense of body ownership may also contribute to a reduced sense of agency. Future studies should explicitly target the precise relation between the two in schizophrenia.

AUTHOR CONTRIBUTIONS

All authors contributed extensively to the final version of this manuscript. HCD and MK both contributed to the initial idea and design. MK provided the first draft of the manuscript. HCD provided critical feedback and rewrote sections of the initial article. Both authors contributed to revision and editing of the final version. HCD and MK approve of the manuscript to be published.

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Non-hierarchical Influence of Visual Form, Touch, and Position Cues on Embodiment, Agency, and Presence in Virtual Reality

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The concept of self-representation is commonly decomposed into three component constructs (sense of embodiment, sense of agency, and sense of presence), and each is typically investigated separately across different experimental contexts. For example, embodiment has been explored in bodily illusions; agency has been investigated in hypnosis research; and presence has been primarily studied in the context of Virtual Reality (VR) technology. Given that each component involves the integration of multiple cues within and across sensory modalities, they may rely on similar underlying mechanisms. However, the degree to which this may be true remains unclear when they are independently studied. As a first step toward addressing this issue, we manipulated a range of cues relevant to these components of self-representation within a single experimental context. Using consumer-grade Oculus Rift VR technology, and a new implementation of the Virtual Hand Illusion, we systematically manipulated *visual form plausibility*, *visual–tactile synchrony*, and *visual–proprioceptive spatial offset* to explore their influence on self-representation. Our results show that these cues differentially influence embodiment, agency, and presence. We provide evidence that each type of cue can independently and non-hierarchically influence self-representation yet none of these cues strictly constrains or gates the influence of the others. We discuss theoretical implications for understanding self-representation as well as practical implications for VR experiment design, including the suitability of consumer-based VR technology in research settings.

Keywords: virtual reality, embodiment, agency, presence, virtual hand illusion, self-representation

INTRODUCTION

Researchers have long puzzled over how best to describe and study the way we experience and represent ourselves. To gain traction on this problem, a common strategy is to decompose the concept of self-representation into several distinct components. These include: sense of embodiment—the experience of owning a body and knowing its location (Longo et al., 2008b); sense of agency—the experience of causing actions and events in the world (Wegner, 2004);

and sense of presence—the experience of "being there," of being situated in an environment (Sanchez-Vives and Slater, 2005).

These components of self-representation have typically been studied independently in a variety of different experimental contexts. For example, embodiment has been investigated using bodily illusions (Botvinick and Cohen, 1998; Longo et al., 2008b; Tsakiris, 2010; Blanke, 2012; Ehrsson, 2012; Blanke et al., 2015); agency has been manipulated using hypnosis techniques (Kihlstrom, 2008; Polito et al., 2014) and in clinical research (Frith and Done, 1989); and presence has been investigated in the context of Virtual Reality (VR) and communication technologies such as videoconferencing (e.g., Ijsselsteijn et al., 2001; Sanchez-Vives and Slater, 2005).

Embodiment Cues

One way to understand these components of self-representation (embodiment, agency, presence) is to explore how they are induced and modified by different sensory cues. For example, research into embodiment has largely focused on the rubber hand illusion (RHI, Botvinick and Cohen, 1998). This paradigm allows researchers to introduce conflicts between multisensory cues and thus to investigate the effect of different cues on self-representation. In the conventional RHI paradigm, an artificial hand is placed next to a participant's hidden hand. When both hands are stroked at the same time, this can induce an experience of embodiment such that the participant feels that the artificial hand is part of their own body. Researchers have manipulated cues such as the synchrony of tactile and visual stimulation or the form of the artificial hand to investigate which signals are important drivers of the sense of embodiment. Embodiment in this paradigm is typically measured by asking participants to report their subjective experience related to body ownership, agency, and the perceived location of their limb (Tsakiris and Haggard, 2005; Longo et al., 2008b), or with action-oriented measures that involve decisions, actions or physiological reactions to stimuli near the body (Armel and Ramachandran, 2003; Aspell et al., 2009; Zopf et al., 2010, 2011, 2013).

Agency Cues

Although agency has sometimes been considered an element of embodiment, there has also been considerable research investigating the sense of agency as an independent construct, using a variety of experimental designs. In some of these designs, specific experimental cue manipulations changed the kind of cognitive attributions or sensory predictions participants made about their own or others' actions. For example, in Wegner and Wheatley's (1999) "I-Spy" task, false audio commentaries describing the motion of a mouse cursor displayed on a computer screen led participants to misattribute their own thoughts as the cause of the actions they observed, even though these actions were actually externally generated. Conversely, in the Blakemore et al. (2000) study of tickle responses, a mechanical device was used to introduce a temporal delay between participants' tickling actions and the tactile stimulus from those actions. This manipulation interfered with participants' sensory predictions regarding the outcome of their intended actions and led them to experience these self-generated movements as if they had been externally generated. In another line of research, hypnotic suggestions have been shown to induce significant changes in the way that susceptible participants generate and monitor actions, leading to marked alterations to the sense of agency (Polito et al., 2014). Sense of agency has been measured in a variety of ways including explicit ratings of first-person experience (Bowers, 1981; Polito et al., 2014, 2015) and indirect, implicit measures such as intentional binding, which uses participants' time judgments regarding causal actions in a behavioral task as a proxy for agency (Haggard et al., 2002).

Presence Cues

Research into cues that influence the sense of presence has typically taken two forms. First, some studies have investigated how the experience of being present in a virtual environment is affected by the technical capacity of the VR hardware to deliver realistic multisensory cues. These studies include the impact on presence of: head tracking and provision of stereoscopic 3D cues (Hendrix and Barfield, 1995; Barfield et al., 1999); VR display resolution and refresh rate (Barfield and Hendrix, 1995); latency between head movement and VR display updating, and the inclusion of haptic feedback (Sanchez-Vives and Slater, 2005). Such studies of presence are also clearly important for the consumer VR industry. For example, the *Oculus Best Practices* (Oculus, 2016) emphasizes the importance of achieving <20 ms latency between head movements and corresponding screen updates, in addition to maximizing screen refresh rate, to avoid negative impacts on user comfort and presence.

The second area of presence research aims to identify the specific cues and content within virtual environments that lead to increased presence. For example, Slater et al. (2009a) and Yu et al. (2012) investigated the extent to which visual realism of the virtual environment affects presence. Their work concluded that it was the dynamic nature of shadows and reflections in response to events rather than mere lighting and reflection quality that primarily drives a sense of presence (Yu et al., 2012).

Post-experiment subjective questionnaires with explicit rating scales are a primary tool for measuring presence. Some researchers, however, have sought to measure presence more objectively by employing implicit behavioral and physiological reactions such as measuring changes in heart rate (Sanchez-Vives and Slater, 2005).

Investigating Self-Representation Using the Virtual Hand Illusion

These separate lines of research into embodiment, agency, and presence have found that each component involves the integration of multiple cues both within and across sensory modalities. This suggests that these components may partly rely on similar underlying mechanisms. However, the degree to which this may be true remains unclear. Some authors, for example, have suggested that components such as ownership and agency may directly influence each other (Tsakiris et al., 2006; Morgan, 2015). Alternatively, these components may simply rely on similar cues (Synofzik et al., 2008; Zhang et al., 2014). As a step toward addressing this issue, in this study we systematically manipulated a range of cues and studied their effect on the different components of self within a single experimental context. The context we chose is a variant of the RHI paradigm. Specifically, we implemented a new VR version of this paradigm—the Virtual Hand Illusion (VHI, Slater et al., 2008).

RHI-type paradigms commonly involve manipulations of various cues across the modalities of vision, touch, and proprioception. The experience of embodiment in the RHI results from the integration of multiple sensory cues that could plausibly provide body relevant information (Tsakiris, 2010; Apps and Tsakiris, 2014; Blanke et al., 2015; Kilteni et al., 2015).

Three key cues that have been found to modulate embodiment in the RHI are: (a) *visual-form plausibility* (hereafter FORM), how realistically the experimental stimulus resembles a body (Tsakiris and Haggard, 2005; Tsakiris et al., 2010); (b) *visual–tactile synchrony* (hereafter TOUCH), the consistency in timing between tactile stimulation applied to a participant's own hand and the visual representation of stimulation applied to the rubber hand (Botvinick and Cohen, 1998); and (c) *visual–proprioceptive spatial position offset* (hereafter OFFSET), the distance between the proprioceptively localized real hand and the visually localized rubber hand. A number of researchers (e.g., Tsakiris, 2010; Blanke et al., 2015) have claimed that introducing discrepancies to these cues can constrain the inclusion of the artificial hand as a part of bodily self-representation.

However, three findings in the literature indicate that introducing discrepancies to these cues may not always act as hard limits on embodiment. First, placing the artificial hand far from the actual hand (i.e., introducing a large spatial OFFSET between vision and proprioception) does not always affect the RHI, especially when the viewed hand is placed near the trunk (Zopf et al., 2010; Preston, 2013). Second, in a recent VHI study where participants were able to move the virtual limb, embodiment effects were found even when the visual form of the target stimulus was a balloon or square rather than a virtual hand (Ma and Hommel, 2015). It is, however, unclear if this is also the case in a passive version of the illusion. Third, previous data suggest that TOUCH might have its strongest effect when there is a spatial offset between the hands (Zopf et al., 2010).

To the best of our knowledge, no previous study has systematically manipulated all three cues (FORM, TOUCH, and OFFSET) within a single experimental context. For each cue, these manipulations involve altering the degree of alignment between the presented visual feedback and other sources of information regarding the body. For example, the effect of FORM can be tested by comparing a condition where the virtual hand form is congruent with that of the real hand, vs. a condition where the virtual form is not at all hand-like, such as presenting a simple block or sphere. Similarly, the effect of TOUCH can be tested by altering the synchronization between seen and felt touch stimuli. Finally, the effect of OFFSET can be tested by introducing a discrepancy between the visually presented and felt real hand position. Exploring each of these cues within a single experimental context permits examination of main effects and interactions, both of which are critically important for determining the relative importance of the individual cues.

In this study, we simultaneously manipulated FORM, TOUCH, and OFFSET to investigate their effects and interactions on embodiment as well as other aspects of self-representation such as the sense of agency and presence in an RHI-type paradigm. For FORM and OFFSET we used two conditions each, a congruent and an incongruent condition. For TOUCH, in addition to the commonly employed synchronous and asynchronous conditions, we also included a "no-touch" control condition in which no active tactile stimulation is delivered, (passive touch still occurs via the hand resting on the table). Little is known about how the mere occurrence of a touch might influence embodiment, since only a few previous studies have employed a no-touch condition (Longo et al., 2008a; Rohde et al., 2011).

Rationale for Using the Virtual Hand Illusion

In this study, we employed a VHI paradigm, which is an adaptation of the RHI to a virtual environment (Slater et al., 2008). The VHI paradigm offers several methodological advantages compared to the standard RHI. Computer simulations allow a high level of experimental control, continuity and precise repeatability for stimulus presentation. Using a virtual hand makes it easy to carefully manipulate many aspects of visual form, for example, changing hand shape while keeping skin texture constant. Also, the contextual break that results from placing a fake hand model in a real world context can be avoided by using VR to seamlessly present a virtual hand model in a similarly virtual environment. Furthermore, the VHI setup allows for consistent matching between the presentation times of tactile and visual stimuli, providing a greater level of temporal reliability compared to the experimenter-generated manual brushing commonly employed in the RHI. Finally, the presentation of visual stimuli is not restricted due to physical interference from the artificial limb. Instead, stimuli can be presented anywhere within the virtual environment making it much easier to achieve true overlap (no apparent spatial OFFSET) between virtual and actual body parts.

A former disadvantage of the VHI compared to the RHI has been the challenge, time and cost of creating virtual environments and acquiring VR equipment. Until very recently, VR technology was limited to specialty research and niche training applications such as flight simulator training or other military applications, but this is no longer true. Affordable, high quality VR head-mounted displays (HMDs) such as the Oculus Rift are now commercially available. The confluence of consumer VR with the mainstreaming of video-game and other computer-generated video media also means that powerful and easy-to-use desktop 3D environment creation software is now readily available, supported by online marketplaces with large user communities of enthusiasts, graphic artists, and developers. Consequently, researchers can now design and implement experiments using VR with relative ease and at reasonable costs. In light of this, a supplementary motivation of this study was to develop and demonstrate the viability of conducting cognitive science research using consumer-grade VR technology.

Investigating the Viability of Consumer VR for Research

Despite the advantages and ease of creating virtual environments, there are a variety of non-trivial sizing and positioning challenges to achieve high congruency between the virtual and the real. A good match means that virtual features such as chairs, tables, hands, and viewing position are visually at the same scale, position and orientation as corresponding real features. Failure to carefully solve these challenges may introduce uncontrolled spatial and sizing conflicts between visual and proprioceptive feedback, which could impact experiment results and obscure analysis of the specific cue manipulations we wished to perform. In this study we therefore also aimed to demonstrate clear methods for matching the real and virtual worlds using consumer VR.

Summary of Aims and Hypotheses

To summarize, in this study we investigate three distinct components of self-representation—embodiment, agency and presence—within a single experimental context. Our first aim was to systematically investigate how FORM, TOUCH, and OFFSET influence these components of self-representation. To measure changes in self-representation we employed rating scales and items that have previously been used in embodiment (Longo et al., 2008b), agency (Polito et al., 2013), and presence (Sanchez-Vives and Slater, 2005) research. Our second aim was to demonstrate that scientific research on self-representation can be conducted successfully using consumer-grade VR technology.

We formulated five specific hypotheses concerning the influence of FORM, TOUCH, and OFFSET cues on self-representation. First, based on previous work (Tsakiris and Haggard, 2005; Tsakiris et al., 2010), we predicted that using an incongruent FORM in our VHI paradigm would negatively impact embodiment ratings compared to the congruent FORM. Second, we predicted that changes in TOUCH would influence embodiment measures for both plausible visual forms (i.e., hands), and for implausible visual forms (i.e., simple geometric volumes that are not hand-shaped, see Ma and Hommel, 2015). In other words, we expected a main effect of TOUCH but no interaction of TOUCH and FORM. Third, based on previous findings (Zopf et al., 2010; Preston, 2013), we expected that spatial OFFSET would not have a strong overall effect on embodiment. Fourth, based on earlier work showing an increased effect of TOUCH on embodiment when a rubber hand is displaced from a participant's actual hand (Zopf et al., 2010), we predicted that TOUCH would be most important when there is a spatial discrepancy between vision and proprioception. That is, we expected an interaction between TOUCH and OFFSET. Our fifth hypothesis concerned the sense of agency. We expected that the occurrence of touch would influence sense of agency since tactile signals indicate that an action is occurring in the external environment, such as contacting a surface while reaching for an object. As agency is robust to noisy sensory signals (Moore and Fletcher, 2012), we specifically expected that the mere occurrence of tactile feedback, rather than visual-tactile synchrony *per se*, would influence agency ratings. Since FORM and OFFSET cues do not provide obvious indications of action, we did not expect these manipulations to influence sense of agency ratings. We did not have strong predictions regarding presence, as the effect of these cues has received relatively little attention in the relevant literature.

METHODS

Participants

We tested 50 participants who either received course credit for participation or payment of $15. Twenty-five participants (16 female, 21 right handed, mean age 21 years, range 18–34 years) completed the experiment with a zero spatial OFFSET condition and 25 participants (14 female, 25 right-handed, mean age 20 years, range 18–32 years) completed the experiment with a non-zero spatial OFFSET condition. This research was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and was approved by the Macquarie University Ethics Review Committee (Human Research). Informed consent was obtained from all participants.

Equipment

The primary device for delivery of all VR experiments was the Oculus Rift Development Kit 2[1] (DK2), depicted in **Figure 1A**. The DK2 is a HMD with positional camera tracking system that allows six degrees of freedom head tracking (head rotation and translation). We chose PC hardware sufficient to maintain the visual frame rate at the maximum DK2 display refresh rate of 75 Hz at the native DK2 display resolution (960*1080 pixels per eye), with no transient drops in frame rate, frame skipping, or latency spikes. Full specifications for the DK2 and PC hardware are included in Appendices A and B in Supplementary Material.

Tactile stimuli were delivered via a vibrating tactor device placed beneath the participant's index finger. Tactor oscillations were driven via 200 Hz sinewave audio outputs from the PC's audio processing card. Technical details for the tactor and PC audio processing are provided in Appendix B in Supplementary Material.

3D Environment and Software

We used the Unity[2] 3D videogame engine, version 5.1.2f1 (64-bit) software to construct the 3D environment. The environment was a simple monochrome space with no complex graphical textures (see **Figures 1B,C**). The virtual space resembled the actual lab environment and consisted of gray floor, desk, chair, and a virtual computer screen that were illuminated via a virtual light source from above. There were no walls and illumination faded to black if the participant looked into the distance.

Our experiment maintained dynamic illumination which has been shown to increase the plausibility of the VR experience (Khanna et al., 2006; Slater et al., 2009a; Yu et al., 2012) and is readily achievable with the Unity 5 engine (including soft-edged shadows and real-time light from the flashing virtual button

[1]http://www.oculus.com/en-us/dk2/.

[2]http://unity3d.com/. Unity 3D allows a number of options for writing supporting programming code. For these experiments we used the C# programming language, which is widely used within the Unity3D user community.

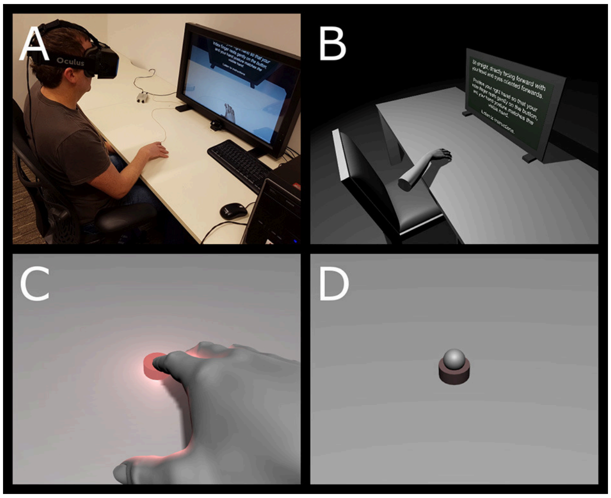

FIGURE 1 | (A) Experimental setup, with the tactor positioned beneath the right index finger. The monitor offers a 2D depiction of the participant's view for the experimenter to observe. **(B)** An overhead view of the entire virtual environment (i.e., not from the participant's viewpoint). **(C)** Virtual hand/finger placement, also depicting the visual feedback corresponding to a touch. Dynamic illumination effects such as the light flash reflection from the hand and table are visible. **(D)** A close up of the virtual button in the "no touch" condition with the incongruent FORM (a sphere).

cast onto nearby objects such as the hand, table and virtual monitor). Virtual objects used in the scene, including furniture and the hand model, were either created directly within Unity (simple geometric solids) or acquired at no cost online. We used a consistent, gender neutral arm model for all participants[3].

Calibrating the Virtual Environment

To ensure that the apparent size and position of virtual objects matched the real environment, and to also calibrate the participant's virtual viewpoint to their real-world viewpoint, we adopted the following procedures.

Similar Plain Appearance for Real and Virtual Objects

We measured the dimensions and placement of real-world objects involved in the experiment, and kept the general appearance of the real desk and walls unadorned and featureless. These object dimensions and similarly plain appearance were reproduced in the virtual environment.

Benchmarking Virtual Space and Size

Aligning the virtual and real environments involved calibration along two separate factors. First, units of distance in the virtual environment were benchmarked against real distances in the physical workspace environment to ensure a close match. We assessed this by moving the HMD 50 cm along the desk within view of the position-tracking camera, and noting the real-time movement of the corresponding viewpoint in the virtual environment. After repeated testing, we established that (at least for our setup) 100 cm in the real workspace environment corresponded to 0.96 distance units in Unity. This ratio was used in creating and positioning virtual objects (e.g., the desk and chair) to achieve close alignment between the physical and virtual environments.

Calibrating Scaling for Each Participant

In VR, depth perception is achieved via binocular stereopsis by presenting an offset camera view to each eye. The distance between these two virtual cameras is directly correlated to what the participant perceives as their own size in the virtual environment, and therefore affects the participant's sense of the relative scale of all virtual objects and distances. So that each participant perceived the virtual world with the same sense of scale as they do in the real world, we measured the distance between each participant's pupils (inter-pupillary distance or IPD), and set a corresponding separation between the virtual camera view for each eye. This separation is readily manipulated by entering the participant's IPD directly into the Oculus Rift DK2 configuration utility[4].

IPD was initially measured using a utility provided with the Oculus runtime. However, this procedure proved time consuming and occasionally produced obviously incorrect measurements, and was abandoned after 18 participants. For the remaining participants, we instead measured IPD using a ruler positioned against the participant's nose. When compared over several tests the two measurement techniques were within ±2 mm of one another.

Positioning the Virtual Viewpoint to Match the Real-World Viewpoint

We used a small, custom-made HMD mount to locate the HMD in a preset real-world position and orientation prior to each experiment, within view of the positional-tracking camera. Once the HMD's real-world position/orientation were fixed by placing it in the mount, the experimenter could shift the virtual viewpoint to align with the HMD's real world position/orientation with a single key press. Following this, the HMD could then be moved around and placed on the participant's head. The positional-tracking camera would maintain an accurate record of its real-world location, and adjust the virtual viewpoint accordingly in real time to maintain alignment with the participant's head movements. This calibration step was repeated after every experiment trial. The HMD mount was removed from the setup while running the experiment trial itself.

Appropriately Situating the Participant's Real Hand

As described below, the experiment design required appropriate positioning and posture of the participant's real right hand to enable a match or mismatch (depending on the OFFSET condition) between the proprioceptive feedback from the real hand and visual feedback from the virtual hand. The location

[3]The hand model was obtained from the Leap Motion Unity core assets package, available at: http://developer.leapmotion.com/unity.

[4]Note: the configuration utility was available for the Oculus DK2 and in the developmental Oculus runtime version 0.6.0.1 as used in our experiments. However, in the commercial release of the Oculus Rift and runtime, this configuration utility is no longer available. IPD adjustments for the commercial release are now made with a slider control on the underside of the commercial release Oculus Rift HMD.

of the participant's real hand and index finger were controlled by adhering the tactor to specific physical locations on the desk for each of the OFFSET conditions and instructing participants to place the tip of their index finger on the tactor. Participants were also instructed to align their real hand posture to that of the virtual hand for trials involving the hand FORM condition.

Multisensory Touch Stimulation in VR

Visual–tactile feedback to the participant consisted of a periodic vibration delivered by a tactor positioned beneath the participant's right index finger. Participants wore headphones to mute both the audible noise resulting from the vibration of the tactor unit, and any other unwanted environmental noise.

Self-Representation Rating Scales

To measure embodiment, agency, and presence, we employed three sets of rating scales.

Embodiment Rating Scales (Botvinick and Cohen, 1998; Longo et al., 2008b)

We used the 10 embodiment rating scale items from Longo et al. (2008b) as well as the item "It seemed like I was feeling the touch in the location where I saw the rubber hand being touched," which is often included in RHI studies and positively rated in synchronous conditions (Botvinick and Cohen, 1998). As the viewed stimulus varied across trials in this task (i.e., a hand or a sphere), the wording of items in this questionnaire was modified to refer to "the target." Based on the findings of Longo et al. we further divided these 11 items into three different subcomponents (see **Table 1** for details): *embodiment–ownership* (for example, "It seemed like the target belonged to me"), *embodiment–location* (for example, "It seemed like the target was in the location where my hand was"), and *embodiment–agency* ("It seemed like I was in control of the target"). For each item participants rated their level of agreement on a 7-point Likert scale from "strongly disagree" to "strongly agree." In the "no touch" condition, the items referring to touch experience (8 and 9) were not presented. We computed average embodiment component scores for ownership, location and agency for each participant and condition.

The Sense of Agency Rating Scale (SOARS; Polito et al., 2013)

The SOARS is a 10-item scale that measures subjective alterations to the sense of agency related to some specific experience. Participants were instructed to think of the preceding experimental task and to rate their level of agreement with a series of statements on a 7-point Likert scale from "strongly disagree" to "strongly agree." The scale has two factors: (1) *involuntariness*, with items such as "I felt that my experiences and actions were not caused by me," which represent a subjectively-experienced reduction in control over one's own actions; and (2) *effortlessness*, with items such as "My experiences and actions occurred effortlessly," which represent a subjectively-experienced increase in the ease and automaticity with which actions occur. Although, the SOARS was originally developed for use in hypnosis, we used a modified, general form with slight edits to the wording of three items (#1, #4, and #10), which is applicable in any context (**Table 2**).

TABLE 1 | Embodiment rating scale (Based on Longo et al., 2008b).

	Item	Subscale
1.	It seemed like I was looking directly at my own hand rather than the target	Ownership
2.	It seemed like the target began to resemble my real hand	Ownership
3.	It seemed like the target belonged to me	Ownership
4.	It seemed like the target was my hand	Ownership
5.	It seemed like the target was part of my body	Ownership
6.	It seemed like my hand was in the location where the target was	Location
7.	It seemed like the target was in the location where my hand was	Location
8.*	It seemed like the touch I felt was caused by the button flash at the target	Location
9.*	It seemed like I was feeling the touch in the location where I saw the target being touched	Location
10.	It seemed like I could have moved the target if I had wanted.	Agency
11.	It seemed like I was in control of the target	Agency

These items not included in "no-touch" conditions.

Presence Rating Items (Sanchez-Vives and Slater, 2005)

Participants rated three presence items on a 7-point Likert scale: (1) "To what extent did you have a sense of being in the virtual environment," rated from "not at all" to "very much so"; (2) "To what extent were there times during the experience when the virtual environment became "reality" for you, and you almost forgot about the "real world" of the laboratory in which the whole experience was really taking place?," rated from "never" to "almost all the time"; and (3) "When you think back to your experience, do you think of the virtual environment more as *images* that you saw, or more as *somewhere that you visited*?," rated from "only images that I saw" to "somewhere that I visited." These items are reported by Sanchez-Vives and Slater (2005) as representative items for assessing alterations in presence. Although the descriptive poles of the Likert scale differ across items, in all cases a score of 1 represents no presence, whereas a score of 7 represents complete presence.

Experimental Design

The experiment included FORM, TOUCH, and OFFSET manipulations. We implemented two within-subject FORM conditions (see **Figures 1C,D**): (a) a congruent feedback condition involving the presentation of a realistically depicted virtual hand and forearm shape, in which the index finger was positioned on top of a realistically depicted virtual tactor on a virtual table. The virtual hand had smooth, unmarked texturing and light gray coloring; and (b) an incongruent hand feedback condition involving the presentation of a smooth, unmarked gray spherical object (∼1.8 cm in apparent diameter), appearing atop the virtual tactor (**Figure 1D**) in the same position as the tip of the participant's real index finger. The virtual tactor could

TABLE 2 | General form of the Sense of Agency Rating Scale (Polito et al., 2013).

	Item	Subscale
1.*	Doing what I was meant to was hard	Effortlessness
2.*	I chose how to respond	Involuntariness
3.*	My experiences and actions felt self-generated	Involuntariness
4.	I went along with my experiences freely	Effortlessness
5.*	My experiences and actions were under my control	Involuntariness
6.	I felt that my experiences and actions were not caused by me	Involuntariness
7.	My experiences and actions occurred effortlessly	Effortlessness
8.	I was mostly absorbed in what was going on	Effortlessness
9.	My responses were involuntarily	Involuntariness
10.*	I was reluctant to go along with my experiences	Effortlessness

**These items are reverse scored.*

be presented in one of two states: either visually vibrating and glowing bright red (an ON state corresponding to the delivery of tactile feedback) or completely motionless with a dull dark red color (an OFF state corresponding to the absence of tactile feedback).

For TOUCH manipulations, there were three within-subject conditions: (a) synchronous touch—visual and tactile stimulation were initiated at the same time and presented for 300 ms every 1000 ms; (b) asynchronous touch—the tactile stimulation was identical to the synchronous case, while the visual flash/vibration was initiated at random intervals between 500 and 1500 ms after the tactile feedback; and (c) no touch—no visual or tactile vibration stimulation was given.

Although they were initiated simultaneously in code, we tested the system delay timing using a 240 frames/second audio-visual camera. We recorded onset of visual feedback through the HMD lenses and onset of tactor vibrations by increasing vibration amplitude sufficiently to produce an audible sound that could be recorded by the camera's microphone. In analysing 25 recorded tactor vibrations, we found that there was a mean delay of 226 ms (*SD* 13 ms) between the visual flash and the tactor vibration. This delay meant that the visual and tactile stimulation was not completely synchronous in the synchronous condition. However, small delays due to human error would also be expected in research employing manual brush stroking. Previous RHI research found no difference between delays as long as 300 ms compared to smaller delays for inducing changes in embodiment (Shimada et al., 2009). In addition, the low variability in delay magnitude from vibration to vibration means that better consistency for this experiment is likely than for RHI research employing manual brush stroking.

Finally, we had two between-subjects OFFSET conditions: (1) 0 cm spatial offset, with the participant's real hand positioned along the body midline, in the same apparent position as the virtual hand, and (2) 30 cm offset, with the participant's real right hand positioned 30 cm to the right of the body midline, while the virtual hand (or sphere) position was maintained in the exact position and orientation as in the 0 cm offset condition. OFFSET was investigated as a between subject condition partly to keep the experiment duration reasonable (a third within-subject condition would double the experiment duration), but also to minimize the potential for leading the participant: for FORM and TOUCH manipulations, participants can receive identical instructions and experiment setup is unchanged. Changing the OFFSET condition requires moving the placement of the tactor on the desk and moving the participant's hand. This may have signaled a change to the participant and influenced their responses.

Each participant was tested in one of these two OFFSET conditions and completed all FORM and TOUCH conditions in a 2-by-3 factorial design—six trials per participant. There are 720 possible orderings of the six conditions. Since we only used 25 orderings, we adopted a pseudo-random ordering selection for each participant. This involved randomly selecting an order from the 720 possible orderings for a participant, and then using the reverse of this for the next participant. The same orderings were used for the 25 participants tested with the 0 cm offset condition as for the 25 participants tested with the 30 cm offset condition.

Procedure

Following IPD measurement and positional calibration, the participant was seated and the HMD placed on the participant's head. We ensured that the positional tracking camera did not lose view of the HMD while this was done, to maintain the virtual-to real-environment match. The experimenter then assisted the participant in adjusting their real chair so that they were sitting with their torso a few centimeters from the edge of the desk, and central to the scene. In discussion with the participant, the experimenter fitted the straps and HMD position to ensure optimal focus. Participants were asked to adjust the HMD on their heads until they had good focus in the center of their vision. Participants were instructed to keep their left arm in their lap where it would be obscured from view by the desk (this ensured consistency with the virtual environment where no left arm was visible), to sit up straight, and avoid leaning back or rotating the chair position. Participants were otherwise free to look around the scene or to lean in to view objects in the scene more closely.

Participants began each trial viewing the desk scene without any local tactile stimulus, with instructions displayed on the virtual monitor. While viewing this scene, the experimenter would ensure the participant was correctly positioned and also place headphones on the participant. At the commencement of each of the six experiment trials, the participant would first see 15 s of darkness, before again viewing the same desk scene for the experiment trial proper. Participants would view the target and experience visual–tactile stimulation (or not, in the case of the "no touch" trials) for a 1-min duration. During this time, participants were instructed to keep their arm still, but were free to move their head as desired to view the target from any angle. Following each trial, participants were prompted to remove the HMD and complete a questionnaire.

At the beginning of responding to the set of rating items the participant was told that the target referred to either the "gray hand" or the "gray sphere" as appropriate. In order to minimize stereotyped responses, the embodiment, agency, and presence rating item sets were presented in random order. Furthermore, the order of items within each set was randomized.

The ratings were presented using Qualtrics Survey Software (www.qualtrics.com) on a separate laptop.

Positional calibration using the HMD mount was performed at the start of each experiment trial. Each of the six variations was prepared in separate executable files. The experiment duration, including IPD measurement, instructions, and the six trials, was typically 30–45 min.

RESULTS

To investigate the effects of FORM, TOUCH, and OFFSET, we entered all rating scale means (*embodiment–ownership, embodiment–location, embodiment–agency, presence, involuntariness, effortlessness*) into a multivariate analysis of variance (MANOVA) with the within-subject factors FORM (hand, sphere) and TOUCH (synchronous, asynchronous, no touch stimulation), and the between-subject factor OFFSET (0 cm spatial offset, 30 cm spatial offset). To further investigate the effect of different cues on each self-representation scale separately, we conducted individual ANOVAs with the factors FORM, TOUCH, and OFFSET. We found non-normal rating response distributions for some rating scales (Shapiro–Wilk-tests). However, ANOVA are robust also for non-normally distributed data when the sample size is equal (Field, 2009).

For FORM, there was a multivariate main effect across all rating scales [Pillai's trace, $V = 0.756$, $F_{(6, 43)} = 22.25$, $p < 0.001$, $\eta_p{}^2 = 0.756$]. ANOVA for each rating scale separately showed that viewing a hand resulted in significantly higher mean values compared to viewing a sphere for *embodiment–ownership, embodiment–agency, embodiment–location, presence* and *effortlessness*, but not *involuntariness* (see **Table 3** for statistics and **Figures 2–4**).

We found a multivariate main effect of TOUCH [Pillai's trace, $V = 0.448$, $F_{(6, 43)} = 2.50$, $p = 0.016$, $\eta_p{}^2 = 0.448$]. ANOVA for each variable separately showed that TOUCH was significant for *embodiment–ownership, embodiment–agency, embodiment–location, presence,* and *involuntariness*. We found a trend for *effortlessness* (**Table 3**). We also used planned, simple contrasts to directly compare the effect of synchronous and asynchronous touch (effect of *touch synchrony*) as well as between synchronous and asynchronous touch combined and compared to no touch (effect of *touch occurrence*). We found a significant effect of touch synchrony for *embodiment–location* and *presence*, such that synchronous touch led to higher self-representation ratings [*embodiment–location*: $F_{(1, 48)} = 8.03$, $p < 0.001$, $\eta_p{}^2 = 0.269$; *presence*: $F_{(1, 48)} = 8.88$, $p = 0.005$, $\eta_p{}^2 = 0.156$]. Surprisingly, there was only a trend for *embodiment–ownership* [$F_{(1, 48)} = 3.93$, $p = 0.053$, $\eta_p{}^2 = 0.076$]. There was no effect of touch

TABLE 3 | Statistics (*F* and *p*-values and effect sizes) for Multivariate and Univariate Main effects for FORM, TOUCH, and OFFSET.

	FORM			TOUCH			OFFSET		
	F	*P*	$\eta_p{}^2$	*F*	*p*	$\eta_p{}^2$	*F*	*p*	$\eta_p{}^2$
Multivariate	**22.25**	**<0.001**	**0.756**	**2.50**	**0.016**	**0.448**	**6.01**	**<0.001**	**0.456**
Ownership	**142.17**	**<0.001**	**0.748**	**8.28**	**<0.001**	**0.147**	2.76	0.103	0.054
Location	**44.70**	**<0.001**	**0.482**	**8.37**	**<0.001**	**0.148**	**28.77**	**<0.001**	**0.375**
Agency	**34.60**	**<0.001**	**0.419**	**5.19**	**0.007**	**0.098**	0.26	0.615	0.005
Involuntariness	0.60	0.443	0.012	**3.79**	**0.026**	**0.073**	2.86	0.097	0.056
Effortlessness	**5.24**	**0.027**	**0.098**	2.79	0.066	0.055	0.65	0.425	0.013
Presence	**29.81**	**<0.001**	**0.383**	**9.81**	**<0.001**	**0.170**	2.85	0.098	0.056

Bold text indicates a significant result.

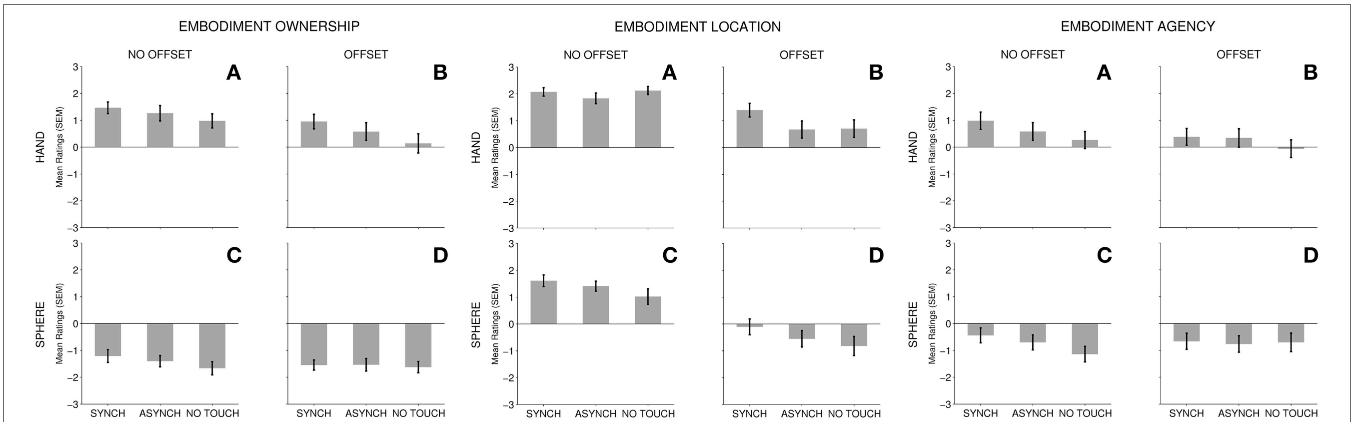

FIGURE 2 | *Embodiment* mean rating scale results. For each subscale, TOUCH conditions (Synchronous, Asynchronous, No Touch) are depicted for all FORM and OFFSET conditions: **(A)** No Offset—Hand; **(B)** Offset—Hand; **(C)** No Offset—Sphere; and **(D)** Offset—Sphere. Error bars present the standard error of the mean.

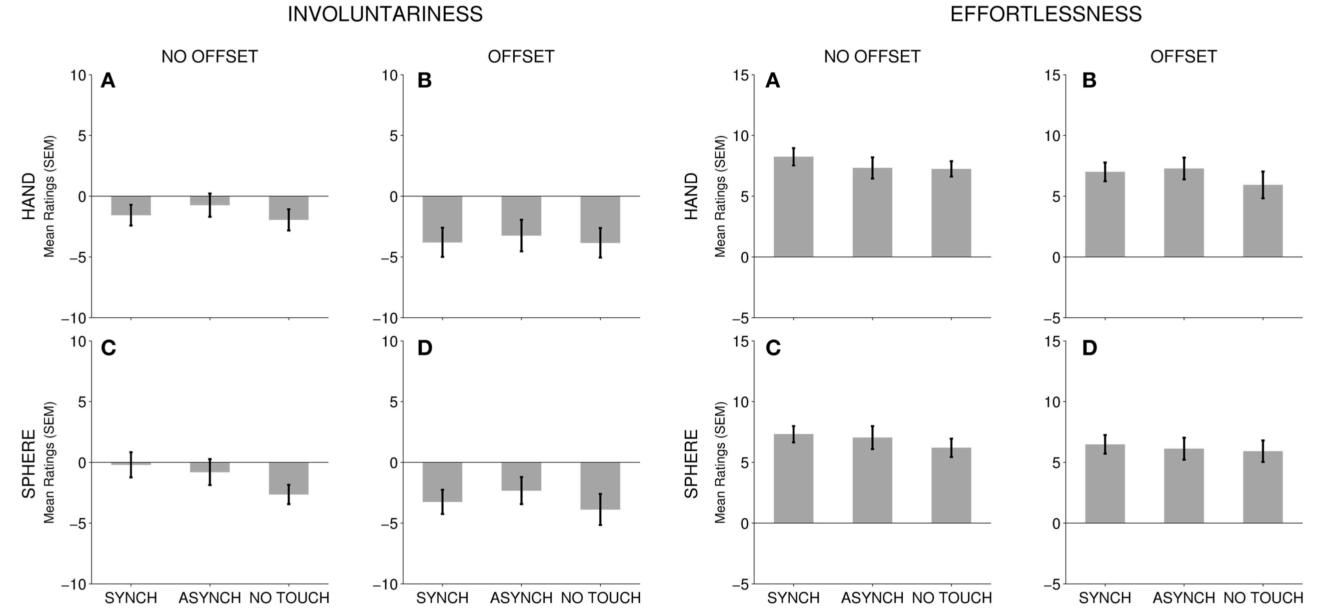

FIGURE 3 | *Agency* mean rating scale results. For each subscale, TOUCH conditions (Synchronous, Asynchronous, No Touch) are depicted for all FORM and OFFSET conditions: **(A)** No Offset—Hand; **(B)** Offset—Hand; **(C)** No Offset—Sphere; and **(D)** Offset—Sphere. Error bars present the standard error of the mean.

synchrony for any of the agency measures [*embodiment–agency*: $F_{(1, 48)} = 2.07$, $p = 0.156$, $\eta_p{}^2 = 0.041$, *involuntariness*: $F_{(1, 48)} = 0.802$, $p = 0.375$, $\eta_p{}^2 = 0.016$, *effortlessness*: $F_{(1, 48)} = 0.802$, $p = 0.375$, $\eta_p{}^2 = 0.016$]. In contrast, we found a significant effect of touch occurrence for all scales [*embodiment–ownership*: $F_{(1, 48)} = 10.71$, $p = 0.002$, $\eta_p{}^2 = 0.182$, *embodiment–agency*: $F_{(1, 48)} = 7.64$, $p = 0.008$, $\eta_p{}^2 = 0.137$, *embodiment–location:* $F_{(1, 48)} = 4.71$, $p = 0.035$, $\eta_p{}^2 = 0.089$, *involuntariness*: $F_{(1, 48)} = 4.06$, $p = 0.050$, $\eta_p{}^2 = 0.078$, *effortlessness:* $F_{(1, 48)} = 6.67$, $p = 0.013$, $\eta_p{}^2 = 0.122$, and *presence:* $F_{(1, 48)} = 10.31$, $p = 0.002$, $\eta_p{}^2 = 0.177$], such that each of these ratings were higher for touch compared to no-touch conditions. To summarize, for *embodiment–ownership*, *embodiment–location,* and *presence*, touch synchrony, and touch occurrence were both significant factors. In contrast, agency measures (*embodiment–agency*, *effortlessness,* and *involuntariness*) were sensitive only to touch occurrence (a trend only for *involuntariness*). We found no significant multivariate or univariate interactions between FORM and TOUCH, or between TOUCH and OFFSET (**Table 4**). This indicates that the effect of TOUCH does not differ for hand and sphere forms, or when the virtual hand location is displaced relative to the actual hand.

