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Evaluating bodily self-consciousness and the brain using multisensory perturbation and fMRI.

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In this article, we consider the usefulness of functional magnetic resonance imaging (fMRI) and perturbation in evaluating causal relationships between bodily self-consciousness and the brain. We argue that fMRI research is not always restricted to correlational statements when it is combined with perturbation techniques and can sometimes permit some degree of causal inferencing, such as when bodily illusions are examined with fMRI. In these instances, one is changing a participant's conscious bodily self by experimentally perturbing mechanisms that are involved in multisensory integration.

Keywords: Functional magnetic resonance imaging (fMRI), bodily self-consciousness, multisensory integration, perturb-and-measure.

Introduction

We are quite familiar and attuned to our conscious bodily self and have a strong personal attachment to it. Yet, paradoxically, this phenomenology remains ineffable and mysterious. The relationships between the contents of this conscious experience and the levels of activity in different brain regions can be characterised by fMRI. However, it is often difficult to infer the true nature of these activations. This is because fMRI is a measurement technique and is therefore inherently correlative and not immune to epiphenomenal results. For example, activation in the visual cortex while we are awake relative to while we are asleep might be epiphenomenal to wakefulness. Wakefulness might not be the primary cause for the activation. Rather, the opening of the eyelids allowing for retinal information to reach the brain for further cortical processing may be the primary cause for this activation. Thus, it can be difficult to establish causation with fMRI. Considering this limitation, the following question arises: How useful is this technique for investigating different facets of consciousness? In this article, we argue that there are instances in which fMRI allows some degree of evaluation of causation when the effects of perturbation are examined, such as the induction of bodily illusions on brain activation.

Can one really evaluate causation?

Evaluations of causality can be achieved to some degree with fMRI through experimental manipulation using perturbation techniques. For example, as illustrated in Fig. 1A, if a given visual stimulus ‘activates’ region X, we do not know whether its activation is due to the stimulus or some other cause such as reciting Shakespeare or thinking about breakfast. However, as illustrated in Fig 1B, if one perturbs region X from processing the visual stimulus

(e.g. asking the participant to close their eyes) and then repeat the experiment again, we can more confidently say something about causation. If region X is no longer activated then its activation is more likely to have something to do with the stimulus. If region X remains activated then its activation does not have something to do with the stimulus.

The notion of a perturb and measure approach for inferring causality in brain-behaviour relationships is nothing new in cognitive neuroscience and it has a long history (Paus, 2005). For example, in some of the most famous experiments in cognitive neuroscience, perturbation by brain lesions informed us that the left inferior frontal cortex is essential for language production (Broca, 1861) and the hippocampus for declarative memory (Scoville & Milner, 1957). Similarly, the somatotopic organization of the motor cortex was first demonstrated in humans by electrical stimulation applied along the precentral cortex in neurological patients during surgery (Penfield & Boldrey, 1937). Today, similar approaches based on less invasive methods (e.g. transcranial magnetic stimulation) are used in combination with functional neuroimaging techniques such as fMRI (Paus, 2005).

The primary focus of this article is to highlight how different kinds of perturbation techniques can change bodily consciousness and consequently brain activity as measured with fMRI, which in turn allow certain inferences to be made about causality. In its simplest form, as shown in Fig. 1C, if the loss of consciousness due to an experimental manipulation causes activation in region X to cease, then its activation is more likely to have something to do with consciousness. If region X remains activated then its activation does not have something to do with consciousness. Note the latter is quite possible as evidenced by a number of studies demonstrating fMRI activation to a passive listening task in comatose patients (Coleman et al., 2009) and healthy participants sedated with general anaesthesia (Davis et al., 2007). In a more complicated form, as shown in Fig. 1D, if consciousness is experimentally altered to create different states of consciousness (e.g. having the sense of bodily self inside versus outside the

physical body) and activation in region X is parametrically modulated in the same manner, then its activation is more likely to have something to do with this consciousness. Otherwise, it does not.

