The Role of Body-Related Afferent Signals in Human Sense of Agency

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ABSTRACT: At present, most of the neurocognitive models of human sense of agency (ie, "this action is due to my own will") have been traditionally rooted in a variety of internal efferent signals arising within the motor system. However, recent neuroscientific evidence has suggested that also the body-related afferent signals that subserve body ownership (ie, "this body is mine") might have a key role in this process. Accordingly, in the present review paper, we briefly examined the literature investigating how and to what extent body ownership contributes to building up human motor consciousness. Evidence suggests that, if required by the context, body ownership per se can act on agency attribution (ie, independently from efferent signals). Hence, a unitary and coherent subjective experience of willed actions (ie, "this willed action is being realized by my own body") requires both awareness of being an agent and of owning the body.

KEYWORDS: Bodily self, body ownership, sense of agency, afferent signals, efferent signals

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When we achieve willed actions, we do not feel as though those acts simply happen to us, we strongly sense to be in charge. Such subjective experience of authorship is known as sense of agency.[1] In other words, we are aware of intending, initiating, and controlling our volitional movements (so-called "body agency"),[2] as well as their consequences in the external world ("external agency"),[2] and this awareness is vital for survival. Indeed, perceiving to be an agent allows distinguishing actions that are self-generated from those that are generated by others. This, in turn, contributes to the key signature of human nature, that is, the phenomenological experience of self-consciousness.[3]

At present, sense of agency is thought to arise from signals within the motor system, such as motor intentions, planning, premotor processing, efference copy, and sensorimotor predictions.[4] In particular, one of the most influential neurocognitive models of such experience focuses on signals related to motor control[5] and puts forward a specific explanation. It is known that any willed action starts with a desire or a goal state on which the brain must create the motor commands necessary to trigger and drive the action to the final goal. Besides the motor commands, the system also creates their efferent copy, which is useful to predict the more likely sensory consequences of the given action.[6] It is stated that the subsequent comparison between predicted and actual outcomes is the main source of signals for the construction of the sense of agency.[4,7-10] Specifically, whenever the actual sensory consequences (reafferences) match the predictions made by the motor system, a feeling of being an agent arises. Being based on a causal relationship between an action and its effect, such mechanism primarily explains the sense of agency over external events (external agency). For instance, if I am thirsty and I quickly get a glass of water, I experience a seemingly coherent feeling of agency over those events. At the neural level, such complex process is subserved by the activity of a large variety of brain structures. In particular, a number of studies[11–15] demonstrated that human sense of agency requires the involvement of the frontoparietal network including the superior/inferior parietal cortex, the supplementary motor area, and the anterior cingulate cortex.

It is worth emphasizing, however, that whenever we successfully achieve volitional actions, we feel not only being in control of our movements and their consequences but also that those movements are being executed through our own body (body agency). For instance, if I am thirsty and I quickly get a glass of water, I experience that my own body is moving toward the glass. In the absence of any movement, such an embodied and enduring sense of being aware of our own body, termed body ownership,[16] is known to be rooted in multisensory integration. In other words, it arises whenever the body-related afferent sensory signals (ie, visual, tactile, proprioceptive, kinesthetic, auditory, etc) that constantly reach our body are integrated in both spatial and temporal terms. For example, if someone else caresses my arm, I experience that body part as my own because I see and I feel the touches at the same time and in the same place. All in all, the stronger the spatiotemporal congruency among these signals, the higher the feeling of body ownership.[17–20] It is thought that in the human brain, body ownership is underpinned by the activity of a network including premotor areas, the occipitotemporal cortex, the primary/secondary somatosensory areas, and the anterior insula.[18,21–23]

Capitalizing on the above-mentioned considerations, it follows that the coherence, the richness, and the completeness of human subjective experience of being the agent of a given voluntary action necessarily requires both awareness of controlling the actions and awareness of owning the body that achieves them. However, whether, how, and to what extent body ownership has a role in building up such experiences is an issue that only very recently has come to the forefront of the scientific investigations. For these reasons, in this article, we aimed at reviewing all studies that, in one way or another, investigated the possible role of body ownership in building up the sense of agency over the body movements.