For OFFSET, we found a multivariate main effect [Pillai's trace, $V = 0.456$, $F_{(6, 43)} = 6.01$, $p < 0.001$, $\eta_p{}^2 = 0.456$]. Individual ANOVAs revealed an unsurprising main effect of *embodiment–location*, such that participants gave higher ratings in the no spatial offset condition compared to the spatial offset condition. No significant OFFSET effect was found for any of the other scales (**Table 4**).

Furthermore, there was a multivariate interaction of FORM-by-OFFSET, indicating that the overall effect of FORM on our measures of self-representation depended on whether the apparent location of the virtual hand was displaced from the location of the actual hand [Pillai's trace, $V = 0.337$, $F_{(6, 43)} = 3.64$, $p = 0.005$, $\eta_p{}^2 = 0.337$]. Univariate ANOVAs for each rating scale separately showed this interaction to be significant

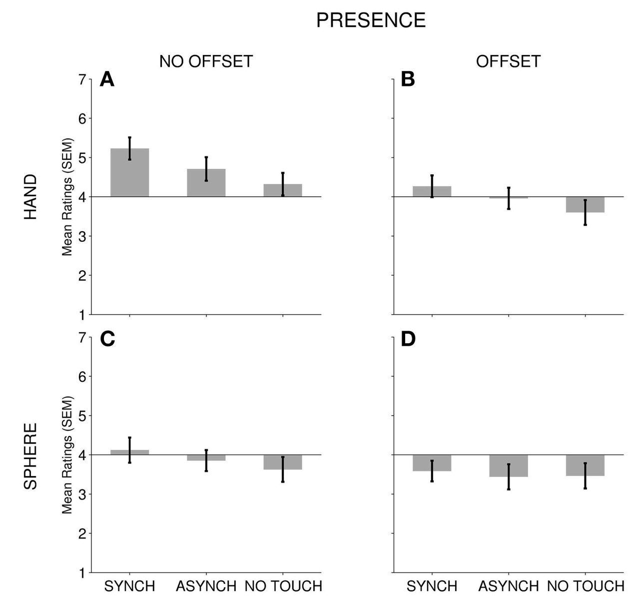

FIGURE 4 | *Presence* mean rating scale results. For each subscale, TOUCH conditions (Synchronous, Asynchronous, No Touch) are depicted for all FORM and OFFSET conditions: **(A)** No Offset—Hand; **(B)** Offset—Hand; **(C)** No Offset—Sphere; and **(D)** Offset—Sphere. Error bars present the standard error of the mean.

TABLE 4 | Statistics (*F* and *p*-values and effect sizes) for Multivariate and Univariate Interaction effects for FORM, TOUCH, and OFFSET.

	FORM × TOUCH			FORM × OFFSET			TOUCH × OFFSET			FORM × TOUCH × OFFSET		
	F	p	η_p^2	F	p	η_p^2	F	p	η_p^2	F	p	η_p^2
Multivariate	1.21	0.311	0.282	**3.64**	**0.005**	**0.337**	1.92	0.063	0.384	0.47	0.920	0.132
Ownership	1.57	0.214	0.032	1.78	0.188	0.036	0.01	0.994	0	1.32	0.273	0.027
Location	2.13	0.124	0.043	**5.89**	**0.019**	**0.109**	1.67	0.194	0.034	0.83	0.441	0.017
Agency	0.37	0.692	0.008	1.27	0.265	0.026	1.27	0.287	0.026	0.65	0.527	0.013
Involuntariness	1.07	0.349	0.022	0.10	0.757	0.002	0.64	0.533	0.013	0.55	0.581	0.011
Effortlessness	0.05	0.950	0.001	0.11	0.745	0.002	0.24	0.786	0.005	0.93	0.399	0.019
Presence	2.08	0.131	0.042	3.27	0.077	0.064	0.77	0.466	0.016	0.12	0.890	0.002

Bold text indicates a significant result.

for *embodiment–location* only (see **Table 4** for statistics). As can be seen in **Figure 2** ("Embodiment Location" panel), the difference between viewing a hand and viewing a sphere was relatively small in the no spatial offset condition, whereas a change in FORM had a much greater effect when there was a spatial offset. Viewing a sphere in the spatial offset condition led to negative *embodiment–location* scores, whereas *embodiment–location* ratings were positive when viewing a hand, regardless of OFFSET. We did not find a FORM-by-OFFSET interaction for any of the other variables (**Table 4**).

There was no multivariate or univariate 3-way interaction of FORM, TOUCH, and OFFSET (**Table 4**).

DISCUSSION

This study utilized a novel consumer grade VR system to test the impacts of FORM, TOUCH and OFFSET on self-representation in a Virtual Hand Illusion paradigm. We used multiple measures including an embodiment scale commonly used in RHI studies (Longo et al., 2008b); the Sense of Agency Rating Scale (SOARS), which has previously been used to assess alterations to feelings of agency in studies of self-generated actions in hypnotic and clinical contexts (Polito et al., 2013, 2014, 2015); and rating scale items for presence typically used in studies of VR experiences (Sanchez-Vives and Slater, 2005). We found multivariate effects of FORM, TOUCH, and OFFSET across all measures, confirming that each of these cues has a broad influence on self-representation. We tested five specific predictions about the effects of our experimental manipulations.

Hypothesis One: The Effect of Form on Embodiment

As expected, we found that a congruent visual representation of the hand led to higher scores on all embodiment subscales compared to the incongruent spherical cursor representation. Previous studies have shown that FORM congruency is an important factor in the traditional RHI setup (Tsakiris and Haggard, 2005; Tsakiris et al., 2010), and these results also confirm this for the VHI. The FORM resemblance of visual body representations thus seems an important driver of embodiment.

Hypothesis Two: The Effect of Touch on Embodiment

In line with our expectations the type of touch influenced all embodiment subscales. This was not modulated by the FORM of the target. This is consistent with findings from a recent study by Ma and Hommel (2015), in which artificial objects on a screen changed either synchronously or asynchronously with the participant's hand movements. Those authors found that movement feedback synchrony modulated embodiment ratings even for non-body objects. Here, we extend this finding and report that FORM does not seem to significantly limit the effect of touch synchrony, even with a static target. We found no evidence that the effect of multimodal synchrony on self-representation is limited or constrained by FORM (Tsakiris, 2010; Blanke et al., 2015).

Hypothesis Three: The Effect of Offset on Embodiment

We hypothesized that OFFSET would not influence embodiment measures in this setup. Although we did find an effect of OFFSET on *embodiment–location*, the subscales of *embodiment–ownership,* and *embodiment–agency* were unaffected by differences in OFFSET (0 vs. 30 cm). This suggests OFFSET is not important for *embodiment–ownership* or *embodiment–agency*, at least not when the artificial hand is viewed near the trunk and the offset is within 45 cm (Zopf et al., 2010; Preston, 2013).

Hypothesis Four: The Interaction Effect of Touch and Offset on Embodiment

Contrary to our expectations, the effect of TOUCH on embodiment did not increase when we introduced a spatial offset between participants viewed and actual hands. This contrasted with earlier findings from our lab, which suggested that increasing lateral distance might increase the influence of TOUCH in the RHI (Zopf et al., 2010), although significant interactions between TOUCH and OFFSET were also not reported in that study. Our previous study employed an even larger distance and compared a 45 cm offset with a 15 cm offset. It is possible that the effect of TOUCH is greater for offsets beyond 30 cm. Taken together, these findings indicate that TOUCH has a direct effect on embodiment independent of the FORM or OFFSET of the depicted hand feedback.

Hypothesis Five: The Effect of Touch Occurrence on Sense of Agency

As expected, contrasts between touch and no touch conditions showed that touch occurrence contributed to significant higher scores for all agency measures. Although, participants' hands remained still, tactile sensations appear to facilitate the perception of action, and a sense of control over one's actions in the experiment. However, there was no effect of touch synchrony, suggesting that when a touch does occur, agency measures are insensitive to temporal delays.

The Effect of TOUCH, FORM, and OFFSET on Presence

We had no strong predictions for the effect of different cues on presence and this part of our study was explorative. We found a significant impact of FORM and TOUCH, as well as both touch occurrence and touch synchrony on *presence*. Furthermore, we found non-significant trends for an OFFSET effect ($p = 0.098$) as well as for an interaction between FORM and OFFSET ($p = 0.077$). This suggests that the experience of *presence* in our VR setup is significantly modulated by the cues that also influence embodiment. This implies in turn, that these cues influence the experience of being situated in a virtual environment, in addition to direct experience of one's own body.

Complex Pattern of Influence of Cues on Components of Self-Representation

Overall, univariate ANOVAs for each rating measure revealed that FORM, TOUCH, and OFFSET influenced different components of self-representation. FORM had a significant impact on all *embodiment* subscales, *effortlessness*, and *presence*. TOUCH had a significant influence on all *embodiment* subscales, *involuntariness* and *presence*. OFFSET had a significant impact on the *embodiment–location* subscale only. Furthermore, touch occurrence had a significant impact on all rating scales, whereas touch synchrony did not significantly impact any of the *agency* scales

In line with previous work, we found no effect of OFFSET on *embodiment–ownership* (Zopf et al., 2010; Kilteni et al., 2012; Preston, 2013). However, we did find that the experience of location for one's own body was significantly affected by OFFSET when directly comparing a no spatial offset with a spatial offset condition. So in contrast to the other components of self-experience, *embodiment–location* was sensitive to a spatial difference between visual- and proprioceptive location information in the virtual hand illusion. This supports the idea that *embodiment–ownership* and *embodiment–location* correspond to different self-components with different mechanisms (Serino et al., 2013).

The pattern of results for *presence* ratings suggests that *presence* tends to be influenced by similar cues as *embodiment-location* ratings (although for OFFSET there were trends for significance only). The current findings suggest that this shift toward prioritizing virtual environment cues over real environment cues is facilitated when there is a visual hand form, multisensory touch signals, and no conflict between the perceived spatial location of an individual's virtual body and the actual location of their real body.

For agency measures, we found an effect of touch occurrence. However, these agency measures were not modulated by touch synchrony. This accords with the previous finding that visual-tactile synchrony affects different components of self-representation such as ownership, location and agency differently (Longo et al., 2008b; Kalckert and Ehrsson, 2012). However, movement synchrony has previously been shown to affect agency ratings (Kalckert and Ehrsson, 2012). Agency seems sensitive to movement synchrony but not to touch synchrony when the hand is passive. Additionally, agency scores were not affected by OFFSET. Agency therefore seems robust to both temporal and spatial multisensory discrepancies, whereas the other self-representation components were not. This is in line with research showing agency can be experienced for spatially and temporally distant events (Faro et al., 2013). However, agency was not immune to all sensory cues. FORM significantly increased *embodiment-agency* as well as *effortlessness* ratings, suggesting that participants were more likely to experience agency for a target that was visually congruent with their own body. Thus overall, visual information and FORM congruency had a significant influence on all measures of self-representation.

Not all agency rating scales were affected by FORM. We found no significant effect on *involuntariness*. In this study we used the SOARS, which conceptualizes sense of agency as comprising two primary dimensions: *involuntariness* and *effortlessness*; and also the *embodiment-agency* subscale, which conceptualizes sense of agency as a subcomponent of embodiment. In earlier work, Polito et al. (2013) showed that *involuntariness* and *effortlessness* are quite distinct conceptual subcomponents of the subjective sense of agency. It may be that *effortlessness* (and also *embodiment–agency*) tap processes related to monitoring of sensory signals, including visual cues; whereas *involuntariness* taps more attributional judgments about agentive experience: for example, tracking whether a movement actually occurred (there were no actual self-generated movements in this task).

This componential view of agency is consistent with research indicating that sense of agency is a multidimensional construct that fluctuates in response to a range of sensory and cognitive signals over time and across domains (Synofzik et al., 2008; Gallagher, 2012; Polito et al., 2014). The current results suggest that body-congruent visual cues may influence the immediate, felt experience of agency (represented by higher *effortlessness* scores), whereas the sensation of touch may influence attributional judgments of agency (represented by higher *involuntariness* scores).

To summarize, these findings highlight similarities and differences between *ownership, location, presence* and the three agency aspects *embodiment–agency*, *effortlessness,* and *involuntariness*. Based on the findings here, there is some overlap but also important differences between the influence of different cues on these components.

No Single Cue Strictly Constrains Self-Representation in the VHI

The common link between the three cues we manipulated is that they all involve comparing a condition where visual information is in harmony with other bodily information, to a condition where a discrepancy is introduced: whether a viewed body form matches an actual body form; whether a viewed touch corresponds to a felt touch, and whether a viewed hand position matches the proprioceptively felt hand position. In all three cases, a better match generally signals that the visual information is more plausible and therefore more likely to be related to one's own body.

Previous accounts of body ownership and self-consciousness proposed that specific cues can operate as strict hierarchical constraints on the processing of subsequent cues (e.g., Tsakiris, 2010; Blanke et al., 2015). For example, one influential model of body-ownership posits a hierarchical sequence of matching stages in which successful matching at one stage permits matching at the next stage, and unsuccessful matching gates or constrains further processing stages (Tsakiris, 2010). According to this account, in the first stage, current visual information about form is matched with a stored model of the way the body typically looks to eliminate gross mismatches. Only if matching is successful in the first stage is a second stage of more fine-grained comparisons performed between visual and proprioceptive information about bodily posture and anatomical position. Finally, only if a postural match is confirmed in the second stage, does a third stage of comparisons commence in which the temporal synchrony between viewed and felt touch is analyzed. According to this model, because matching at each stage is hypothesized to occur in a strict hierarchy, a form mismatch, for example, will restrict or gate the sense of body ownership even if other cue comparisons such as visual-tactile synchrony suggest congruency. This model therefore predicts specific interactions between the different cues involved in the various comparison stages.

We found no evidence for strict hierarchical interactions. Instead, we primarily observed main effects for different cues on self-representation. This implies that whereas each of the cues is important for self-representation, none hierarchically constrains or limits the influence of any of the other cues. Congruent information from all types of cue can, to some extent, independently and non-hierarchically influence self-representation. This finding indicates a flexible self-representation system that can readily adapt to different combinations of multisensory cues.

Implications for VR Methods

Overall, this study demonstrated that consumer-grade VR equipment can be used in the lab to investigate cues that influence self-representation. Studying self-representation in VR allows for a high level of experimental control, continuity, and accurate repeatability of stimulus presentation. We have successfully set up a VR laboratory environment using less than AU$1000 in VR hardware and software (not including PC equipment), that allowed us to manipulate visual, tactile, and proprioceptive cues. Equipment and software is readily available, with a number of consumer VR HMD vendors entering the market in 2016.

We successfully demonstrated a calibration procedure for appropriately registering the virtual environment as viewed by each participant so that it aligned with the real environment. We achieved this by measuring participant inter-pupillary distance, determining the ratio between units of measurement in the virtual environment and real world measurements, and by appropriately sizing virtual objects to achieve a good match. By correctly locating the HMD in real space, we can, with a single keypress, move the virtual viewpoint to the corresponding position. Good calibration is important for avoiding unwanted or unmeasured experimental influences. Following calibration, the built-in head position tracking of the VR system ensures that the participant's virtual viewpoint is thereafter constantly aligned to their real head and view position. This procedure demonstrates the simplicity with which consumer VR systems can be used for research where a requirement is close calibration between real and virtual environment features.

Our findings also have implications for human-computer interface design and a variety of consumer VR applications. VR software designers aim to create virtual worlds, games and experiences that distinguish their software from conventional 2D software. This means maximizing user experiences of presence, embodiment, and agency over virtual avatars. Understanding the relationships between specific sensory cues and users' subjective self-representations can inform this intention, giving developers more detailed information on the features and controls important for achieving good design. There are five findings from this study that may inform VR applications. First, that both visual form congruency and touch synchrony are generally important for compelling self-representation in VR. Second, relative to those cues, a spatial discrepancy between the proprioceptively felt real hand location and the visually apparent virtual hand location is not a sensitive influence on most elements of self-representation. Third, agency and presence seem to depend on the same multisensory cues (FORM, TOUCH, and OFFSET) that have been identified as important in the embodiment literature. Fourth, touch stimuli can be used in different ways: synchronous touch influences feelings of embodiment and presence, whereas the simple occurrence of touch may be sufficient to influence a sense of agency. Fifth, cues differ in their relevance for different components of self-experience in VR. So, depending on what self-experience is important for a specific VR implementation or product (e.g., ownership vs. agency), the designer may focus on different cues. Furthermore, these results can inform the design of VR software for therapeutical settings, where modulating the intensity of self-representation with different cues (e.g., employing graduated exposure treatments in anxiety disorders) could be important.

Limitations

An important innovation of our study was that we investigated the influence of a set of cues on a set of components thought to be important for self-representation. To do this we employed rating scales. Rating scales require participants to make explicit judgment responses and these may be subject to responses biases. For example, participants may have responded to different rating scales in a similar manner or responded to the repetition of the questionnaires similarly. We tried to provide a safe-guard for repetitive response patterns by randomizing the rating scales. That we found different patterns for different rating scales suggests that we did tap into differences in self-representation that were not simply due to the way participants tended to respond to these items. In future research, converging evidence from implicit measures will be useful to further investigate the mechanisms that support the representation of one's own body and actions.

For presence we only employed a small set of ratings (Sanchez-Vives and Slater, 2005). In future studies a full presence rating scale measure could be used (e.g., Lessiter et al., 2001; but see Slater et al., 2009b, for a critique of questionnaires for measuring presence, and suggested alternatives such as physiological measures).

In this study we manipulated a combination of visual, tactile and proprioceptive cues while the body was static. However, in many real-world scenarios as well as VR-applications the body is moving. Additional cues related to initiating a movement and processing movement feedback are likely crucial for self-representation, particularly for agency. To further study these cues and interactions with FORM, TOUCH, and OFFSET on several aspects of self-representation, an active Virtual Hand Illusion paradigm could be implemented.

Lastly, in our experimental design there is room for improvement in achieving synchrony between visual and tactile feedback relating to the experience of a touch. Since the system delay from the onset of visual feedback to onset of the tactor vibration is so steady, hardware based delays could be overcome by hard-coding a countering delay for the visual feedback, such that delay between the two is extinguished.

CONCLUSION

Our findings shed light on the multivariate influence of visual form congruency (whether the virtual hand appears similar in form to the participant's real hand), touch synchrony (whether virtual visual feedback about touch is temporally synchronized with physically experienced sensations of touch) and hand position alignment (whether or not visual and proprioceptive feedback about hand position are in agreement) on participants' experiences of embodiment, presence and sense of agency. We provided evidence that each type of cue can independently influence self-representation, but that none of these cues strictly constrains or gates the influence of the others. We also demonstrated that consumer-grade VR equipment can be used successfully in the cognitive and brain sciences to investigate self-representation.

AUTHOR CONTRIBUTIONS

All authors together designed the experiments; SP setup the VR-equipment and programmed the experiments; SP and VP collected the data; RZ and VP analyzed the data; SP, VP, and RZ wrote the paper with input from DK and MW.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpsyg.2016.01649

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The Effect of Visual, Spatial and Temporal Manipulations on Embodiment and Action

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The feeling of owning and controlling the body relies on the integration and interpretation of sensory input from multiple sources with respect to existing representations of the bodily self. Illusion paradigms involving multisensory manipulations have demonstrated that while the senses of ownership and agency are strongly related, these two components of bodily experience may be dissociable and differentially affected by alterations to sensory input. Importantly, however, much of the current literature has focused on the application of sensory manipulations to external objects or virtual representations of the self that are visually incongruent with the viewer's own body and which are not part of the existing body representation. The current experiment used MIRAGE-mediated reality to investigate how manipulating the visual, spatial and temporal properties of the participant's own hand (as opposed to a fake/virtual limb) affected embodiment and action. Participants viewed two representations of their right hand inside a MIRAGE multisensory illusions box with opposing visual (normal or grossly distorted), temporal (synchronous or asynchronous) and spatial (precise real location or false location) manipulations applied to each hand. Subjective experiences of ownership and agency towards each hand were measured alongside an objective measure of perceived hand location using a pointing task. The subjective sense of agency was always anchored to the synchronous hand, regardless of physical appearance and location. Subjective ownership also moved with the synchronous hand, except when both the location and appearance of the synchronous limb were incongruent with that of the real limb. Objective pointing measures displayed a similar pattern, however movement synchrony was not sufficient to drive a complete shift in perceived hand location, indicating a greater reliance on the spatial location of the real hand. The results suggest that while the congruence of self-generated movement is a sufficient driver for the sense of agency, the sense of ownership is additionally sensitive to cues about the visual appearance and spatial location of one's own body.

Keywords: body ownership, sense of agency, MIRAGE, multisensory integration, body representation, visual distortion

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INTRODUCTION

Experiencing a body as one's own is dependent upon the integration and interpretation of information from various sensory sources. Incoming information from the visual, tactile, vestibular, auditory and proprioceptive systems is integrated to form "bottom-up" contributions to body representation. These must also be interpreted with respect to "top-down" knowledge about the body, which modulates perceptual experience (Tsakiris, 2017). Under normal circumstances, the sense of body ownership seems effortless; that is, we do not have to decide whether or not our body belongs to us. However, experimental paradigms that involve the manipulation of multisensory inputs allow investigation into how this sense of body ownership is formed. In particular, introducing conflict between sensory inputs and top-down knowledge can reveal to what extent each contributes to the sense of owning and controlling the body.

The rubber hand illusion (RHI), first reported by Botvinick and Cohen (1998), has provided much insight into how multisensory interactions contribute to the experience of body ownership. In the basic paradigm, participants watch a rubber hand being stroked at the same time as their unseen real hand is stroked. When the site of stimulation between the two hands is visually congruent and the hands are stroked in synchrony, participants typically report the feeling that the rubber hand starts to become part of their body, and when asked to indicate the location of their real hand, estimates are displaced towards the rubber hand. However when the timing or site of stroking between the real limb and fake hand is asynchronous or incongruent, the illusion is diminished. This finding is replicated throughout the literature (Ehrsson et al., 2004; Tsakiris and Haggard, 2005; Costantini and Haggard, 2007; Shimada et al., 2009) and highlights the importance of intermodal correlations for the experience of body ownership; in this case, the correlation between visual and tactile inputs leads to the experience of ownership over the rubber hand and a modulation of proprioception (Botvinick and Cohen, 1998). Armel and Ramachandran (2003) extend this finding, reporting that synchronous visual and tactile inputs were sufficient to induce a referral of tactile sensations on to a wooden table and furthermore, led to physiological responses consistent with embodiment of the table. The authors suggested that perception is driven by Bayesian inference, implying that so long as stimulation is synchronous, any object may be experienced as belonging to oneself. However, subsequent research has failed to support this assumption, and instead demonstrates that while so-called "bottom-up" sensory correlations are necessary for the illusion, they are not sufficient; "top-down" knowledge constrains the feeling of ownership under certain conditions (Tsakiris and Haggard, 2005). The strength of the illusion is significantly reduced when the rubber hand is replaced with a wooden hand or a block (Tsakiris and Haggard, 2005; Tsakiris et al., 2010a) and when the rubber hand is rotated to an implausible/incongruent posture (Ehrsson et al., 2004; Holle et al., 2011; Ferri et al., 2013). Interestingly, the physical characteristics of the fake hand and their similarity to the participant's real hand appear to be less crucial; illusion experience is comparable for fake hands of different skin colors (Farmer et al., 2012) and the illusion is maintained for enlarged fake hands (although less so for visually reduced hands; Pavani and Zampini, 2007). Overall, the literature on body-ownership illusions demonstrates that both bottom-up and top-down factors are important in shaping bodily experience. Whilst spatiotemporal correlations between seen and felt stimulation/movements are crucial for the induction of ownership illusions, they are not sufficient; the to-be-integrated stimulus must also be compatible with semantic information about the body (Kilteni et al., 2015). However, the latter component appears somewhat flexible, and under normal conditions, visuo-tactile correlations are able to override some aspects of cognitive knowledge (Farmer et al., 2012; Newport et al., 2015). It is likely that the modification of top-town constraints and the experience of sensory input are bidirectional in nature as the brain attempts to minimize error between predictions and incoming sensory data (see Tsakiris, 2017).

Although the RHI can inform our understanding of some aspects of sensory integration and interaction between bottom-up and top-down components, the traditional paradigm is somewhat restricted, thus limiting what we can infer about how sensory and cognitive factors affect perception of the body. First, the illusion requires the participant to embody a static object, over which they have no motor control. This limits the intermodal correlations that can be investigated; typically only visuo-tactile correspondences are considered as long as the proprioceptive discrepancy is within acceptable limits. Recently, modified versions of the RHI paradigm have emerged that allow a basic motor correspondence between the movements of the participant's hand and the fake hand (Dummer et al., 2009; Kalckert and Ehrsson, 2012, 2014), but this does not extend to full control over the fake limb. Furthermore, this paradigm required the real and fake hand/fingers to be physically linked, which may affect top-down expectations during the illusion.

Second, the focus of the paradigm is on the application of manipulations to a fake limb, but it is theoretically important to consider how feelings of ownership are affected when these manipulations are applied to the real hand. In the RHI, exploration of the interactions between visual, temporal and spatial properties of the hand is constrained by the possible manipulations that can be applied, and by the requirement that the real hand be hidden from view (vision of the real hand diminishes the illusion; Armel and Ramachandran, 2003). For example, the real hand (based on appearance) can never be moved to an incorrect spatial location, nor can the synchrony between the seen and felt touch on the real hand be manipulated.

Some of these limitations are addressed in the use of virtual reality paradigms, in which participants view a virtual representation of their limb(s) through a head mounted display (Slater et al., 2008). In the virtual hand illusion, the size and position of the virtual hand is programmed such that it appears as though the participant is looking directly at their own hand, and the use of motion tracking technology allows the virtual limb to mimic the participant's movements. This has enabled more precise investigation into the factors affecting body ownership, with studies investigating the influence of visuomotor correlations, and violations to semantic information including size distortions and body discontinuity (Slater et al., 2009; Sanchez-Vives et al., 2010; Kilteni et al., 2012; Tieri et al., 2015). However, while virtual environments are realistic, the visual characteristics of the limb make it apparent that one is viewing a virtual representation as opposed to one's own hand. This produces conflict between the existing visual body representation and the seen limb, which may influence interactions between top-down and bottom-up information (Azañón et al., 2016). Since the perceptual aberrations experienced in disorders affecting body representation are misperceptions arising from the real body, it is important to determine whether the principles of body ownership are similar under conditions in which manipulations are applied to the participant's own hand, i.e., the seen hand matches the existing visual body representation.

Although manipulating the physical properties of the real hand when viewed directly is not possible, manipulations can be applied using video technology. Gentile et al. (2013) manipulated the synchrony and location of seen and felt tactile stimulation using video recordings of the participants' real hands taken prior to the experiment. Participants viewed the video image through a head-mounted display, creating the impression that they were looking directly at their own hand. However, a drawback of this method is that discrepancies may occur between the pre-recorded video image and the participant's real hand. The use of pre-recorded videos also limits flexibility in the application of experimental manipulations. These restrictions can be overcome by using a live video image of the participant's hand. In the video-version of the RHI (the "projected hand illusion (PHI)"; Graham et al., 2015), the rubber hand is replaced by a live video image of the participant's own hand. As well as allowing precise manipulation of the synchrony of seen and felt brush strokes, the PHI allows the congruency between seen and felt movements to be manipulated. This has been particularly useful for investigating contributions to the sense of agency, including distinctions between active vs. passive movement generation (Tsakiris et al., 2006; Longo and Haggard, 2009; Shimada et al., 2010).

In the PHI, an unmanipulated video image of the participant's hand is typically either projected onto the surface of a table (e.g., Tsakiris et al., 2006) or shown via a display screen embedded within a table (e.g., Graham et al., 2015). A disadvantage of this set-up is that the viewed hand is in a different plane to the real hand, which may require additional computation factors for the brain to overcome. In addition, by displaying an unmanipulated hand, the top-down factors that can be investigated are restricted. This can be remedied by using more immersive set-ups, such as virtual or mediated reality. The MIRAGE device is an example of such a system, presenting participants with a real-time video image of their own hand that appears in the same spatial location as the participant's real hand, creating the impression that the participant is viewing their hand directly. This enables visual, spatial and temporal manipulations to be applied concurrently to the participant's own hand, revealing how such manipulations affect bodily experience.

Previously, Newport et al. (2010) used the MIRAGE to investigate how manipulating the congruency of seen and felt tactile stimulation affected embodiment when participants were presented with two competing representations of the hand. Healthy participants viewed two images of their left hand, and the synchrony of visual information was varied whilst participants engaged in active touch. When one hand was synchronous and the other was not, ownership and reaching movements were consistent with embodiment of the synchronous hand. This finding is consistent with previous literature demonstrating the importance of intermodal correlations in determining ownership. In this study, both hand images were offset at an equal distance away from the participant's real hand, meaning that spatial (proprioceptive) information was not used to determine ownership. The effect of spatial location was explored in a later study by Newport and Preston (2011), who found that participants disowned the hand in the correct spatial location when feedback was asynchronous, instead taking ownership over the spatially displaced synchronous hand. The manipulation also reduced the accuracy of pointing responses, although reaches were not consistent with complete embodiment of the synchronous hand. Taken together, the findings of these studies demonstrate a strong link between agency and ownership, with ownership of the hand switching with motor synchrony. In both those experiments, however, the appearance of the hand was not manipulated and the two hand images were identical, meaning that only bottom-up contributions to bodily experience were explored. Here, we aim to extend the supernumerary limb paradigm by additionally manipulating the visual appearance of one of the images in order to investigate top-down influences on embodiment. Specifically, we wanted to explore how changing semantic information affects embodiment when manipulations are applied to a realistic representation of the participant's own limb, rather than a fake hand or virtual limb (Kilteni et al., 2015). By manipulating the congruency of visual, temporal and spatial information of two virtual hands at the same time, the aim is to directly compare the extent to which these factors contribute to body perception and the sense of self. Showing two hands simultaneously, with one always appearing in the same location as the participant's actual hand, allowed us to explore to what extent certain characteristics "override" others with respect to the sense of embodiment. The question being addressed is whether temporal motor synchrony (and the associated sense of agency) is powerful enough to override top-down visual factors related to ownership of the hand, and whether the addition of congruent proprioceptive information will modulate this. Whereas the previous studies focused on the sense of ownership, the present study aimed to capture a more detailed subjective experience of embodiment by also measuring agency and sense of location (Longo et al., 2008). Along with the inclusion of manual pointing responses, which provided an implicit measure of the "location" component of embodiment, this enabled a more detailed investigation into how sensory manipulations affect different components of embodiment.

Temporal synchrony of movement was predicted to be the strongest driver of embodiment. It was hypothesized that participants would report stronger embodiment over the synchronous hand compared to the asynchronous hand, even when spatial location of the synchronous hand was incongruent, in line with previous findings (Newport et al., 2010; Newport and Preston, 2011). In addition, it was predicted that the experience of embodiment would be modulated by the appearance of the hand, reflecting the influence of top-down knowledge about the body. However, the extent of this modulation was expected to depend on the spatial and temporal properties of the hands, i.e., smaller effect when temporal and spatial information was congruent. Furthermore, visual manipulations were predicted to have a stronger influence on subjective reports compared to pointing responses.

MATERIALS AND METHODS

Participants

Thirty-nine participants (24 female) were recruited using online advertisements and posters. The majority were students at the University of Nottingham. The mean age of participants was 22.12 years (*SD* = 4.05) and 35 self-reported being right handed. This study was carried out in accordance with the recommendations of the School of Psychology ethics committee with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the School of Psychology ethics committee.

Apparatus and Procedure

The experiment was carried out using MIRAGE mediated-reality that duplicated a live (delay ∼10 ms) digital representation of the participant's own right hand and presented both of these hands in the same spatial plane as the real hand. Both hands appeared to the right of the body midline and direct view of the upper limb was obscured using a black bib.

Before the experiment began, the participant was given a short time to view his or her unmanipulated and unduplicated right hand in MIRAGE. During this time participants responded to a six-item baseline questionnaire (see **Table 1**) to verify embodiment of their hand under normal conditions. Responses were on a 7-point scale running from −3 (strongly disagree) to +3 (strongly agree). As expected, all participants immediately reported strong embodiment of the hand in this unmanipulated viewing condition. Following this, participants were given a demonstration of the pointing task (see below), which was demonstrated using two identical images of the participant's right hand, with no visual distortion applied.

At the start of each condition, the MIRAGE-mediated view was blank and the participant placed his or her (unseen) hand inside MIRAGE. The experimenter moved the hand to a specified start location that varied between conditions. A regular short tone, repeated at a rate of ∼1 Hz, was played via a computer as a metronome beat and the participant tapped the index finger of the right hand in time to the beat. When tapping in time, the MIRAGE-mediated view presented the participant with two images of his or her right hand. On each trial, the participant saw two hands with opposing characteristics. One hand moved in synchrony with the participant's movements whilst the other was asynchronous (factor: synchrony). The asynchrony was produced by adding a fixed delay of 500 ms to the video image via software control. At the same time, on the same trial, one hand appeared normal whilst the other was distorted (factor: appearance) and one hand was presented in the same location as the participant's real hand while the other was presented in a false spatial location, displaced by 12 cm (factor: hand; see **Figure 1**). After 30 s, the participant stopped tapping the finger and completed either the questionnaire or the pointing task (see below; order randomized across conditions). Following completion, the experimenter picked up the participant's hand and moved it around before placing it on a start location. To ensure that stimulation was equivalent before each task, the trial was then repeated, with the participant completing the other task after 30 s of tapping.

The distortion was created by defining a region of interest around the hand within the original captured image that was then extracted and transformed to fill a space defined by four new co-ordinates within the workspace. Bicubic filters ensured the smooth transformation of the selected image region in a process that took less than 2 ms with a modal transformation time of 1 ms. The appearance of the distorted hand was selected based on the results of a pilot study in which participants (*N* = 51) rated the appearance of several different hand images. The hand distortion used in the current study was rated as significantly less realistic, less "hand-like" and more distorted than an unmanipulated hand.

To control for the physical location of the real hand (left or right), each condition was presented twice with the physical location of the hand varied such that the false hand appeared either to the left or right of the real hand,

TABLE 1 | Items 1–6 assessed feelings of ownership, agency and sense of location towards each hand (hand on the left vs. hand on the right) resulting in 12 experimental questions.

	It seemed like...	Category
1	... the hand on the left/right belonged to me	Ownership
2	... the hand on the left/right was part of my body	Ownership
3	... I caused the movement of the left/right hand	Agency
4	... I was in control of the left/right hand	Agency
5	... my hand was in the location where the left/right hand was	Location
6	... when I was tapping, my hand was moving in the location where I saw the left/right hand moving	Location
7	... I had three right hands	Control
8	... I no longer had a right hand	Control

Two control items (items 7 and 8) were included to check for response bias. Items 1–5 were included in the baseline questionnaire, reworded to refer to the "hand image". Since there was no tapping in the baseline condition, item 6 was substituted for the following question in the baseline questionnaire: "it seems like the hand in the image is my hand".

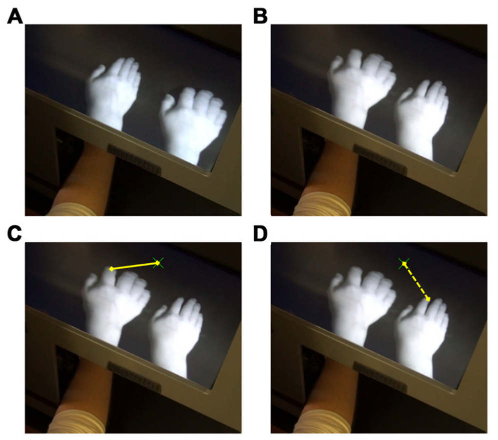

FIGURE 1 | TOP: example of the appearance and location of the hands in two conditions: (A) Veridical hand normal; **(B)** Veridical hand distorted. The physical location (real hand on left/right) and synchrony of finger movements (real hand synchronous/asynchronous) was balanced, resulting in a total of eight conditions. In the actual experiment, a black bib occluded vision of the arm. BOTTOM: the yellow lines show example reach trajectories in the pointing task. **(C)** illustrates a reach of the correct distance consistent with perceiving the hand to be in the location of the veridical hand, whilst **(D)** illustrates a reach of the correct distance consistent with perceiving the hand to be in the location of the displaced hand. Note that during the actual task, only the green cross was visible to participants—the hand images were hidden.

but not overlapping, with both hands falling within the right hemispace (see **Figure 1**). This resulted in a total of eight different conditions, with participants completing the questionnaire and pointing task once for each condition (order randomized). Conditions were completed in a pseudorandom order and counterbalanced between participants. There was a short break between conditions, during which the participant was encouraged to take his or her hand out of MIRAGE and move it around to prevent any stiffness and carry-over effects.

Questionnaire

At the end of the tapping period, the MIRAGE-mediated view of the hands remained visible. Participants responded to 12 statements designed to assess embodiment of the two hands. The construct of embodiment was based on three distinct components identified by Longo et al. (2008): ownership, agency and location. The items were adapted from those used in previous research (Longo et al., 2008; Tsakiris et al., 2010b) and contained six items relating to embodiment, each asked in reference to the seen left and right hands separately. Two control questions were included to check for response bias, giving a total of 14-items (see **Table 1**). Participants gave verbal responses to each item using a 7-point scale ranging from −3 (strongly disagree) to + 3 (strongly agree) and the experimenter recorded the response.

Pointing Task

At the end of the tapping period, the MIRAGE-mediated view of the hands was replaced with a blank workspace except for a green cross located equidistant between the index fingers of the two (now unseen) hands. The participant's task was to reach, in one smooth movement, and point to the green cross using the index finger such that the finger (if visible) would land at the center of the cross. Reaching movements were recorded via the MIRAGE device.