The perturbation and imaging of resting states

Neuroimaging research has revealed that two distinct brain networks, the default mode (DMN) and executive-control (ECN) networks, are associated with general states of mental rest and task related cognition, respectively (Fox et al., 2005). Research using fMRI has been useful in describing how these networks operate. For instance, Fox et al. (2005) examined the relationship between DMN and ECN during spontaneous fluctuations in fMRI BOLD activity. In this experiment, participants underwent fMRI during different resting conditions: eyes closed, eyes open in low light, and fixation of a visual crosshair. Six predefined regions of interest were examined for resting state correlations in brain areas pertaining to the DMN and ECN. The correlational coefficients between the regions of interest and the time course were then computed for each participant. An important finding was that the DMN and ECN were anti-correlated in the absence of any overt task.

ECN and DMN research have demonstrated clear implications for how we understand consciousness to be functionally related to brain activity. Firstly, the phenomenon of mind wandering, when attention drifts from a current train of thought to content generated by the individual, is a fundamental aspect of consciousness that appears to have a neural basis. The oscillations between DMN and ECN have indeed been found to coincide with reports of mind wandering (Smallwood & Schooler, 2015). Secondly, the phenomena of social reflection (Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008) and self-recollection (Spreng & Grady, 2010) both show similar oscillations between DMN and ECN. These studies

highlight an important strength of fMRI in that global activity can be assessed throughout the brain and that the contents of different conscious states can be inferred. However, causality can be drawn from these studies only when these networks are perturbed using methods such as anaesthesia in conjunction with fMRI. To demonstrate this, an fMRI study by (Schrouff et al., 2011) aimed to investigate how the function and connectivity of brain networks were implicated in conscious states after being affected by varying levels of induced unconsciousness by the administration of propofol. Their results demonstrated that synchronous activity, both between and within brain networks, reduced accordingly as the level of consciousness was decreased.

fMRI and illusions of ownership for body parts

Bodily self-consciousness pertains to the experience of owning a physical body and having a first person perspective from that body. One can experimentally perturb this experience by providing conflicting information from the different senses, resulting in powerful illusions of where the self is located relative to the physical body. It is important to underscore the perturbation aspect of these illusions, which relies on mechanisms that would normally be helpful for bodily self-consciousness but tricks us into experiencing a disturbance when we are presented with conflicting information from the different senses, which is something that ordinarily does not occur under normal circumstances.

For instance, in the rubber-hand illusion (Botvinick & Cohen, 1998), the participant watches a rubber hand being stroked with a brush while they feel their own hand, which is hidden from view, being stroked in synchrony with the rubber hand. When this procedure is done properly, the participant quickly begins to experience a transfer of ownership from their own hand to the rubber hand. fMRI studies have demonstrated how activity in a number of

multisensory brain areas, such as the posterior parietal cortex and the ventral premotor area, is modulated during the rubber-hand illusion, highlighting the role played by these areas in integrating visuo-tactile signals necessary for the self-attribution of a hand (Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004; Gentile, Guterstam, Brozzoli, & Ehrsson, 2013). When multisensory signals are perturbed, self-attribution of a hand transfers from the real hand to an artificial hand, which suggests a causal link between processing in these brain areas and ownership.

fMRI and out-of-body experiences

In the next two sections, we will discuss how experimentally-induced disturbances of bodily self-consciousness can be extended to the whole body and how fMRI has been used to examine their neural underpinnings. Out-of-body experiences are illusory experiences characterised by three phenomenological features: i) disembodiment, i.e. the impression of being 'teleported' outside of a body to another location in space; ii) the impression of seeing the world from a different visuo-spatial perspective; and iii) the impression of seeing a body from this new perspective (Bunning & Blanke, 2005). This phenomenon can be observed in some patients with neurological (Blanke, Landis, Spinelli, & Seeck, 2004) and psychiatric (Simeon, 2004) conditions as well as drug abuse (Wilkins, Girard, & Cheyne, 2012).