Most of the existing literature that examined the role of being aware of one's own body in sense of agency is obtained in experimental conditions where actual participant's movements are always present.[2,24,25] Such approach is not trivial but, rather, strongly driven by the above-mentioned predominant notion that the sense of agency relies almost entirely on the match between predicted and actual action outcomes.[3,6-9] Hence, considering action execution as a necessary condition to trigger sense of agency implies that body ownership can have only an additive role. Among those studies, the work by Tsakiris et al[26] suggested, for the first time, that the two senses might share some anatomo-functional features. This claim had the merit of sparking and strengthening the interest around this topic. Accordingly, another study directly tested this hypothesis in an experimental setting.[27] More specifically, the authors of the study manipulated body ownership and examined any possible causal effect on sense of agency. To do so, they employed the rubber hand illusion paradigm, a well-known experimental manipulation that allows to induce a temporary feeling of ownership over a fake life-sized hand.[28] The illusion occurs when temporally synchronous (but not asynchronous) touches are delivered onto a visible rubber hand and onto the hidden participants' hand and when the rubber hand is placed in a congruent (0°), but not in an incongruent (eg, rotated 180°) position with respect to the participant's body. Such paradigm was integrated with a phenomenon typically considered an implicit signature of sense of agency,[27] namely sensory attenuation.[29–32] This phenomenon consists in the fact that the perceived intensity of the sensory consequences of an agent's voluntary actions is attenuated with respect to the intensity of physically identical externally generated events. Hence, the ability to set apart sensations originating from external causes from self-generated sensations is thought to contribute to creating and maintaining the sense of agency. Overall, the study showed that when a seen dummy hand that was perceived as one's own moved repeatedly and synchronously with the participants' hand, somatosensory stimuli delivered to the participants' body by that hand were attenuated exactly as it happened when the own real hand delivered the stimuli. The attenuation did not occur if the hand was not perceived as one's own. Similar conclusions have been obtained by means of another experimental manipulation of body awareness able to induce an illusory ownership of the whole body rather than of a body part only. Such paradigm, known as the full body illusion,[33] induces the illusory experience of owning the body of a life-sized virtual avatar in immersive virtual reality. As with the rubber hand illusion, this experience occurred only with synchronous touches and with the avatar seen from a congruent posture (0°). Two different studies employed the full-body illusion and measured the sense of agency explicitly through an ad hoc questionnaire on the subjective experience of being an agent.[34,35] Both studies demonstrated that when the seen avatar perceived as the own body moved its limbs synchronously with participants' actual limbs, participants falsely attributed to themselves the words uttered by the avatar only.[34] On the contrary, no illusory agency were present when the avatar was not perceived as the own body. In summary, this first set of studies showed that if an external object that is perceived as part of one's own body moves together with the participant's body, an illusory sense of agency over the movements of that object arises. This does not happen if the moving external object is not perceived as part of one's own body.

As all the studies mentioned so far always included actual participant's movements, they did not allow clarifying if body ownership has a role per se in building up the sense of agency. However, there is another part of the literature that attempted to solve this problem by excluding the movements. Within this perspective, interesting findings come out from a recently discovered stroke-induced disorder of body ownership.[36] In such delusion, hemiplegic patients (ie, with complete full unilateral motor deficits) treat and care for someone else's hand as their own hand. As for the rubber hand illusion, the delusion emerges only if the alien hand is located in congruent postural positions (0°). Garbarini et al[37] asked whether such pathological embodiment affected the conscious experience of voluntary action. These authors reported that whenever the patients were asked to move their impaired hand, but only the "alien" embodied hand actually moved (due to the complete plegia), they misattributed the movement to their own will. This did not happen when the alien hand was rotated 180°. Similarly, two different studies[38,39] with brain-computer interface showed that if participants' imagined movements matched the movements of mind-controlled robotic arm, an illusory agency over those movements occurred.

Another evidence came from a study employing the full-body illusion showing that when a virtual embodied avatar was walking repeatedly along a route, while the participant remained still, an illusion of walking occurred.[40] This did not happen when the avatar was not embodied. It is also worth noting that highly automated actions, as walking, are thought to prime the movements and intentions to move in advance. In summary, this second set of studies showed that, if participants' motor representations (eg, motor intentions, motor imagery or motor plan) match the movements of an external object perceived as part of one's own body, an illusion of agency arises. This does not happen if the moving external object is not perceived as part of one's own body.