Analysis

Participants gave separate questionnaire responses for each hand. A mean score for each component of embodiment (ownership, agency and location), and the control questions, was calculated by averaging each participant's responses across the relevant items (note that collating scores from individual items in this way produces interval data; see Carifio and Perla, 2008). Positive scores for ownership/agency indicate that the participant experienced a sense of ownership/agency over the specified hand. Positive scores for location indicate that the participant felt as though their hand was in the location of the specified seen hand. Preliminary analysis showed no effect of physical location. Therefore the eight conditions were averaged across physical location (left/right), resulting in four conditions that describe the synchrony (synchronous vs. asynchronous) and appearance (normal vs. distorted) of each hand (the veridical hand, i.e., the hand in the same spatial location as the participant's actual hand, and the displaced hand, i.e., the hand in a different spatial location to the participant's actual hand). For brevity, the conditions are referred to by reference to the synchrony and appearance of one hand, (e.g., veridical hand synchronous and normal), but note that the characteristics of the other hand are simply the opposite (in this case, the displaced hand is asynchronous and distorted). The data were analyzed using 3-way repeated measures analysis of variances (ANOVAs) with the factors HAND (Veridical; Displaced), SYNCHRONY (Synchronous; Asynchronous) and APPEARANCE (Normal, Distorted). A potential consequence of analyzing questionnaire data this way is that the assumption of normality of residuals is violated. Exploration of the data from each of the measures showed that the distribution of residuals significantly differed from normal in several conditions (ownership: 4/8; agency: 4/8; location: 3/8; pointing: 1/4). One option was to transform the data, although this would have made the data difficult to interpret. Given the factorial design of the study, non-parametric analysis was considered unsuitable due to the inability of such procedures to investigate interactions between factors. The 3-way design would also have required a large number of *post hoc* comparisons, which after correction for multiple comparisons would dramatically reduce the likelihood of detecting true significant effects (increased type II error). Furthermore, a number of stimulation studies have concluded that ANOVA is "robust" to deviations from normality, particularly when sample size and variance is equal across groups (Glass et al., 1972; Harwell, 1992; Norman, 2010; Schmider et al., 2010). Therefore, the decision was made to proceed with the ANOVA analysis, taking care to interpret statistical findings with respect to measures of central tendency, the spread of the data and effect sizes. In addition to the means displayed in figures, median scores are presented in **Table 2** for comparison.

TABLE 2 | Median and interquartile range for ownership, agency and location scores for each hand in each condition.

Hand	Synchrony	Appearance	Ownership		Agency		Location	
			Median	IQR	Median	IQR	Median	IQR
Veridical	Sync	Normal	2.75	1.00	2.75	0.50	2.50	0.75
		Distorted	1.50	2.00	2.50	1.00	2.00	1.00
	Async	Normal	0.50	2.00	0.50	2.25	0.50	2.25
		Distorted	−1.50	1.75	−0.50	3.00	0.00	2.25
Displaced	Sync	Normal	−2.00	1.50	−0.50	2.25	−2.00	1.25
		Distorted	−0.75	2.25	−0.25	2.50	−1.75	1.25
	Async	Normal	0.50	2.75	2.00	0.75	0.00	2.00
		Distorted	2.00	1.75	2.50	1.00	0.75	2.75

Additionally, to ascertain whether or not participants reported positive experience of each component, one-sample t-tests were conducted to test whether means in each condition were significantly greater than zero (Bonferroni method used to control family-wise error rate). This procedure was to ensure that positive ratings for each component represented a meaningful rating of ownership/agency/location.

Reaches made during the pointing task were recorded via video and data was extracted offline using a LabVIEW script that identified the x-coordinates of the finger start location, finger endpoint and the target, in pixels. The difference between the finger start point and finger endpoint was calculated with respect to the target location and converted into centimeters (1 cm = 13 pixels), resulting in either a positive or negative value that indicated both the distance and direction of the reach. The distance between the veridical finger and the target was 6 cm. Therefore, a reach of 6 cm indicates a reach of the correct distance consistent with reaching "with" (i.e., from the location of) the veridical hand. Alternatively, a value of −6 cm indicates a reach of the correct distance consistent with reaching "with" (from the location of) the displaced hand (see **Figure 1**). As with the questionnaire measure, the eight conditions were averaged across left/right location, resulting in four conditions. Again, these are referred to in terms of the characteristics of the real hand in each condition (false hand the opposite). The data were analyzed using a 2-way repeated measures ANOVA with the factors SYNCHRONY (Synchronous; Asynchronous) and APPEARANCE (Normal, Distorted).

RESULTS

Ownership

Figure 2 shows the mean ownership score for each condition. The analysis revealed a significant effect of hand, $F_{(1,38)} = 23.47$, $p < 0.001$, $\eta_p^2 = 0.382$, as well as significant two-way interactions for hand by synchrony, $F_{(1,38)} = 100.70$, $p < 0.001$, $\eta_p^2 = 0.72$, and hand by appearance, $F_{(1,38)} = 47.01$, $p < 0.001$, $\eta_p^2 = 0.553$. Simple main effects analysis comparing hand at each level of synchrony showed that when the veridical hand was synchronous, ownership scores were higher for the veridical hand compared to the displaced hand, $F_{(1,38)} = 149.70$, $p < 0.001$, $\eta_p^2 = 0.798$ (*M [SE]* veridical vs. displaced: 1.78 [0.16] vs. −1.17 [0.16]). This pattern was reversed when the veridical hand was asynchronous, $F_{(1,38)} = 19.29$, $p < 0.001$, $\eta_p^2 = 0.337$ (*M [SE]* veridical vs. displaced: −0.45 [0.16] vs. 0.87 [0.19]).

Simple main effects analysis comparing hand at each level of appearance showed that when the veridical hand was normal in appearance, ownership scores were higher for the veridical hand compared to the displaced hand, $F_{(1,38)} = 79.54$, $p < 0.001$, $\eta_p^2 = 0.677$ (*M [SE]* veridical vs. displaced: 1.35 [0.11] vs. −0.71 [0.18]). However, there was no difference in ownership scores when the veridical hand was distorted, $F_{(1,38)} = 2.48$, $p = 0.124$, $\eta_p^2 = 0.061$ (*M [SE]* veridical vs. displaced: −0.01 [0.17] vs. 0.41 [0.16]).

In addition, one-sample t-tests were conducted to determine in which conditions ownership scores were significantly greater than zero, indicating a positive experience of ownership. Scores for the veridical hand were significantly bigger than zero in both conditions for which the veridical hand was synchronous (normal: $t_{(38)} = 20.30$, $p < 0.001$; distorted: $t_{(38)} = 5.22$, $p < 0.001$). Scores for the displaced hand were only significantly bigger than zero when the veridical hand was asynchronous and distorted ($t_{(38)} = 7.54$, $p < 0.001$).

In summary, ownership was expressed for the veridical hand when it was synchronous and either of normal or distorted

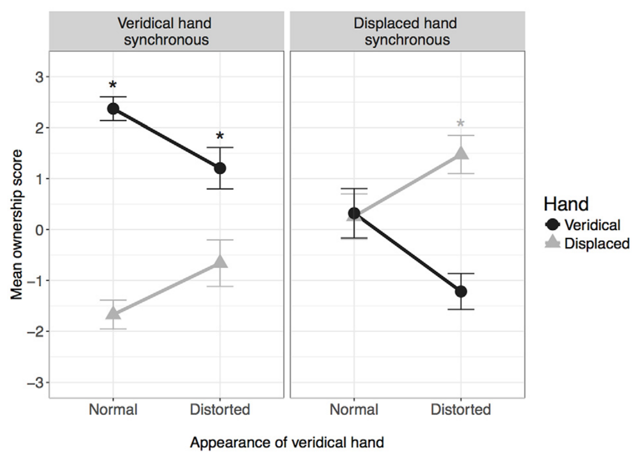

FIGURE 2 | Mean ownership score in each condition. *Indicates mean is significantly greater than zero after correcting for multiple comparisons. Error bars: 95% CI.

appearance, and for the displaced hand when it was synchronous and normal in appearance.

Agency

Figure 3 shows agency scores for each condition. The analysis revealed a significant effect of hand, $F_{(1,38)} = 13.96$, $p = 0.001$, $\eta^2_p = 0.269$, along with a significant hand by synchrony interaction, $F_{(1,38)} = 115.85$, $p < 0.001$, $\eta^2_p = 0.753$, and a hand by appearance interaction, $F_{(1,38)} = 20.22$, $p < 0.001$, $\eta^2_p = 0.347$.

Simple main effects analysis comparing hand at each level of synchrony showed that when the veridical hand was synchronous, agency scores were higher for the veridical hand, $F_{(1,38)} = 126.39$, $p < 0.001$, $\eta^2_p = 0.769$ (*M [SE]* veridical vs. displaced: 2.47 [0.09] vs. −0.48 [0.24]). The reverse pattern was observed when the veridical hand was asynchronous, $F_{(1,38)} = 78.50$, $p < 0.001$, $\eta^2_p = 0.674$ (*M [SE]* veridical vs. displaced: −0.19 [0.21] vs. 2.07 [0.12]).

Simple main effects analysis comparing hand at each level of appearance showed that when the veridical hand was normal, agency scores were higher for the veridical hand compared to the displaced hand, $F_{(1,38)} = 35.66$, $p < 0.001$, $\eta^2_p = 0.48$ (*M [SE]* veridical vs. displaced: 1.36 [0.11] vs. −0.60 [0.15]). However, there was no difference in agency scores when the veridical hand was distorted, $F_{(1,38)} = 0.26$, $p = 0.615$, $\eta^2_p = 0.007$ (*M [SE]* veridical vs. displaced: 0.92 [0.13] vs. 0.99 [0.14]).

One-sampled *t*-tests revealed that agency scores for the veridical hand were significantly bigger than zero in both conditions for which the veridical hand was synchronous (normal: $t_{(38)} = 32.22$, $p < 0.001$; distorted: $t_{(38)} = 20.87$, $p < 0.001$). Furthermore, agency scores for the displaced hand were significantly bigger than zero in both conditions for which the veridical hand was asynchronous i.e., the displaced hand was synchronous (normal: $t_{(38)} = 14.71$, $p < 0.001$; distorted: $t_{(38)} = 14.99$, $p < 0.001$).

In summary, agency was expressed for the hand that was in temporal synchrony with the movements of the veridical hand, regardless of location or appearance.

Location

Figure 4 shows location scores for each condition. Again, there was a main effect of hand, $F_{(1,38)} = 60.93$, $p < 0.001$, $\eta^2_p = 0.62$, and significant two-way interactions for hand by synchrony, $F_{(1,38)} = 88.71$, $p < 0.001$, $\eta^2_p = 0.700$, and hand by appearance, $F_{(1,38)} = 19.65$, $p < 0.001$, $\eta^2_p = 0.341$.

Simple main effects analysis comparing hand at each level of synchrony showed that when the veridical hand was synchronous, location scores were significantly higher for the veridical hand, $F_{(1,38)} = 363.78$, $p < 0.001$, $\eta^2_p = 0.905$ (*M [SE]* veridical vs. displaced: 2.25 [0.09] vs. −1.73 [0.15]). However, there was no difference in location scores when the veridical hand was asynchronous, $F_{(1,38)} = 0.100$, $p = 0.754$, $\eta^2_p = 0.003$ (*M [SE]* veridical vs. displaced: 0.23 [0.20] vs. 0.37 [0.23]).

Simple main effects analysis comparing hand at each level of appearance showed that when the veridical hand was normal, location scores were higher for the veridical hand compared to the displaced hand, $F_{(1,38)} = 90.67$, $p < 0.001$, $\eta^2_p = 0.705$ (*M [SE]* veridical vs. displaced: 1.52 [0.12] vs. −0.87 [0.16]). The reverse pattern was observed when the veridical hand was distorted, $F_{(1,38)} = 26.46$, $p < 0.001$, $\eta^2_p = 0.411$ (*M [SE]* veridical vs. displaced: 0.97 [0.14] vs. −0.49 [0.17]).

One-sampled *t*-tests revealed that location scores for the veridical hand were significantly bigger than zero in both conditions for which the veridical hand was synchronous (normal: $t_{(38)} = 29.92$, $p < 0.001$; distorted: $t_{(38)} = 15.27$, $p < 0.001$). When the veridical hand was asynchronous, location scores were not significantly greater than zero for either the normal or distorted hand after correcting for multiple comparisons.

In summary, participants felt as though their hand was in the same location as the veridical hand regardless of whether

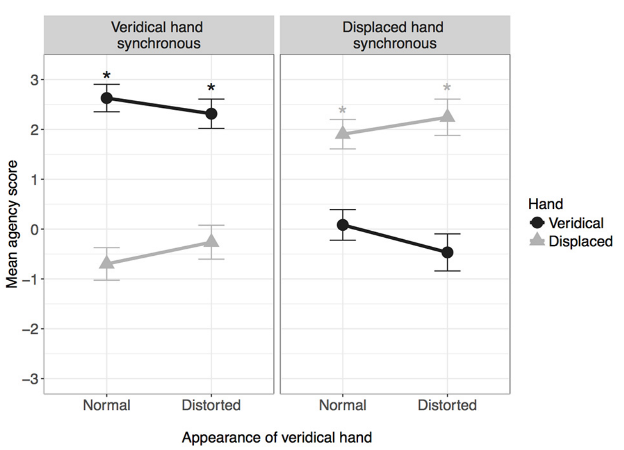

FIGURE 3 | Mean agency score in each condition. *Indicates mean is significantly greater than zero after correcting for multiple comparisons. Error bars: 95% CI.

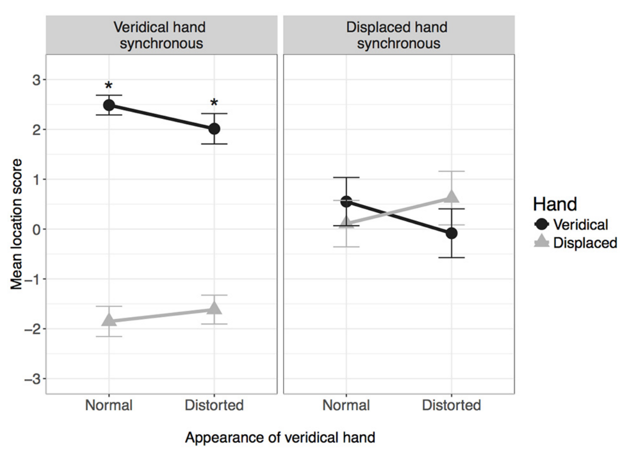

FIGURE 4 | Mean location score in each condition. *Indicates mean is significantly greater than zero after correcting for multiple comparisons. Error bars: 95% CI.

it appeared normal or distorted, but only when the veridical hand was synchronous; when it was asynchronous (and thus the displaced hand was synchronous), the perceived location of the hand was ambiguous.

Pointing Task

Mean distance reached (cm) is displayed in **Figure 5**, with lower values reflecting reduced accuracy. The analysis revealed a main effect of synchrony, $F_{(1,37)} = 75.72$, $p < 0.001$, $\eta_p^2 = 0.672$, and a main effect of appearance, $F_{(1,37)} = 49.95$, $p < 0.001$, $\eta_p^2 = 0.574$, as well as a significant interaction between the two, $F_{(1,37)} = 11.55$, $p = 0.002$, $\eta_p^2 = 0.238$.

Simple main effects analysis of appearance at each level of synchrony revealed a significant effect of appearance both when the veridical hand was synchronous, $F_{(1,37)} = 6.44$, $p = 0.016$, $\eta_p^2 = 0.148$, and when it was asynchronous, $F_{(1,37)} = 31.78$, $p < 0.001$, $\eta_p^2 = 0.462$. When the veridical hand was synchronous, accuracy was lower when the hand was distorted compared to when it was normal (mean difference: 0.47 cm), although it should be noted that overall accuracy remained high. The same pattern was observed when the veridical hand was asynchronous, with lower accuracy for when the veridical hand was distorted compared to when it appeared normal, although the difference between the means was much larger compared to when the veridical hand was synchronous (mean difference: 1.95 cm), and overall accuracy was lower.

In summary, when the synchronous hand was proprioceptively congruent with the real hand, participants pointed with the synchronous hand (that is, from the location of the synchronous hand) regardless of physical appearance. When the synchronous hand was incongruent with the location of the real hand, the inferred origin of reaches was shifted towards the displaced, synchronous hand, but not completely. This effect was modulated by appearance and was greater when the displaced, synchronous hand was normal in appearance.

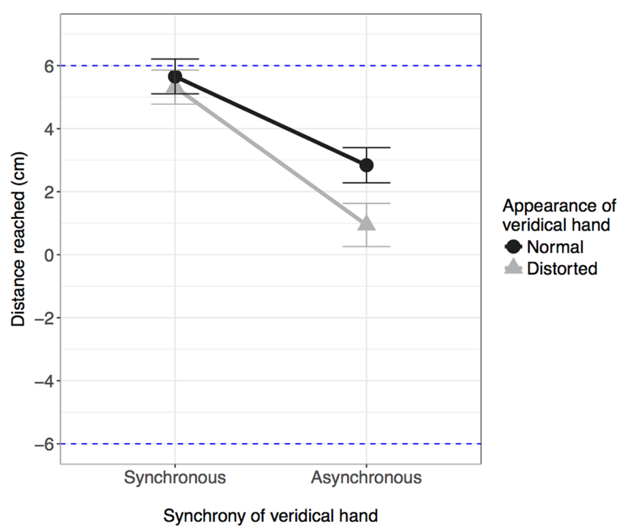

FIGURE 5 | Mean distance reached (cm) in the pointing task (in horizontal plane). The dotted line at 6 cm represents a reach of the correct distance consistent with reaching "with" (i.e., from the location of) the veridical hand. Alternatively, the dotted line at −6 cm indicates a reach of the correct distance consistent with reaching "with" (from the location of) the displaced hand. A reach of 0 cm indicates that the participant reach straight-ahead, consistent with the perception that their hand was located directly between the two hand images they saw. Error bars: 95% CI.

Correlations between Components

In addition to the main analyses, exploratory correlational analyses were conducted to assess the relationship between the different components of embodiment in each condition. For the subjective components, correlations were conducted on scores for the veridical hand only.

Pearson correlations (shown in **Table 3**) revealed significant positive correlations between the subjective components, ownership, agency and location, in all conditions except when the veridical hand was synchronous and distorted (displaced hand asynchronous and normal). In that condition, location scores were significantly correlated with both ownership and agency, however ownership and agency were not significantly correlated with each other.

Pointing accuracy was significantly correlated (positively) with location scores for all conditions except when the veridical hand was synchronous and distorted. Aside from a significant correlation between pointing accuracy and ownership scores in one condition, all other correlations were not significant (see **Table 3**).

DISCUSSION

This study investigated how manipulating visual, temporal and spatial information about the hand influenced body perception in

TABLE 3 | Pearson correlations between the four measures for each condition.

	Ownership	Agency	Location
Veridical hand synchronous and normal			
Ownership	–		
Agency	0.404*	–	
Location	0.421**	0.504**	–
Pointing	−0.060	0.251	0.331*
Veridical hand synchronous and distorted			
Ownership	–		
Agency	0.178	–	
Location	0.382*	0.792**	–
Pointing	0.100	0.200	0.242
Veridical hand asynchronous and normal			
Ownership	–		
Agency	0.452**	–	
Location	0.727**	0.490**	–
Pointing	0.458**	0.045	0.577**
Veridical hand asynchronous and distorted			
Ownership	–		
Agency	0.494**	–	
Location	0.489**	0.545**	–
Pointing	−0.079	−0.116	0.326**

*Significant associations are indicated by asterisks, where *p < 0.05, **p < 0.01. N = 39 for all.*

relation to agency and ownership. Participants tapped the index finger up and down whilst viewing two representations of his or her own hand that had opposing visual (normal or distorted), temporal (synchronous or asynchronous movement) and spatial (real location or false location) characteristics. Questionnaire responses captured perceived ownership, agency and sense of location for each hand, and pointing responses served as an implicit measure of embodiment.

For agency, the strongest driver was temporal synchrony; participants felt a sense of control over whichever hand moved in synchrony with their own movements, and the sense of agency remained regardless of visual appearance or location relative to the real hand (see **Figure 3**). The effects were somewhat different with regards to ownership; whilst temporal synchrony remained an important factor, the sense of ownership was additionally modulated by visual appearance and location: while ownership was reported for the synchronous hand in either location, the strength of feeling was lessened if that hand was grossly distorted or if the location was incongruent with the real hand (see **Figure 2**), to the extent that ownership was not claimed if the hand was both distorted AND in an incongruent location. Subjectively, the real hand was felt to be in the same location as the synchronous hand only when the synchronous hand was in the same location as the real hand in reality (veridical hand synchronous conditions in **Figure 4**). When the asynchronous hand was in the same location as the real hand in reality (veridical hand asynchronous conditions in **Figure 4**), subjective location became uncertain and was reported to be in neither the location of the synchronous nor asynchronous hand. Subjective reports were consistent with objective pointing data: the inferred start locations were consistent with reaching "with" (from the location of) the synchronous hand when it was in the same physical location as the real hand, but from between the two hands when the hand seen in the same location as the real hand was asynchronous (see **Figure 5**). That is, start locations were dragged towards the synchronous hand, but not completely, suggesting modulation by proprioception and congruence with the real hand location.

The present work is the first study to investigate how distorting the appearance of the participant's own hand affects embodiment when simultaneous spatial and/or temporal manipulations are applied. Previous experiments have demonstrated how manipulating the appearance, temporal synchrony or the spatial location of fake or virtual limbs influences feelings of embodiment. However, it is unclear whether the same mechanisms apply when manipulations are applied to (an image of) one's own hand. Experiencing an external object as part of your own body is likely to involve different multisensory interactions compared to when manipulations are applied to an image of one's own hand. In comparison to a fake hand, viewing a representation of one's own hand might be expected to evoke stronger top-down influences, due to the fact that the visual appearance of the hand is consistent with the visual representation in the existing internal model (Tsakiris, 2010). This may influence the integration of top-down and bottom-up inputs, potentially causing visual information regarding the appearance of the hand to be given a stronger weighting compared to situations in which visual information is obviously inaccurate or false. Such strong visual information may even be sufficient to overcome other sensory discrepancies, such as incongruence between seen and felt movements (or touch), contradicting results from fake/virtual body paradigms. Such a finding would also have important implications for our understanding of disorders of body representation, where perceptual aberrations arise from one's own body rather than misperceptions of external objects.

Importantly, the findings show that even when participants view normal and distorted representations of their own hand, visuomotor synchrony is the strongest driver of both agency and ownership: in all four conditions, participants reported a strong sense of agency for whichever hand was synchronous, and a sense of ownership was reported over the synchronous hand in all but one condition. However, the results also show that violations of top-down knowledge about the body, introduced through the visual distortion, have different implications for agency and ownership. While the contrasting visual appearance between the two hands had little effect on agency, participants reported significantly less ownership over the hand when it was distorted, indicating that ownership is more influenced by the visual information about the hand form/appearance compared to agency. This is in line with findings showing that postural manipulations of fake/virtual hands have a greater effect on ownership compared to agency (Kalckert and Ehrsson, 2012; Salomon et al., 2016). Here, we extend these findings by showing a similar effect when manipulating the visual characteristics of the participant's own hand, indicating that agency and ownership are at least partially independent processes. Further evidence for this is found in the comparison of ownership and agency ratings in the condition for which the veridical hand was both asynchronous and of normal appearance (displaced hand synchronous-distorted); participants reported a strong sense of agency over the displaced hand but no sense of ownership over either hand. This demonstrates first that ownership is not necessary for agency, and second that agency is not sufficient for ownership, supporting previous suggestions that ownership and agency are dissociable (Tsakiris et al., 2010b; Kalckert and Ehrsson, 2012). However, the present results cannot conclude that agency and ownership are completely independent. It is notable that participants did not report ownership for a hand that they did not also have a sense of agency for although see Kalckert and Ehrsson (2012), and furthermore under no circumstances did participants claim ownership of one hand, but agency of another.

The significant associations between the subjective experiences of ownership, agency and location support the notion that these three factors can be considered as subcomponents of a broader bodily experience, termed embodiment (Longo et al., 2008; Graham et al., 2015). In particular, the strong association between ownership and agency suggests that these two components share at least some common mechanisms. Although both ownership and agency correlated with the subjective sense of location, neither correlated with pointing accuracy, the implicit measure of perceived hand location (with the exception of ownership in one condition). However, pointing accuracy did correlate with subjective location scores in all but one condition, supporting the suggestion that the pointing task provides an implicit measure of the location component of embodiment.

The current study extends previous findings from the supernumerary limb paradigm, which found that ownership of the hand moved with visuomotor synchrony (Newport et al., 2010; Newport and Preston, 2011). However, in those experiments, the two hands were identical in appearance. The current experiment demonstrates that visuomotor synchrony does not completely dictate ownership when competing top-down (appearance) and bottom-up (proprioception) factors provide additional, conflicting information. Similarly, ownership is not driven by appearance alone; seeing a representation of one's own hand (normal appearance) is not sufficient to override the influences of incongruent temporal and spatial information. Rather unsurprisingly, perhaps, the brain seems to weigh up the available sensory information and make sense of the body accordingly. When the hand is synchronous, in the same location and with veridical appearance, it is owned; when it is asynchronous, in the wrong location and looks wrong, it is not; all other combinations are somewhere in between.

While the present study demonstrates that altering the appearance of the hand reduces the sense of ownership, participants still experienced ownership over the distorted hand when it was temporally and spatially congruent with their actual limb (see **Figure 2**, veridical hand synchronous and distorted condition). The extent to which the appearance of the hand can be altered whilst maintaining a sense of ownership (when all other factors are constant) remains unclear. In future work we aim to clarify this by manipulating the visual similarity between the participant's own hand and the viewed limb in different stages, gradually increasing the level of distortion/dissimilarity. This will shed further light on the interplay between bottom-up and top-down factors during body representation.

Overall, the findings reveal important information about the way in which different sensory information is used to form a representation of the body. Few studies have examined how specific visual characteristics of the hand affect experience of embodiment, despite vision providing a key source of information used to distinguish between self and other. When visual characteristics have been explored, these have been limited to altering the appearance of a fake limb, rather than changing the appearance of the participant's own hand (e.g., Heed et al., 2011; Bertamini and O'Sullivan, 2014). In line with previous research, the results showed that temporal synchrony had the strongest effect on the sense of ownership, agency and perceived location of the hand as measured by both the questionnaire and pointing responses. Importantly, the visual appearance of the hand also had a smaller but significant effect on responses. The difference between normal and distorted hands was minimal for both agency and location scores, but the effect was larger for ownership scores, suggesting visual information is weighted more strongly in determining the sense of ownership. Visual information also had an effect on pointing responses, but only in conditions for which the veridical hand was asynchronous (displaced hand synchronous). The findings also demonstrate that participants were sensitive to the spatial location of the hands, although the extent to which this affected responses differed across components. Both questionnaire scores of perceived location and pointing responses were particularly sensitive to hand location; specifically, synchronous movement of the displaced hand was not sufficient to result in a shift in perceived hand location towards that hand, even when it also appeared normal.

Taken together, the findings support the distinction between agency and ownership. While visuomotor synchrony is sufficient for the sense of agency, the sense of ownership is reduced when the visual appearance or physical location of the hand is manipulated. Furthermore, the study highlights how distinct sensory inputs are weighted differently, and combined with top-down knowledge of the body, to contribute to individual components of embodiment.

AUTHOR CONTRIBUTIONS

NR and RN designed the study, interpreted the data and wrote the manuscript. NR conducted the experiment and analyzed the data.

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Manipulating Bodily Presence Affects Cross-Modal Spatial Attention: A Virtual-Reality-Based ERP Study

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Earlier studies have revealed cross-modal visuo-tactile interactions in endogenous spatial attention. The current research used event-related potentials (ERPs) and virtual reality (VR) to identify how the visual cues of the perceiver's body affect visuo-tactile interaction in endogenous spatial attention and at what point in time the effect takes place. A bimodal oddball task with lateralized tactile and visual stimuli was presented in two VR conditions, one with and one without visible hands, and one VR-free control with hands in view. Participants were required to silently count one type of stimulus and ignore all other stimuli presented in irrelevant modality or location. The presence of hands was found to modulate early and late components of somatosensory and visual evoked potentials. For sensory-perceptual stages, the presence of virtual or real hands was found to amplify attention-related negativity on the somatosensory N140 and cross-modal interaction in somatosensory and visual P200. For postperceptual stages, an amplified N200 component was obtained in somatosensory and visual evoked potentials, indicating increased response inhibition in response to non-target stimuli. The effect of somatosensory, but not visual, N200 enhanced when the virtual hands were present. The findings suggest that bodily presence affects sustained cross-modal spatial attention between vision and touch and that this effect is specifically present in ERPs related to early- and late-sensory processing, as well as response inhibition, but do not affect later attention and memory-related P3 activity. Finally, the experiments provide commeasurable scenarios for the estimation of the signal and noise ratio to quantify effects related to the use of a head mounted display (HMD). However, despite valid a-priori reasons for fearing signal interference due to a HMD, we observed no significant drop in the robustness of our ERP measurements.

Keywords: virtual reality, head mounted display, event-related potentials, bodily presence, cross-modal spatial attention

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INTRODUCTION

Our ability to focus on a specific location while ignoring events occurring in other directions is a vital requirement for successful interaction with the surrounding world. While early research on selective spatial attention focused on attention processes within a single sensory modality (Woods, 1990), over the last two decades evidence has cumulated on the degree that voluntary—or endogenous—attention in one modality and spatial location strongly affects processing in the other, task-irrelevant, sensory modalities if presented on the attended side (Spence, 2014). For example, in a study by Spence et al. (2000), asking participants to respond to visual stimuli presented at certain location was shown to speed up participants' reactions to visual and tactile events if presented on the attended side.

Recordings of ERPs have been found particularly useful in the investigation of the mechanisms underlying endogenous cross-modal spatial attention. A typical ERP experiment involves a stream of stimuli presented in two sensory modalities and from two spatial locations (e.g., left and right). Participants are asked to respond to stimuli of a certain combination of modality and location while ignoring all other stimuli. The general finding is that attending to a location amplifies evoked potentials in the target modality and in the irrelevant modality (Eimer, 2001). In other words, even if the participants should completely ignore stimuli in the irrelevant modality and merely respond to, for example, left vibrations, visual ERPs show enhanced processing if they appear in the relevant location (left). Such cross-modal interactions have been observed in various modalities: as suggested between vision and audition, as well as between vision and audition and audition and touch (Teder-Sälejärvi et al., 1999; Eimer et al., 2002).

In EEG-based ERP measurements, the effect of spatial attention usually occurs in the sensory-specific N1 component, suggesting the modulation takes place at a very early, sensory-perceptual stage (Hötting et al., 2003). This observation with the findings that preparatory attentional states are similarly affected regardless of the target modality, have led researchers to conclude that endogenous spatial attention operates at a supramodal level (Eimer et al., 2002). That is, rather than being divided into separate unimodal attention systems, our spatial selection seems to be regulated by a modality independent control system operating across different sensory systems.

Cross-modal links also have been demonstrated in completely different settings, demonstrating the special role of the visual body in spatial attention. Sambo et al. (2009), for instance, investigated whether the visual input of one's hands would influence the somatosensory processing of tactile targets in a sustained spatial attention task. Participants were instructed to covertly attend to infrequent tactile targets presented to one hand while completely ignoring targets sent to the other hand, as well as all non-targets. Attending to the stimulated hand was found to enhance early somatosensory processing. The attentional modulation, however, occurred earlier (from 100 ms poststimulus) if the participant' hands were visible when they were covered, or if the participant was blindfolded. Similarly, a positron emission topography study by Macaluso et al. (2000) revealed that covertly attending to one's left or right hand resulted in greater activity in intraparietal sulcus and secondary somatosensory cortex when a tactile stimulus was delivered to the attended hand. Finally, a more recent study on this visual enhancement of touch (VET) showed that viewing one's body affected processing of the tactile stimuli and that the effect was observed as early as 27 ms poststimulus in primary somatosensory cortex (Longo et al., 2011).

Thus, it is clear that seeing our body affects even the earliest levels of perceptual processes (Harris et al., 2015). Previous findings suggest, however, that attentional modulation can also affect later stages of processing, such as response inhibition and execution. Pavani et al. (2000), for instance, examined the attentional link between vision and touch using a spatial tactile discrimination task with visual distractors. In all conditions, the visual distractors were presented well away from participants' hands, which, in turn, were occluded from view by a table. Reaction times in the spatial discrimination task were substantially delayed if the visual distractors were spatially incongruent with the responses. Interestingly, however, the researchers found even greater delay if placing a pair or rubber hands close to the distractors, suggesting the visual body, whether rubber or real, is used to locate events in the tactile modality. To some extent, this is similar to the VET (Sambo et al., 2009; Longo et al., 2011) but there are also crucial differences. First, in the VET studies, the visual body cues were shown to enhance *tactile* perception while in Pavani et al.'s (2000) study, visual input of the hands enhanced processing of *visual* stimuli. Second, in the VET, the visual body input mainly affected the early sensory–perceptual processes while the Pavani et al.'s (2000) results indicate seeing one's hands influenced later executive functions, such as response inhibition.

Unfortunately, Pavani et al. (2000) did not investigate physiological responses, leaving us to speculate about the brain stages affected by the rubber hand effect. Taking into account that reaction times are commonly correlated with the P3 potential (Conroy and Polich, 2007), one could expect the tactile target-related P3 to be more enhanced if one's hands are visible than when they are occluded. Similarly, if seeing a visual distractor close to one's hands makes it more distracting, as Pavani et al. (2000) suggested, one would predict that more of an inhibitory effort would be required if the hands are visually present than when they are not. Because the anterior N2 component—a negative potential occurring just before the P300—has been found to be particular to inhibitory processes (Spapé et al., 2011; for a review, see Folstein and Van Petten, 2008), one could predict the visual presence of hands may result in an amplified anterior N2. On the other hand, earlier research on cross-modal spatial attention (for review, see Eimer et al., 2002) shows the cross-modal interactions are clearly present in early sensory processes while completely absent in late postperceptual processes. It is thus possible the modulating effect of bodily presence is likewise limited to sensory-related components, such as the N1, which has been linked to early sensory gain control that amplifies spatially relevant sensory stimuli (Hillyard et al., 1998b), and P200, which has been thought to reflect the attentional enhancement of late sensory processing (Freunberger et al., 2007).

Thus, the goals of the current ERP study were to verify whether seeing one's body affects the spatial attentional link between vision and touch and to determine at which point the effect takes place. Similar to earlier studies, we utilized a bimodal oddball paradigm with two sensory modalities and two locations leading to four stimulus types: left- and right-handed vibrations and left- and right-located flashes. Participants reacted to one stimulus type by silently counting the occurrences while ignoring all other stimuli arising from the other modality and direction. The effect of bodily presence on cross-modal spatial attention was then investigated by manipulating participants' visual body cues under three viewing conditions. In the *VR hands* condition, motion tracking sensors, and a head mounted display (HMD) were used to show the task in a virtual scenario with simulated hands. In the *VR without hands* condition, no virtual hands were provided, leaving the participant virtually disembodied in visual space. Finally, a control condition was provided with the task shown in the traditional setup without any VR. To determine whether and when the bodily presence affects cross-modal interaction, we measured the effect of visible hands on the attentional modulation of visual and tactile evoked N1, P2, N2, and P3 potentials, contrasting the virtual hand condition with both a no-hand VR condition and a VR-free control condition.

Further, we were interested in measuring the effect of using an HMD on the reliability of the EEG signal. Given the anecdotal findings of HMDs' adverse influences on ERPs (Bayliss and Ballard, 2000), we took special care to make conditions between the different scenarios commeasurable and to quantify the degree to which the HMD induces noise in the EEG signal. To do so, we concentrated on the most common ERP, the P3, and compared the signal to noise results obtained in VR conditions with equivalent ERP data collected in traditional experimental settings with an LCD screen (HMD-free control). After taking into account that the type of stimulus and the location of the experiment affects ERPs (Debener et al., 2012), we created a virtual replica of our real laboratory environment, including the EEG amplifier and other objects, such as the LCD screen. As the participants put on the HMD, they found themselves in seemingly the same room, but now in VR. Finally, the same experimental procedure was used to project the stimuli on the real screen in the control condition as it appeared on the virtual animated screen. Thus, additional noise could not be ascribed to differences in the scenario or task and must instead be due to the HMD itself.

MATERIALS AND METHODS

Participants

Twelve right-handed participants (seven female, five male) volunteered to take part in the experiment. They all self-reported as healthy adults (age 29.5 ± 5.7 years) with normal vision. In accordance with the Declaration of Helsinki, participants were fully briefed on the nature of the study and on their rights as volunteers—including the right to withdraw at any point without fearing negative consequences—prior to signing informed consent forms. The order of the experimental conditions was counterbalanced among participants so that one-third of the participants took part in the control condition (real hands) first. After the three conditions, the participants received two movie tickets in return for their participation. The study did not concern medical research, and in accordance with Finnish law, the need for formal approval was waived by both the vice president of Aalto University and by the chairman of the Ethics Review Board of Aalto.

Procedure and Design

A 3 (viewing condition: control [HMD-free], VR with hands, VR without hands) × 24 (blocks) × 4 (target stimulus: vibration on the left, vibration on the right, circle on the left, circle on the right) × 4 (presented stimulus: vibration on the left, vibration on the right, circle on the left, circle on the right) within-subject design was employed. **Figure 1** shows the setups of each viewing condition.

In the Oddball task, participants were instructed to silently count a certain stimulus type (e.g., flashes on the left) while a stream of tactile and visual stimuli was presented on both the left and right sides of a central fixation cross. The cross was presented at the center of the screen throughout the stream of stimuli, and participants were told to keep their gaze on it while counting the stimuli. Following the block, participants were asked to indicate the correct number of the target stimuli. The task was the same in all three viewing conditions (control, VR with hands, and VR without hands, order counterbalanced among participants). Each condition consisted of 24 blocks of 60 stimulus trials. All four stimulus types (vibrations on left, vibrations on right, flashes on left, and flashes on right) were presented with equal probability of 25% within the block. However, to keep participants from guessing the correct answer, the number of target stimuli was randomly varied (15 ± 3) among blocks.

Each block proceeded uniformly, beginning with a task instruction presented on the screen (e.g., "Count the flashes left") for 3 s, after which the white central fixation cross was shown on a black background. Following an interval of 100–300 ms (randomized), the stream of stimuli started with a 500-ms stimulus duration and 100–300-ms (randomized) inter-stimulus interval. The next block started immediately after participants indicated the number of targets. The entire experiment took approximately 100 min, including breaks and EEG preparation.

Apparatus and Stimulus Material

In all three viewing conditions, participants were seated at a desk equipped with a glass table. Vibrotactile devices were placed on each participant's left and right palms and kept stationary with rubber bands. Vibrations were presented using two ATAC C-2 Tactors[1] that each delivered 125-Hz sinusoid signals with a 500-ms stimulus duration. To prevent the C-2 from providing auditory cues, masking white noise was played throughout the experiment.

The source of the visual stimuli differed depending on the viewing condition. In the control condition, the visual stimuli and task instructions were presented on a 24′′ TFT monitor (1920 pixel × 1200 pixel resolution; 60 Hz refresh rate), whereas in the VR conditions, an Oculus Rift VR headset (Oculus Rift Developer Kit 2; 960 × 1080 resolution per eye; 75 Hz refresh rate; 100° nominal field of view) was used. However, in all conditions, the visual stimuli that had to be counted were white, filled circles (200 pixels/5.4 cm diameter) presented for 500 ms to the left or right of a central fixation cross. The validity of comparing the control with the VR conditions was further supported by

[1] www.atactech.com/PR_tactors.html

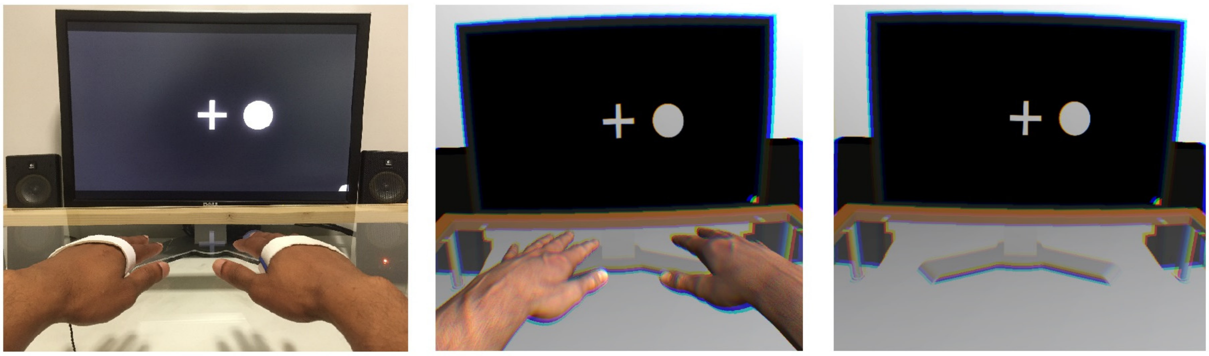

FIGURE 1 | Experimental setups used in the control (A), virtual-hand **(B)**, and no-hand **(C)** conditions. An EEG was recorded while a stream of tactile and visual stimuli was presented on the left and right sides. Participants were instructed to place their hands on the table in alignment with the visual stimuli.

adding a photorealistic 3-D model of the lab room to the VR setting, including all of the physical lab's central visual objects (e.g., computer screen, amplifier, speakers, and a glass table; see Supplementary Figure 2). No visual body cues were present in the first VR condition. However, to investigate how bodily presence affects cross-modal spatial attention, a pair of virtual arms—the appearance of which matched participants' real arms—was included in the second VR condition. To allow participants to move their 3-D arms in the virtual space, we placed a Leap Motion[2] movement tracker under the glass table 16 cm below each participant's real hands.