Ehrsson (2007) demonstrated that it is possible to experimentally generate an out-of-body experience in healthy participants in a systematic manner using virtual reality and tactile stimulation (Fig. 2). In this study, participants sat on a chair and wore a pair of head-mounted displays. Video cameras were used to show the participants' back with a perspective of a person sitting 2 m behind them. The experimenter touched the participant's actual chest (not visible) with a rod as well as an 'illusory' chest right below the recording cameras with a second rod

(visible). Participants reported an out-of-body experience of sitting behind their own body and seeing themselves from a third-person perspective, as revealed by their responses to a questionnaire. These out-of-body experiences were also measured in a more objective manner using skin conductance response as an indicator of arousal in another experimental condition in which the illusory chest was 'hurt' by hitting it with a hammer. In agreement with the perceptual experience, the physiological response also indicated that participants were experiencing themselves as being located behind their real body. Importantly, both perceptual ratings and skin conductance responses were weaker under asynchronous conditions, whereby the participant's actual and illusory chests were touched in alternation, suggesting that this phenomenon requires congruent visuo-proprioceptive signals for successful visuo-tactile integrations.

In a similar manner, Lenggenhager, Tadi, Metzinger, & Blanke (2007) used visuotactile stimulation to systematically induce disturbances in bodily self-consciousness (Fig. 2). Participants wore head-mounted display goggles while they stood inside a room. With the goggles, the participants viewed their backs being stroked with a brush from a different visual perspective. This perspective was filmed using a closed-circuit television camera directly behind them. The key manipulation was whether the strokes they saw were synchronous or asynchronous to what was actually delivered to their backs. When the two were synchronous, participants reported a feeling of their self moving forwards to their virtual body they saw through the head-mounted display goggles. This was measured by questionnaires and by the experimenter physically displacing the participant to a new location after each trial and asking the participant to return to their original starting position. The participants tended to return to a position that was in front of their original starting position in the synchronous but not asynchronous stroking conditions.

In an fMRI study, Ionta et al. (2011) repeated similar procedures but with the participant laying down in the MRI scanner. For tactile stimulation, a brush was embedded inside the bed of the scanner which could be remotely controlled to move up and down along the participant's back and stroke it with precision timing. For visual stimulation, the participant wore head-mounted display goggles and watched a video of somebody else's back being brushed. The videos were filmed with a camera behind this person. Again, the key manipulation was whether the strokes applied to the participant's back were synchronous or asynchronous to what they saw on the video.

Under the synchronous brush stroke condition, two thirds of the participants experienced seeing a virtual body above them and feeling their self moving upwards while the remaining participants experienced seeing a virtual body below them and feeling their self moving downwards. The authors suggested that these discrepancies arose from individual differences in how vestibular and visual cues are weighted for the purposes of creating a perception of the spatial orientation of the self. Specifically, the participants relying more heavily on vestibular cues took a perspective from a supine position, which is the same position they were in as they laid on the bed the scanner. In contrast, the participants relying more heavily on visual cues took a perspective from a prone position, which was a perspective that was perhaps suggestive from the videos. These differences in illusory experiences of the self were confirmed by having participants perform a mental ball dropping task. In this task, the participants held a ball in one hand and were asked to indicate by button pressing with the other hand when it would hit the ground if they were to release the ball. The former group reported longer times relative to the latter, confirming that the former group took possession of a virtual body above them while the latter took possession of a virtual body below them.

The fMRI results revealed that activation in the temporal-parietal junction (TPJ) in the two hemispheres not only predicted a displacement in bodily self but also whether this

displacement went upwards towards a virtual body above the participants or downwards towards a virtual body below the participants. Therefore, TPJ not only fulfils a role in multisensory integration, but it also contributes to the nature of the actual experience of the conscious self (i.e. the self being displaced upwards vs. downwards). The fMRI experiment was further complimented with a quantitative MRI lesion analysis on a cohort of out-of-body experience patients. This analysis showed maximal overlap in the location of their lesions with the fMRI activation observed in the right TPJ in their typical sample, implying a crucial role of this area in bodily self-consciousness and establishing a casual relationship between this area and bodily self-consciousness.