All just-mentioned studies have the merit of excluding actual participant's movements. However, as motor representations were (or could still be) present, none of them could fully guarantee that any kind of efferent signals was prevented. Hence, also this literature cannot provide unequivocal evidence of the role of body ownership independently from any kind of motor-related signals. However, other studies seem to able to create an experimental setup preventing the presence of any possible efferent signals. Braun et al[41] capitalized on another well-known implicit index of sense of agency, the temporal binding.[42–44] This phenomenon consists in the fact that the temporal interval between a voluntary action and its external sensory consequence is subjectively perceived as compressed with respect to when the action and consequences are not causally linked. As sensory attenuation, this phenomenon contributes to creating our awareness of voluntary action. The authors simply capitalized on this phenomenon and measured whether certain temporal binding was present also for the actions of an embodied dummy hand. It is worth noting that the study reported conflicting findings. Indeed, it described both double dissociations and associations between ownership and agency. Other studies were specifically designed to strongly control for the problem of efferent signals.[45–47] They employed the same logic already mentioned above, that is manipulating body ownership (by means of the rubber hand illusion) and examining any possible causal effect on sense of agency. Furthermore, the movements of the embodied body part were quite unpredictable and quick. Hence, even more hidden signals, such as primed motor intentions, were almost certainly prevented. These two studies employed an already mentioned index of the sense of agency (ie, sensory attenuation) and an hoc questionnaire on the subjective experience of agency. It is worth emphasizing that measuring both implicit (ie, sensory suppression) and explicit (ie, questionnaire) aspects of sense of agency allows, in principle, to obtain more solid findings and an in-depth picture of the topic. This is relevant as there is also some evidence suggesting that sensory attenuation could not be strictly related to sense of agency.[48,49] Results showed that when a dummy hand, perceived as one's own, pressed a button delivering an electrical stimulus to the participant's body, such movement was subjectively misattributed to the participant's own will and the stimulus intensity was attenuated (exactly as it happened when one's own hand delivered the stimulus). As in the other studies, the pattern was not present when the dummy hand delivering the somatosensory stimulus was not embodied. It is worth noticing that one of those studies[47] attempted also to obtain neural evidence of the role of body ownership on sense of agency. The authors found that disrupting the activity of the brain structures known to subserve sensory attenuation eliminated sensory attenuation effect for both one's own movements and the movements of an embodied dummy hand. In summary, these latter studies demonstrated that if an external object is perceived as one's own, an illusion of authorship over that object's actions can arise.

To sum up, here we reviewed evidence supporting the idea that body ownership does have a role in human sense of agency, specifically body agency. The review shows that being aware of one's own body has a role per se in building and maintaining the sense of agency, namely it can act on agency attribution in the absence of any efferent signals, such as motor intentions and feedforward predictions, and causes preceding effects and so on. First, it is worth noticing that giving any role to body ownership is not trivial but, rather, consistent with human nature. Indeed, our actions are achieved mainly through the physical body,[50] and the body is a prerequisite for any successful interaction with the environment.[51] Indeed, it is already known that body ownership affects motor control, allowing to estimate limb positions,[52] to tune motor commands,[53] and to adjust errors.[54] Hence, discovering its role also within motor consciousness would not be surprising. Here, we suggest that the signals that give rise to body ownership might have a key role in sense of agency by acting on agency attribution in the absence of any efferent signals. How is it possible to reconcile in a concrete manner this idea with the current neurocognitive model of the sense of agency? As already mentioned, the classical motor control model of sense of agency states that the experience of being an agent arises from the comparison between predicted and actual outcomes.[4,7-10] This, in turn, means that action preparation is a necessary condition to have any experience of being an agent. We put forward the idea that under some circumstances, only seeing the own body moving would be enough to activate the neurocognitive processes subserving action preparation. At this point, the feeling of agency over that specific given act would be triggered. Such a process could be exemplified by the inference: "since this is my body part, any action performed by it would be intended by me." Furthermore, in dynamic conditions, that is when we actually achieve the willed actions, body ownership would provide additional signals to the efferent motor-related signals and would contribute to the subjective experience of being an agent. Within this view, sense of agency is conceived as a very flexible neurocognitive mechanism. Indeed, it is rooted in the dynamic and optimal integration among efferent and afferent signals. Any given source of information would be weighted according to the specificity of the context and the actual availability of signals.[55]

We have to emphasize that the present review did not aim to investigate the interactions between human body ownership and sense of agency but, rather, it focused on the role of the former in the construction of the latter. Therefore, this article cannot provide an exhaustive picture of the complex interplay between the two senses, and future studies in this direction should allow gaining key hints to understand human bodily self-consciousness.

Author Contributions

All authors contributed to manuscript preparation as well as drafting and finalyzing the text.

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