The stimuli timing and the behavioral data recording were enabled via the Unity3D platform (Unity Technologies, San Francisco, CA, USA; version 4.6.9), using custom C#-programmed routines to facilitate timing accuracy and sending triggers via parallel port to the EEG amplifier. The same experimental code was used in all viewing conditions to present the visual and tactile stimuli. Integration with the HMD was achieved using the Oculus Unity Integration Package (Oculus VR, Irvine, CA, USA; version 0.4.3). Finally, all conditions were presented using the same Intel desktop PC, which ran Windows 7.

EEG Recording and Preprocessing

A QuickAmp amplifier (Brain Products GmbH, Gilching, Germany) recorded the EEG at 1,000 Hz from 32 Ag/AgCl scalp electrodes, which were positioned using an elastic EEG cap (EasyCap GmbH, Herrsching, Germany) on the approximately equidistant electrode sites of the 10% system. The initial recording reference was the common average reference; this was used throughout all preprocessing steps before the data were re-referenced to the linked mastoids (at TP9/TP10) to facilitate a comparison with the P3 and Oddball literature. Horizontal electro-oculographic activity was recorded using bipolar electrodes placed 1 cm to the left and to the right of the outer canthi of the eyes. Vertical electro-oculographic activity was acquired using a similar setup, 1 cm below and above the pupil of the right eye. Offline preprocessing of the EEG and electro-oculographic activity included bandpass filtering in the range $0.2 < \text{Hz} < 40$.

The artifact correction procedure was based on an independent component analysis (ICA) using the Infomax algorithm in EEGLAB (Delorme and Makeig, 2004). The ICA aims to find a linear representation of non-Gaussian data so that the components are statistically as independent as possible (Hyvärinen and Oja, 2000). Since its introduction to EEG data analysis (Makeig et al., 1996), it has become one of the most popular methods of artifact correction. Components are often manually identified as either EEG sources or artifact sources (related to muscles, eye movements, noise, etc.). In the present study, ICA was used to decompose the 3 (condition) × 12 (subject) data sets independently. To reduce the possibility that preconceived notions would influence how the HMD affected the EEG, the classification of components was conducted in a blind manner. Following this, the weights obtained from all non-artefactual components were used to recompute the scalp-level EEG. In the signal-to-noise analysis, the ICA technique with no artifact correction was contrasted with the more traditional, linear-regression-based correction (Gratton et al., 1983). After the artifact correction, EEG was further analyzed using the Brain Vision Analyzer (Brain Products GmbH, Gilching, Germany). This included segmentation into 1 s epochs that were time-locked to the onset of target stimuli, including 200 ms of baseline activity. The baseline was subtracted before a threshold-based artifact-rejection procedure was applied; this involved removing epochs with an absolute amplitude greater than the maximum of 40 μV or with peak differences greater than 60 μV.

Peak Detection and Analysis

The windows of ERP peaks were established separately for somatosensory evoked potentials (SEPs) and visual evoked potentials (VEPs) using the grand-average ERPs at the lateral (C3/4) and midline (Fz, Cz, and Pz) channels. When visually scanning the standardized, lateralized activity, the somatosensory N140 was identified as a negative peak in the contralateral sites from 140 to 170 ms, with $T(11) > 3$. The windows of subsequent

[2]www.leapmotion.com

SEPs and VEPs were based on a visual inspection of the grand-average ERPs and on identification of the local peaks and the zero-crossing points of the grand-average ERP waveform. The resulting windows were averaged over three midline electrodes (Fz, Cz, and Pz) and rounded to the nearest 10 ms interval, yielding three latency windows each for SEPs (P200: 160–310; N200: 280–380; P3: 380–500) and VEPs (P200: 150–260; N200: 200–340; P3: 260–400). Finally, peak-to-peak difference values were calculated for the SEP and VEP N200 and P3 components by subtracting the peak amplitude from the preceding peak value (i.e., N200 – P200 and P3 – N200).

The effects that spatial attention had on ERP peak amplitudes were investigated by conducting full factorial repeated measures ANOVAs for each peak latency window and for each SEP and VEP. ANOVAs were performed using the GLM command of SPSS 23.0. Trials were not included in the analysis if participants responded inaccurately (a difference of 5 or more from the true count). In all ANOVA models, modality relevance (relevant vs. irrelevant), location relevance (relevant vs. irrelevant), channel (Fz vs. Cz vs. Pz), and viewing condition (control vs. VR with hand [VR+H] vs. VR without hand [VR−H]) were set as factors; peak amplitudes or peak-to-peak values were set as dependent variables. As an exception, the ANOVA for the somatosensory evoked N140 was performed on the ERP peak amplitude values obtained at C3/4 site. Also, an additional factor of hemisphere (contralateral vs. ipsilateral) was included in this model because the early somatosensory activity was expected to be stronger at the central sites contralateral to the stimulus side. Visual N1 was not analyzed with ANOVA because there was no control for the lateral eye movements other than asking people to keep their gazes focused on the fixation cross. Peak amplitudes were used as the predicted values, both for early SEPs (N140 and P200) and for VEPs (P200), whereas peak-to-peak values were used for the analysis of subsequent potentials (N2 and P3). Follow-up ANOVAs were conducted separately for each viewing condition in case significant effects of viewing condition or attention were found. Whenever required, Greenhouse-Geisser adjustments for degrees of freedom were performed, and the adjusted *p*-values were reported.

RESULTS

Signal and Noise

To compare the efficacy of obtaining relevance-induced ERP components in the VR conditions with hand (VR+H) and without hand (VR−H), we compared the signal and noise for these conditions with the HMD-free control. For each viewing condition, we calculated the noise as the effect size (in root mean square, RMS) of the relevant (vs. irrelevant) modality in the baseline and the signal as the same comparison except within an area of similar length as the noise interval (but within the P3 window). To show how artifact correction affects these comparisons, we provided the same analyses for three common types of corrective procedures: raw (i.e., no correction), regression (based on Gratton et al., 1983) and ICA (Vigário, 1997).

Historically, artefactual data has been removed from the analysis using visual inspection, but as artifacts (such as ocular artifacts, head movements and muscle twitches) tend to cause extreme voltages, it is now more common to apply a threshold for the absolute amplitude or largest difference value within epochs (see Luck, 2005, pp. 152–170 for the general artifact rejection process). One can assume that if a large percentage of epochs is removed due to crossing said threshold, the data are likely strongly confounded by noise. Similarly, if thresholds are changed to remove no more than a certain proportion of the data, then a high threshold indicates a large quantity of noise.

As shown in **Table 1**, linear regression reduces the number of epochs removed in the artifact rejection and decreases the threshold for removing artifacts. ICA again shows its use (Hyvärinen and Oja, 2000) as a technique to reduce noise, as only 3–5% of trials are removed with a 50-μV absolute threshold, and a threshold of 36–40 μV removes 10% of epochs. More importantly, the HMD was not found to induce noise; in fact, the VR−H and VR+H conditions had fewer trials removed than did the control conditions and generally could use a lower threshold for artifact rejections.

This pattern is to some extent repeated in **Table 2**, which provides the results of the signal and noise ratios (following artifact rejection). In particular, the VEPs, although they were expected to be most affected by the use of the HMD, had a signal that was higher for VR−H and VR+H conditions; the VEPs' noise was also somewhat lower. For the SEPs, the signal in VR−H was similar to that of the control but was somewhat lower in VR+H; the SEPs' noise was lower for VR−H and similar for VR+H. Finally, an examination of the topography images showed that HDM had no systematic influence on the ERPs (see Supplementary Figure 1).

Effects of Spatial Attention on SEPs

Figure 2 shows ERPs elicited by tactile stimuli at both the midline and lateral sites. The figure is separated into three panels, one for each viewing condition (control, VR+H, and VR−H). The left side of each panel shows the SEPs induced by a tactile stimulus when the tactile modality was relevant—that is, when tactile cues had to be counted. The right side shows the SEPs elicited by task-irrelevant tactile stimuli. First, enhanced contralateral negativity was observed in response to task-relevant tactile stimuli presented on the relevant (vs. irrelevant) side at the range of N140. The effect was similar in all viewing conditions but was present only if tactile stimuli had to be counted. N140 was followed by attentional effects in the subsequent P200, N200, and P3 components; enhanced P200 elicited by a task-relevant tactile target was visible in the control and VR+H conditions but not in the VR−H condition. Interestingly, the same effect was also present in SEPs evoked by modality-irrelevant tactile stimuli if they were presented on the relevant side. However, this cross-modal interaction was mainly present in the VR+H condition. P200 was followed by enhanced attentional negativity in the range of N200. When tactile stimuli had to be counted, the N200 was most enhanced in response to tactile stimuli shown on the irrelevant side. However, if the task was to count visual stimuli, task irrelevant tactile stimuli shown on the relevant side

TABLE 1 | Artifact rejection.

	Epochs removed (%) above 50 μV			Threshold (μV) removing > 10%		
	Control	**VR−H**	**VR+H**	**Control**	**VR−H**	**VR+H**
Raw	43.90 (9.21)	27.79 (6.00)	30.63 (6.22)	87.00 (12.08)	64.67 (5.98)	69.42 (7.42)
Regression	26.23 (8.89)*	19.81 (5.28)*	25.42 (6.79)*	67.92 (11.28)	56.42 (5.55)*	73.50 (14.78)
ICA	5.44 (2.13)***	3.25 (1.99)***	2.75 (1.24)***	39.83 (2.89)**	36.67 (2.63)***	37.58 (1.91)**

*Artifact rejection as a function of the artifact correction procedure and the experimental condition: Control, VR without hands (VR−H) and VR with hands (VR+H). *p < 0.05, **p < 0.01, ***p < 0.001.*

TABLE 2 | Signal and noise ratios.

VEPs	Signal: RMS (REL-IRR [280, 480])			Noise: RMS (REL−IRR [−200, 0])		
	Control	**VR−H**	**VR+H**	**Control**	**VR−H**	**VR+H**
Raw	2.74 (0.39)	3.20 (0.46)	3.56 (0.56)	0.99 (0.20)	0.82 (0.06)	0.80 (0.05)
Regression	2.40 (0.24)	2.99 (0.47)	3.36 (0.55)	0.71 (0.07)	0.75 (0.07)	0.78 (0.11)
ICA	2.08 (0.19)*	2.34 (0.54)*	2.81 (0.41)*	0.64 (0.06)	0.63 (0.07)**	0.58 (0.05)**
SEPs	**Signal: RMS (REL−IRR [350, 500])**			**Noise: RMS (REL-IRR [−200, 0])**		
Raw	2.62 (0.51)	2.67 (0.42)	2.32 (0.39)	0.95 (0.14)	0.74 (0.07)	0.86 (0.08)
Regression	2.32 (0.50)	2.57 (0.42)	2.26 (0.41)	0.68 (0.08)	0.65 (0.07)*	0.97 (0.20)
ICA	2.06 (0.35)	1.93 (0.35)*	2.08 (0.36)	0.65 (0.07)	0.57 (0.10)	0.73 (0.09)*

*Signal calculations using the root mean square (RMS) of the difference between relevant (REL) and irrelevant (IRR) conditions at the P3 interval; the noise (as RMS) for the same conditions around the baseline; and the signal-to-noise ratio (SNR). The table shows the effects of the artifact correction procedure for each of the three conditions of bodily presence: Control, VR without hands (VR–H) and VR with hands (VR+H). The difference of artifact corrections was tested with a series of t-tests contrasting the Raw condition to the Regression and ICA. *p < 0.05, **p < 0.01, ***p < 0.001.*

caused the strongest decline, but the effect was again mainly present in the VR+H condition. Finally, a clear P3 component was observed, with the strongest positivity found at the Pz channel. The P3 was clearly present when the tactile stimuli had to be counted but was almost completely absent when the tactile modality was task irrelevant. Contrary to preceding components, no clear differences were found between the viewing conditions.

Supporting the observations of the early negative component, significant main effects of modality relevance, $F(1,11) = 13.38$, $p = 0.004$, $\eta_p^2 = 0.55$, location relevance, $F(1,11) = 7.15$, $p = 0.022$, $\eta_p^2 = 0.39$, and hemisphere, $F(1,11) = 21.99$, $p = 0.001$, $\eta_p^2 = 0.67$, were found in the N140 latency window. The N140 was most enhanced at the sites contralateral to stimulus location and showed stronger negativities in response to modality-relevant tactile stimuli. The significant effect of location relevance indicated that stimuli sent to the irrelevant location resulted in larger N140. Further ANOVAs calculated separately for each hemisphere revealed that modality relevance affected similarly the N140 obtained from the contralateral, $F(1,11) = 14.83$, $p = 0.003$, $\eta_p^2 = 0.57$, and ipsilateral sides, $F(1,11) = 7.60$, $p = 0.019$, $\eta_p^2 = 0.41$, but the effect of location relevance was only present on the ipsilateral side, $F(1,11) = 10.39$, $p = 0.019$, $\eta_p^2 = 0.41$. Although no main or interaction effects of viewing condition were found (ps > 0.076), follow-up ANOVAs conducted separately for each viewing condition revealed that modality relevant tactile stimuli resulted in enhanced N140 both in the control and VR+H conditions (ps < 0.05, η_p^2s > 0.31) but not in the VR–H condition ($p = 0.09$).

In the range of P200, we observed significant effects of location relevance, $F(1,11) = 9.69$, $p = 0.010$, $\eta_p^2 = 0.47$, and channel, $F(1,11) = 12.32$, $p < 0.001$, $\eta_p^2 = 0.53$, indicating increased positivity evoked by tactile stimuli presented at the relevant location. As shown in **Figure 2**, somatosensory P200 was similarly affected by location relevance, regardless of modality relevance. The ANOVA results supported this observation, revealing no effect of modality relevance, $F(1,11) = 1.66$, $p = 0.23$. Based on visual inspection, P200 seemed to be most enhanced in the VR+H condition. In contrast, no main or interaction effects of viewing condition were found (ps > 0.17). However, conducting the follow-up ANOVAs separately for each viewing condition revealed a significant effect of side in the VR+H condition, $F(1,11) = 6.66$, $p = 0.026$, but not in the control ($p = 0.06$) or VR−H condition ($p = 0.20$).

Investigating the peak-to-peak difference between P200 and N200 revealed significant effects for the modality relevance, $F(1,11) = 6.48$, $p = 0.027$, $\eta_p^2 = 0.37$; channel, $F(1,11) = 12.12$, $p < 0.001$, $\eta_p^2 = 0.52$; and modality relevance × location relevance interaction, $F(1,11) = 19.02$, $p = 0.001$, $\eta_p^2 = 0.63$. This reflects the strongest negativity for modality-irrelevant tactile stimuli presented at the target location. A significant three-way interaction of modality relevance, location relevance, and channel, $F(2,22) = 4.31$, $p = 0.026$, $\eta_p^2 = 0.28$, revealed that the attentional modulation was particularly strong at Fz and Cz. Finally, a modality relevance × location relevance × channel × viewing condition interaction,

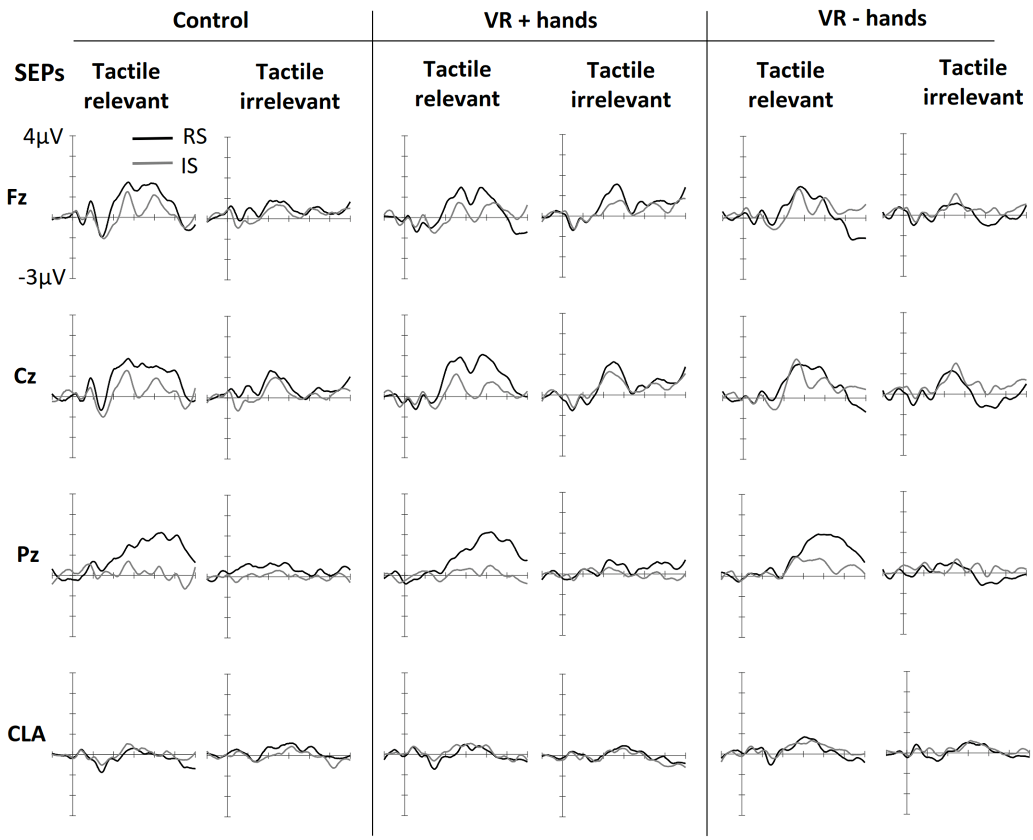

FIGURE 2 | Grand averaged somatosensory evoked potentials (SEPs) elicited in three conditions of bodily presence (Control, VR+hands, and VR−hands) and obtained at midline (Fz, Cz, and Pz) and contralateral C3/4 sites (CLA). Black lines represent SEPs elicited by side-relevant (RS) tactile stimuli, and gray lines represent SEPs elicited by side-irrelevant (IS) tactile stimuli. In each column, the left side shows SEPs elicited by stimuli from the task-relevant modality whereas the right side plots present SEPs elicited by stimuli from task-irrelevant modalities.

$F(1.86,20.43) = 4.34$, $p = 0.029$, $\eta_p^2 = 0.28$, revealed that the effect of spatial attention on frontal N200 was particularly enhanced in both the control and VR+H conditions; it was not present in the VR−H condition. The same effect is presented in **Figure 3**, which also shows that modality-irrelevant tactile stimuli presented on the relevant side caused N200's attentional enhancement. This attentional negativity occurs in both the control and VR+H condition but reaches significance only in the VR+H condition, $F(2,22) = 5.79$, $p = 0.010$, $\eta_p^2 = 0.34$.

In the range of P3, we found a significant main effect of viewing condition, $F(2,22) = 4.76$, $p = 0.019$, $\eta_p^2 = 0.30$, suggesting that the control and VR+H conditions induced more enhanced P3 activity than did the VR−H condition regardless of spatial attention. No other main effects were found. However, in line with the pattern shown in **Figure 2**, we found that attention was enhanced in P3 only when participants were instructed to count tactile stimuli, $F(1.26,13.84) = 15.15$, $p = 0.001$, $\eta_p^2 = 0.58$. This target-related positivity was particularly present at central sites, as reflected by a modality relevance × location relevance × channel interaction, $F(1.27,14.01) = 7.78$, $p = 0.011$, $\eta_p^2 = 0.41$. Viewing condition did not affect the attentional modulation of the P3 component (ps > 0.10).

Effects of Spatial Attention on VEPs

Figure 4 shows ERPs elicited by visual stimuli in three viewing conditions (one panel for each) and measured at three midline sites. The left side of each panel shows ERPs elicited by visual stimuli when the visual stimuli were modality-relevant. The right side shows the VEPs elicited by visual stimuli when the visual modality was irrelevant and tactile stimuli had to be counted. Visual targets elicited larger N1 components at frontal midline sites. The effect was similar for all viewing conditions. N1 was followed by attention-related positivity in the range of 150–260 ms post stimulus. The P200 was most enhanced at posterior sites and in vision-relevant stimulus conditions. No clear difference between viewing conditions was perceived. P200 was followed by attention-related negativity between 200 and 340 ms and was most enhanced at the central site. Similarly to SEPs, modality-relevant visual stimuli presented on the irrelevant side and modality-irrelevant visual stimuli presented on the relevant side resulted in the strongest N200. The pattern was the same in all three viewing conditions, although the decline was strongest in the VR+H condition. Finally, in the range of 260–500 ms, we found a P3 component with strongest positivity at the Pz channel. As with SEPs, the P3 was again more strongly

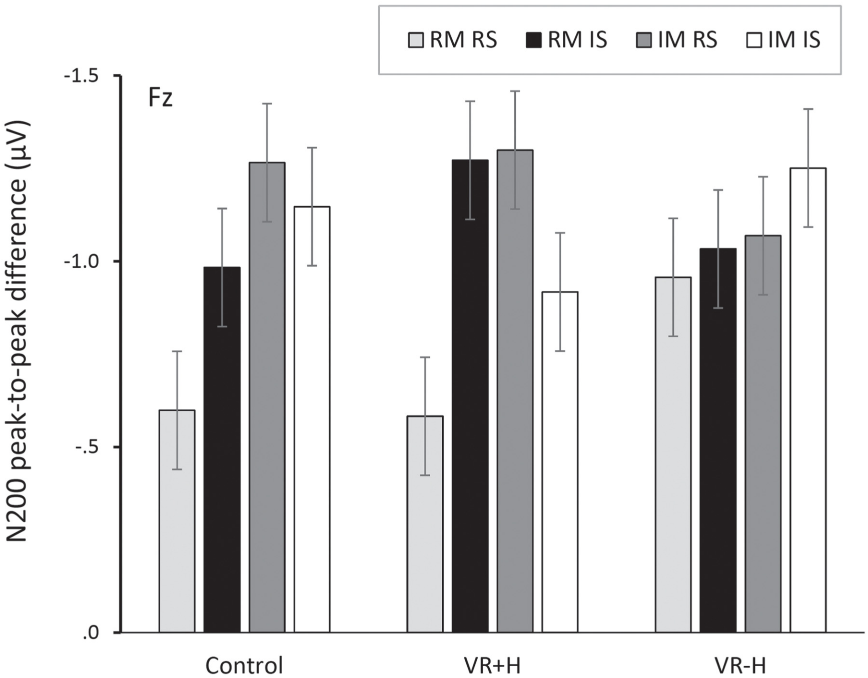

FIGURE 3 | Peak-to-peak difference between P200 and N200, presented as a function of viewing condition (VR+H vs. VR−H vs. HMD-free control), modality relevance [relevant modality (RM) vs. irrelevant modality (IM)] and location relevance [relevant side (RS) vs. irrelevant side (IS)]. The figure shows that both modality-relevant and modality-irrelevant tactile stimuli, when presented on the relevant side, are related to enhanced negativity in the range of N200. This attentional negativity occurs both in the control and the virtual-hands conditions.

present in visual-relevant stimulus conditions when compared to the visual-irrelevant condition. However, in the control and VR+H conditions, a small P3 component was observed resulting from modality-irrelevant stimuli shown on the irrelevant side.

ANOVAs revealed a significant main effect of modality relevance, $F(1,11) = 15.67$, $p = 0.002$, $\eta_p^2 = 0.59$, indicating an enhancement in P200 in response to the visual stimuli when the visual modality was relevant. A main effect of viewing condition was also found, $F(2,22) = 4.31$, $p = 0.026$, $\eta_p^2 = 0.28$, implying that more enhanced P200 amplitudes occurred in the control condition rather than in the VR condition. This effect was accompanied by a significant location relevance × channel × bodily presence interaction, $F(4,44) = 2.93$, $p = 0.031$, $\eta_p^2 = 0.21$, suggesting that the visual stimuli presented on the cued side resulted in enhanced positivity at the posterior site and that this effect was stronger in the VR+H condition than in the VR−H condition—and was totally absent in the control condition.

No significant main effects of modality relevance or location were found in the N200 range when subtracted from the previous P200 peak, $F(1,11) < 1.08$, $ps > 0.32$. However, main effects were found for viewing condition, $F(2,22) = 5.36$, $p = 0.013$, $\eta_p^2 = 0.33$, and channel, $F(2, 22) = 8.05$, $p = 0.002$, $\eta_p^2 = 0.42$. These effects were accompanied by a significant viewing condition × channel interaction, $F(4,44) = 4.20$, $p = 0.006$, $\eta_p^2 = 0.28$, indicating enhanced negativity at the central sites. This negativity was particularly pronounced in the control condition regardless of the modality or side. Modality relevance was also found to affect N200, but the effect was opposite at the frontal and parietal sites, $F(2,22) = 17.41$, $p < 0.001$, $\eta_p^2 = 0.61$. Furthermore, we found particularly strong negativities for task-relevant visual stimuli presented on the irrelevant side and modality-irrelevant visual stimuli shown on the relevant side, $F(1,11) = 5.71$, $p = 0.036$, $\eta_p^2 = 0.34$. This modality relevance × location relevance interaction was most evident in the central and parietal midline electrodes, $F(2,22) = 16.81$, $p < 0.001$, $\eta_p^2 = 0.60$. Unlike SEPs, viewing condition did not affect this attentional modulation ($ps > 0.19$). Further ANOVAs conducted separately for each viewing condition confirmed this finding reveals a significant three-way interaction of modality relevance, location relevance interaction, and channel in all three conditions ($ps < 0.12$).

Finally, both modality relevance, $F(1,11) = 11.21$, $p = 0.006$, $\eta_p^2 = 0.51$, location relevance, $F(1,11) = 11.83$, $p = 0.006$, $\eta_p^2 = 0.36$, and channel, $F(1.55,17.02) = 6.25$, $p = 0.013$, $\eta_p^2 = 0.36$, were found to affect P3. Presenting a visual, task-relevant stimulus on the relevant side resulted in the strongest positivity, whereas no difference between the relevant and irrelevant sides was found when the tactile stimuli had to be counted, $F(1,11) = 9.50$ $p = 0.010$, $\eta_p^2 = 0.46$. This interaction effect was accompanied by a three-way interaction between modality relevance, location relevance, and channel, $F(1.27,13.95) = 5.15$, $p = 0.033$, $\eta_p^2 = 0.32$, indicating that the aforementioned effect was particularly pronounced at the central and parietal midline sites. Similarly to SEPs, viewing condition

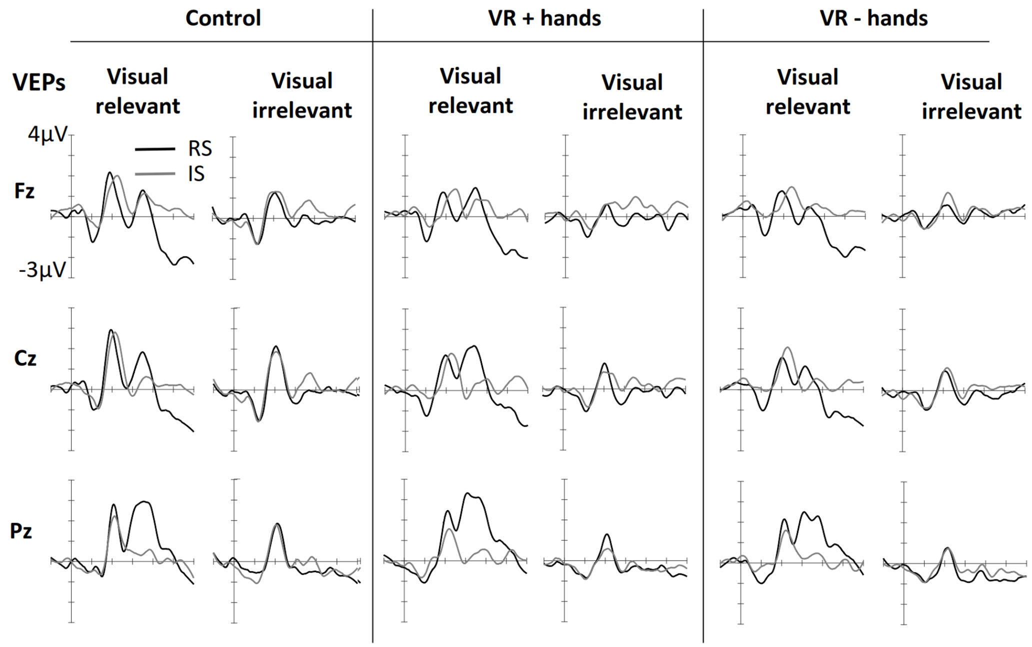

FIGURE 4 | Grand averaged VEPs elicited in three conditions of bodily presence (Control, VR+hands, and VR−hands) obtained at midline sites. Black lines represent VEPs elicited by side-relevant (RS) visual stimuli, and gray lines represent VEPs elicited by side-irrelevant (IS) visual stimuli. In each column the left side shows VEPs elicited by visual stimuli when the tactile modality was relevant whereas the right side plots present VEPs elicited by stimuli arising from the irrelevant modality.

did not affect the attentional modulation of visually evoked P3 (*p*s > 0.22).

DISCUSSION

Although the visual enhancement of tactile attention has been demonstrated both with behavioral and neurophysiological recordings (e.g., Longo et al., 2008), the neural underpinnings of body-induced cross-modal interference have remained unclear. Thus, the present ERP study investigated whether viewing one's real or virtual hands modulates visuo-tactile interaction in endogenous spatial attention at different levels of visual and somatosensory processing. For this purpose, a bimodal oddball task with tactile and visual stimuli was performed under three different viewing conditions: VR with hands, VR without hands, and VR-free control with real hands visible. Based on the previous findings, we assumed the presence of hands would influence attentional modulation of visual and tactile ERPs at both the sensory-perceptual stage (N1, P200) and later, post-perceptual, stages (N200, P3).

Effect of Bodily Presence on Sensory-Perceptual Processing

As described earlier, attending to a certain spot or stimulus modality potentiates early sensory processing of the attended stimuli (Hillyard et al., 1998a; Hötting et al., 2003) and focusing on the left or right tactile stimuli enhances early visual processing if the visual cue is presented on the attended side (Eimer, 2001). These so-called intramodal, intermodal, and cross-modal spatial modulations were also found in the present study. First, for somatosensory ERPs, an early attentional negativity was obtained at the range of the N140 component. As an example of intermodal attentional modulation, this early negativity was found to be more enhanced in response to modality-relevant tactile stimuli. The amplitude of N140 differed also in terms of stimulus location. Tactile stimuli presented on the irrelevant side resulted in greater negativity than those presented on the relevant side. This effect occurred regardless of the attended modality and was mainly present at the ipsilateral electrodes. In VEPs, the N1 component has been shown to be responsive to task-irrelevant visual stimuli if shown on the attended side. However, in SEPs such an effect does not usually occur, which has been suggested to indicate that, contrary to other modalities, touch can be decoupled from cross-modal attention when being task-irrelevant (Eimer and Driver, 2000). This decoupling was not observed in the current data given that the somatosensory N140 obtained at ipsilateral sites was similarly enhanced in the tactile relevant and irrelevant trials.

More importantly, we found that attentional enhancement of N140 occurred only if the participants could see their real or virtual hands resting on the table. This so-called VET effect has also been found in earlier studies (e.g., Longo et al., 2008; Sambo et al., 2009). However, in these studies the visual body cues were shown to affect spatial attention whereas in the present study seeing one's hands modulated mainly the intermodal selection (i.e., effects of modality relevance). Although unclear, the contrasting finding may be due to differences in the tasks and target stimuli.

In the range of somatosensory P200, we observed that tactile stimuli presented on the relevant side elicited larger P200 both in tactile and visual relevant trials. This cross-modal interaction in spatial attention was also present in visual P200. Further ANOVAs revealed that the attentional modulation of tactile and visual P200 occurred mainly when virtual or real hands were present, suggesting that the hands made participants more sensitive to both modality-relevant and -irrelevant visual stimuli when presented on the attended side. It is unclear, however, why in VEPs the effect was only present in the VR+H condition but was not found in the control condition, in which participants could also see their hands lying on the table. One reason for this could be the novelty of the 3-D arms, which caused participants to pay more attention to their new limbs than they would to their real hands when seeing them resting on the table. Another explanation is that the vertical distance between tactile and visual cues was slightly different in the VR and HMD-free condition. In correlation to the second explanation, researchers using single-cell recordings from non-human primates have revealed populations of neurons in the parietal region, premotor area, and putamen responding similarly to tactile stimulus presented on the hand and visual stimulus shown near the hand (Graziano and Gross, 1993; for a review, see Reed et al., 2006). Presenting visual stimulus farther away from the hands results in attenuated firing in the neurons (Graziano and Gross, 1995). These body-centered multisensory representations have been suggested to underlie the effects of bodily presence on tactile-spatial selective processing (Sambo et al., 2009), but they can also explain why in the current study the presence of hands enhanced attentional modulation of visual-evoked P200.

Effect of Bodily Presence on Post-perceptual Processing

Based on the findings of Pavani et al. (2000), we suggested that seeing one's hands would make the tactile non-targets more distracting, and thus lead to response inhibition indexed by an enhanced N200 component (Azizian et al., 2006). This was exactly what we found. Participants responded with more negative N200 to tactile distractors when they either arose from the same modality or were presented on the same side as the target. This effect was stronger in the VR hands and control conditions than in the VR no-hands condition. Contrary to the expectations, the presence of hands had no effect on visual-evoked N200. Despite this, visual N200 was likewise more sensitive to target-like distractors, indicating an inhibitory role similar to what was observed in SEPs. Thus, although visual target-like distractors also resulted in enhanced response inhibition in VEPs, no extra inhibitory effort was required when (virtual or real) hands were present. The observed discrepancy between visual and tactile N200 is interesting as it shows that visual input of one's body affects the tuning of tactile spatial attention more strongly than it affects the tuning of visual spatial attention. The finding is important as it confirms and extends previous ERP evidence which suggests that visual body rather than ambient visual information (e.g., the lab environment) is used for remapping tactile stimuli (Sambo et al., 2009). Also, in addition to earlier ERP evidence, here we show how the presence of body affects not only the sensory-perceptual processes but also later executive function.

Finally, we sought to investigate whether bodily presence would influence late attention and memory-related processing. Contrary to preceding components, both visual and tactile P3 were selectively responsible only to target stimuli. Also the viewing condition affected P3, although only in SEPs. The attentional modulation at the P3 range was, however, no different between viewing conditions, suggesting that both target and non-target tactile stimuli resulted in enhanced P3 if the hands were shown. The finding of P3's selective responsiveness is in line with earlier literature showing that cross-modal interaction in spatial attention is dismissed at the later ranges (Eimer, 2001).

To sum up, the present study was able to show that bodily presence modulates cross-modal spatial attention. This modulation appears mainly between early (N140) and late sensory-perceptual processing (P200) and subsequent inhibition-related processes (N200) but is absent in the later attention- and memory-related P3 component. However, the relatively small sample size and numerous estimated ANOVA models increase the risk of type 1 error; therefore, replications are required to draw more solid conclusions. On the other hand, many recent studies are consistent with the obtained findings. For example, evidence from various behavioral, ERP, and imaging studies has demonstrated that seeing one's stimulated body part amplifies early somatosensory processing (Macaluso et al., 2000; Longo et al., 2008; Sambo et al., 2009). Our observation that somatosensory processing is affected and visual-evoked potentials are modulated by bodily presence is likewise in line with earlier findings (Graziano and Gross, 1993, 1995). To our knowledge, there is no earlier ERP evidence showing that bodily presence has an amplifying effect on response inhibition in the context of cross-modal spatial attention tasks. Thus, the current findings confirm and extend previous evidence for the role of visual body in endogenous spatial attention.

Opportunities and Challenges for Future VR-EEG Research

Besides investigating the effect of spatial attention on SEPs and VEPs, we ensured the reliability of ERPs obtained in VR conditions with signal-to-noise-ratio (SNR) analyses. Comparing the SNRs of viewing conditions, we were able to show that the VR conditions had a stronger P3 signal and less noise than what was observed in the HMD-free control condition. The finding was surprising as we assumed that HMD would induce electrical interference in the EEG signal. However, it seems that the higher SNR in the VR conditions could be due to more restricted head movements and ocular artifacts. That is, in the control condition, participants were not wearing the display, which might have encouraged them to move more freely, whereas in the VR condition, their movements were more limited due to the substantial number of cables. Altogether, HMD did not adversely affect the ERPs, which implies that current commercially available VR headsets can safely be used in ERP research without compromising the reliability of EEG recordings.

In future, the EEG-VR research can be utilized in more complex settings. There are, however, some practical limitations that we would like to point out. The HMDs' immersive visual experience is in part caused by occluding the user's vision of the peripheral environment. Despite the benefits of this, occluding also causes increased simulator sickness (Moss and Muth, 2011). Such simulator sickness has long slowed down the diffusion of HMD technologies. The new wave of HMDs promises to eliminate the symptoms by expanding the field of view, but some users still feel nausea and have headaches after extended use (Moss and Muth, 2011). Given that EEG experiments normally last for more than an hour, it is possible that such symptoms may appear. However, as a subtype of motion sickness, simulator sickness is highly dependent on the user's movements (Merhi et al., 2007). Given that, in most cognitive neuroscience experiments, the participants are encouraged to keep still rather than move around, the risk of simulator sickness remains low. In the present study, only one participant reported feeling mild nausea at the end of the experiment. If, however, constant movements are required, the risk of nausea will exist, and that risk should be taken into account when designing the study.

In ordinary experimental paradigms, the potential of VR simulations is nevertheless evident. This has long been acknowledged among cognitive scientists, who have found virtual environments to be particularly useful in research on body-related processes (e.g., Slater et al., 2009; for a review, Blanke, 2012). Virtual versions of the Rubber Hand Illusion have, for instance, revealed how the integration of tactile, visual, and proprioceptive cues is integral to the feeling that our body belongs to us (Sanchez-Vives et al., 2010; Ma and Hommel, 2013). So far, however, the VR-based research on body representation has mainly relied on behavioral and autonomic measures (Sanchez-Vives et al., 2010; Slater et al., 2010; Ma and Hommel, 2015). Additionally, more attention has been paid to how sensory body cues affect body representation than to how perceiving the body influences perception of the extracorporeal world (Harris et al., 2015). Here, we demonstrate how seeing one's body modifies the cross-modal attentional system and associated electrophysiological features. In future, the same VR-EEG approach can be used to better understand the influences that the body has on more complex cognitive processes, such as self-body relations and out-of-body experiences.

ETHICS STATEMENT

This study was carried out in accordance with the recommendations of guidelines issued by the National Advisory Body on Research Ethics in Finland with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the Ethics Review Board of Aalto University.

AUTHOR CONTRIBUTIONS

VH collected the data, conducted the analyses, and wrote the manuscript. IA designed and created the 3-D environment, programmed the experiment, and assisted in writing the manuscript. GJ contributed to writing the manuscript. NR was involved in the study design and contributed to the writing. MS designed the study and contributed to the analyses, data interpretation, and manuscript drafting. All authors approved the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fnhum.2017.00079/full#supplementary-material

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Altered Sense of Body Ownership and Agency in Posttraumatic Stress Disorder and Its Dissociative Subtype: A Rubber Hand Illusion Study

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Traumatic experiences have been linked to the development of altered states of consciousness affecting bodily perception, including alterations in body ownership and in sense of agency, the conscious experience of the body as one's own and under voluntary control. Severe psychological trauma and prolonged distress may lead to posttraumatic stress disorder (PTSD). Together, symptoms of derealization and, related specifically to the sense of body ownership and agency, of depersonalization (where parts of the body or the entire body itself is perceived as detached and out of control), constitute the dissociative subtype (PTSD+DS). In this study, we explored the Rubber Hand Illusion, an experimental paradigm utilized to manipulate sense of body ownership in PTSD ($n = 4$) and PTSD+DS ($n = 6$) as compared to healthy controls ($n = 7$). Perceived finger location and self-report questionnaires were used as behavioral and subjective measures of the illusion, respectively. In addition, the correlation between the illusion's effect and sense of agency as a continuous feeling of controlling one's own body movements was explored. Here, a lower illusion effect was observed in the PTSD as compared to the control group after synchronous stimulation for both the proprioceptive drift and subjectively perceived illusion. Moreover, by both proprioceptive drift and by subjective ratings, the PTSD+DS group showed a response characterized by high variance, ranging from a very strong to a very weak effect of the illusion. Finally, sense of agency showed a trend toward a negative correlation with the strength of the illusion as subjectively perceived by participants with PTSD and PTSD+DS. These findings suggest individuals with PTSD may, at times, maintain a rigid representation of the body as an avoidance strategy, with top-down cognitive processes weakening the impact of manipulation of body ownership. By contrast, the response elicited in PTSD+DS appeared to be driven by either an increased vulnerability to manipulation of embodiment or by a dominant top-down cognitive representation of the body, with disruption of multisensory integration processes likely in both cases. Taken together, these findings further our understanding of bodily consciousness in PTSD and its dissociative subtype and highlight the supportive role played by sense of agency for the maintenance of body ownership.