The involvement of TPJ in this bodily illusion has been further confirmed by a recent single-case study in which fMRI responses were measured in a woman who reported to be able to wilfully produce out-of-body-experiences (Smith & Messier, 2014). The participant was asked to either perform her extra-corporeal experience or guided motor imagery tasks (e.g. jumping jacks; finger movements). The experimenter gave her cues on when to start and stop the task. Findings revealed a network of brain areas associated with the reported extracorporeal experience that differed from those observed during motor imagery. In particular, the left supplementary motor area, the supramarginal and posterior superior temporal gyri, which overlap with TPJ, the cerebellum as well as frontal areas were active during the out-of-body-experience.

FMRI and body-swap illusions

The above research relates to the conscious self being removed from the physical body. One can take this even further and have the conscious self experimentally transferred to a completely different body such that one obtains the experience of inhabiting this body as

opposed to their own. In the body-swap illusion, as the name implies, a person consciously experiences ownership of another body. As first demonstrated by Petkova & Ehrsson (2008), this illusion can be induced by applying tactile stimulation on a person's body while they watch simultaneously, by means of virtual reality, the same tactile stimulation applied to a mannequin from the first person visual perspective of the mannequin (Fig. 3). The illusion of a body swap is reported to be so powerful that significant skin conductive responses can be induced in participants by stabbing the mannequin with a knife (Petkova et al., 2011; Petkova & Ehrsson, 2008).

In their seminal paper, Petkova & Ehrsson (2008) noted the importance of three conditions for creating their illusion. First, a continuous match between visual and tactile information is absolutely necessary. Without this, the illusion does not occur. Second, the usage of a sufficiently humanoid body is also required. The body swap does not transfer to blocks and other inanimate objects that are not shaped like human bodies. Third, the adoption of a first person visual perspective of the other body is required. Based on their findings, and the importance of these three factors in creating the illusion, Petkova & Ehrsson (2008) proposed that bodily self-consciousness arises from the brain's assumption that visual information is received under an egocentric frame of reference relative to a point between the two eyes and that the body produces patterns of sensory signals from other modalities in step with this information. If the former changes in such a way that the latter becomes congruent with the first-person visual perspective of a different body, such as a mannequin's, then a body swap will occur.

In a subsequent study, the same authors investigated their illusion using fMRI (Petkova et al., 2011). Specifically, the authors aimed to determine how neuronal populations that integrate multisensory information across different body segments might merge together to form a single experience of bodily self. The illusion was controlled by having participants

observe tactile stimulation on the body of a mannequin from the mannequin's first-person view point while identical synchronous touches were applied to both the participant and mannequin. In doing this, the participants experienced a body swap illusion coinciding with fMRI activation in a network of brain regions, including bilateral ventral premotor (PMv), the left intraparietal sulcus, and the left putamen.

Conditions were also created in which the participant saw different parts of the mannequin being stroked in isolation without seeing the rest of the mannequin's body, effectively creating illusions of changes in body-part ownership much like the rubber-hand illusion. Replicating earlier fMRI work on the rubber-hand illusion (Ehrsson et al., 2005; Ehrsson et al., 2004), Petkova et al. (2011) demonstrated how bilateral activation in PMv was strongly associated with the ownership for specific body parts. However, using multi-voxel pattern analysis, a technique that examines data from individual voxels within a region of interest jointly in a multivariate analysis, the authors found that a specific set of neuronal populations within PMv in the two hemispheres could code for the ownership of a full body as opposed to a different body part like the hand or the abdomen. In other words, activation for PMv can reflect a genuine full-body ownership representation, which will not be invoked when the transfer of ownership is restricted to just one body part, such as the rubber-hand illusion. Such specificity during illusory conditions cannot be explained easily by epiphenomena, underscoring an important role of PMv in the bodily consciousness of self and the ownership of different body parts. Taken together, these fMRI results provide compelling evidence that the conscious self is produced by neural populations within a specialised network that integrate multisensory information across the different segments of the physical body.

Electrophysiological studies in the macaque monkey have found bimodal neurons in both PMv and the putamen that fire when the monkey either sees or feels by touch a stimulus being applied to a specific body part (Graziano & Gross, 1993; Graziano, Yap, & Gross, 1994).

The receptive fields of these cells do not move with the eyes but with the body part and the strength of their response diminishes as a function of the distance from the body part. Moreover, it has been demonstrated that somatosensory and visual inputs can be combined together in individual neurons in parietal area 5 to represent limb positioning (Graziano, 1999; Graziano, Cooke, & Taylor, 2000). Importantly, these neurons can code for the felt position of the monkey's arm while it is covered from view (Graziano, 1999) and are sensitive to the position of a realistic false arm but only when false and real arm are stroked synchronously, much like in the rubber-hand illusion (Graziano et al., 2000). Therefore, the functional role of these bimodal neurons might be to provide representations of the body configurations, which are fundamental for the visual control of actions. Given the properties of these neurons, it is expected that one's body scheme can be extended so as to incorporate foreign objects, even the outer edges of a car (Graziano et al., 2000), and give rise to the bodily illusions described in our paper.

Conclusions

This paper has considered the usefulness of fMRI in establishing causal relationships between bodily self-consciousness and the brain. We reviewed seminal fMRI papers on bodily illusions, arguing that that these types of illusions are created from a perturbation in multisensory integration that would normally provide accurate conscious experiences of the bodily self. For illusions of self-location outside a physical body, bilateral TPJ has been reported to be functionally engaged. The necessity of the right TPJ has further been validated in an MRI lesion analysis in patients who had out-of-body experiences. For body-swap illusions, bilateral PMv has been reported to be functionally engaged. As demonstrated by multi-voxel pattern analysis, activation within this area reflects specificity for different kinds of body-part illusions as well

as specificity for a whole-body illusion. If one considers the implications of these findings with regards to advancing our understanding the conscious bodily self, we contend that further study and advances in fMRI will continue to progressively unlock its mysteries.