Keywords: body ownership, sense of agency, PTSD, dissociation, rubber hand illusion

INTRODUCTION

Conscious experience of the self is a complex phenomenon that assumes a bodily representation of the self, including thoughts, feelings, and actions (Damasio, 1994; Gallagher, 2000, 2013). Here, the representation of the body in humans has been described as multidimensional, involving both "bottom-up" multiple sensory inputs (vision, touch, and proprioception) and "top-down" conceptual representations of the body (Tsakiris and Haggard, 2005; Longo et al., 2008). The integration of low-level sensorimotor processes coherent with top-down meta-representations of the body is thought to lead an individual to experience a comprehensive and ongoing bodily experience (Balconi, 2010) and has been associated with body ownership, the sense of the body as belonging to the self (Ghallager, 2000; Tsakiris, 2010). Moreover, the self-consciousness of having/owning a body comprises not only a sense of ownership but also the sense of agency over one's own body, two components crucial to building a sense of bodily self-consciousness (Longo et al., 2008; Serino et al., 2013). Critically, embodiment, the self-awareness of being located in one's own body (Longo et al., 2008; Lewis and Lloyd, 2010), has been described as compromised in both neurological and psychiatric conditions (Kenna and Sedman, 1965; Alper et al., 1997; Baker et al., 2013), including in posttraumatic stress disorder (PTSD; Ataria, 2015; Frewen and Lanius, 2015; Lanius, 2015; Rabellino et al., 2016), a psychiatric disorder following the experience of severe and/or multiple psychological trauma.

PTSD includes re-experiencing, avoidance, hyperarousal symptoms, and negative alterations in mood and cognition, symptoms that often have bodily manifestations, including bodily distress and activation of bodily defensive actions such as fight-and-flight responses. These symptoms suggest a link between high-level and low-level cognitive/sensory mechanisms. Bottom-up multisensory processing is thought to be particularly involved during re-experiencing and hyper-arousal symptoms, where the traumatic event is relived as if it were re-occurring at the present moment with concurrent bodily perceptions and reactions. By contrast, avoidance symptoms have been linked to a top-down over-modulation of emotional reaction and to a coping style characterized by active avoidance of trauma reminders and potential triggers, as well as emotional detachment/restricted affect (such as emotional numbing, often associated with alexithymia; Frewen et al., 2008, 2012; Lanius et al., 2010; APA, 2013).

Critically, a dissociative subtype of PTSD (PTSD+DS) has been added recently to the DSM-5 (APA, 2013) and is characterized by derealization (feeling that one's external surroundings are unreal, dreamlike, or distorted) and depersonalization, symptoms that target specifically alterations in body ownership (feeling detached from the body and that part of or the whole body is not one's own; Lanius et al., 2012; Spiegel et al., 2013). Depersonalization symptoms in PTSD may represent a unique opportunity to investigate the phenomenology of body ownership and agency, where the detachment from one's own body leads the individual to experience a failure of the perceptual integrated self (Spiegel et al., 2013). Depersonalization symptoms can be characterized by partial disembodiment (or partial loss of body ownership), where part of the body (e.g., a hand or a foot) is experienced as "non-self," namely alien, not one's own, as well as by full disembodiment (or complete loss of body ownership), where the whole body is felt as "non-self" (Sierra and David, 2011; Frewen and Lanius, 2015).

Furthermore, individuals that develop PTSD may experience a weakened sense of agency (Ataria, 2015), where impairment of intentional control over one's own movements occurs, with consequent feelings of helplessness. During trauma, the loss of agency can be experienced as loss of control because someone else is controlling the subject's body movements (e.g., in the case of rape or torture). In addition, an extreme loss of agency can be experienced when an individual feels unable to voluntarily control his/her own body as occurs, for example, during freezing states (Herman, 1992; Ataria, 2015). During freezing states, which can be a form of death feigning in order to protect the individual from a predator during the traumatic event, the individual experiences extreme fear, muscle tension, and an inability to move, with dual activation of the sympathetic and parasympathetic nervous system (Schauer and Elbert, 2010; Kozlowska et al., 2015).

As described above, sense of body ownership and sense of agency represent two dissociable aspects of embodiment and self-consciousness (Tsakiris et al., 2007; Balconi, 2010; Kalckert and Ehrsson, 2012) that also appear to share a close interaction. Indeed, both afferent peripheral signals and efferent bodily movements contribute to bodily ownership, as agency has been proposed to contribute to building the sense of bodily ownership (Tsakiris et al., 2006). Their reciprocal interplay, however, is yet to be completely understood (Dummer et al., 2009; Kalckert and Ehrsson, 2012; Burin et al., 2015).

Given the relation between PTSD symptomatology and disturbances in bodily self-consciousness, the objective of the current study was to explore the phenomenology of body ownership alterations and loss of agency via the Rubber Hand Illusion (RHI) paradigm. The RHI manipulates visual, tactile, and proprioceptive inputs from one's hidden hand through synchronous brushing of the hidden real hand and a plausible visible rubber hand. The illusion temporarily alters the sense of ownership of the hidden hand, where the rubber hand seems to substitute for the real hand in the subjective representation of the body (Botvinick and Cohen, 1998; Ehrsson et al., 2004). The RHI procedure therefore provides an ideal paradigm for the manipulation and investigation of body ownership and its alterations in individuals with dissociative symptoms. A case study with participants diagnosed with the dissociative subtype of PTSD showed a strong illusion effect of the RHI task, with associated alterations in body ownership and temporary exacerbation of depersonalization and derealization during the task (Rabellino et al., 2016). Critically, however, investigations comparing PTSD with and without the dissociative subtype and healthy controls are currently lacking.

We hypothesized that PTSD individuals with the dissociative subtype (PTSD+DS) would show a significantly stronger effect of the illusion, with relative alterations in the sense of body ownership as compared to healthy controls. We were also interested in exploring possible differences in the effects on body ownership between the two PTSD groups (PTSD vs. PTSD+DS). Here, whereas avoidance symptoms characterizing the PTSD group were expected to induce a more rigid top-down representation of the body aimed at avoiding any possible manipulation (a potential trigger), depersonalization symptoms characterizing the PTSD+DS group were expected to result in flexible and more easily alterable body representation (Sierra and David, 2011; Frewen and Lanius, 2014, 2015) linked to a stronger illusion effect of the RHI. Moreover, we hypothesized that an initial weaker sense of agency, here interpreted as the continuous feeling that one's own body is under one's own control (Haggard and Chambon, 2012), would show a significant correlation with the strength of the illusion induced by the RHI paradigm in individuals with PTSD. In summary, our study objectives were to investigate: (a) body ownership in PTSD during the RHI; (b) body ownership in the dissociative subtype of PTSD during the RHI; and (c) the correlation between body ownership and sense of agency in the whole PTSD sample.

MATERIALS AND METHODS

Participants

Four participants with a primary diagnosis of PTSD (PTSD) and six participants with a diagnosis of PTSD with the dissociative subtype (PTSD+DS) were enrolled through community advertisement in London, ON, Canada. Seven healthy controls (HC) were enrolled through community advertisement in Turin, Italy. Whereas the Structured Clinical Interview for DSM-IV Axis I disorders [SCID-I; First et al., 2000, 2002 (Italian edition)] was administered to assess the participants for psychiatric disorders, PTSD symptom severity was assessed through the Clinician Administered PTSD Scale for DSM-4 and for DSM-5[1] (CAPS-4, Blake et al., 1995; CAPS-5, Weathers et al., 2013; cut-off score ≥50 for CAPS-4 and criteria met for CAPS-5). The two CAPS items on depersonalization (measuring persistent or recurrent experience of feeling detached from one's mental processes or body) and derealization (measuring persistent or recurrent experience of unreality of surroundings) were utilized to identify PTSD participants that met criteria for the dissociative subtype (on CAPS-4 individual item scores range is 0–4 on two separate subscales—frequency of the experience and intensity of the experience -; when the total score frequency + intensity ≥4, the participant was included in the dissociative subtype of PTSD group; on CAPS-5 individual item scores range is 0–4 on a single scale, when the score was ≥2, the participant was included in the dissociative subtype of PTSD group) as per standard methods (Weathers et al., 1999; Rabellino et al., 2015). Dissociative symptomatology was further assessed with the Multiscale Dissociation Inventory (MDI; Briere, 2002), a 30-item self-report questionnaire that measures dissociative symptoms (disengagement, depersonalization, derealization, emotional constriction, memory disturbance, and identity dissociation), and the Structured Clinical Interview for Dissociative Disorders (SCID-D; Steinberg et al., 1993), designed specifically to assess dissociative symptomatology (depersonalization, derealization, and amnesia). Participants with a diagnosis of psychosis, bipolar disorder, significant medical or neurologic conditions, history of head injury (loss of consciousness), and/or alcohol or substance abuse not in sustained full remission were excluded. HC had no current history of psychiatric disorder or neurological injury. All participants were right-handed (Oldfield, 1971). The study was approved by the Health Sciences Research Ethics Board of Western University, Canada, and by the local Bioethical Committee from University of Turin, Italy, and all participants provided informed written consent.

Materials

As described in Rabellino et al. (2016) and following standard procedures (Burin et al., 2015), the RHI task was performed using a black box (60 × 40 × 20 cm) divided in half (30 × 40 × 20 cm) by a perpendicular panel. One half of the box (where the participants inserted their own hand) was covered in order to hide the participant's real hand from view and to allow a view of the life-like rubber hand (positioned in the other half) only. Participants wore a cape to ensure that only the rubber hand was in view, while the alignment of the rubber hand with the participant's shoulder rendered the rubber hand position plausible, closer to the body midline with respect to the real participant's hand. Either the real or the rubber hand were positioned to point fingers forward and to face palms down, while an approximate distance of 15 cm separated the real and the rubber hand. An illustration of the setting is provided in **Figure 1**.

The procedure consisted of brushing synchronously vs. asynchronously the index finger of the rubber hand and the real dominant hand (right hand for all participants) during two consecutive 2-minute trials (Costantini and Haggard, 2007; Ocklenburg et al., 2011). The trial order (synchronous vs. asynchronous) was counterbalanced between participants.

[1] Depending on time of enrolment.

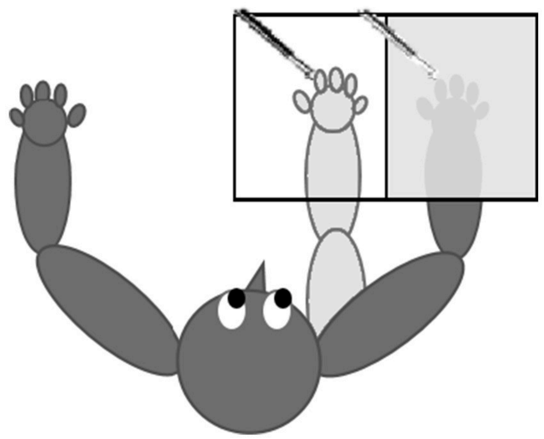

FIGURE 1 | Setting of the RHI procedure. The participant is seated with both hands (dark gray) placed on a table; the real right hand is inside a covered box that prevents visual feedback of the real right hand. The rubber hand (light gray) is aligned with participant's shoulder and is placed visibly in the opened part of the box. Both the rubber hand's and the real hand's index fingers are stimulated synchronously or asynchronously.

Procedure

Proprioceptive Drift

Prior to each trial, a flat lid was used to cover the box. After placing a soft ruler (in centimeters) upon the lid, the participant was asked to report the number on the ruler that corresponded to her/his perceived index finger's location (Burin et al., 2015). This inquiry was repeated six times with a random change of the ruler's position each time, in order to prevent the participants from repeating their previous answers. The same procedure was applied after each trial (synchronous and asynchronous) to determine proprioceptive drift, obtained by subtracting the average post-trial estimations from the average pre-trial estimations for each subject (Botvinick and Cohen, 1998). Proprioceptive drift, the perception that one's own hand is closer to the rubber hand after the illusion procedure, is considered a reliable and objective measure of the illusion effect (Longo et al., 2008; Ehrsson, 2012), particularly when confirmed by subjective measures of the illusion (see questionnaires presented below). Although there is no standard cut-off measure of proprioceptive drift in healthy subjects for the illusion to be considered effective, previous studies have documented a drift that ranged from 0.76 cm (Longo et al., 2008) to 9 cm (Botvinick and Cohen, 1998) when the illusion effect took place.

Questionnaires

The nine-item questionnaire created by Botvinick and Cohen (1998; here referred to as RHI Likert scale) was administered verbally to assess subjective perception of the illusion after each trial. Scores ranged from −3 indicating complete disagreement to +3 indicating complete agreement. Whereas the first three questions consist of target questions relative to the illusion effect, the remaining questions are administered to control for task compliance (see Supplementary Material S1). Items were administered in a random order for each trial and for each participant.

A questionnaire, here named the Sense of Agency questionnaire, investigated the sense of agency as the general and usual feeling of having intentional control over movements acted by one's own body (considering the last month; see Supplementary Material S2) and was administered prior to the experiment. Items of the Sense of Agency questionnaire were adapted from a previous study by Kalckert and Ehrsson (2012) and included six items (3 target and 3 control items) scored on the same scale used for the RHI Likert scale (see Supplementary Material S2 for details). Items were administered in a random order for each participant.

At the end of the experimental session, participants were encouraged to describe sensations and feelings during the experiment. Indeed, the phenomenology of the response to the RHI paradigm represents a unique opportunity for the understanding of the dissociative subtype of PTSD, where dissociative states can affect the perception of one's own body and its relationship with the surrounding world.

Data Analyses

Statistical analyses were performed using SPSS v24 (IBM Corporation). Descriptive analyses were initially conducted to explore the distribution of the data (Shapiro-Wilk to test normality) and the homogeneity of the variance (Levene's test). Averages on psychological and demographic data, as well as between-group comparisons (one-way ANOVA) were then computed.

In order to compare the effect of synchronous vs. asynchronous trial on drift (post- pre-measurements) in the whole sample, a Wilcoxon signed ranks test (2-tailed) was conducted collapsing the groups in one sample. We then focused on the effect of drift after synchronous trials by performing a one-way Welch's ANOVA (three groups: CNTR, PTSD, PTSD+DS), a test taking into account unequal sample sizes and inhomogeneity of the variance, followed by *post-hoc* Games-Howell between-group comparisons. Additional comparisons were run for the PTSD+DS group to explore the high variance observed as compared to the PTSD and the control group (Levene's test).

With regard to the subjective effect of the illusion, as measured by the RHI Likert scale, ratings for each item were standardized by means of an ipsatization procedure (to control for response bias; Romano et al., 2014; Burin et al., 2015). Due to the nature of the data (non-normal distribution), we compared the subjective ratings during synchronous vs. asynchronous trial through a Wilcoxon non-parametric test within the whole sample (CNTR, PTSD, PTSD+DS) on each of the target items (first three items: Q1, Q2, Q3, here referred as "real" items), the average of the real items as well as the real items after subtraction of the control items (real – control items). Subsequently, we conducted Kruskal-Wallis H tests (3 groups: CNTR, PTSD, PTSD+DS) to investigate between-group differences on the subjective ratings after synchronous trials for the first three items (Q1, Q2, Q3, here referred as "real" items), the average of the real items as well as the real – control items. As the PTSD+DS group showed a significantly higher variance than the other groups (Levene's test), we explored between-group comparisons on the subjective ratings in the PTSD group as compared to the control group after synchronous trials. Here, Mann-Whitney tests were performed on each item, as well as on the real items collapsed and the real – control items. Again, the high degree of variance present in the PTSD+DS group was compared to the other groups' variance at each item of the RHI Likert scale.

Correlations (Spearman's rho, two-tailed) between either drift measurements and RHI Likert scale ratings (average of the first three items, here referred as "real" items) and the sense of agency ratings (average of the first three items, here referred as "real" items) within the whole PTSD sample (PTSD and PTSD+DS) were performed.

Finally, direct reports from participants were categorized into themes using qualitative methods (Boyatzis, 1998; Braun and Clarke, 2006).

RESULTS

Participants

No significant group differences were found relative to age, sex, or education. See **Table 1** for a complete report on psychological and demographic characteristics.

Proprioceptive Drift

Data were normally distributed for drift during the synchronous condition and non-normally distributed during the asynchronous condition.

Synchronous vs. Asynchronous Trials

A comparison between trials (synchronous-SYN vs. asynchronous-ASYN) showed a trend toward a significantly higher drift during the SYN as compared to the ASYN condition within the whole sample (SYN>ASYN: $Z = 1.752$, $p = 0.080$, $r = -0.425$; see **Table 2**).

Between-Groups Results for Post- Pre-synchronous Trials

Significant results emerged from the one-way Welch's ANOVA $[F_{(2, 14)} = 4.853, p = 0.041]$.

Post- Pre-synchronous Trials in PTSD vs. HC

With respect to the proprioceptive drift during the SYN condition only, *post-hoc* tests showed that the PTSD group had a significantly *lower* illusion effect as compared to the control group (CNTR: M = 2.71 ± 1.36 cm, PTSD: M = 0.46 ± 1.04 cm; CNTR > PTSD: $p = 0.036$; see **Table 2**). No other significant differences were found between groups (all $p > 0.469$). Proprioceptive drifts during synchronous and asynchronous trials are illustrated in **Figure 2**.

TABLE 1 | Demographic and psychological characteristics.

Clinical and demographical characteristics	HC ($n = 7$)	PTSD ($n = 4$)	PTSD+DS ($n = 6$)	ANOVA/ttest/$\chi 2$ (p)
Age (mean ± SD) years	41.86 ± 9.68	38 ± 9.57	51.17 ± 9.35	0.105
Gender (F) frequency	6	3	5	0.902
Education	16.42 ± 3.73	16.5 ± 1	16.6 ± 2.3	0.989
CAPS tot score (mean ± SD)	5.28 ± 9.14 (CAPS-4)	33.25 ± 8.8 (CAPS-5)	63 ± 7.07 (CAPS-4) 46.5 ± 10.34 (CAPS-5)	0.100 (CAPS-5)*
MDI tot score (mean ± SD)	N/A	40.75 ± 4.11	93.33 ± 35.34	0.014
SCID_D comorbidity frequency	N/A	–	DDNOS (2) DDNOS-in partial remission (4)	–
SCID_I comorbidity (current [past]) frequency	Adjustment disorder [2]	Major depressive disorder (1 [2])	Major depressive disorder (3 [3])	–
		Major Depressive Episode [1]	Panic disorder with agoraphobia [1]	
		Lifetime history of alcohol abuse or dependence [2]	Obsessive-compulsive disorder [1]	
			Eating disorders (1)	
			Somatoform disorder [2]	
			Lifetime history of alcohol abuse or dependence [3]	
			Lifetime history of substance abuse or dependence [3]	

CAPS, Clinician Administered PTSD Scale; DDNOS, Dissociative Disorder Not Otherwise Specified; HC, healthy controls; MDI, Multiscale Dissociation Inventory; PTSD, posttraumatic stress disorder group; PTSD+DS, dissociative subtype of the posttraumatic stress disorder group; SCID-D, Structured Clinical Interview for Dissociative Disorders; SCID-I, Structured Clinical Interview for DSM-IV Axis I disorders.
**t-test between PTSD and PTSD+DS based on CAPS-5.*

Levene's Tests on the Homogeneity of the Variance in Post- Pre-synchronous Trials

The PTSD+DS group showed a grossly higher variance in the drift measurements (variance: SYN = 95.642, ASYN = 24.335) as compared to the PTSD group (variance: SYN = 1.081, ASYN = 0.951) and the HC (variance: SYN = 1.849, ASYN = 7.791). These results were supported by the Levene's test of the homogeneity of variance for the post- pre-SYN condition (CNTR vs. PTSD+DS: Levene stat = 9.410, $p = 0.011$; PTSD vs. PTSD+DS: Levene stat = 5.633, $p = 0.045$; PTSD vs. CNTR: Levene stat = 0.491, $p = 0.501$; see **Table 2**).

TABLE 2 | Proprioceptive drift.

SYN vs. ASYN (Wilcoxon signed-rank test)	Z	*p*
Collapsed across groups	−1.752	0.080
post- pre-SYN	**Welch test**	***p***
One-way Welch's ANOVA	4.853	0.041*
CNTR>PTSD (Games-Howell *post-hoc*)	2.256 (mean difference)	0.036*
Homogeneity of the variance post- pre-SYN (Levene's test)	**Levene stat**	***p***
CNTR vs. PTSD+DS	9.410	0.011*
PTSD vs. PTSD+DS	5.633	0.045*
PTSD vs. CNTR	0.491	0.591

*ASYN, asynchronous condition; CNTR, control group, PTSD; posttraumatic stress disorder group; PTSD+DS, dissociative subtype of PTSD; SYN, synchronous condition. *denotes p< 0.05.*

Subjective Ratings

Synchronous vs. Asynchronous

As compared to the ASYN condition, the SYN condition showed a significantly higher perception of the illusion using all of the real items of the RHI Likert scale (Q1, Q2, Q3), considered either separately or as an average (SYN > ASYN Q1: Z = 2.816, $p = 0.005$, Q2: Z = 2.599, $p = 0.009$; Q3: Z = 2.047, $p = 0.041$, average of the real items: Z = 2.921, $p = 0.003$), as well as for the real—control items (SYN > ASYN: Z = 2.586, $p = 0.010$; see **Table 3**) within the whole sample.

Between-Groups Results for Synchronous Trials

No significant between-group results emerged when considering scores on Q1 ($\chi^2 = 1.018, p = 0.601$), Q3 ($\chi^2 = 3.721, p = 0.156$), and the real—control items ($\chi^2 = 4.251$, $p = 0.119$). However, between-group results showed a trend toward significance when considering scores on Q2 ($\chi^2 = 5.708, p = 0.058, \eta^2 = 0.131$) and the average of the real items ($\chi^2 = 5.032, p = 0.081, \eta^2 = 0.079$).

Synchronous Trials in PTSD vs. HC

Comparing PTSD to HC, the PTSD group showed a significantly lower perception of the illusion during the SYN condition for item Q2(U = 1, $p = 0.014$). Similarly, as compared to HC, the PTSD group showed a lower illusion perception during the SYN condition for the average of the real items (U = 2, $p = 0.023$), and for the real—control items (U = 3, $p = 0.037$; see **Table 2**; **Figure 3**). Considered separately, items Q1 and Q3 did not show any significant difference between groups (see Supplementary Material S2 for items Q1, Q2, and Q3).

Levene's Tests on the Homogeneity of the Variance in Synchronous Trials

The PTSD+DS again showed a significantly higher variance for Q2 as compared to the control group (Levene stat = 6.457,

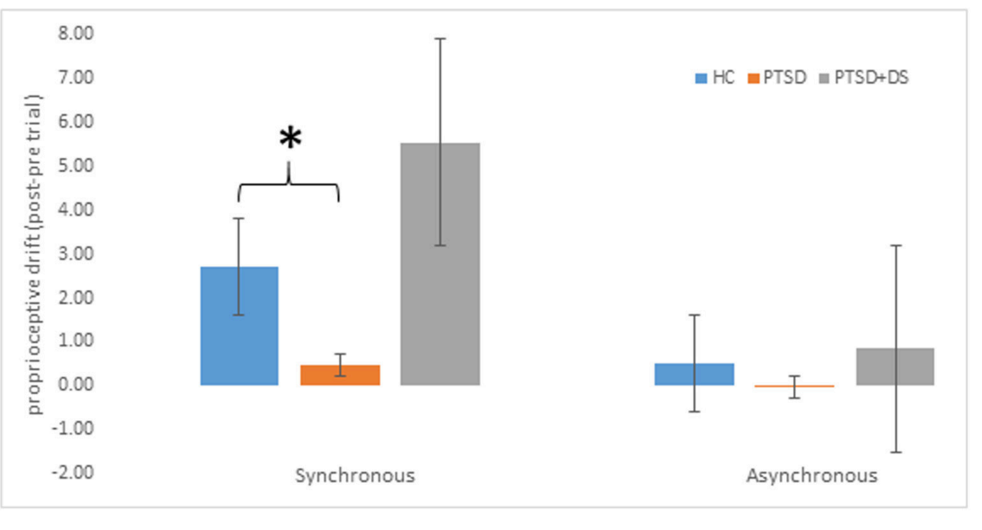

FIGURE 2 | Proprioceptive drift (averaged post-pre- trial estimation) in the three groups. Positive scores refer to perceived location closer to the rubber hand (in cm). Error bars represent standard errors. Asterisks indicate significant comparisons (*$p < 0.05$). HC: healthy controls, PTSD: posttraumatic stress disorder group, PTSD+DS: dissociative subtype of the posttraumatic stress disorder group.

TABLE 3 | Subjective ratings.

	Q1		Q2		Q3		Average real Q		Average real–control Q	
SYN > ASYN (Wilcoxon signed-rank test)	**Z**	***p***	**Z**	***p***	**Z**	***p***	**Z**	***p***	**Z**	***p***
Collapsed across groups	2.816	0.005*	2.599	0.009*	2.047	0.041*	2.921	0.003*	2.586	0.01*
SYN (Mann-Whitney test)	**U**	***p***	**U**	***p***	**U**	***p***	**U**	***p***	**U**	***p***
CNTR>PTSD	13	0.850	1	0.014*	5	0.089	2	0.023*	3	0.037*
Homogeneity of the variance SYN (Levene's test)	**Levene stat**	***p***	**Levene stat**	***p***	**Levene stat**	***p***	**Levene stat**	***p***	**Levene stat**	***p***
CNTR vs. PTSD+DS	1.163	0.304	6.457	0.027*	1.189	0.299	1.245	0.288	1.225	0.292
PTSD vs. PTSD+DS	0.070	0.798	5.54	0.046*	6.28	0.037*	0.193	0.672	0.605	0.459

ASYN, asynchronous condition; CNTR, control group; PTSD, posttraumatic stress disorder group; PTSD+DS, dissociative subtype of PTSD; Q, question item; SYN, synchronous condition.
**denotes p < 0.05.*

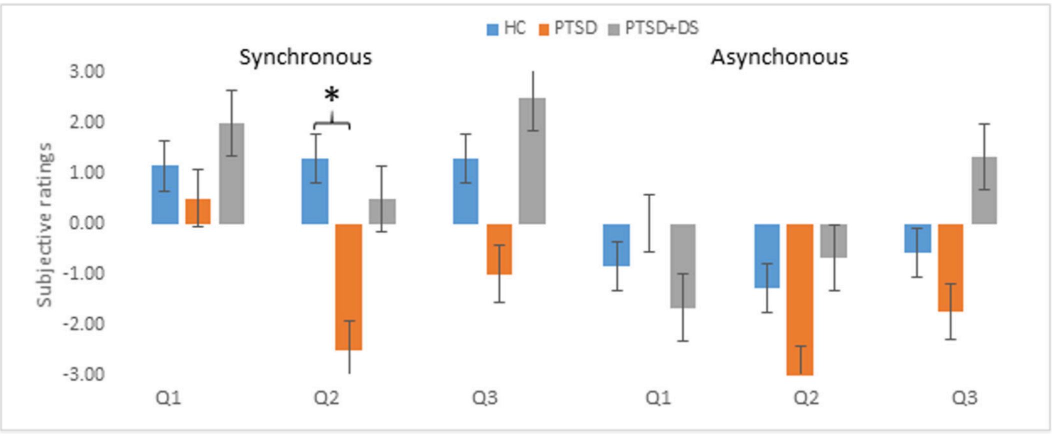

FIGURE 3 | Subjective ratings of RHI in the three groups. Positive scores refer to the subjective experience of the illusion. Error bars represent standard errors. Asterisks indicate significant comparisons (*$p < 0.05$). HC, healthy controls; PTSD, posttraumatic stress disorder group; PTSD+DS, dissociative subtype of the posttraumatic stress disorder group.

$p = 0.027$), and for Q2 (Levene stat = 5.54, $p = 0.046$) and Q3 (Levene stat = 6.28, $p = 0.037$) as compared to the PTSD group. No significant differences in variance emerged in the PTSD vs. the control group (see **Table 3**).

Sense of Agency

Subjective ratings on the illusion perception showed a trend toward a significant negative correlation with the sense of agency (rho = −0.614, $p = 0.079$) after synchronous trials (see **Figure 4**). No other significant correlations emerged with the sense of agency.

Phenomenology

Following drift measurements and the administration of questionnaires, PTSD participants were prompted to describe their subjective experience of the experiment (detailed reports of three of the PTSD+DS participants can be found in Rabellino et al., 2016).

Coping Strategies in PTSD+DS

The diverse experiences reported by PTSD+DS participants (here referred to as P1, P2, P3, etc. for convenience) in response to the RHI followed three distinct patterns: (a) perceiving that one's own hidden hand is moving back and forth between the real hand's and the rubber hand's position; (b) feeling that one's own hand has jumped through the box division and become one with the rubber hand; (c) feeling that one's own hand is located somewhere in the space between the two hands. Individual reports detailing each coping strategy are described below:

(a) *Perceiving that one's own hidden hand is moving back and forth between the real hand's and the rubber hand's position.* This experience was described by one PTSD+DS participant as: P4 "It feels like it [index finger] is going between numbers [referring to the drift measurements], like it's going back and forth, back and forth." Another participant reported the following after asynchronous brushing: P5 "It seems like the hand is going back and forth, almost jumping like

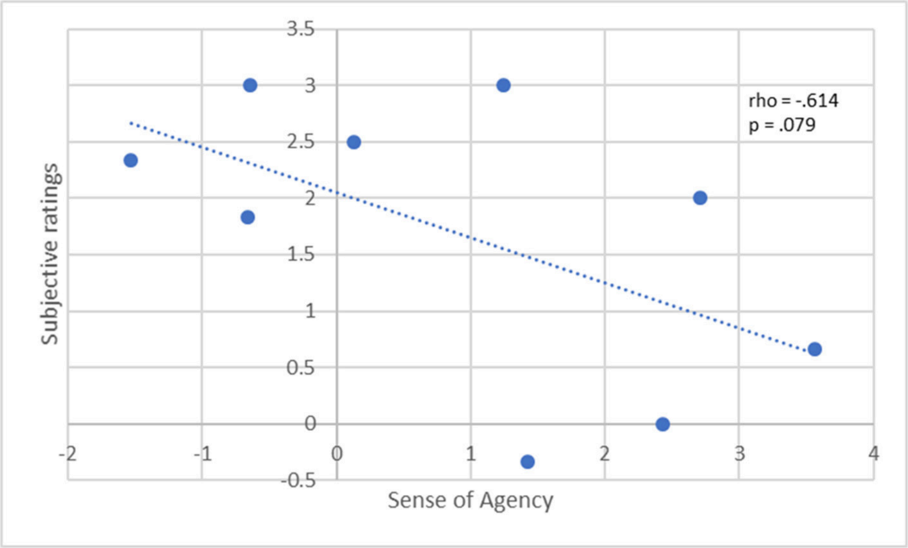

FIGURE 4 | Correlation between subjective ratings of RHI (average real Q) and Sense of Agency (average real items) in the whole PTSD group (PTSD and PTSD+DS). The dotted line depicts a negative correlation; Spearman's rho and *p*-value are reported at the top right. Sense of Agency scores are missing for one subject.

the brushing," and during the synchronous condition: "The hand was going back and forth, afterwards my hand was where the rubber hand was" (this participant showed a drift after SYN = 10.5 cm, and after ASYN = 3.3 cm, while the subjective perception of the illusion after SYN = −0.06, and after ASYN = −1.06 using the average score for the real items);

(b) *Feeling that one's own hand has jumped through the box division and become one with the rubber hand.* This experience was reported by a participant showing a strong illusion effect (drift after SYN = 22.83 cm, drift after ASYN = 1.17 cm; subjective ratings after SYN = 2.3, after ASYN = −0.03 using the average score for the real items) in these terms: P1 "it didn't drift it flew [...] it's like it jumped [...] once it jumped over it was there, there was no more coming back" (also reported in (Rabellino et al., 2016));

(c) *Feeling that one's own hand is located somewhere in the space between the two hands.* For example, one participant described this experience as being like a non-specific location of one's own hand in space: P6 "I felt the sensation but there was no location to it. [...] I was looking at the hand, and the feeling was somewhere off in space [...] You can see in your body where it's happening ...but it's not really happening there, just hanging off in space somewhere."

Top-Down Body Representation vs. Bottom-Up Sensory Processing

PTSD+DS participants described the conflict occurring between cognitive representation of their own body and the incoming sensory information as follows: P5 "Logically, I knew [it couldn't be], but it felt like in front of me; as the measurements went on, it felt like it went back where it should be," P2 "Because it is a disconnect, it's not mine and I should be able to figure that out but it wasn't ... near the end I wasn't sure and so that was difficult," P1 "... knowing that it should be there but this is where it feels like ... and so I was really having problems at that point with a number "cause I could intellectualize it but that's not what it was feeling like." These feelings appeared to trigger a familiar sensation of uncertainty with respect to their own beliefs and feelings, and ability to discern between what is or is not real: P5 "With PTSD you learn you cannot trust your feelings ... the uncertainty," P6 "What disturbed me is that the feeling was actually very familiar [...] you always question: is this normal? Do I actually experience this stuff? Is everybody experiencing this?" One participant explicitly reported that the feeling experienced during the RHI closely resembled the dissociative experience: "It is a perfect illustration of when you feel and not feel a sensation [...] when you feel it and then don't feel it in connection with your body [...] that's the experience when you are really ... in the middle of something."

Body Ownership and Sense of Agency

Finally, one participant described the correlation between body awareness and the body in movement: P6 "If I don't use a part [of my body] I am not aware of it. I am aware of them when I use them," where moving the body (sense of agency) appears to support the sense of body ownership. Also, not being allowed to move the hands during the experiment alters the ability to identify and respond to feelings of disconnection from parts of the body: P4 "I couldn't fix what was happening," P3 "It was hard to stay still when you were doing it," P2 [asked what makes it difficult to stay present] "Staying in one position."

DISCUSSION

The aim of this study was to investigate sense of body ownership and its relation to sense of agency in PTSD and its dissociative subtype (PTSD+DS) through manipulation of multisensory integration processes via the RHI paradigm. As expected, the results of the study revealed an overall stronger effect of the illusion during the synchronous as compared to the asynchronous condition, measured by both proprioceptive drift and by subjective ratings on the perception of the illusion. During the synchronous condition, the PTSD group showed a significantly *lower* effect of the illusion as compared to the healthy control group, indicated by lower proprioceptive drift and subjective rating on the perception of the illusion. By contrast, the PTSD+DS group exhibited a high variance in response to the RHI, ranging from very strong to very weak, both in terms of proprioceptive drift and the subjective perception of the illusion. Moreover, the results showed a trend indicating that the lower the sense of agency, the stronger the effect of the RHI, as measured by subjective ratings of the illusory perception in PTSD.

Despite a small sample size, these results nonetheless suggest a pattern of response to manipulation of body representation in the PTSD group. Specifically, overall PTSD participants showed a very small illusion effect (see **Figures 2**, **3** for proprioceptive drift and subjective ratings) that was significantly lower than that observed in the HC group. As previously indicated, typical symptoms of PTSD include effortful avoidance of trauma-related distress as well as emotional numbing represented in mind and body (Frewen et al., 2012; APA, 2013). In PTSD, the top-down representation of the body, responsible in part for cognitive control, may predominate, filtering and suppressing sensory information that can lead to the manifestation of other typical PTSD symptoms, such as re-experiencing and hyperarousal. Indeed, the data captured here suggest that, overall, PTSD participants may have resorted to avoidant coping strategies in an attempt to maintain control of the body, reacting to sensory manipulation with a sustained rigid body image, which comprises perceptions, beliefs, and emotional representations relative to one's own body (Costantini and Haggard, 2007; de Vignemont, 2011).

By contrast, the PTSD+DS group displayed a highly variant response to the RHI, both in terms of proprioceptive drift and of subjective perception of the illusion. Phenomenological reports suggest that the conflict between top-down representation of the body and bottom-up sensory information was a familiar feeling to these participants. They described becoming uncertain about the reality of their perceptions and/or the quality of their body representation. Broadly speaking, two coping/defensive strategies were observed. The first strategy involved the individual reacting to the presumed unresolved conflict between top-down representation of the body and bottom-up sensory information with depersonalization, where both the sense of agency and the sense of ownership were reported to be affected. These individuals reported experiencing both detachment from the body or parts of the body (an extreme example represented by out-of-body experiences) and/or freezing responses during which he/she was unable to move parts of his/her body (Bracha, 2004; Schauer and Elbert, 2010; Panksepp and Biven, 2012; Ataria, 2015; Frewen and Lanius, 2015). Such freezing responses have been proposed to involve thalamocortical deafferentiation, where bottom-up sensory signals no longer influence higher cortical regions mediating integration of the experience (Longo et al., 2008; Lanius et al., 2014), a reaction also observed in animal models under threat (Kalin et al., 2005; Mobbs et al., 2009; Porges, 2009; Kozlowska et al., 2015). For example, one PTSD+DS participant who experienced freezing of the hand during the RHI reported the following sensation at the end of the experimental session: "Feeling tingling, like wearing a glove… like when I'm freezing and then the sensation comes back." We hypothesize that severely traumatized individuals would resort to this strategy as an extreme defense to a potential threat, when all other coping strategies (e.g., avoidance) are unavailable or unhelpful (Herman, 1992), with consequent drifting toward a dissociative state involving depersonalization and derealization.

The second defensive strategy to cope with the presumed conflict between top-down representation of the body and bottom-up sensory information observed in the PTSD+DS group was similar to the strategy proposed for the PTSD group. Here, top-down cognitive representation dominated, thus having the potential to suppress afferent signals in order to maintain control over the body, body ownership and sense of agency. Given the high variance characterizing the response in the PTSD+DS group, our results suggest that patterns of response to the manipulation of body ownership in the dissociative subtype of PTSD may be critically dependent on an individual's state at the time of testing, which can change over time and which is characterized by alterations in integrating multisensory information. Here, it is also interesting to note that previous neuroimaging studies of dissociative states in PTSD involving depersonalization have suggested altered activity in brain regions involved in multisensory integration during states of depersonalization/derealization (Simeon et al., 2000; Lanius et al., 2002; Felmingham et al., 2008). Future research examining the RHI illusion at multiple time points will therefore be of utmost importance.

Taken together, these results support the notion that high-level cortical processes (as interpretation of experienced body-related event) can modulate low-level subcortical mechanisms such as multisensory integration. Here, psychiatric symptoms originating from traumatic events would affect not only the psychological domain, but also somatic processes (Eshkevari et al., 2012; Walsh et al., 2015), with effects on embodiment and body ownership partially resembling those demonstrated previously in neurological patients with somatosensory system lesions (Lenggenhager et al., 2012).

Finally, these results point toward a close interrelation between sense of agency and sense of body ownership (in terms of subjective perception of the illusion) in PTSD. Specifically, a weaker sense of agency (measured here as a continuous feeling of being in control of one's body movements; Haggard and Chambon, 2012) showed a trend toward a significant correlation with a stronger perception of the illusion. Participants' self-reports were in line with this observation where they described utilizing intentioned movement as a means to reinforce sense of agency when they began to perceive that they were losing their sense of body ownership. Critically, severe dissociative symptoms have been associated with the loss of either body ownership and sense of agency (Ataria, 2015, 2016).

Limitations of the current study need to be considered along with the conclusions. Firstly, the small sample size within the three groups does not allow for generalization of the results. Further investigation in larger samples is required. Secondly, data were collected at a single time point, whereas a longitudinal design would allow for investigation of differential psychological/physiological states in PTSD+DS. Moreover, the different location of the control group recruitment and data collection might represent a confounding variable, although experimental protocols have been accurately compared and followed. Finally, the RHI protocol did not include directly procedures to manipulate sense of agency. Future studies investigating the RHI in PTSD should include manipulation of either sense of agency and sense of body ownership in order to explore the impact of each independently and in combination. In addition, future studies should enrich behavioral observations with physiological and neuroimaging data to delineate the neurophenomenology of body ownership and sense of agency in PTSD and its dissociative subtype.