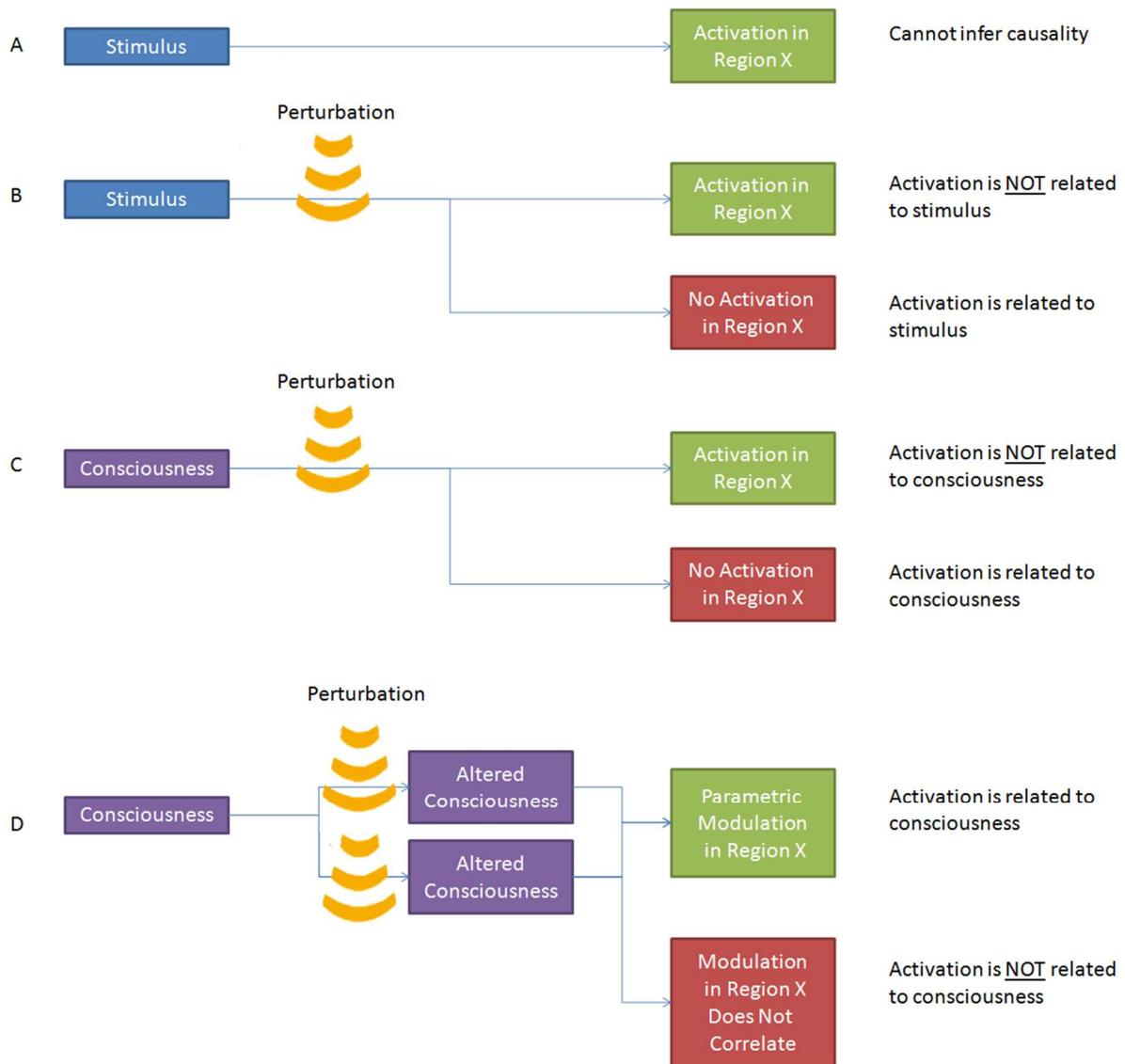


Fig. 1. Inferring causality with perturbation techniques and fMRI. Evaluations of causality can be achieved to some degree with fMRI through experimental manipulation using perturbation techniques. This figure provides some examples. A) Any correlational measurement, such as fMRI, by itself can never be used to imply causation. Activation may or may not be related to the stimulus. B) If one were to perturb the system and the activation remains then one can infer the two are unrelated. If one were to perturb the system and the activation disappears then one can infer some causal relationship. C) The same logic for B) can be applied to investigate consciousness. D) Creating different states of consciousness through

perturbation should lead to different levels of fMRI activation that correspond to the differences in perturbation should a causal relationship exist.

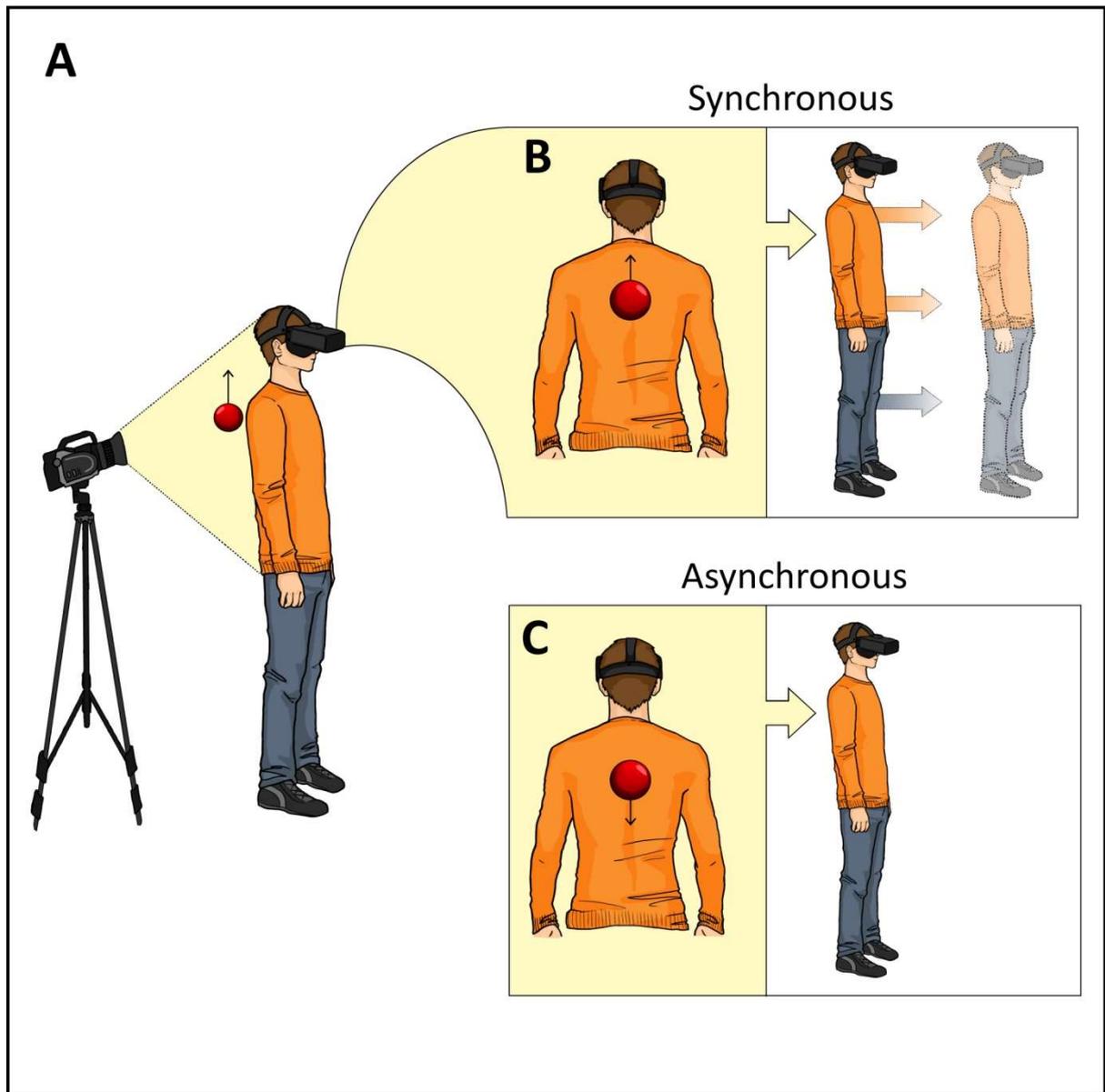


Fig. 2. Experimentally inducing out-of-body experiences. A number of studies, such as those performed by Ehrsson (2007), Lenggenhager et al. (2007), and Ionta et al. (2011), demonstrate how one can experimentally alter bodily self-consciousness to a location outside of the physical body. The basic underlying principles are as follows. A) Virtual reality is used to show participants the filming of a body part being brushed (in this case, the back). B) In the synchronous condition, when the filming is presented in real-time and the somatosensory and visual information about the brush strokes are simultaneous, participants perceive their self moving in space away from their physical body (in this case, forward). C) In the asynchronous

condition, when a delay between the visual and the somatosensory information is introduced, participants do not experience their self as being in a location different from their physical body.