In conclusion, this study contributes to a deeper understanding of the complex defensive reaction occurring during manipulation of body ownership in traumatized individuals with PTSD and its dissociative subtype. Furthermore, our results highlight key differences in patterns of response to the RHI between the two groups. Whereas a top-down filtering of sensory information as a cognitive avoidance strategy aimed at maintenance of a rigid body representation may characterize the PTSD group, a changing state-dependent representation of the body appears to better describe individuals with PTSD+DS. Crucially, sense of agency is thought to play a primary role in the maintenance and recovery of body ownership in PTSD. Indeed, our findings showed that a lower sense of agency correlated with a stronger illusion effect, with PTSD individuals resorting frequently to intentional movements in order to regain a sense of body ownership during dissociative experiences. Taken together, these findings point toward the need for development of specific treatments for the dissociative subtype of PTSD that are tailored to address not only alterations in body representation but also potential loss of body ownership. Interventions that focus on increasing the feeling of connection with one's own body such as body scan mindfulness training (Lanius et al., 2015; Boyd et al., 2017) or sensorimotor psychotherapy (Ogden and Fisher, 2014; Frewen and Lanius, 2015) may be helpful in this regard. Finally, improving and restoring an embodied sense of agency may be critical to trauma recovery.

AUTHOR CONTRIBUTIONS

DR, PF, and RL: conception and study design; DR, DB, SH, CL, and RL: study execution and supervision; DR, DB, PF, MM, and RL: data analysis and interpretation; DR, DB, SH, CL, PF, MM, and RL: manuscript drafting and revision.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnhum.2018.00163/full#supplementary-material

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When Playing Is a Problem: An Atypical Case of Alien Hand Syndrome in a Professional Pianist

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Alien hand syndrome (AHS) is a neurological illness characterized by limb movements which are carried out without being aware of it. Many patients describe these movements as aggressive and some perceive a strong feeling of estrangement and go so far as to deny ownership. The sense of body ownership is the perception that parts of one's body pertain to oneself, despite it is moving or not and if movement is intentional or unintentional. These anomalous self-experiences may arise in patients with focal brain lesions and provide unique opportunities to disclose the neural components underlying self-body perception. The feeling of foreignness described in AHS is often observed in post-central cortical lesions in the non-dominant hemisphere and is typical of the "posterior alien hand variant". We used Diffusion-Tensor magnetic resonance imaging (DT-MRI) in an unusual case of posterior AHS of the dominant hand in a professional pianist with corticobasal syndrome (CBS). The patient showed uncontrolled levitation with the right arm while playing the piano and perceived as if her hand had a "mind of its own" which prevented her from playing. MRI-scans show asymmetric brain atrophy, mainly involving left post-central regions and SPECT-Tc99m-ECD patterns of hypometabolism over the left parietal-occipital cortices. DT-MRI revealed extensive damage which comprised left fronto-temporal cortex and extends into the ipsilateral parietal cortex causing a disruption of corpus callosum (CC) projections from the rostrum to the splenium. Our case illustrates that posterior AHS may occur in the dominant hemisphere due to widespread damage, which exceed parietal cortex. The parietal lobe has been recognized as a multimodal association region that gets input from several networks and organizes motor output. We suggest that the disturbance to this pathway could result in disruption of motor output and associate an abnormal motor control and anomalous self-body perception.

Keywords: alien hand syndrome, corticobasal syndrome, diffusion tensor imaging (DTI), piano playing, self-body perception

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INTRODUCTION

Alien hand syndrome (AHS) is one of the most gripping disconnection disorders in neurology. It could be described as the perception that one limb "has its own volition" together with recognizable uncontrolled motor activity which pries with the voluntary movements of the unaffected limb (Doody and Jankovic, 1992). It is fairly common that the affected arm holds clothes, parts of the body, adjacent objects or even people (Josephs and Rossor, 2004). Moreover, patients are usually unaware of it, and could display signs of inattention of the affected limb, perceiving that it is not theirs (Josephs and Rossor, 2004).

AHS is observed in post-stroke patients, secondary to vascular malformations and brain tumors, neurosurgical lesions, trauma and neurodegenerative diseases, particularly in atypical parkinsonian syndromes as corticobasal syndrome (CBS) and progressive supranuclear palsy (Scepkowski and Cronin-Golomb, 2003; Chang et al., 2012; Alexander et al., 2014). The presence of limb apraxia, visuospatial dysfunction and AHS is suggestive of CBS, particularly when it develops in a progressive way. In fact, alien hand phenomenon appears in around 30% of compiled CBS cases (Armstrong et al., 2013). Neural mechanisms of AHS have remained speculative and the combination of lesions necessary to produce this phenomenon is uncertain (Scepkowski and Cronin-Golomb, 2003). According to the anatomical lesions and clinical features, three different categories: callosal, frontal and posterior AHS have been described. The first two types are classified as an anterior form of AHS whereas the third one is also defined as a posterior form (Scepkowski and Cronin-Golomb, 2003). The more common "anterior or motor" AHS is characterized by uncontrollable manipulation of objects and involuntary grasping of the dominant hand. Posterior subtype (pAHS) is uncommon and usually associated with involuntary movements such as a position-dependent levitation of the arm in addition to a sensation of strangeness in the limb (Scepkowski and Cronin-Golomb, 2003). The etiology of involuntary movements in pAHS is not elucidated yet and remains unclear (Armstrong et al., 2013). It mostly, though not exclusively, affects the non-dominant hand with lesions involving the posterior right hemisphere (Kessler and Hathout, 2009). Shared mechanisms between AHS variants have been described and the data seem to indicate that most cases of AHS arise from lesions of interhemispheric networks or between the frontal and the parietal lobes (Sarva et al., 2014). However, the case-report descriptions of patients with damage distant from the typical affected areas reflects our partial knowledge of the processes producing AHS (Sarva et al., 2014).

We describe a case of pAHS of the dominant right hand secondary to CBS in a 65-year-old professional pianist with unusually increased alien limb symptoms while playing. Diffusion-Tensor magnetic resonance imaging (DT-MRI) and fiber tractography could offer the opportunity to shed light on the pathophysiology of AHS and other neurological disorders affecting the perception of one's own body.

CASE REPORT

Patient History

A 65-year-old woman, right-handed professional pianist suffered from increasing awkwardness of her dominant arm during the last 5 years. She was healthy until the age of 60, when she first felt impairment of the voluntary movement of her right hand while playing the piano. She experienced as whether her arm "didn't do what it was ought to" and declined to play due to it was "too clumsy to practice". Rarely, when she moved her left hand, the right one raised involuntarily. She felt strange and surprise with the behavior of her affected arm and believed that "it had an entity of its own". After 2 years, she had severe difficulties with playing and, although her right hand was not paretic, her movement was significantly slowed down. The hand carried on its odd compartment, which utterly hampered her from playing. No history of any other illnesses, toxins or drugs were reported. The patient underwent a detailed assessment by a neurology specialist. Its main features on clinical examination were asymmetric hand clumsiness, rigidity and bradykinesia with reduced right arm swing, prominent right constructional and ideomotor apraxia and feelings of estrangement of the right limb coupled with non-purposeful movements such as levitation, especially when attention decreased well distinguishable from distal pseudo-athetosis which was not presented. She exhibited other cortical sensory deficits such as decreased pain sensation in the right side besides transcortical motor aphasia. Clinical criteria for dementia were absent.

The patient was diagnosed as having probable CBS based on recently published criteria (Armstrong et al., 2013; Alexander et al., 2014) furthermore, she displayed the typical features of pAHS. She was treated with levodopa (until 800 mg per day) and clonazepam (1 mg per day). However, she had modest response to it.

Methods

As part of the clinical assessment, MRI was performed in a 3T MR scanner (Philips Achieva, Philips Medical Systems, Nederlands) with a SENSE Neurovascular coil (16 elements). No contrast agent or sedation was utilized. For the MRI protocol a high-resolution T1-weighted gradient-echo scan: 212 slices, 0.8 mm isotropic voxels, FOV 250 × 250 mm, TR 11 ms and TE 4.9 ms was acquired. DT Imaging (DTI) was acquired in axial slice orientation, using a single-shot EPI sequence with diffusion encoding in 32 directions (values 0 and 800 s/mm^2, voxel size was 2 × 2 × 2 mm^3, 60 slices, SENSE factor 1.9). The diffusion-weighted data were transferred to a workstation for analysis and eddy current compensation was performed by affine registration to B0 image. Tractography was carried out using the PRIDE fiber-tracking tool (Philips Medical Systems) as described previously (Alfaro et al., 2015; Bernabeu et al., 2016) and was fulfilled based on the connection between two areas of regions of interest (ROIs), the ROIs were drawn manually based on the anatomical MRI and on published atlases (Wakana et al., 2004). The fibers were computed automatically by the software with the following parameters as stopping criteria: minimum fractional anisotropy value (FA) of 0.3, maximum fiber angle between fibers of 27° and minimum fiber length of 10 mm.

Additionally, brain perfusion studies with SPECT-Tc99m-ECD were performed with a Philips Forte Gamma Camera System (Philips Medical Systems, US) using Tc-99m radiopharmaceuticals. Imaging acquisition and reconstruction was carried out with the usual specified protocols (Delrieu et al., 2010).

The study adhered to the Declaration of Helsinki. The protocol was approved by the institutional review board (Hospital Vega Baja Ethics Committee). The patient gave her written informed consent before entering the study and for publishing the information appearing in this case report.

Results

MR imaging of the brain revealed severe atrophy in the left hemisphere, mainly in the left posterior post-central gyrus, anterior and posterior parietal lobe and ipsilateral occipital cortex (**Figure 1A**) consistent with the SPECT-Tc99m-ECD result, which displayed deficient cerebral perfusion in all these regions (**Figure 1B**). DTI-MRI showed right corpus callosum (CC) fibers connected properly to frontal, temporal, parietal and occipital cortex (**Figure 2A**). By contrast, left CC fibers displayed serious and wide disruption, which affected left premotor, supplementary motor and motor cortex connections besides left temporal, parietal and occipital cortices connections further extensive damage in the left superior longitudinal fascicule (**Figure 2B**). A little group of CC fibers in both brain hemispheres, crossing through the rostrum and the genu, were preserved (**Figure 2C**).

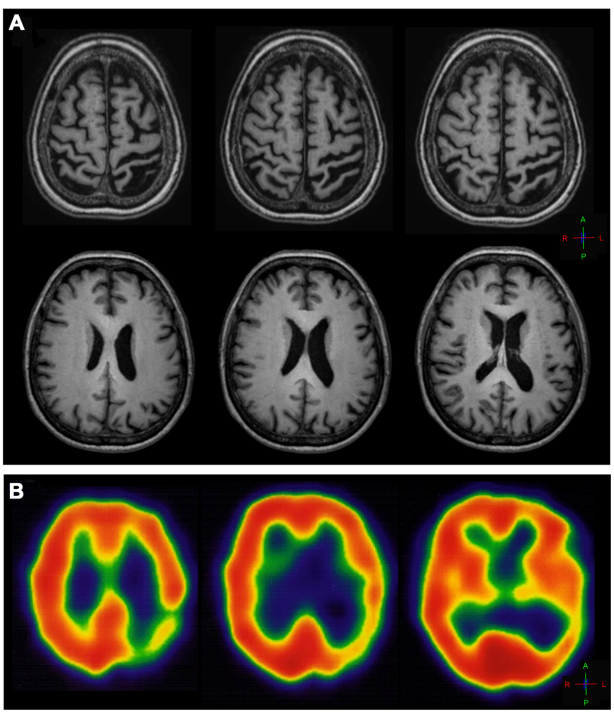

FIGURE 1 | (A) T1-weighted axial MR image of the brain showing diffuse cortical atrophy and ventriculomegaly in the left hemisphere, marked in the left central sulcus and precentral gyrus and more prominent on the left post-central gyrus and parietal-posterior area. **(B)** SPECT axial slices of thechnetium-99m-HMPO brain perfusion scan showing deficient cerebral perfusion in the left posterior parietal-occipital cortex.

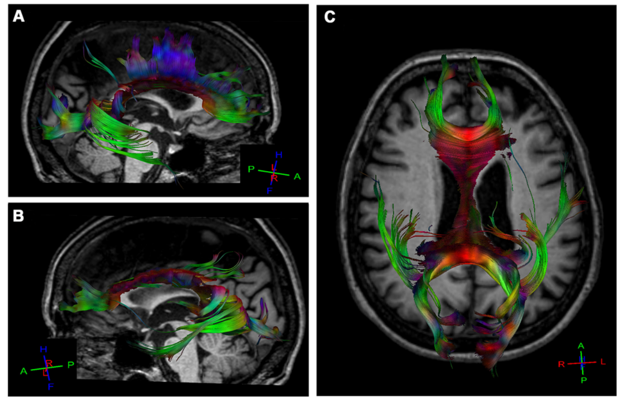

FIGURE 2 | Diffusion tensor tractography (DTT) for corpus callosum (CC) fibers using a sensitive-encoding head coil on a 3.0T Philips Achieva system. DTT was performed based on the connection between two regions of interest (ROI) in order to minimize the risk of including other tracks. **(A)** Right CC fibers extended normally to frontal, temporal, parietal and occipital cortices. **(B)** Extensive disruption of the left CC connections from the rostral body to the splenium. A small group of CC fibers in both brain hemispheres are preserved. **(C)** Axial reconstructed of CC fibers in the patient.

BACKGROUND

Studying the abnormalities of self-body perception due to brain damage has a key role in addressing questions regarding the structure and functional signature of body consciousness (Pia et al., 2013). This is the case of patients with pAHS who commonly manifest body schema distortions such as the strong feeling of foreignness or strangeness of one limb and other parietal sensory deficits (Doody and Jankovic, 1992; Scepkowski and Cronin-Golomb, 2003; Josephs and Rossor, 2004).

In the last 20 years our understanding of AHS subtypes has evolved to the three, well-defined variants: the two anterior (frontal and callosal) variants and the relatively recent added posterior one (Sarva et al., 2014). The "posterior form" of AHS has been related with impairment to the thalamus, the posterolateral parietal cortex and the occipital lobe (Scepkowski and Cronin-Golomb, 2003; Prakash et al., 2011). This variant usually, though not exclusively, involves the non-dominant limb (Kessler and Hathout, 2009; Kloesel et al., 2010). The alien limb movements appear non-purposeful and non-conflictual and patients could experience involuntary levitation of the arm which may be task specific (Rohde et al., 2002; Gondim et al., 2005; Prakash et al., 2011). In some cases, the alien hand also could exhibit a bizarre position, called "parietal hand" in which the palmar surface is withdrawn from approaching tools and the fingers move into an extremely extended posture (Prakash et al., 2011; Sarva et al., 2014). Additionally, pAHS can be accompanied by hemianesthesia, hemianopia, visuospatial neglect (Yuan et al., 2011) and optic ataxia (Levine and Rinn, 1986) and some patients may have significant sensory deficits without weakness (Spector et al., 2009).

pAHS could be produced by different neurodegenerative conditions for instance, Creutzfeld–Jacob disease (Rubin et al., 2012), Alzheimer's disease, CBS or progressive supranuclear palsy (Chand et al., 2006) as well as cerebrovascular accidents in the thalamus, parietal cortex or posterior cerebral artery (Marey-Lopez et al., 2002; Rohde et al., 2002; Gondim et al., 2005; Hassan and Josephs, 2016).

Due to the relative low prevalence of this syndrome and the limited reports of pAHS described, our understanding of underlying mechanisms remains incomplete. On the one hand, some authors noted the necessary implication of parietal lobe in pathophysiology of pAHS. The parietal lobe is a multimodal association area required for formation of proprioceptive schemes which assist in the integration of body image (Perez-Velazquez, 2012). Additionally, it receives inputs from primary somatosensory and prefrontal cortices and coordinates motor output (Perez-Velazquez, 2012). Because of this, damage to parietal lobe could produce inability to combine sensory input and motor output and may induce impaired volitional movement execution, involuntary arm levitation and release a pronounced feeling of estrangement of a limb (Graff-Radford et al., 2013). On the other hand, a distortion of body representation due to an anomalous cortico-striato-thalamic network without significant parietal lobe injury has been recently described as a cause of pAHS (Filevich et al., 2012). Moreover, it is known that a thalamic stroke with no frontal and parietal involvement may result in pAHS with slight sensory loss (Bartolo et al., 2011). Likewise, posterior cerebral artery stroke may evoke sensation of limb foreignness secondary to the damage to the medial paralimbic fibers implicated in limb awareness (Groom et al., 1999). According to this, we could say that nowadays, the neuroanatomical circuitry involved in pAHS is diverse and yet poorly understood.

DISCUSSION

Here we focused on an unusual patient affected by CBS who exhibited a constellation of symptoms consistent with pAHS in her dominant right limb. Nevertheless, our case differs from other reported cases of pAHS.

First of all, pAHS is classically described in non-dominant limb (Scepkowski and Cronin-Golomb, 2003) and there have been very few reports of lesions in the left hemisphere causing pAHS of the dominant right upper extremity (Carrilho et al., 2001; Rohde et al., 2002; Kessler and Hathout, 2009; Kloesel et al., 2010). Leiguarda et al. (1993) described a patient who developed right AHS following neurosurgical removal of a vascular malformation from the left parietal cortex and Gondim et al. (2005) reported a position-dependent levitation of the dominant limb afterward left parietal cerebrovascular accident. Nevertheless, there is anecdotal evidence from dominant pAHS with atrophy in the left dominant parietal lobe. Kessler and Hathout (2009) propose a precise localization of AHS of the dominant hand through the report of a patient with left parietal stroke and suggests that Brodmann area 5, which coincides with the tertiary somatosensory cortex and is required in stereognosis and post-central circumvolution, which is entailed in kinesthesia, could trigger the anomalous movements and the sensations of strangeness of an alien arm, even in the dominant limb (Sarva et al., 2014). In the light of these observations and our reported findings, it seems that pAHS variant could not be restricted to non-dominant hemispheric lesions.

Otherwise, although clinically our patient presented symptoms that remind one of the posterior alien hand variant, neuroimaging revealed extensive damage that exceeds the posterior parietal cortex causing a widespread disruption of left CC connections from the rostral body to the splenium. These results suggest that the sense of ownership over the alien hand could be established by a wide spectrum of lesions, ranging from purely anterior to purely posterior forms and hinted that disruption of the motor centers from the parietal cortex probably cause misperception, and developing an abnormal integration between afferent multisensory signals and pre-existing body presentations and the loss of consciousness of movement (Graff-Radford et al., 2013; Sarva et al., 2014).

Furthermore, our patient exhibited a previously unreported feature: apparently her posterior alien arm symptoms exacerbated while piano playing. Playing the piano requires the activation of multisensory and motor networks located in distant but functionally related brain regions such as frontal, parietal, and temporo-occipital cortices besides subcortical structures such as basal ganglia, thalamus and cerebellum (Altenmüller and Schlaug, 2015). Indeed, parietal lobe and temporo-occipital cortices play a critical role for conscious perception of sensory information. These areas work together in order to integrate inputs from the auditory, visual, and somatosensory system into a combined sensory impression (Altenmüller and Schlaug, 2015). The functional links between all these brain regions make possible the coupling of perception and action for playing. As we described before, our patient suffered from a widespread disruption of brain networks involved frontal, parietal and temporo-occipital cortices and first perceived impairment of the conscious and voluntary movements of her right arm while playing the piano. It has been known that uncoordinated hand movements or involuntary levitation in patients with pAHS may be task-specific. Kloesel et al. (2010) described a patient with pAHS secondary to CBS who had exaggerated arm elevation only while walking (Prakash et al., 2011) and in other cases, involuntary movements are triggered or worsened by tactile stimulation (Gondim et al., 2005), sudden noises or coughing (Rohde et al., 2002). Levitation in our patient appeared when attention decreased and were not related to a specific position of the arm. It is certain that levitation exacerbated while piano playing. In addition, she first noticed impairment of the controlled movement of her right hand during piano execution. However, we consider that playing a musical instrument demands the suitable perception of the limb position and motion in space and requires a fine visual, proprioceptive and motor integration (Pascual-Leone, 2001). Most of the networks which take part in these processes are damaged in our patient.

Regarding the differential aspects of our findings with task-specific dystonia in pianists, our patient did not display the typical cramps, hyperextensions and flexions of the hand while playing the piano which is commonly described in task-specific dystonia of musicians. It is known that the posterior variant of AHS can be accompanied by other features such as atypical hand posture sometimes referred to as a "parietal hand" (Prakash et al., 2011) and other cortical sensory deficits like hemianesthesia and hemineglect which cause a poor proprioceptive awareness and could restrict the skill for playing (Scepkowski and Cronin-Golomb, 2003).

CONCLUDING REMARKS

This case report shows that pAHS could appear in the dominant limb from a widespread disruption of brain networks which exceeds left posterolateral parietal and occipital cortices. Moreover, these symptoms could get worse during a specific task as playing the piano. Further imaging research is needed in order to understand the neural pathways involved in pAHS. A combination of neurological assessment and anatomical and functional imaging may provide invaluable information about relationship between clinical features and anatomic localization of pAHS and contribute to further expand our knowledge about this rare condition and anomalous self-body perception.

AUTHOR CONTRIBUTIONS

AA, AB and EF designed the study. AA was responsible for clinical data on the case. AB contributed to the acquisition and analysis of images. AA, EF, AB, FJB and NG carried out the interpretation of data. AA and EF prepared the final version of the article.

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Subjectivity of the Anomalous Sense of Self Is Represented in Gray Matter Volume in the Brain

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The self includes complicated and heterogeneous functions. Researchers have divided the self into three distinct functions called "agency," "ownership," and "narrative self". These correspond to psychiatric symptoms, behavioral characteristics and neural responses, but their relationship with brain structure is unclear. This study examined the relationship between the subjectivity of self-related malfunctions and brain structure in terms of gray matter (GM) volume in 96 healthy people. They completed a recently developed self-reported questionnaire called the Embodied Sense of Self Scale (ESSS) that measures self-related malfunctions. The ESSS has three subscales reflecting the three distinct functions of the self. We also determined the participants' brain structures using magnetic resonance imaging (MRI) and voxel-based morphometry (VBM). Multiple regression analysis revealed a significant negative correlation between ownership malfunction and the insular cortex GM volume. A relationship with brain structure could thus only be confirmed for the ESSS "ownership" subscale. This finding suggests that distinct brain structures feel ownership and that the ESSS could partly screen for distinct brain structures.

Keywords: voxel-based morphometry, minimal self, ownership, agency, narrative self

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INTRODUCTION

For centuries, researchers have searched for the "self" (consciousness) in the brain, but no specific region seems to be dedicated to this (Legrand and Ruby, 2009). This is probably because the entire brain is involved in multiple functions and works as a network, forming what is called the default mode network (Northoff et al., 2006; Grimm et al., 2011; Qin and Northoff, 2011; Lipsman et al., 2014). The self can be regarded as surveilling the body, actions, and even the external environment (i.e., perception), which suggests that activity and functions corresponding to the self are distributed throughout the brain.

To better understand the self and its neural correlates, researchers have divided the self into essential and distinct functions. For example, Gallagher (2000) has postulated two

Abbreviations: DARTEL, diffeomorphic anatomical registration through exponentiated Lie algebra; DLPFC, dorsolateral prefrontal cortex; ESSS, Embodied Sense of Self Scale; GM, gray matter; VBM, voxel-based morphometry.

components of the self: the minimal self and the narrative self. The minimal self is the online sensation of self and includes the sense of body (i.e., ownership) and action (i.e., agency). The narrative self is the offline storage for maintaining the sense of past and future self and includes autobiographical memory, personality and identity.

This categorization is still used in many studies because these concepts can be studied and, more importantly, tested using cognitive or neuroscientific methodologies. These functional selves have been examined theoretically through philosophy, clinical investigations and even computer models; subjectively through questionnaires and interviews; behaviorally through observations and experiments; electro-physiologically through electroencephalography (EEG) and skin conductance responses; and neurologically through functional and structural brain imaging. For example, the rubber hand illusion modulates our sense of ownership of our hand (Botvinick and Cohen, 1998). This has been examined using behavioral responses (Pavani et al., 2000), skin conductance responses (Armel and Ramachandran, 2003), skin temperature (Moseley et al., 2008), EEG (Kanayama et al., 2007, 2017; Press et al., 2008; Evans and Blanke, 2013), functional magnetic resonance imaging (fMRI; Ehrsson et al., 2004; Tsakiris et al., 2010; Brozzoli et al., 2012), and Bayesian causal modeling (Samad et al., 2015). The relationship between ownership and agency has also been experimentally investigated (Kalckert and Ehrsson, 2012, 2014). As a result, we now know that in healthy people, the subjectively reported minimal and narrative selves are expressed through behavior, physiological responses and brain activity.

However, previous studies have produced inconsistent results even when using the same measurements. This suggests the existence of individual differences in consciousness of the self. Traditional psychological studies have repeatedly shown the impact of individual differences using validated questionnaires (for schizophrenia, see Asai et al., 2011; Kanayama et al., 2009 for depersonalization; and Kanayama et al., 2008 for dissociative disorder). In cognitive neuroscience, some recent studies have shown that neural responses may be modulated by cortical structure (Suzuki et al., 2013), spontaneous cortical activation (Northoff et al., 2010; Nakao et al., 2013), and their interaction (Tavor et al., 2016), suggesting individual differences in neural responses as well. For a deeper understanding of the functional self, including the individual differences found in cognitive neuroscience studies, it is important to elucidate the relationship between individual differences measured using subjective reports and those measured neurologically. Some studies have shown that experience and learning induce structural changes in the human brain (Draganski and May, 2008; May, 2011). It may therefore be informative to compare anatomical brain structure with individual differences in the subjectively reported functional self. However, the relationship between anatomical brain structure and subjectivity of the functional self remains unclear. While some neuropsychological and psychiatric studies of patients with schizophrenia or brain lesions have investigated this, they did not measure subjectivity of the functional self in healthy subjects in daily life (rather than during a specific task) as an individual difference variable.

A previous study that applied exploratory factor analysis to a self-related questionnaire (Longo et al., 2008) showed that the factor structures of subjective response were related to the functional self, but the study was highly optimized for its own data. This data-driven approach failed to find a common factor structure for the functional self across studies. One difficulty was the lack of correspondence with studies that used different methodologies (e.g., fMRI). Therefore, a self-reported questionnaire for conceptions of the self was recently developed in a theory-driven manner. It is called the Embodied Sense of Self Scale (ESSS), and it measures three subfactors: "agency," "ownership," and "narrative" (Asai et al., 2016). The ESSS was developed by first listing 120 items related to the embodied sense of self, including items to assess schizotypal, depersonalizing and dissociative tendencies that relate to agency, ownership and narrative, respectively. Twenty-five items were ultimately selected for the short version, which is a reliable, valid and statistically usable scale. It significantly correlates with some related scales and clearly distinguishes healthy controls and patients with chronic schizophrenia (thought to be a disorder of the embodied sense of self).

This is the first study to examine how the subjectivity of self-related malfunctions correlates with brain structure in healthy people. For this, we searched for correlations between the ESSS subscales and measured gray matter (GM) volumes.

We focused on cortical regions that were related to the self-subscales in previous studies. We have a clear model of agency-related brain area networks because many experimental and schizophrenia patient studies have examined self-agency. These studies indicated that the cerebellum and left dorsolateral prefrontal area were involved in agency-related psychological functions. Cerebellar activation in particular was observed in subjects predicting the sensory consequences of self-action (Blakemore et al., 1999; Farrer and Frith, 2002) and those recognizing discrepancies between actual and predicted sensory consequences (Blakemore et al., 2001; Leube et al., 2003). Some studies have shown that the middle frontal gyrus detects visuomotor incongruencies (David et al., 2007; Farrer et al., 2008) and the agency of a self-propelled moving ball (Stosic et al., 2014). Schnell et al. (2007) also showed that a wide area of the middle frontal gyrus responded to the onset of visuomotor incongruence in a video game. This suggests that the dorsolateral prefrontal cortex (DLPFC) could be involved in switching the internal model of visuomotor contingency to predict body movement and sensory feedback (Imamizu et al., 2004; Imamizu and Kawato, 2008). The DLPFC is anatomically connected to the cerebellum (Kelly and Strick, 2003), which suggests that the DLPFC also has a role in switching the internal visuomotor model stored in the cerebellum in response to changing circumstances. However, structural abnormalities of the prefrontal cortex have been repeatedly reported in schizophrenic (Nickl-Jockschat et al., 2011; Schnack et al., 2014) and schizotypal individuals (Nenadic et al., 2015), while cerebellum atrophy has been less frequently reported (Zhang et al., 2015). We therefore focused on the DLPFC as an area of interest for the agency subscale.

We do not have as clear a model of the cortical networks and structural abnormalities relevant to the ownership subscale. The postcentral gyrus and insular cortex might be relevant because they are activated during the synchronous visuotactile stimulation of the rubber hand illusion (Ehrsson et al., 2004; Tsakiris et al., 2010). Additionally, the angular gyrus is a sensory association area commonly damaged in patients who frequently have out-of-body or autoscopic experiences (Blanke et al., 2004). Of these areas, the postcentral gyrus is an unlikely candidate because it is a primary somatosensory area with no reported abnormalities even in depersonalization disorder (Sierra et al., 2002), which is closely related to ownership dysfunction. The inferior parietal cortex, which contains the angular gyrus, is structurally abnormal in schizophrenic (Schnack et al., 2014) and schizotypal individuals (Nenadic et al., 2015), suggesting that it is not exclusively related to body ownership dysfunctions. However, the insular cortex is a good candidate because a body ownership-related task activates it (Tsakiris et al., 2007), but damage to this area has no impact on self-agency as measured by a task that requires distinguishing between self-generated and other-generated actions (Philippi et al., 2012). Additionally, a positron emission tomography study reported that the feeling of movement control in schizophrenia patients was related to regional cerebral blood flow in the right angular gyrus but not in the insular cortex (Farrer et al., 2004). We therefore examined the insular cortex as an area possibly correlated with the ownership subscale and irrelevant to the agency subscale.

It is difficult to identify any specific cortical region that is likely associated with the narrative self-ubscale. Araujo et al. (2015) tried to separate the core (minimal) self and autobiographical self using fMRI and showed that numerous cortical regions, including the temporal pole, precuneus and lateral occipital cortex, were involved in autobiographical self-recognition as measured with personality trait questionnaires. Legrand and Ruby (2009) showed that a task requiring self-relatedness evaluation, which is closely related to personality as an important concept of narrative self, activated cortical areas distributed over a wide cerebral network, including the medial prefrontal cortex, precuneus, temporoparietal junction and temporal poles. They suggested that this cortical network could be explained by two cognitive processes: inferential processing and memory recall. If the narrative self is a temporal expansion of the minimal self (Gallagher, 2000), it must include a process to retrieve autobiographical memory (memory recall) and a process to use these retrieved memories to generate behavioral patterns (e.g., personality) for optimizing future behavior (inferential processing). We therefore examined the network areas from Legrand and Ruby (2009) for possible correlations with the ESSS narrative self-subscale.

We hypothesized that in healthy participants regularly experiencing self anomalies in daily life, ESSS-measured subjectively reported self-related malfunctions would predict GM volume in the target cortical areas mentioned above.

MATERIALS AND METHODS

Participants

Ninety-six healthy participants were recruited from two sites (Site A and B). Fifty-one participants (26 women and 25 men, mean age = 22.50 years, standard deviation (SD) = 3.39 years) were recruited from Site A. Forty-five participants (10 women and 35 men, mean age = 22.60 years, SD = 4.81 years) were recruited from Site B. All participants were right-handed, had no history of psychiatric or neurological disorders, and met our magnetic resonance imaging (MRI) safety criteria (e.g., not wearing any magnetic material, non-claustrophobic). Participants were paid for their participation.

This study was carried out in accordance with the recommendations of Human Research Ethics Committee of Hiroshima University and the Research Ethics Committee of Kochi University of Technology with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the Human Research Ethics Committee of Hiroshima University and the Research Ethics Committee of Kochi University of Technology independently.

Questionnaires

Participants from Site A completed an 80-item version of the ESSS, while participants from Site B completed a 25-item version. Fifty-five items from the Site A ESSS were excluded, and the remaining 25 items were identical to those of the Site B ESSS. The total score and sub-scores were calculated from these 25 items.

Participants answered each item by clicking a radio button on a personal computer, with ratings on a 5-point Likert scale ranging from "Strongly disagree" to "Strongly agree". Based on a previously reported factor analysis of this questionnaire (Asai et al., 2016), we calculated three sub-scores. The first was "ownership," which included nine items related to malfunction of bodily awareness or body perception. The second was "narrative," which included eights items describing the consistency of personality or self-identification. The last was "agency," which included eight items related to the sense of controlling oneself or one's own movement. The details of these subscales are described in Asai et al. (2016).

MRI Data Acquisition

The participants at Site A and B both underwent MRI on a 3.0-tesla Siemens Verio Scanner (Siemens Ltd., Munich, Germany). We obtained structural MRI scans using a 32-channel head coil and whole-brain T1 weighted volumetric sequence using magnetization-prepared rapid-acquisition gradient echo (MP-RAGE). The following acquisition parameters were identical at both sites: inversion time = 900 ms, flip angle = 9°, matrix size = 256 × 256, voxel size = 1 × 1 × 1 mm, slice thickness = 1 mm, and sagittal acquisition. The Site A-specific parameters were as follows: echo time (TE) = 2.98 ms, repetition time (TR) = 2300 ms, field of view (FOV) = 256 × 256 × 176 mm, and number of slices = 176. The Site B-specific parameters were as follows: TE = 3.06 ms, TR = 2250 ms, FOV = 256 × 256 × 192 mm, and number of slices = 192.

Preprocessing and Voxel-Based Morphometry (VBM) Analysis

Before voxel-based morphometry (VBM) analysis, all images were aligned to the anterior-posterior commissure axis to set the origin to the anterior commissure and set the images parallel to the axis. This was done using the auto_reorient.m MATLAB (MathWorks, Natick, MA, USA) script[1], and unexpected errors were confirmed by visually inspecting the aligned images.

VBM analysis was conducted using SPM12 (rev 6225; The Welcome Department of Cognitive Neurology, London, UK) in MATLAB v. 8.3. First, all images were segmented into GM, white matter, cerebrospinal fluid, or non-brain parts after intensity non-uniformity correction. For this segmentation, we used the strong criterion (labeled "Thorough") in SPM12 because we observed that non-brain tissue remained when we used the light criterion ("Light"). Furthermore, for anatomical normalization (affine regularization), the East Asian Brain template was selected. All other parameters were SPM12's default settings.

Next, GM and white matter population templates were generated from all dataset images using the diffeomorphic anatomical registration through exponentiated Lie algebra (DARTEL; Ashburner, 2007). The DARTEL technique was implemented in SPM12 with default settings. First, an affine transformation was initially applied to the GM and white matter DARTEL templates to align them to the tissue probability maps in Montreal Neurological Institute space[2]. The GM images were then non-linearly warped to the DARTEL GM template in Montreal Neurological Institute space. The warped images were modulated using Jacobian determinants calculated by the nonlinear deformation field to preserve relative GM volumes even after spatial normalization. The modulated images were smoothed with an 8-mm full-width at half-maximum Gaussian kernel. The smoothed, modulated and normalized GM datasets were then statistically analyzed.

Statistical Analysis

We performed multiple regression analysis to investigate correlations between ESSS subscale scores and regional GM volumes. For all subsequent regression analyses, the covariates included age, sex and total intracranial brain volume. The three ESSS subscales were registered as independent variables, and regional GM volume was registered as a dependent variable. To exclude any effect of site on correlations between GM volumes and ESSS scores, we made the site a dummy variable (0 = Site A, 1 = Site B) and made the dummy variable a statistical test covariate based on a suggestion made by Pardoe et al. (2008).

Region of Interest (ROI) Analysis

For statistical VBM analysis, a mask image of the cortical region of interest (ROI) was made for each ESSS subscale. For the agency subscale, we used a mask image of Brodmann area 46 to represent the middle and inferior frontal gyri. For the ownership subscale, we used a mask image of the insular cortex. For the narrative subscale, we used a mask image of the superior medial frontal and medial orbitofrontal cortices to represent the medial prefrontal cortex, the precuneus and the angular gyrus and a mask image of the supramarginal gyrus to represent the temporoparietal junction and the middle and superior temporal poles. The mask images were generated based on Automated Anatomical Labeling and the Brodmann area separations. Statistical significance was defined as $p < 0.05$ after correction with the family-wise error (FWE) method at peak level.

Whole-Brain Analysis

We conducted whole-brain analysis using several statistical thresholds. Based on Lieberman and Cunningham (2009), we first created a statistical map with an uncorrected $p < 0.001$ threshold and 20-voxel extent to balance Type-I and Type-II errors, but the 20-voxel extent was arbitrary and insufficiently strict for controlling Type-I errors, as shown in a study using permutation testing (Eklund et al., 2016). To confirm a statistically significant voxel extent, we calculated alternative cluster size thresholds using: (1) permutation testing of the participants' original questionnaire scores and GM volumes; (2) the original questionnaire score sets and 96 GM volume sets randomly sampled from two open datasets (198 Beijing participants and 198 Cambridge participants) registered with the Functional Connectomes Project (Biswal et al., 2010); and (3) 96 dummy questionnaire score sets randomly generated in ranges appropriate for each scale (for example, 9–45 for the ownership subscale because it has nine 5-point scale items) and 96 GM volume sets from the same open sources used in (2). For (1), each individual's questionnaire score set was randomly assigned to another individual's GM volume set. For (2) and (3), 51 GM volume sets were selected from one data source and another 45 volume sets were selected from the other to imitate the original data sets coming from two different sites.

The preprocessing and statistical testing for the permuted and random sampled data were identical to those for the original data. Statistical tests were repeated 1000 times, and the 1000 maximum brain region cluster sizes that were significantly correlated with the ESSS subscales (uncorrected $p < 0.001$) were calculated and sorted in ascending order. The 950th highest value in the sorted vector was used as a statistical significance threshold for cluster size. By testing for positive or negative correlations for three subscales, we conducted six tests and generated six cluster size significance thresholds for each repetition. The maximum value among these six thresholds was finally adopted as the statistical analysis threshold.

RESULTS

Averages and SDs of ESSS total and subscale scores are listed in **Table 1**, and total brain volumes are listed in **Table 2**.

ROI Analysis

Correlation analysis revealed a significant negative correlation between ownership subscale scores and GM volumes in the

[1] http://www.nemotos.net/?p=17
[2] http://www.mni.mcgill.ca/

TABLE 1 | Average ESSS total and subscale scores.

	ESSS agency	ESSS ownership	ESSS narrative	ESSS total
Average	22.40	16.75	24.56	63.71
SD	5.79	5.88	5.91	15.00

Abbreviations: ESSS, Embodied Sense of Self Scale; SD, standard deviation.

left posterior insular cortex (peak coordinates: $x = -47$, $y = 2$, $z = -2$; number of voxels = 42; $t = 3.91$, $p < 0.05$ after FWE correction at peak level; **Figure 1**). There were no other significant correlations between regional GM volumes and ESSS subscale scores.

Whole-Brain Analysis

Permutation testing of the original data calculated 615 as the minimum significant cluster size. Random sampling tests that paired open source cortical structure data with either the original questionnaire scores or randomly generated questionnaire scores calculated significance thresholds of 797 or 682, respectively.

With an uncorrected $p < 0.001$ threshold and a 20-voxel extent, all significant correlations between GM volumes and questionnaire scores are listed in **Table 3**. As listed in **Table 3**, no cortical area had a cluster size greater than the lowest statistical threshold (615 voxles). The greatest cluster size which was found in analysis with our original data was 224 for the positive correlation between the narrative subscale scores and GM volumes in the left inferior temporal gyrus. There were therefore no significant correlations in whole-brain analysis using corrected cluster size criteria.

The significant correlations between ESSS subscales and GM volumes in whole-brain analysis with an uncorrected $p < 0.001$ threshold and a 20-voxel extent were described below.

Correlation between Agency Subscale Scores and GM Volumes

Agency subscale scores were positively correlated with GM volumes in the right cerebellum (peak coordinates: $x = 44$, $y = -59$, $z = -36$; number of voxels = 90; $t = 3.46$; **Figure 2A**). Agency scores were negatively correlated with GM volumes in two cortical areas: the left medial orbitofrontal cortex (peak coordinates: $x = -15$, $y = 38$, $z = -24$; number of voxels = 68; $t = 3.72$; **Figure 2B**) and the left medial frontal cortex (peak coordinates: $x = -30$, $y = 35$, $z = 26$; number of voxels = 60; $t = 3.69$).

Correlation between Ownership Subscale Scores and GM Volumes

Ownership subscale scores were negatively correlated with GM volumes in three brain areas: the left insular cortex (peak coordinates: $x = -47$, $y = 2$, $z = -2$; number of voxels = 134; $t = 3.91$; **Figure 2C**), left angular gyrus (peak coordinates: $x = -53$, $y = -56$, $z = 30$; number of voxels = 31; $t = 3.48$), and right postcentral gyrus (peak coordinates: $x = 59$, $y = -21$, $z = 47$; number of voxels = 32; $t = 3.37$). Ownership scores were not significantly positively correlated with GM volumes in any examined area.

TABLE 2 | Average volumes and SDs of gray matter, white matter and total brain.

	Gray matter	White matter	Total brain
Average (cm^3)	773.09	464.86	1237.95
SD (cm^3)	58.23	48.59	97.69

Abbreviations: SD, standard deviation.

Correlation between Narrative Subscale Scores and GM Volumes

Narrative subscale scores were positively correlated with GM volumes in five cortical areas: the left lingual gyrus (peak coordinates: $x = -35$, $y = -92$, $z = -20$; number of voxels = 96; $t = 3.89$), left inferior temporal gyrus (peak coordinates: $x = -47$, $y = -57$, $z = -11$; number of voxels = 224; $t = 3.85$; **Figure 2D**), right cuneus (peak coordinates: $x = 9$, $y = -101$, $z = 15$; number of voxels = 60; $t = 3.80$), left superior temporal pole (peak coordinates: $x = -50$, $y = 9$, $z = -2$; number of voxels = 107; $t = 3.80$), and left precuneus (peak coordinates: $x = -11$, $y = -39$, $z = 56$; number of voxels = 46; $t = 3.37$). Narrative scores were not significantly negatively correlated with GM volumes in any examined area.

DISCUSSION

We aimed to determine the relationship between subjectively reported self-related malfunction and GM volume. Self-related malfunctions were subjectively measured using our recently developed ESSS questionnaire (Asai et al., 2016). The ESSS measures daily experiences rather than illusory feelings induced by specific experimental tasks (e.g., the rubber hand illusion). ROI analysis showed that ownership subscale scores were negatively correlated with left posterior insula GM volumes. This association suggests that daily experiences of self-related malfunctions could induce cortical structure changes. We also conducted whole-brain analysis, but this showed no significant correlations between cortical areas and ESSS subscale scores.

Correlations between the Left Posterior Insula and the Ownership Subscale

As expected, we observed a significant correlation between ownership subscale scores and left posterior insula GM volumes. The insular cortex has been repeatedly shown to be related to body ownership through such tests as the rubber hand illusion (Tsakiris et al., 2007; Limanowski et al., 2014), but it is not strictly limited to body ownership because agency-related tasks can also activate it (Leube et al., 2003). Additionally, both the right and left insular cortices are activated by viewing a video consistently subject to self-controlled movement (Farrer and Frith, 2002; Farrer et al., 2004). Given that some lesion studies

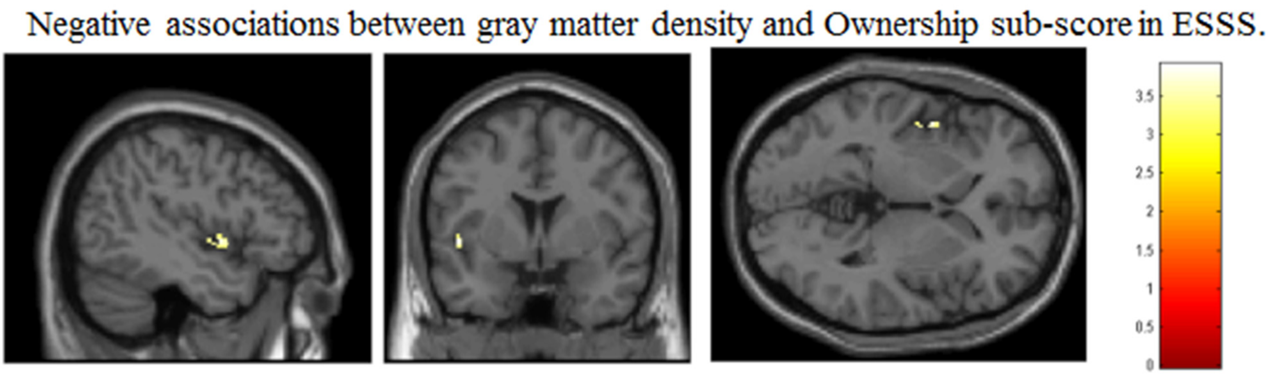

FIGURE 1 | Significant correlations between GM volumes and ESSS ownership subscale scores by ROI analysis. Abbreviations: GM, gray matter; ESSS, Embodied Sense of Self Scale; ROI, region of interest.

have shown that the bilateral insular cortex is not responsible for self agency (Philippi et al., 2012; Damasio et al., 2013), the insular cortex is not solely related to agency or ownership but includes additional complex cognitive functions. Indeed, Kurth et al. (2010) conducted a meta-analysis of the insular cortex's psychological functions and showed their differentiation into emotional, chemosensory, sensorimotor and cognitive domains. From these, interoception in the sensorimotor domain had the location (−41, 2, 3 for the left hemisphere) closest to that of the left insular cortex in our results (−47, 2, −2). The insular cortex is also activated by such tasks as listening to one's own heartbeat or suppressing the urge to void, consistent with Seth's model in which the insular cortex is related to interoceptive inference and self-embodiment (Seth, 2013). This suggests that the insular cortex might be reduced in size by impaired self-awareness of body ownership due to altered interoceptive inference.

However, the ESSS ownership subscale includes the following item: "Sometimes it feels like my body is jerky like a robot". The term "jerky" in this sentence could mean uncontrollable movement, suggesting that altered body sensation is closely related to movement related malfunctions (for all the items, see Asai et al., 2016). This suggests that the ownership subscale is not fully separated from the agency domain. Altogether, it remains unclear whether the two minimal self factors, agency and ownership, are sufficiently separated in the ESSS. Future studies should directly investigate this.

Correlations of GM Volume with ESSS Subscale Scores

Whole-brain analysis based on the criteria by Lieberman and Cunningham (2009) revealed that ESSS subscale scores were significantly correlated with GM volumes in some areas, and these regions were highly predictable based on the findings from previous studies. For example, agency subscale scores were correlated with GM volumes in the cerebellum and middle frontal gyrus, which were activated during active movement inducing a sense of agency over a rubber hand (Tsakiris et al.,

TABLE 3 | Brain regions in which local GM volume was significantly correlated with ESSS subscale scores.

Location name	*x*	*y*	*z*	*k*	*t*
Negative correlations between GM volumes and ownership scores					
L insula (BA 13)	−47	2	−2	134	3.91
L angular gyrus (BA 39)	−53	−56	30	31	3.48
R postcentral gyrus (BA 2)	59	−21	47	32	3.37
Positive correlations between GM volumes and narrative scores					
L lingual gyrus (BA 18)	−35	−92	−20	96	3.89
L inferior temporal gyrus	−47	−57	−11	224	3.85
R cuneus (BA 18)	9	−101	15	60	3.80
L superior temporal pole (BA 22)	−50	9	−2	107	3.80
L precuneus (BA 5)	−11	−39	56	46	3.37
Positive correlation between GM volumes and agency scores					
R cerebellum crus 1	44	−59	−36	90	3.46
Negative correlations between GM volumes and agency scores					
L medial orbitofrontal cortex (BA 11)	−15	38	−24	68	3.72
L middle frontal cortex (BA 9)	−30	35	26	60	3.69

Regions significantly correlated with each ESSS subscale are listed. The codes in parentheses indicate Brodmann areas (e.g., BA13 = Brodmann area 13). In the first row, x, y and z refer to Montreal Neurological Institute coordinates, k refers to the number of voxels in each significant area and t refers to the t-score in each brain region (local maxima). Abbreviations: GM, gray matter; ESSS, Embodied Sense of Self Scale; L, left; R, right.

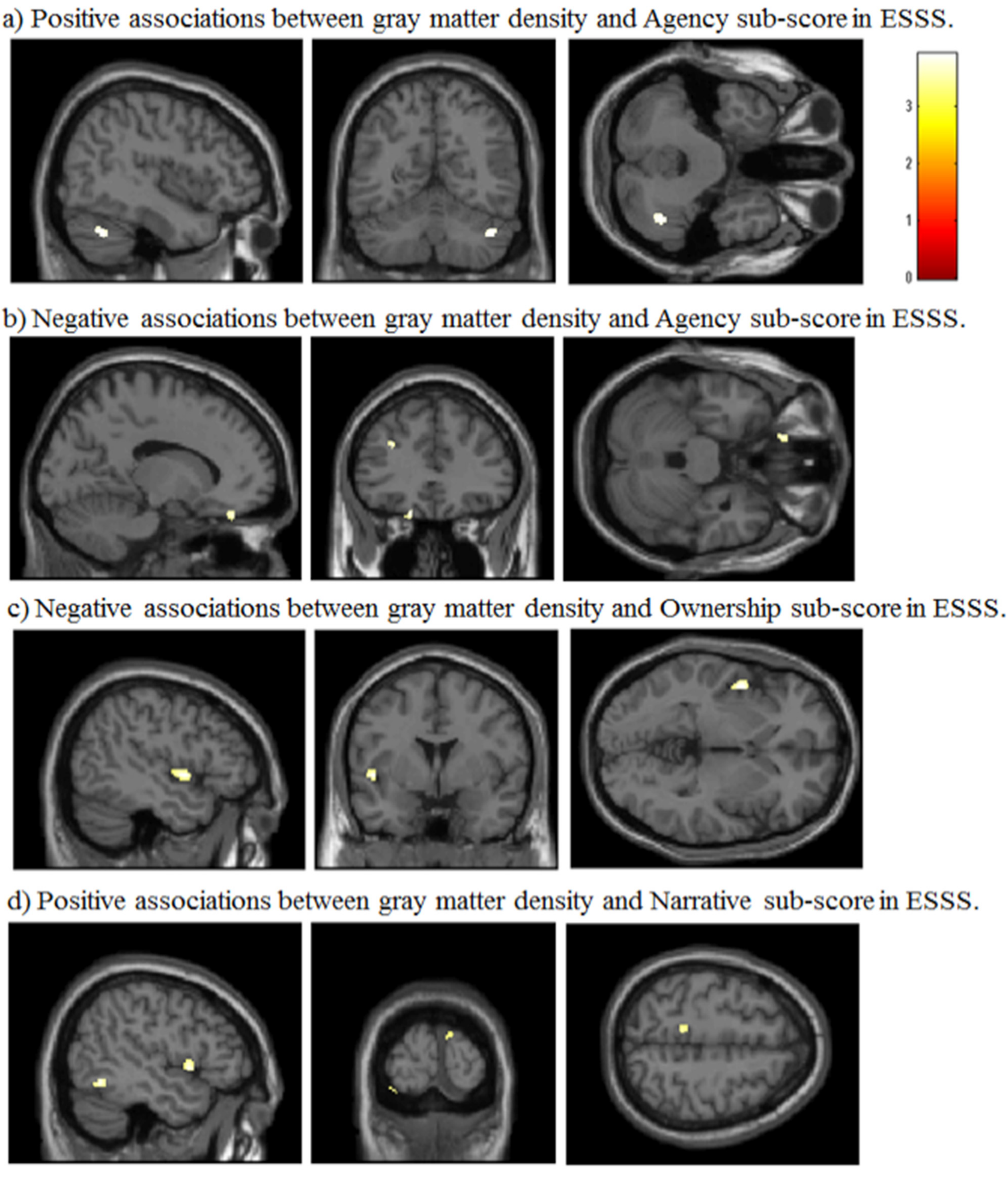

FIGURE 2 | Significant correlations between GM volumes and ESSS subscale scores by whole-brain analysis. (A) Positive correlations between GM volumes and ESSS agency subscale scores. The right cerebellum is highlighted in the sagittal, coronal and transverse views [44, −59 −36]. **(B)** Negative correlations between GM volumes and ESSS agency subscale scores. The left medial orbitofrontal cortex is focused in the sagittal, transverse view. The left medial orbitofrontal and left medial frontal cortices are highlighted in the coronal view [−14, 34 −27]. **(C)** Negative correlations between GM volumes and ESSS ownership subscale scores. The left insular cortex is focused in the sagittal, coronal and transverse views [−47, 2, −2]. **(D)** Positive correlations between GM volumes and ESSS narrative subscale scores. The left superior temporal pole and left inferior temporal gyrus are highlighted in the sagittal view. The left lingual gyrus and right cuneus are highlighted in the coronal view. The left precuneus is highlighted in the transverse view [−47, −96, 56]. Abbreviations: GM, gray matter; ESSS, Embodied Sense of Self Scale.

2010). Ownership subscale scores were correlated with GM volumes in the postcentral gyrus, insula and angular gyrus, which might be engaged in bodily self-consciousness, including body ownership (Blanke et al., 2004; Ehrsson et al., 2004; Tsakiris et al., 2010). We found that narrative subscale scores were positively correlated with GM volumes in the left lingual gyrus, the left inferior temporal gyrus, the right cuneus, the left superior temporal pole and the left precuneus. These areas overlapped with the network activated by a self-relatedness evaluation task (Legrand and Ruby, 2009). However, these correlations could not survive under strict criteria using permutation testing, which suggests that they are not statistically robust.

Limitations

One limitation of this study is that scanning was conducted at two sites. Although almost all scan parameters were identical, this might have contaminated the results, as might other uncontrolled variables such as region, culture and experimenter. The two sites were located in different prefectures on different islands, so the cultural differences could be sufficient to affect the results. Additionally, the scanning method may have differed between experimenters (e.g., fixation of the head or the degree of detail given in instructions), which could have affected the structural image. We attempted to control for site effects by following a recommendation in Pardoe et al. (2008). Some studies (e.g., Moorhead et al., 2009) have shown that a VBM study's statistical power can be improved by adjusting probability maps for the distribution of gray and white matter. Since this requires at least two scans on each scanner, we could not apply it to our results, so we should consider the possibility that important relationships between brain areas and questionnaire scores may have gone undetected.

One major limitation of our study is that no significant correlations between regional GM volumes and ESSS subscale scores were found in cluster size analysis. A recent study cautioned that statistical significance thresholds using cluster size tend to cause 60%–80% Type I error rates (Eklund et al., 2016). This can be mitigated by using permutation testing (Eklund et al., 2016), but we found that this led to a significance threshold of more than 600 voxels, far greater than the highest observed value at 224 voxels. Consequently, our whole-brain analysis showed no significant correlations between ESSS subscales and GM volumes. The significance threshold was little different even if we used open source human brain structure data from the Functional Connectomes Project (Biswal et al., 2010) that were also used in Eklund et al. (2016). This analysis assumes that there is no relationship between ESSS scores and GM volumes, so we expected a low significance threshold. However, the minimum significant cluster size was 797, which was even higher than that obtained with our own data. To further generalize this criterion, we also conducted the same repetition test using the same open source GM volume data but with dummy questionnaire data generated with a score range restriction. This analysis too calculated a significance threshold of more than 600 voxels. Altogether, these findings suggest that when analyzing correlations between GM volumes and questionnaire scores in a relatively small organ like the cortex, it might not be appropriate to use cluster size as a criterion, at least if the ESSS is the questionnaire.

CONCLUSION

Collectively, ESSS-measured, ownership-related self malfunctions in daily life were confirmed to be associated with the insular cortex. This is consistent with previous findings about the cortical areas related to self ownership. It also shows that the ESSS can be a quick assessment tool to predict individual differences in cortical volume related to ownership malfunction.

AUTHOR CONTRIBUTIONS

NK and TA designed the study. NK, TA, KM, RK, TU, TY, and HK performed the experiment. NK and TN analyzed the data. NK, TA, and TN wrote the manuscript. SY supervised the project. All authors approved the final version of the manuscript.

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Attentive Observation Is Essential for the Misattribution of Agency to Self-Performance

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Recent studies have repeatedly demonstrated a false memory phenomenon in which people falsely remember having performed an action by oneself when in fact they have only observed the action by another person. We investigated the attentional effect to the action itself on the observation inflation. Fifty-four participants first performed and read actions (Phase 1); then, they observed the action video that showed another's actions (Phase 2), some of which they had not performed in Phase 1. In the Phase 2, they were required to focus on either the actor's performance (i.e., attentive observation condition) or irrelevant objects, which were presented in the background (i.e., inattentive observation condition) to modulate their attention. Around 2 weeks later, participants took a surprise source-memory test (Phase 3). In this phase, we asked them to judge whether they "performed," "read," or "not presented" the action in Phase 1. Three participants were removed from analysis, because they could not attend Phase 3 within 10–16 days after completion of the second phase. We found observation inflation only in the attentive condition, which contradicted the notions from other false memory studies that showed that attention to the target stimuli reduced false memory in general. We discussed the observation inflation mechanism from the perspective of the "like me" system, including the mirror neuron system, self-ownership, and self-agency.

Keywords: attention, false memory, observation inflation, mirror neuron system, agency, ownership, self-other confusion

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INTRODUCTION

Recent studies have demonstrated a false memory phenomenon which is thought to be due to self-other confusion in the action memory of healthy individuals (e.g., Lindner et al., 2010, 2016; Schain et al., 2012). This phenomenon has been called the OI, in which people falsely remember having performed an action by oneself when in fact they have only observed the action by another person (Lindner et al., 2010). OI represents that people possibly misattribute the sense of agency of the observed action to the self by just observing other people's actions. Originally, self-other confusion as an agent of a certain action has been a symptom observed in psychiatric patients, for example, auditory hallucinations in most schizophrenic patients (Nayani and David, 1996). This is caused by a patient's actual utterances, as stated by previous researchers (e.g., McGuigan, 1966; Green and Preston, 1981). Thus, "self-other confusion" as one of a symptom means the confusion of agency judgment "who is the agent of a certain action." Healthy adults do not likely to confuse own action with others at the moment, however, such confusion can occur in memory.

Abbreviations: OI, observation inflation effect; MNS, mirror neuron system; TPJ, temporo-parietal junction.

Since the first study addressing this phenomenon, which developed and used methodology to approach it (i.e., Lindner et al., 2010), OI has been demonstrated per the following experimental paradigm: first, participants perform or read simple action statements (Phase 1; e.g., "shake the bottle!"). Then, they are asked to observe video clips that show another person's actions (Phase 2). Two weeks later, they take a surprise source-memory test where they are asked to judge whether they "performed," "read," or "not presented" the action in Phase 1 (Phase 3). OI is thought to arise when they believe they performed some of the actions in Phase 1 that in fact they only observed in Phase 2.

Previous researchers studying OI have demonstrated that both facilitating and disturbing factors affect this misattribution during observation of another's actions. When we observe another's action, we can obtain information to induce a feeling "as if I do it," whereas we can find any clue to be conscious of the fact that the agent of the action is other. These ideas have already been advocated in the "like me" hypothesis, which is a system to determine whether a certain agent is close to oneself (Meltzoff, 2007).

Regarding OI's facilitating factor, it has been suggested that motor simulation using the MNS, which is activated both during performing an action and observing another's action (Rizzolatti and Craighero, 2004), is one of the critical processes that induce false memories of self-performance (e.g., Lindner et al., 2016). Much evidence has shown the overlap of neural activation during the performance of an action and during the observation of another's action (e.g., Grèzes and Decety, 2001); therefore, it has been considered that motor representation is created during one's own action performance and likewise during observation of another's actions. Previous studies on OI suggested that motor representation created by motor simulation induces the false attribution of self-performance (Lindner et al., 2016).

Regarding OI's disturbing factor, previous research showed that the information in the action video indicating "the actor is not me" decreases the occurrence rate of this misattribution. For example, Lindner et al. (2012) manipulated group membership by actor's complexion (dark vs. fair), and found that when fair-skinned participants observed actions performed by a dark-skinned actor (i.e., out-group actor for participants), the rate of OI was significantly decreased. In addition, Schain et al. (2012) suggested that when the action video showed an actor's face (vs. concealing the actor's face), the rate of OI was significantly reduced. Previous research on a sense of ownership has suggested that body ownership illusion on virtual objects decreased when the object was a black cuboid ("it is not like my own body") compared with when the object was a dummy body ("it is like my own body," Lenggenhager et al., 2007).

Given that OI could be induced during observation of "another's action," the observed body is not, in principle, the observer's body; however, it contains many characteristics indicating the fact that "it is not the observer's body." While attentive observation of only the target action itself may be likely to increase OI because of facilitation of MNS, careful observation of actor in OI paradigm (Lindner et al., 2010) will provide participants with not only motor information but also information about actor's visual features. If so, it is possible that the careful and attentive observation of the other's action decreases the occurrence of OI because participants can feel less ownership of the people in action video. Schain et al. (2012) examined the effect of the actor's face on OI manipulating attentional focus to the action video. They used three experimental conditions. In the first (the face-invisible condition), the actor's face could not be observed by participants. In the second (the face-visible/action-focus condition), the actor's face could be observed by the participants and they were asked to focus on the actor's action. In the third (the face-visible/face-focus condition), the actor's face could be observed by the participants and they were asked to focus on the actor's face. Consequently, in the face-visible/face-focus condition, the occurrence of OI was eliminated. In addition, even if participants focused on the action, the appearance of another's face in the action video (i.e., in face-visible/action-focus condition) decreased OI occurrence rate compared to the face-invisible condition. Per these results, they concluded that attention on the other's face is a crucial factor to disturb OI.

However, Schain et al.'s (2012) experimental design had a possibility to confound two types of attentional effects: the first was attention on the actor's face as to disturb illusory ownership on an actor in the action video (face-visible/face-focus > face-visible/action-focus > face-invisible condition); the second, was attention on the action itself as a factor to facilitate false agency attribution on the other's action (face-invisible ≥ face-visible/action-focus > face-visible/face-focus condition). That is, it still is not clear how attention to the action itself affects the occurrence of OI. Schain et al.'s (2012) findings may be due to the use of a unique stimulus of the face as a distractor. In accordance with Leonetti et al. (2015), MNS activation is enhanced by peripheral vision. In other words, OI should occur in a situation where the observer's attention is not directed to an action itself (i.e., the inattentive observation condition).

In this study, we modulated observer's attention and investigated the impact of the attention on OI to elucidate the top-down influence on the agency misattribution without any modification of the video contents. We focused on the effect of attention on the action itself using visual distractor unrelated to the actor in the action video, instead of the actor's face. We instructed participants to focus on the objects appearing in the background of the action video to investigate the attentional effects of other's actions on OI.

MATERIALS AND METHODS

Participants

Fifty-four healthy undergraduates (29 females, age range = 18–22 years, mean age = 20.3 years, $SD = 1.2$) participated in our experiment. This study was conducted per the recommendations of the Research Ethics Committee of Hiroshima University with written informed consent from all participants. This study was conducted in accordance with the Declaration of Helsinki.

Design

We used a one-way design (observation condition: attentive observation vs. inattentive observation) manipulated within-participants. Both observation conditions used a randomized block design. In the attentive observation condition, participants were instructed to focus on the action of an actor in the video while ignoring objects appearing in the background that were unrelated to the task and actor. In the inattentive observation condition, participants were instructed to focus on some objects in the background of the action video.

Materials

We generated 60 action statements and action videos consistent with Lindner et al. (2010). The action statements described actions to manipulate objects (e.g., "shake the bottle" in Japanese). Each action video was the 15-s composite video that randomly combined 60 movies showing the actor's action performance with 30 landscape photographs by using Adobe After Effects CC 2014.1.1 (13.1.1, Adobe Systems Software Ireland Ltd.: see **Figure 1B**). To distract participants' attention from the actor's action, 6–10 unrelated objects per video randomly appeared in the background of the video (e.g., some books appeared in the picture of the library as part of the background).

The action video was made in accordance with Lindner et al. (2010): that is, the video filmed a female actor's torso, arms, and hands from a third-person perspective. In each video, she performed the actions described in the action statements. Importantly, to conceal the actor's facial characteristics, we omitted the actor's face from the action video. To strengthen homogeneity of the materials, only one female actor performed all actions in the video.

Procedure

The experiment was controlled by a computer and consisted of three phases following Lindner et al.'s (2010) experimental paradigm (**Figure 1**). In Phase 1, in accordance with the previous research, we set the condition for asking participants to read aloud action statements (read condition) in addition to the condition for actually performing an action themselves (perform condition) to secure the task-difficulty. In Phase 2, two observation condition (attentive vs. inattentive) were prepared to investigate the attentional effect. In Phase 3, which was conducted 2 weeks later by Phase 2, we measured their memory for self-performance in Phase 1. The action statements were counterbalanced across participants.

Figure 1A shows the flow of Phase 1. In the first phase, participants performed 15 actions, and read 15 action statements aloud. The item lists shown in each encoding condition were randomly chosen from all 60 action statements, and they were presented at the center of a 24″ BenQ LCD Monitor display in a random order. We presented the following stimuli using Microsoft PowerPoint 2010, which was manually operated by the experimenter. At the beginning of each trial, the experimenter handed an object (e.g., a plastic bottle filled with water) directly to participants after its name and picture appeared on the screen. Then, Japanese instruction to the next action statement appeared on the screen. The instruction meant either "please perform" or "please read." After that, the experimenter told them to obey the instruction (i.e., perform or read the action statement) for 15 s [during this time, the monitor showed both the instruction and the action statement (e.g., "shake the bottle" in Japanese)].

Between the first and second phase, a 5-min arithmetic task was administered as a distractor. **Figure 1B** indicates the flow of Phase 2. In the second phase, participants observed the 15 action videos per condition that showed other's actions. Some videos presented in this phase were not performed earlier (i.e., 5 action statements were performed, 5 were read, and 5 were not performed in Phase 1). In this phase, participants were required to pay attention to an actor's performance (attentive observation condition) or the irrelevant objects, which were presented in the background (inattentive observation condition) while watching the action video. Each observation condition had a different task after watching the video: participants rated the familiarity with the action in everyday life on a five-point Likert scale (attentive observation condition), or participants reported the number of objects that appeared in the background in the video.

Figure 1C demonstrates the flow of Phase 3. The third phase was conducted 10–16 days after the first and second phases. Participants were invited to the laboratory to participate in another experiment and took a surprise source-memory test for all 60 action statements. At the source-memory test, they were asked to judge whether they performed or did not perform (read or not presented) each action described in the statement presented in Phase 1.

According to Lindner et al. (2010), the occurrence rate of OI was calculated as follows: (a) all action statements were assigned into two categories [actually performed/not performed (i.e., read or not presented) in Phase 1], (b) the performed-response (i.e., participants labeled as "I have done the action in Phase 1" in Phase 3; **Table 1**) to the action statements that were not performed in Phase 1 was considered as a false-response, and (c) the subtraction of the proportion of the false-response not observed in Phase 2 from the proportion of the false-response observed in Phase 2 was defined as the OI effect.

We analyzed participants' OI rate in each observation condition. To investigate the differences in OI between both observation conditions, we conducted paired t-tests. In addition, we conducted a one-sample t-test to confirm the occurrence of OI in each observation condition. The alpha level was set at $\alpha = 0.05$. All analyzes were conducted by R studio (R Core Team, 2016). Furthermore, we adopted Cohen's d as an effect size of t-tests calculated by the R package "compute.es" (Del Re, 2013).

RESULTS

All participants who joined the first and second phase of the experiment took part in the third phase. Three participants could not attend the third phase within 10–16 days after from the completion of the second phase. Therefore, we conducted the analysis for the data from 51 participants.

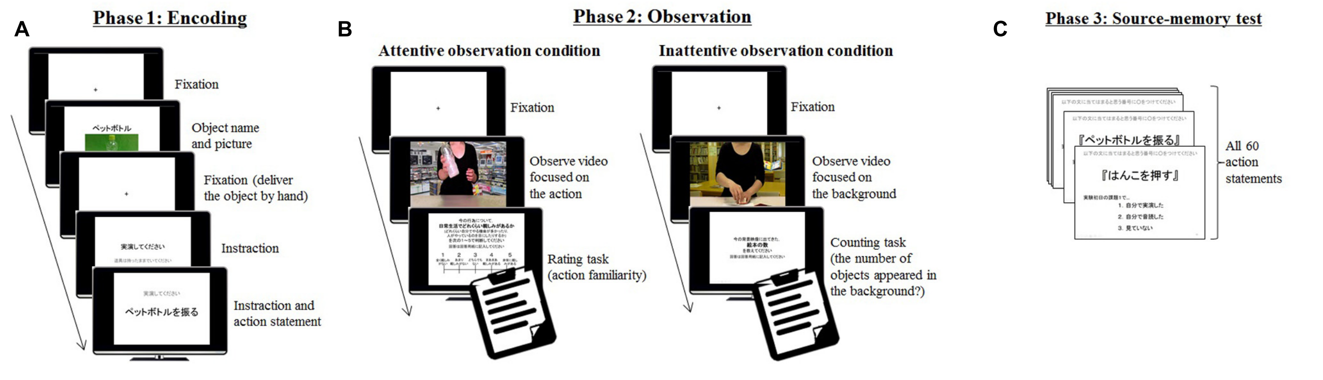

FIGURE 1 | The flow of the procedure. **(A)** Demonstrates the flow of Phase 1, where participants performed or read action statements. **(B)** Demonstrates the flow of Phase 2, including the observation of other's action. **(C)** Demonstrates the flow of Phase 3, where participants completed a source-memory test including whether they performed, read, or did not see a certain action statement in Phase 1. This phase was conducted 2 weeks after Phases 1 and 2.

TABLE 1 | Mean proportion of performed-responses as a function of Phase 1 encoding and Phase 2 observing.

Phase 1: encoding	Phase 2: observing		
	Attentive	**Inattentive**	**No observation**
Performed	0.91 (0.12)	0.84 (0.17)	0.82 (0.20)
Read	0.14 (0.15)	0.04 (0.08)	0.04 (0.09)
Not presented	0.04 (0.10)	0.02 (0.05)	0.00 (0.01)

Performed-responses means the responses that participants labeled as "I have done the action in Phase 1" in Phase 3. All variables varied within participants. Standard deviations are given in parentheses.

Table 1 shows the mean proportions of participants' performed-responses in Phase 3.

The OI effect in each observation condition demonstrated in **Figure 2**.

The Shapiro–Wilk test revealed that the data did not satisfy the assumption of a normal population (for the size of the OI effect in the attentive condition, $w = 0.90$, $p < 0.001$; in the inattentive condition, $w = 0.75$, $p < 0.001$); therefore, we applied the logarithmic transformation.

We found that OI was significantly larger in the attentive condition than it was in the inattentive condition [$t(50) = 5.35$, $p < 0.001$, $d = 1.06$]. In addition, we conducted one-sample t-tests to ascertain whether OI significantly occurred in each condition. Thereby OI was found in the attentive condition [$t(50) = 5.70$, $p < 0.001$, $d = 1.13$], but not in the inattentive condition [$t(50) = 1.93$, $p = 0.06$, $d = 0.38$].

Since the data did not satisfy the assumption of a normal population, we also conducted a non-parametric test (i.e., Wilcoxon signed-rank test) on the OI occurrence rate just to be certain. We also found a trend similar to the results of parametric tests in non-parametric tests: There was still significant differences in the occurrence of OI for the difference between the two observation conditions ($V = 383$, $p < 0.001$), for a one-sample test in the attentive condition ($V = 672$, $p < 0.001$). Note that there was also a significant difference in a one-sample Wilcoxon signed-rank test in the inattentive condition ($V = 145$, $p = 0.04$). However, this result contains 0 in the 95% confidence interval [95% CI = (−0.01, 0.10)].

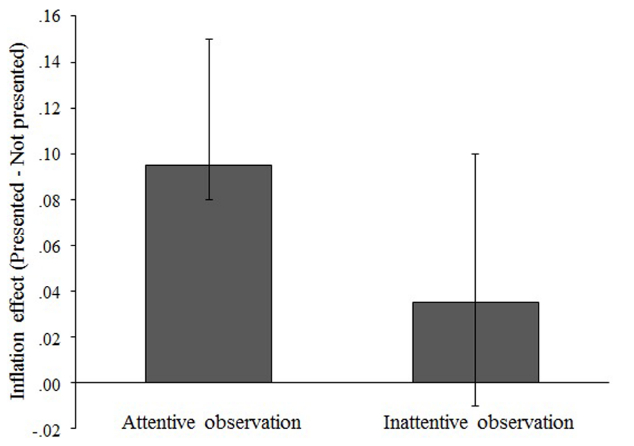

FIGURE 2 | The magnitude of the inflation effect. Results are shown for both Phase 2 observing conditions. Each value shows the (pseudo-) median calculated by the Wilcoxon signed-rank test. The magnitude of the inflation effect was calculated as the difference between the proportion of false performed-responses for action statements presented in Phase 2 and the proportion of false performed-responses for corresponding action statements not presented in Phase 2. Error bars represent the Wilcoxon signed-rank 95% confidence intervals.

DISCUSSION

The aim of this study was to confirm the pure effect of attention to other's action on OI, expanding the findings in Schain et al. (2012).

Observation inflation effect occurred at a significantly higher rate after attentive observation of another's action video compared with after inattentive observation. Considering the studies on MNS, which demonstrated the enhancement of MNS activations when participants observed target action attentively (Muthukumaraswamy and Singh, 2008), attention to action could facilitate "like me" judgment even if it was a misattribution; therefore, greater OI might arise. However, it cannot be said that the MNS activity declined in the inattentive observation condition per the evidence on motor resonance indicating that peripheral vision facilitates the activation of motor resonance, which are supported by MNS activity (Leonetti et al., 2015). Given the circumstances, conversely, another possibility is considered: higher-order cognitive control. Brass and Haggard (2008) and Brass et al. (2009) have suggested that the higher brain mechanism that judges agency (e.g., TPJ) also monitors or controls the agency judgment supported by lower-order system for motor simulation (e.g., MNS). Considering this, the agency judgment confusion occurred at a different cognitive-hierarchical level, which would involve TPJ regardless of MNS activation in the inattentive observation condition.

Further findings from a one-sample *t*-test showed that significant OI was found only in the attentive observation condition. This finding indicates that directing the attention to the action performed by others is a requisite condition for OI occurrence. Typical memory studies have demonstrated that attention to the target content could help us to keep the content in mind (e.g., Craik et al., 1996; Berryhill et al., 2011). Although it seems inconsistent with the typical theory of memory function, our results have higher affinity with the findings about sense of ownership or agency (e.g., Haggard and Cole, 2007; Lenggenhager et al., 2007; Moore and Fletcher, 2012; Kokkinara et al., 2016). In previous research on ownership or agency, it has been suggested that directing attention to a target was related to the occurrence of a sense of agency or ownership. For example, Haggard and Cole (2007) used the method called "intentional binding effect," which was one of the objective ways to investigate participants' sense of agency, and showed that the binding effect was increased when participants could focus their attention to stimuli. Furthermore, in previous studies on memory of involuntary actions, it was suggested that a voluntary action that attends to a sense of agency affects the memory of involuntary actions, which never have sense of agency (e.g., Jensen et al., 2014; Khalighinejad and Haggard, 2016). Altogether, this false attribution of self-performance may not just be typical false memory, but also something concerning the sense of ownership as a distracting factor or agency when observing another's action as a facilitating factor.

From this perspective, as discussed in the introduction section, OI could be decreased by a disrupted sense of ownership, which was induced by an actor's face (Schain et al., 2012) or skin color as a clear indicator of "not like me." Whereas, our results suggested that the decreased OI from focusing on the actor's face in Schain et al. (2012) can be explained by just distracting participant's attention from the action itself. It is indicated that the effect of attention to OI will be determined by the amount of the attention to the action itself rather than by the amount of attention is paid to the visual appearance that allows us to discriminate self from other.

As discussed above, we have suggested new insights concerning the OI mechanism. First, it was not a typical false memory because the occurrence rate was high when participants paid attention to the target. Second, it could be worthy to reconsider the OI mechanism from the perspective of the "like me" system, including MNS, self-ownership, and self-agency. Per this perspective, we propose the process of the occurrence of OI in the OI paradigm (Lindner et al., 2010) as follows: (1) First, participants get a sense of agency to their own action when they performed some actions in Phase 1. (2) Then, they can have a vicarious-agency (Wegner et al., 2004) to observed other's actions by the motor simulation based on MNS when they directed their attention to target action during observing the other's action in Phase 2. (3) The judgment of "who is the agent," that is, "the agent is me or not me" is started in conjunction with the second process. If they recognize the obvious "sense of others" at this point, such as the actor's face, clothes or complexion, the vicarious sense of ownership to an actor's body can be remarkably disturbed. (4) Finally, the misattribution for self-performance on the action that they did not perform, namely, the OI arises at the source-memory test in Phase 3 when they confuse a real agency gained in Phase 1 and vicarious agency accidentally obtained in Phase 2 during remembering their action in Phase 1. It is possible that the OI never occurred when they made the judgment of "the agent was other" (i.e., they inhibited their ownership to observing another) in the third process.

CONCLUSION

We shed light on the possible relationship between self-ownership/agency and false agency attribution in memory, namely OI, and investigated the pure effect of the attention to the action itself. We demonstrated the effect of attention to the action itself as a fundamental factor to induce OI. Given that attentive observation of another's action could facilitate MNS activation as a lure to misattribute the other's action to our self, our findings might reflect that MNS activation facilitates the occurrence of OI. On the other hand, it is possible to form a different interpretation. Given that motor resonance is thought to reflect MNS activation to facilitate in peripheral vision (Leonetti et al., 2015), and that there may be a higher cognitive mechanism for self-other distinction controlling our self-agency judgment (Brass et al., 2009), our result might be explained by another mechanism [i.e., the agency-judgment mechanism including TPJ suggested by Brass et al. (2009)] even though MNS is actually activated in the inattentive condition. However, our study did not directly modulate and measure MNS, so it cannot be mentioned properly. Furthermore, it is conceivable that the instruction in the experimental procedure may affects the occurrence of OI. In future, it is necessary to carry out OI experiments with full attention to the influence of the instruction, such as translation. Further investigations are required to directly examine the relationship between OI and MNS as an index of agency misattribution with participants' self-reports (e.g., Tieri et al., 2015) or other indirect methods (e.g., intentional binding;

Haggard et al., 2002; Haggard and Cole, 2007). Then, we can better understand the mechanisms of agency misattribution.

AUTHOR CONTRIBUTIONS

SK designed the experiment, collected and analyzed the data, and wrote the manuscript. NK, MM, and TN reviewed and revised the manuscript. All authors approved the manuscript.

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frontiers in Human Neuroscience

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Music Upper Limb Therapy—Integrated: An Enriched Collaborative Approach for Stroke Rehabilitation

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Stroke is a leading cause of disability worldwide. It leads to a sudden and overwhelming disruption in one's physical body, and alters the stroke survivors' sense of self. Long-term recovery requires that bodily perception, social participation and sense of self are restored; this is challenging to achieve, particularly with a single intervention. However, rhythmic synchronization of movement to external stimuli facilitates sensorimotor coupling for movement recovery, enhances emotional engagement and has positive effects on interpersonal relationships. In this proof-of-concept study, we designed a group music-making intervention, Music Upper Limb Therapy-Integrated (MULT-I), to address the physical, psychological and social domains of rehabilitation simultaneously, and investigated its effects on long-term post-stroke upper limb recovery. The study used a mixed-method pre-post design with 1-year follow up. Thirteen subjects completed the 45-min intervention twice a week for 6 weeks. The primary outcome was reduced upper limb motor impairment on the Fugl-Meyer Scale (FMS). Secondary outcomes included sensory impairment (two-point discrimination test), activity limitation (Modified Rankin Scale, MRS), well-being (WHO well-being index), and participation (Stroke Impact Scale, SIS). Repeated measures analysis of variance (ANOVA) was used to test for differences between pre- and post-intervention, and 1-year follow up scores. Significant improvement was found in upper limb motor impairment, sensory impairment, activity limitation and well-being immediately post-intervention that persisted at 1 year. Activities of daily living and social participation improved only from post-intervention to 1-year follow up. The improvement in upper limb motor impairment was more pronounced in a subset of lower functioning individuals as determined by their pre-intervention wrist range of motion. Qualitatively, subjects reported new feelings of ownership of their impaired limb, more spontaneous movement, and enhanced emotional engagement. The results suggest that the MULT-I intervention may help stroke

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survivors re-create their sense of self by integrating sensorimotor, emotional and interoceptive information and facilitate long-term recovery across multiple domains of disability, even in the chronic stage post-stroke. Randomized controlled trials are warranted to confirm the efficacy of this approach. Clinical Trial Registration: National Institutes of Health, clinicaltrials.gov, NCT01586221.

Keywords: rehabilitation, functional recovery, music therapy, enriched environment, bodily perception, social participation, psycho-social adjustment, sense of self

INTRODUCTION

Stroke affects one in six individuals worldwide, and is the leading cause of disability (Thrift et al., 2014). In the vast majority of survivors, the sudden and lasting physical effects of stroke lead to a catastrophic disruption in their sense of self and in relationships with the physical and social world (Ellis-Hill and Horn, 2000; Ellis-Hill et al., 2000; Secrest and Zeller, 2007; Salter et al., 2008). Depressed mood, social isolation, poor subjective well-being and mental distress contribute to increased motor impairment, disability and risk of future stroke (Ostir et al., 2001; Northcott et al., 2015). Long-term recovery is thought to be strongly influenced by coherence between the stroke survivor's bodily perception, participation in everyday life, and sense of self (Arntzen et al., 2015). Traditional multi-disciplinary rehabilitation addresses physical limitations such as immobility and reduced functional independence, psychological limitations such as depressed mood and lack of motivation, and societal limitations such as social isolation one at a time. For example, patients may receive physical therapy for a few weeks, and subsequently or separately receive cognitive therapy or psychotherapy. Each type of therapy leads to changes in network connectivity between specific regions of the brain depending on the information that is processed during the therapy tasks (Bajaj et al., 2015a). In contrast, combination therapies can increase the connectivity between multiple brain regions that are disconnected after stroke, leading to better functional outcomes (Bajaj et al., 2015b). Since multi-disciplinary rehabilitation is not widely available—only 30% of individuals who need rehabilitation actually receive it (Go et al., 2013), and there are increasing disparities in accessibility to rehabilitation in the chronic post-stroke period (Roth et al., 2011; Winstein et al., 2016)—combination therapies may be the solution to address limitations across multiple domains simultaneously. Here we asked if a single combined intervention could be designed to address physical, psychological and social domains of rehabilitation simultaneously to facilitate long-term post-stroke upper limb recovery.

Music is one of the most powerful elicitors of spontaneous motor actions (Jäncke, 2008). It motivates people to adhere to exercise regimens (Wininger and Pargman, 2003), distracts attention from physical effort, and reduces perceived exertion (Dyrlund and Wininger, 2008). In addition, auditory-motor coupling has been shown to facilitate repetitive movements post-stroke (Roerdink et al., 2009; Rojo et al., 2011; Rodriguez-Fornells et al., 2012), and repetitive and rhythmic movement synchrony between individuals can establish and reinforce social bonds (Hove and Risen, 2009; Miles et al., 2009; Cirelli et al., 2014). Live interactive music-making engages individuals to interact spontaneously and promotes relationship building (Guerrero et al., 2014). Several studies have also shown positive effects of music listening on mood, and on cognitive and motor processing post-stroke (Särkämö et al., 2008; Malcolm et al., 2009; Särkämö and Soto, 2012). Taken together, these studies suggest that music-making activities may be used to integrate physical, psychological and social facets of rehabilitation, creating an enriched environment for post-stroke recovery. Animal studies have shown that in enriched environments the simultaneous physical and mental activity in socially interactive contexts act synergistically to promote neurogenesis, neuronal integration and recovery (Madroñal et al., 2010; Krakauer et al., 2012).

We therefore designed a novel collaborative group music-making intervention, Music Upper Limb Therapy-Integrated (MULT-I), that combined music therapy with occupational therapy to support physical effort, social participation and psychological well-being simultaneously. This study tested the hypothesis that the MULT-I intervention, provided twice a week for 6 weeks, will lead to reduced upper limb motor impairment (primary outcome); and reduced sensory impairment and activity limitation along with increased well-being and participation (secondary outcomes) post-intervention. Since the interaction among physical, psychological and social facets is thought to support long-term recovery, we further hypothesized that the improvement would persist at 1-year follow up.

PATIENTS AND METHODS

Setting and Study Population

Sixteen ethnically diverse subjects with chronic post-stroke hemiparesis were recruited by referral from physicians and therapists from Rusk Rehabilitation, New York University Langone Medical Center and other hospitals in the New York City metropolitan area (**Table 1**). Inclusion criteria included chronic unilateral stroke at least 6 months prior, the ability to ambulate independently in the community with or without an assistive device, and the ability to grasp implements, such as a wooden mallet, at least partially to participate effectively in the study. Exclusion criteria included hearing deficits that might affect reaction and response to music, as assessed using the Hearing Handicap Inventory for Adults (Newman et al.,

TABLE 1 | Subject characteristics.

Subject	FMS (/66)	Age (years)	Ethnic group	Gender	Time since stroke (months)	Handedness/ Hemiparesis	Stroke subtype	Lesion location	Amount of OT (months)
1201	17	54	White	M	144	R/R	N/A	Left MCA	8
1237	18	33	Hispanic	F	45	R/L	Hemorrhagic	Right BG/Insula	6
1243	19	49	Black	M	25	R/L	N/A	Right MCA	1
1300	29	21	White	F	48	R/L	Hemorrhagic	Right temporal lobe	2
1257	34	64	White	F	24	R/L	Ischemic	Right MCA	1
1198	36	67	Black	M	75	R/R	Hemorrhagic	Left MCA	60
1248	36	39	White	M	30	R/L	Hemorrhagic	Right MCA	6
1195	42	68	Black	M	81	R/R	Ischemic	Left MCA (BG/IC)	0.5
1318	44	54	Asian	M	8	R/R	Ischemic	Left MCA	8
1228	56	44	Black	F	54	R/L	Ischemic	Right MCA	6
1280	57	62	White	M	25	R/L	Hemorrhagic	Right MCA	3
1291	58	58	American Indian	M	20	R/R	N/A	Left MCA	2
1317	58	59	Black	M	24	R/L	Ischemic	Right MCA	7
N = 13	38.8 (15.4)	52 (14)	Diverse ethnicities	9M/4F	46.4 (36.5)	5 R hemi/ 8 L hemi	5 Hemorrhage 5 Ischemia	Mostly MCA territory	8.5 (15.7)

FMS, Fugl-Meyer Scale; OT, Occupational therapy, M, Male; F, Female; R, Right; L, Left; MCA, Middle Cerebral Artery.

1991), history of other neurological or psychiatric disorder, prior injury or surgery in the upper limbs, severe aphasia, cognitive or perceptual deficits including inability to follow directions and attend to task, visual impairment and motor and ideational apraxia or neglect that would prevent participation in the intervention. Subjects did not need to have prior musical training to participate. The New York University Institutional Review Board approved this study (i11-02284) and the subjects gave written informed consent as per the Helsinki Declaration prior to participation in the study. The clinical trial was registered at http://clinicaltrials.gov, NCT01586221.

Study Design and Intervention

We used a quasi-experimental mixed-method pre-test post-test design with 1-year follow up. Subjects received the 45-min intervention twice a week for 6 weeks in groups of three for a total of 12 sessions. One extra make-up session was provided for missed sessions due to holidays or illness. One music therapist (MT) provided the musical framework while playing the piano, while the occupational therapist (OT) and second MT facilitated subjects' instrument playing. The therapists used hand-over-hand assistance or demonstration to encourage repetitive isolated movements of the affected upper limb while they played various musical instruments (**Table 2**). Abnormal compensatory movement patterns were discouraged by selecting appropriate instruments as described below. The group sessions were organized into introduction, interactive live music making and wrap-up intervals. The 5-min introduction consisted of the OT leading musically supported stretches of the trunk and upper limb, and a focus group discussion about the experience of living with stroke. The subjects were encouraged to openly share their feelings about their stroke with respect to physical, emotional, and/or psychosocial challenges and their overall well-being and quality of life. The 35-min music making consisted of improvised live music, with the MT and all subjects playing a variety of instruments, such as drums, bells, shakers, mallets, chimes, piano and harp with their affected upper limb as detailed below. Short breaks were provided as needed to change musical instruments, or to rest at the end of a "piece of music". The therapists provided hand-over-hand support when subjects were particularly challenged, to maintain the flow of the music and facilitate engagement. Hand-over-hand support included the MT or OT grasping a subject's affected upper limb and helping the subject to move through the range of motion needed to play the instrument. Specific attention was given to ensure that the subject's movement was successful in creating a sound that contributed to the music, both with enough volume to be heard and with synchronization to the rhythm and, when applicable, to the melodic elements of the music. The instruments were adapted to make it easier for the subjects to use them. For example, instrument handles were enlarged using foam or rubber grips, Coban wrap was used to reinforce grasp, and devices such as adaptive picks for the harp or guitar were used. The orientation of the instrument was altered to enable playing (e.g., having the xylophone closer to the subject or at a different angle allowed for easier movements), and the subjects were encouraged to use both hands when they were unable to play the instrument with the affected hand alone (e.g., when using the maracas). When open chain movements were not possible to perform, closed-chain movements were used (e.g., holding the cabasa and rolling it on the thigh). In addition, the MT provided musical support to reflect the effort and expression of the subjects by adjusting the accompaniment. For example, dissonance was used to reflect physical exertion, high melodic registers were used to help extend arm reach, and the style of music was adapted to the mood of subjects while playing. The pulse and flow of the music was also adjusted to encourage smoother movements. When fatigue or use of compensatory strategies was noted, the MT reduced the intensity of the music or stopped the music for a period of rest. The 5-min wrap up involved final thoughts and feedback on the sessions

TABLE 2 | Movements performed during MULT-I.

Movement	Musical activity
Shoulder external rotation/internal rotation	1. Hold **maraca** in both hands with elbows at side, internally and externally rotate both shoulders together. 2. Hold **mallet** in affected hand, reach to side repeatedly by externally and internally rotating shoulder to hit **drum**. 3. Hold **tambourine** with one hand, straighten the elbow, hit the tambourine with other hand repeatedly by internally and externally rotating at the shoulder; switch hands.
Shoulder flexion/extension	1. Hold **maraca** in both hands, reach up and down by flexing and extending at the shoulder. 2. Hold **mallet** in affected hand, reach forward by flexing the shoulder to hit **vertical bells**. 3. Hold **wind chime stand** with the affected hand, push back and forth by extending and flexing at the shoulder.
Elbow flexion/extension	1. Hold **mallet** in both hands, hit **xylophone or drum** repeatedly by extending and flexing at the elbow. 2. Hold **horn** with affected hand, bring to mouth to **blow** then bring down by flexing and extending at the elbow. 3. Hold **cabasa** with affected hand, slide down leg and back by extending and flexing at the elbow.
Forearm supination/pronation	1. Hold **maraca** in affected hand with the elbow at side, then supinate and pronate forearm repeatedly. 2. Hold **rain stick** with both hands, unaffected forearm supinated and affected forearm pronated; pronate unaffected forearm twisting affected forearm into supination, repeat.
Wrist flexion/extension and ulnar/radial deviation	1. Hold **maracas** in both hands, move up and down using wrist extension-flexion or radial-ulnar deviation. 2. Hold **hand chimes** in affected hand, move briskly using wrist extension-flexion or radial-ulnar deviation. 3. Hold **rain stick** with both hands, extend and flex both wrists repeatedly.
Hand grasp/release	1. Grasp similarly sized **musical instruments** with one hand, release to other hand; alternate hands. 2. Grasp corn kernels with affected hand, release onto **steel drum.**
Finger individuation	1. Press keys on a **piano.** 2. Pluck strings on **harp or guitar.**

from each of the subjects. The group discussions encouraged social participation as part of the intervention, and enabled the subjects to provide feedback on how the intervention affected them. All sessions were video-recorded for qualitative analysis.

Instrument selection was based on subjects' preferences, as well as their abilities and deficits. For example, subjects with some finger movement but decreased fine motor coordination played the piano or the harp, whereas subjects with decreased hand function but adequate proximal arm movement played the drums. As several instruments can support similar movement goals, instruments that complemented one another in terms of tonality, timbre, volume and register were selected. The MULT-I intervention employed the Nordoff-Robbins approach to music therapy, which focuses on offering each group member an opportunity to feel successful and personally fulfilled in their experience of making music (Nordoff and Robbins, 2007/1977). This philosophy also influenced choice of instrument as it was important that each group member could be heard, and that individuals playing a melodic instrument would easily find notes fitting within the tonal structure of the music. Adaptations were made to the instruments to fit within the overall musical framework. For example, tone bars were added or removed from the xylophone to fit within the tonal framework of the music, and mallets were adjusted to change the volume of the instrument (yarn or felt tips were used to dampen the sound, and wooden or rubber tips were used to enhance the sound). Adaptations were also made to instruments to enable subjects to play their selected instrument successfully, as described above. Engagement in MULT-I required individuals to listen attentively to others, generate appropriately timed movements of sufficient velocity to produce sound, and sustain music making. The therapeutic goals were to enhance emotional awareness and expression, motivate spontaneous creative movement and interaction within the context of the intervention, and promote interpersonal communication, and sense of belonging to the group. Subjects were encouraged to bring in music that was meaningful to them to play during the sessions, to create a shared experience with personal investment in the music-making.

Assessments

Clinical assessments were administered before and after the 6-week intervention and at 1-year follow up by a researcher who was not involved in the intervention. The primary outcome was reduction in motor impairment on the Fugl-Meyer Scale (FMS;

Fugl-Meyer et al., 1975). This is a standard, validated, and widely-used scale of motor impairment post-stroke. It consists of 33 tasks, each of which is scored on a 3-point scale (0 = unable to perform, 1 = partially perform, 2 = faultless performance); the maximum score for the upper extremity is 66. The FMS score reflects the degree to which joint movements can be isolated. Secondary outcomes included reduction of sensory impairment (on the two-point discrimination test) and activity limitation (Modified Rankin Scale, MRS), and increase in well-being (World Health Organization well-being index) and participation post- stroke (Stroke Impact Scale (SIS) for activities of daily living and participation subscales, respectively). The two-point discrimination test (Mackinnon and Dellon, 1985) is a sensitive test for tactile sensibility, and has been shown to be predictive for upper limb dexterity after stroke (Meyer et al., 2014). The MRS (Rankin, 1957) is a six-level outcome scale to assess limitation in mobility and activities of daily living using a structured interview (Wilson et al., 2002). It has excellent inter-rater reliability (Wolfe et al., 1991) and criterion validity (Kwon et al., 2004). Well-being was measured using the World Health Organization (Five) well-being index (Tibaek et al., 2011). The SIS assesses stroke specific quality of life in eight domains (physical problems, memory and thinking, feelings and emotions, communication, activities of daily living, community mobility, use of the hand, and participation). The SIS has excellent test/re-test reliability, internal consistency and responsiveness (Duncan et al., 1999).

Kinematic data during wrist flexion/extension were also collected using a custom-made wrist independence trainer (WIT) pre- and post-intervention, but not at 1-year follow up (Aluru et al., 2014). The device was designed to limit movement to the wrist in the sagittal plane by stabilizing the forearm and arm on a platform using straps; it therefore discouraged compensatory movements. The height of the table was maintained across all subjects, with the front edge of the WIT aligned with the table. The height of the chair was adjusted for each subject to keep their shoulders level, trunk in proper alignment, and elbows at approximately 135° of extension. The arm rests on the WIT were adjusted to keep the forearms shoulder distance apart. Electromagnetic motion sensors (trakSTAR, Ascension Technology Corporation, Shelburne, VT, USA) affixed to the forearm and hand measured wrist kinematics. The data were captured using The Motion Monitor (Innovative Sports Training Inc., Chicago, IL, USA), and analysis was performed offline using Spike 2 (Cambridge Electronic Design, Cambridge, England). At the start position, the hand grasped the handle of the WIT and the wrist was in full flexion. The subject was instructed to perform as many wrist extension/flexion movements as possible within a 10-s period; this constituted one trial. The trials were performed first with the affected hand (unimanual), then with both hands (bimanual) in an alternating manner for a total of 11 trials: six trials with the affected hand interspersed with five trials with both hands. Transfer of learning from bimanual-to-unimanual trials was examined by plotting the range-of-motion of the affected wrist across the six trials with the affected hand (Aluru et al., 2014).

During the MULT-I intervention, qualitative information regarding the experience of life with stroke and reactions to the treatment intervention was obtained by video recordings of the sessions. While the treating OT and MTs initiated conversations on these topics, they promoted an open-ended discussion among the participants. The sessions were transcribed through the process of indexing (Aigen, 1993; Guerrero et al., 2014), which involves a detailed time-based index of the events of each session with transcription of both verbal and musical exchanges.

Statistical Analysis

The General Linear Model (GENLIN) in IBM SPSS Statistics version 23 (IBM Corp., Armonk, NY, USA), was used to perform repeated measures analysis of variance (ANOVA) to test for differences in the means between pre-intervention, immediate post-intervention, and 1-year follow up scores, as the data were normally distributed. The analyses on the primary outcome measure (Fugl-Meyer scores) and secondary outcome measures (two-point discrimination, MRS, WHO well-being index and SIS subscales) included only subjects who completed all three assessments. Differences between the assessments were computed using the Wald Chi-square test. The reliability estimates (Cronbach's alpha) for this sample were: FMS (0.954), static Two-point Discrimination test (0.879), WHO well-being index (0.816), and SIS activities of daily living (0.759) and participation (0.855) subscales. Exploratory analyses were conducted using repeated measures analysis of covariance (ANCOVA) to examine change in Fugl-Meyer Score over time by functional status, defined as the maximum extent of wrist extension pre-intervention: low-functioning subjects had $<15°$ of wrist extension, whereas high-functioning subjects had $>30°$ of wrist extension when using the WIT (Aluru et al., 2014). For these analyses, all subjects were included. The EM algorithm (Dempster et al., 1977) was used to impute missing data. The wrist kinematic data of the affected hand were also analyzed using ANCOVA to examine maximum change in wrist extension with bimanual-to-unimanual learning from pre- to post-intervention by functional status. Pearson's correlation was performed to determine the relationship between pre-intervention Fugl-Meyer scores and maximum change in wrist extension. Qualitative analysis of focus group discussions recorded during the sessions was performed by compiling the indexes for the sessions, analyzing the content, and sorting it into emergent categories (by Nina Guerrero and Daniel Geller; Guerrero et al., 2014). The content was further analyzed in the context of the quantitative data to explore plausible explanations for the results obtained.

RESULTS

Sixteen subjects were enrolled; of these, thirteen subjects completed the intervention, and ten returned for follow up at 1 year. Two subjects dropped out in the first week due to pre-existing pain syndromes: one had a history of rheumatoid arthritis and the other had neuropathic pain in the upper limb. One subject participated in the sessions but fractured the wrist on his affected hand as a result of an unrelated fall prior to the post-intervention assessments. These subjects were not included in the analyses.

For subjects who completed all three assessments, based on the repeated measures ANOVA, significant improvements in motor impairment were noted on the FMS (overall $p = 0.021$), sensory impairment on the two-point discrimination test (overall $p = 0.002$), disability on the MRS (overall $p = 0.002$), and well-being on the WHO well-being scale (overall $p = 0.003$) immediately post-intervention and were retained from pre-intervention to 1-year follow up (**Figures 1A–D**). There were no significant differences between post-intervention and 1-year follow-up.

Interestingly, the SIS scores for activities of daily living did not change significantly from pre-intervention to post-intervention ($p = 0.79$); however they increased significantly from post-intervention to 1-year follow up. Similarly, the SIS scores for participation did not change significantly from pre-intervention to post-intervention ($p = 0.84$), but showed a trend toward significance from post-intervention to 1-year follow up (**Figures 1E,F**).

Exploratory analyses using repeated measures ANCOVA revealed a significant increase in the Fugl-Meyer scores over time based on functional status defined by degree of active wrist range-of-motion pre-intervention ($p = 0.007$; **Table 3**). Low-functioning subjects, who had less than 15° of active wrist extension pre-intervention ($n = 5$), showed higher gains on the FMS post-intervention and at 1-year follow up compared with high-functioning ($n = 8$) subjects who had greater than 30° of active wrist extension (**Figure 2A**). Maximum change in wrist extension with bimanual-to-unimanual learning was significantly different between the low-functioning and high-functioning groups pre-intervention ($p = 0.003$). Low-functioning subjects showed a trend toward significance for improvement in maximum wrist extension with bimanual-to-unimanual learning post-intervention compared to the high-functioning subjects ($p = 0.06$; **Figure 2B**). The study was powered to detect only large effects. Pre-intervention Fugl-Meyer scores were positively correlated with the pre-intervention maximum change in wrist extension with bimanual-to-unimanual learning ($r = 0.85$), but were negatively correlated with the change in maximum wrist extension from pre- to post-intervention ($r = -0.52$).

The qualitative data obtained from the therapy sessions were explored for plausible explanations for the quantitative results obtained, particularly with regard to feelings of body ownership and agency of action. Qualitative data were also

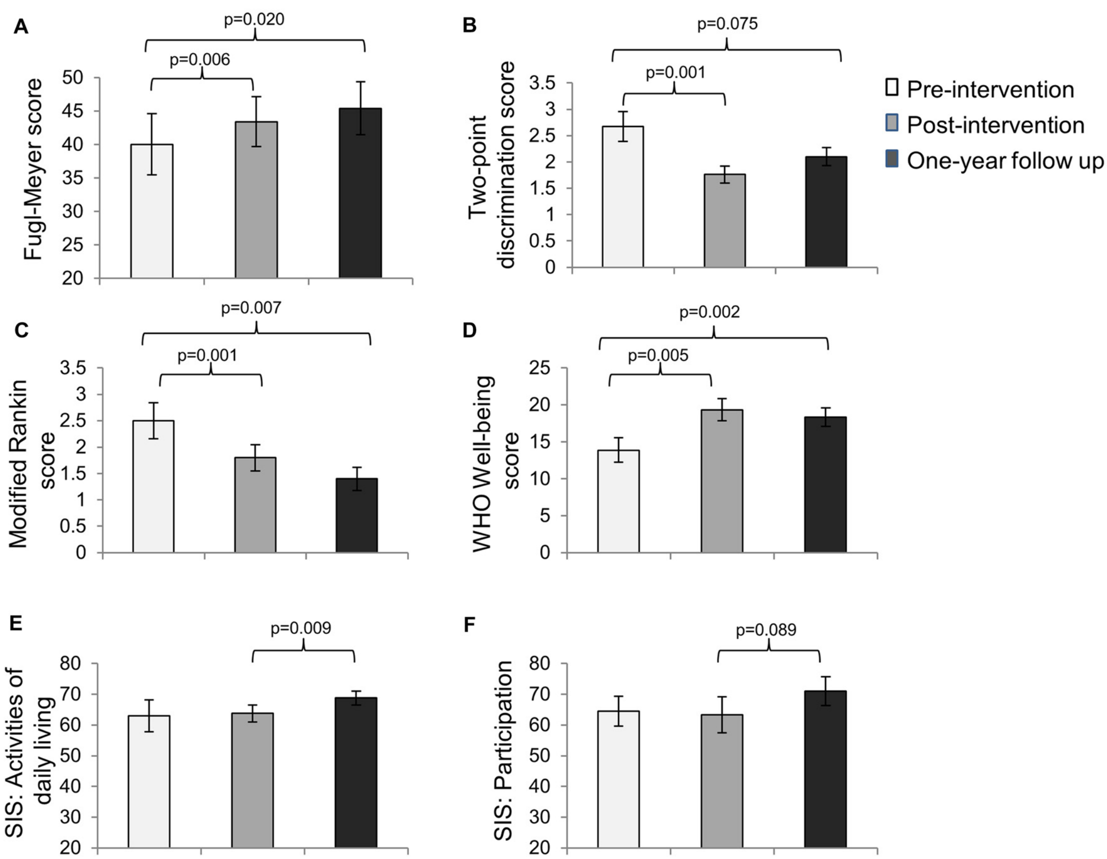

FIGURE 1 | Mean scores (±SE) on the (A) Fugl-Meyer Scale (FMS; $n = 10$), (B) Two-point Discrimination test ($n = 7$), (C) Modified Rankin Scale (MRS; $n = 10$), (D) the WHO Well-being scale ($n = 9$), (E) the activities of daily living subscale of the Stroke Impact Scale (SIS; $n = 10$) and (F) the participation subscale of the SIS ($n = 10$) at pre-intervention, immediate post-intervention and 1-year follow up assessments.

TABLE 3 | Predicting change in Fugl-Meyer Score over time by functional status.

	Estimate	Std. Error	Wald Chi-Square	*p*-value
Intercept	24.99	4.02	38.602	<0.001
Fugl-Meyer Score	5.83	1.05	31.009	<0.001
Functional Status	22.95	5.45	17.700	<0.001
Fugl-Meyer Score by Functional Status	−4.91	1.82	7.244	0.007

explored for moments when subjects shared their challenges regarding their overall recovery process and participation in the intervention. Sharing challenges was considered a significant aspect of the intervention, as these challenges could then be addressed, through physical, emotional and social support. Five main themes were noted: challenges with feelings of ownership of the impaired arm, increased feelings of ownership of the impaired arm with MULT-I, more spontaneous movement, enhanced emotional engagement, and challenges during the intervention. The statements below were captured during group discussions, organized by session. Statements from all 13 subjects who completed the intervention, including both low- and high-functioning subjects, are represented under each theme.

Theme 1: Challenges with feelings of ownership of the impaired arm

> 1228 (session 3) *"I forget my [affected] arm doesn't do what I want it to do."*
> 1257 (session 3) *"I need to improve. I totally forget about the left side. I put stuff [under my left arm] and forget it."*
> 1195 (session 3) *"My brain has to tell my arm it's there."*
> 1248 (session 7) *"It's hard to get my arm involved in the things I do every day."*
> 1280 (session 7) *"I can't get my arm to do what my brain tells it to do."*
> 1257 (session 9) *"I used to be the kind of person who always helped—now people do things for me."*
> 1257 (session 11) *"This is really sad. . .they tell me eventually I will feel [my arm]. But every morning I wake up, and it's still the same."*

Theme 2: Increased feelings of ownership of the impaired arm with MULT-I

> 1300 (session 2) *"I felt a lot more strength in my left [affected] arm toward the end of the music."*
> 1198 (session 7) *"I feel relief, to be able to move the arm."*
> 1257 (session 8) *"I'm much more conscious of my left arm now—certainly in the sessions, but also throughout the day. I at least try to use it."*
> 1228 (session 8) "*Music stimulates lots of different movements, more movements than usual and different kinds. People make comments about my [affected] arm. They say 'you're moving it better'.*"
> 1237 (session *11)*"*This morning, it was so cool. . .I was lying down and could totally feel my left [affected] arm, and I could feel the weight of it against my body*."

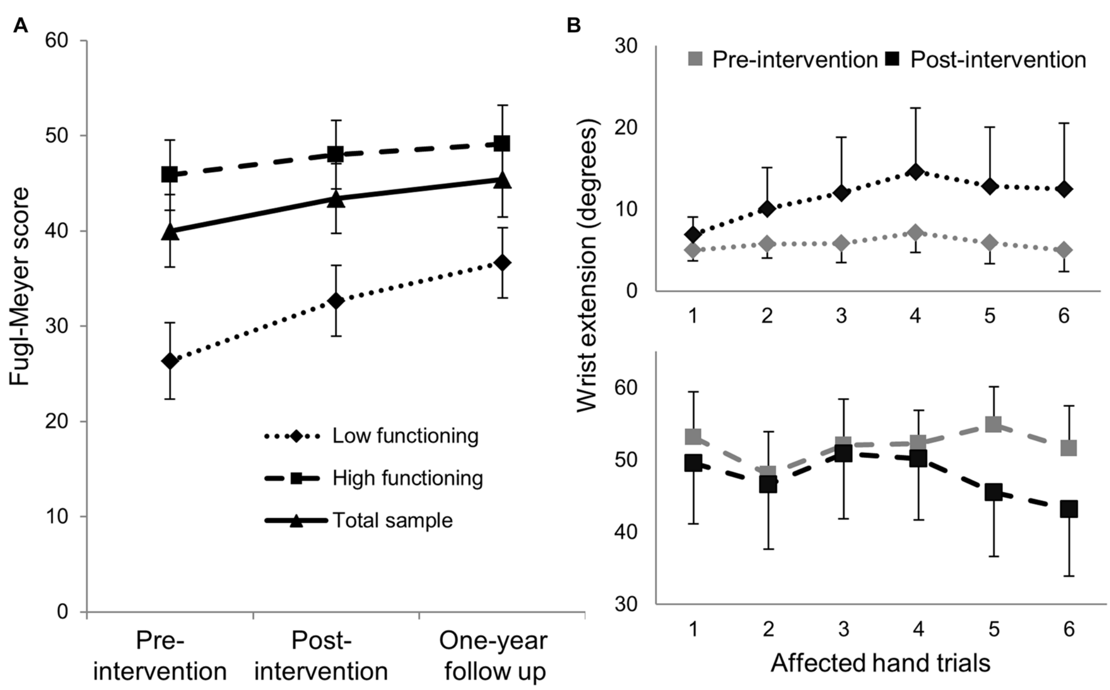

FIGURE 2 | (A) Mean (±SE) Fugl-Meyer scores in low-functioning subjects (*n* = 5) showed greater improvement compared with high-functioning subjects (*n* = 8). **(B)** The low-functioning subjects (active wrist range-of-motion <15°) showed better bimanual-to-unimanual learning across trials with the affected hand post-intervention than the high-functioning subjects (active wrist range-of-motion >30°).

Theme 3: More spontaneous movement

1195 (session 2) *"I was cooking and I spontaneously reached out with my right [affected] arm."*
1198 (session 2) *"My wife observed that I put on my jacket by myself."*
1201 (session 7) *"I can now open my hand supporting my weight on the bed."*
1237 (session 8)*"I started taking the train, and gave up using my cane."*
1237 (session 10) *"I started dancing with my son to his favorite music."*

Theme 4: Enhanced emotional engagement

1198 (session 1) *"I feel the music!"*
1317 (session 1) *"Music calms the soul."*
1228 (session 2) *"This is fun."*
1291 (session 2) *"I feel more joy."*
1198 (session 2) "*[The intervention] allows participants to have healthy interaction with others in similar circumstances, and is just plain fun!*"
1237 (session 8) *"I get lost in the music; I could do this all day."*
1228 (session 9) *"There are still certain movements. . .that I hate to do because they give me that sickly feeling. . .[but] the music lets us ride it out."*
1257 (session 9) *"I've been through many different therapies, and with no disrespect to all the therapists I've had, this is more fun! More interesting and varied."*
1318 (session 13) "*Music makes movement less tiring and less boring.*"
1280 (session 13) *"We're creating something together; the whole is greater than the sum of its parts."*

Theme 5: Challenges during the intervention

1291 (session 8) *"My arm is going crazy. . ..All this isn't helping with my arm! It's very difficult, uncomfortable."*
1237 (session 8) "*With all of the sensations I'm getting in my left arm, it triggers my spasticity. My arm is tingling.*"
1243 (session 8) *"The length of treatment is too short."*
1228 (session 9) *"I hate it. . .it's boring. . .the tone chime swings back and hits my left knuckles. . .it hurts!"*
1291 (session 11) *"I'm having trouble with my voice. . . I sound retarded."*

DISCUSSION

This proof-of-concept study tested the hypothesis that an enriched collaborative group music-making intervention, Music Upper Limb Therapy-Integrated (MULT-I), that combined music therapy with occupational therapy to support physical effort, psychological well-being and social participation simultaneously, will lead to reduced upper limb motor impairment (primary outcome), and reduced sensory impairment and activity limitation along with increased well-being and participation (secondary outcomes) post-intervention, and that the improvement would persist at 1-year follow up. The results support our hypotheses. Interestingly, activities of daily living and social participation improved only from post-intervention to 1-year follow up. Furthermore, low-functioning subjects showed greater improvement on motor impairment with this intervention compared with high-functioning subjects. Qualitative analyses of group discussions that were part of the intervention, suggest that the subjects experienced challenges with feelings of ownership of the impaired arm, but that the MULT-I intervention helped increase their feelings of ownership of the impaired arm, promoted spontaneous movement, and enhanced emotional engagement, despite challenges during the intervention. These results are discussed below.

Impacting Disability Across Multiple Domains with MULT-I

The goal of rehabilitation is to impact disability in all three domains of the International Classification of Functioning, Disability and Health's (ICF) model (Geyh et al., 2004)—impairment, activity and participation. The relationships among these domains are complex and influenced by many factors which are difficult to address with any single intervention. Combination therapies or interventions that are designed to address multiple facets of rehabilitation simultaneously may be one solution. The MULT-I intervention offers several advantages over traditional therapy that can contribute to enhanced network connectivity conducive to post-stroke recovery. Music modulates activity in a broad bilateral network of mesolimbic structures involved in processing emotions and reward information (Menon and Levitin, 2005). The recruitment of limbic circuits, for example during creative musical activity (Bashwiner et al., 2016), may facilitate motor recovery after stroke (Marshall et al., 2009). Repetitive sensory stimulation from the use of percussion instruments may enhance functional connectivity in the sensorimotor network (Freyer et al., 2012). In addition, moving in synchrony to an auditory beat enhances the perception of beat timing (Manning and Schutz, 2013), leading to coordination of perception and action for sensorimotor integration. Auditory-motor coupling during rhythmic tasks activates a cortico-subcortical network including the auditory cortex, putamen, supplementary motor area and the premotor cortex, engaged in the analysis of temporal sequences, prediction of beat and beat generation (Grahn and Rowe, 2009; Rodriguez-Fornells et al., 2012). Furthermore, music can enhance social cognition (Koelsch, 2014, 2015). Taken together with the present findings, these data suggest that the MULT-I intervention created an enriched environment that provided simultaneous physical, psychological and social engagement leading to improvement in all three domains of disability over the long-term.

Longer-Term Improvement in Activities of Daily Living and Participation

Our results showed no significant improvement in activities of daily living and participation subscales of the SIS immediately post-intervention, but the improvement was significant (or trended towards it) between post-intervention and 1-year follow up. The SIS is a valid and reliable outcome measure with robust psychometric characteristics to measure the impact of stroke on activities of daily living and participation (Duncan et al., 2003), and the participation subscale effectively captures social well-being and quality of life in patients with stroke (Lai et al., 2003). However, the responsiveness to change is affected by stroke severity and time since stroke, and changes in quality of life are typically measured at 3-month intervals with rehabilitation interventions (Duncan et al., 1999). The 6-week interval between pre- and post-intervention in this study may have been insufficient for changes in quality of life to take place. Overall, the improvement in upper limb motor and sensory impairment, activity limitation, and well-being from pre- to post-intervention, and the improvement in activities of daily living and participation from post-intervention to 1-year follow up, suggest that the MULT-I intervention is promising to effect long-term post-stroke recovery.

Functional Status Predicts Improvement with MULT-I

Rehabilitation trials typically show greater improvement in subjects with higher pre-intervention Fugl-Meyer scores, compared to those with lower Fugl-Meyer scores (Gebruers et al., 2014), because the higher scores reflect lower stroke severity and the availability of neural substrates to mediate recovery. Interestingly, in this study, low-functioning subjects, who had limited movement in their wrist and hand, showed a significantly greater reduction in motor impairment than the higher- functioning subjects who had more movement to begin with, but were still far from complete recovery. Furthermore, the lower the pre-intervention Fugl-Meyer score, the greater was the increase in maximum wrist extension from pre- to post-intervention with bimanual-to-unimanual learning. We have previously suggested that subjects with predominant paresis, i.e., with limited active wrist range of motion and low Fugl-Meyer scores, may be particularly responsive to rhythm and music (Aluru et al., 2014). Rhythmic auditory stimulation has been shown to produce more efficient motor unit synchronization (Thaut et al., 1999), which can directly facilitate movement. It also excites a bilaterally distributed sensorimotor network (Pollok et al., 2005; Serrien, 2008) and increases excitability of spinal motor neurons via the reticulospinal pathway (Paltsev and Elner, 1967; Rossignol and Jones, 1976), that can increase co-activation across both the agonist and antagonist muscles. While any muscle activation may contribute to increased movement in low-functioning individuals, as previously shown (Aluru et al., 2014), and exemplified by subject #1237 in this cohort (see statements under Theme 5), excessive muscle co-activation in higher-functioning individuals (e.g., subject #1291 (session 8) under Theme 5) may actually reinforce abnormal synergy patterns, produce discomfort, and decrease movement. Hence, rhythmic auditory engagement in sensorimotor tasks may be particularly beneficial to facilitate movement in low-functioning individuals.

Adjusting to a New Identity Post-Stroke

Stroke is experienced as a sudden and overwhelming disruption, impeding engagement in previously easy tasks, and altering stroke survivors' sense of self (Salter et al., 2008). Experiences that support re-connection with a new body and positive social interactions are important to the recovery process and for re-establishing a positive sense of self. Activities for which there is no perceived consequence for failure support the process of re-establishing a connection with the body after a stroke (Guidetti et al., 2007). Music-making activities, particularly involving rhythmic use of the body in conjunction with others, provide an opportunity to reconnect with the body. The temporal structure of musical rhythm facilitates sensorimotor synchronization (Merker et al., 2009; Ravignani et al., 2014). Perceiving rhythm (Maes et al., 2014) and observing rhythmic movements (Kirsch and Cross, 2015) enable the formation of internal representations of familiar movement kinematics (Stadler et al., 2012). Furthermore, rhythmic music-making activities, as in the MULT-I intervention (**Table 2**), are not part of most participants' activities of daily living, which reduces the perceived consequences of failure.

Additionally, different instruments require different degrees of bodily engagement and control. Thus, instrument selection is important to help the stroke survivor feel successful in his or her ability to make music effectively, and receive positive feedback through the sounds created and the physical sensation of playing. Instrument selection was performed collaboratively by the subject, MT and OT. Moreover, the musical framework created by the therapists highlighted even the smallest movement or sound made by a subject. The qualitative data presented under Themes 2 and 3 suggest that the MULT-I intervention was successful in helping subjects reconnect with their body, increase feelings of ownership of the impaired arm, and move more spontaneously.

Group music therapy has been shown to improve social interaction among stroke survivors (Nayak et al., 2000). The live interactive music-making in MULT-I created a psychologically safe environment that reflected the emotional expressions and physical activities of the group. Through music, individual members expressed a full range of emotions and connected with other members in the group. The qualitative data presented under Theme 4 suggest that the group music-making during MULT-I successfully enhanced emotional engagement. Subjects not only reported feeling a part of creating something together, but were also able to explore difficult feelings of loss, grief and frustration (under Themes 1 and 5), and emerged from the experience with an improved sense of well-being. Taken together, the improved awareness of the affected limb combined with enhanced emotional engagement suggest that the MULT-I intervention supported the creation of a positive sense of self post-stroke.

Integrating the Benefits of Music Therapy to Enhance Stroke Rehabilitation

Current practice in music therapy and stroke rehabilitation includes multiple theoretical perspectives (Magee and Baker, 2009). Neurologic Music Therapy harnesses the benefits of auditory-motor coupling to facilitate gait training and upper limb rehabilitation (Thaut et al., 2007; Malcolm et al., 2009). Other music therapy methods facilitate self-expression, connection with others, and emotional well-being through instrumental improvisation and group singing (Magee and Baker, 2009). Music-listening, alone, has been shown to improve cognition and mood among stroke survivors (Särkämö et al., 2008). There is a need to develop a music-based intervention that effectively integrates these benefits of music therapy into a comprehensive approach for stroke rehabilitation.

The MULT-I intervention leverages the benefits of auditory-motor coupling, while allowing flexibility in the music-making process through selection of instrument, musical style, and improvisation to support the psychosocial aspects of stroke rehabilitation, which contribute significantly to overall rehabilitation outcome (Ostir et al., 2001). The collaboration between music therapy and occupational therapy further supports functional goal attainment within a group music-making process. In addition, enjoyable tasks motivate individuals to engage in movement, and provide a positively reinforcing experience for post-stroke re-learning (Sabini et al., 2013). The results of this study suggest that it is feasible to integrate the physical, psychological and social benefits of music into a single effective intervention for stroke rehabilitation.

Limitations and Conclusions

This quasi-experimental study had a pre-test post-test design and a small sample size. There was no control group because the purpose of the study was to determine the feasibility of the enriched collaborative MULT-I intervention in facilitating long-term upper limb recovery across multiple domains of disability. This study is innovative in many respects. First, the intervention is based on the synergistic effects of physical, psychological and social rhythmic entrainment which can help create both a sense of ownership and agency with regard to the impaired limb. Second, the study evaluates the feasibility of a collaborative intervention for post-stroke recovery which involves not only inter-disciplinary collaboration between MTs and OTs but also collaboration among patients and therapists. Such collaborative interventions could potentially increase cost-effective access to rehabilitation. Third, our results demonstrate that it is possible to impact all three domains of disability, i.e., impairment, activity and participation limitations, with a single relatively short-term intervention with long-lasting results. Finally, this study provides preliminary evidence that this intervention may be more effective in a lower functioning subgroup of patients. This is important for resource allocation to target the right patients and obtain the best outcomes. Taken together, our results suggest that the MULT-I intervention may constitute a practical model of an enriched environment for post-stroke rehabilitation even in the chronic stage post stroke. This holds significant implications for further research and clinical use of enriched interventions for post-stroke rehabilitation. The next step is to perform a larger randomized controlled study to confirm the results. We are now testing the translatability of the MULT-I intervention with larger group sizes and fewer therapists, and in low-resource settings, for more cost-effective resource utilization.

AUTHOR CONTRIBUTIONS

PR and AT: conception and study design. DG, NG, VA, AT: study execution. JPE, JAT, GO, VA, PR: data analysis and interpretation. PR, DG, NG, AP, VA: manuscript drafting.

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