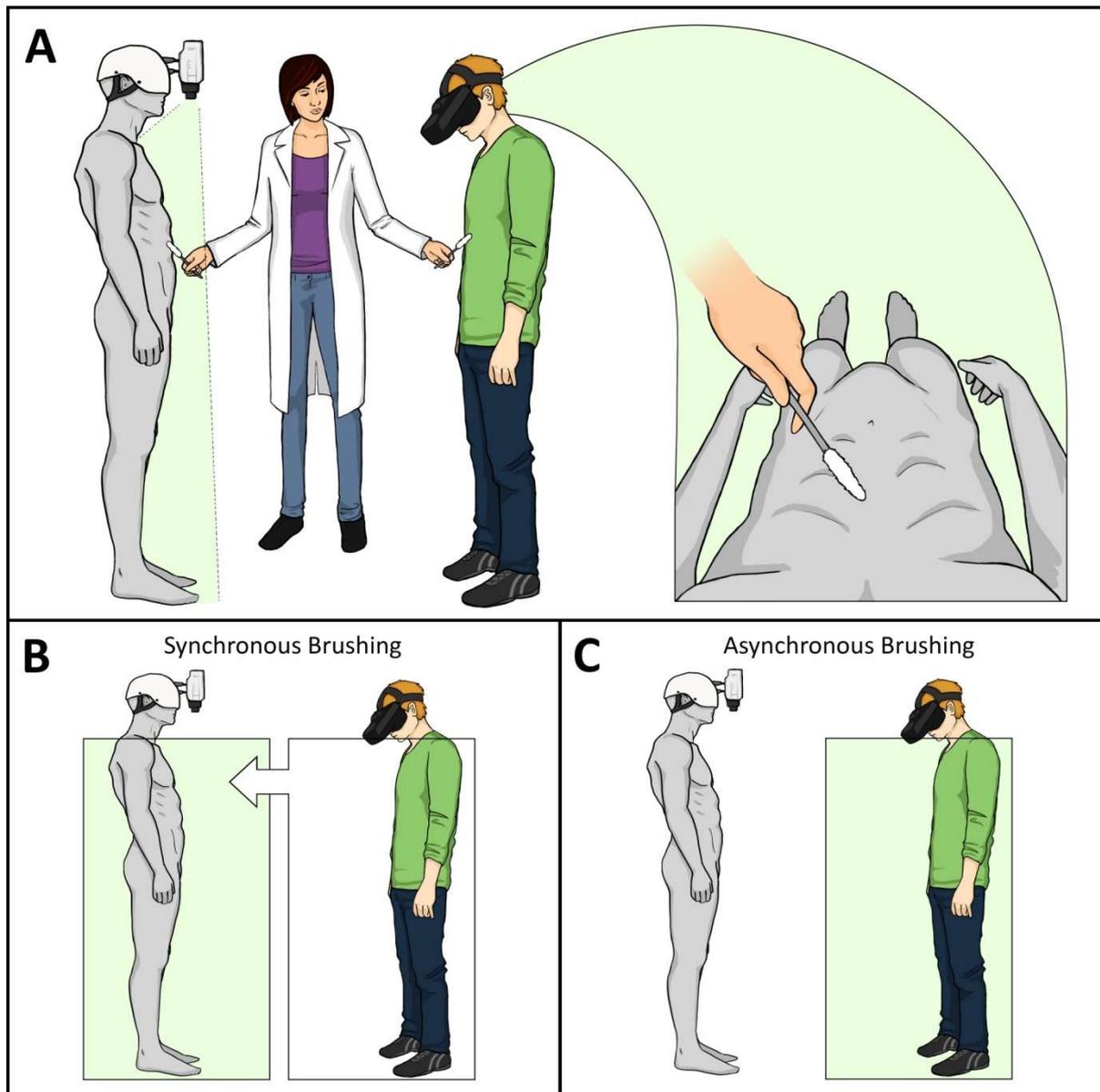


Fig. 3. Experimentally inducing body-swap illusions. A number of studies, such as those performed by Petkova & Ehrsson (2008) and Petkova et al. (2011), demonstrate how one can experimentally alter bodily self-consciousness to a different physical body. The basic underlying principles are as follows. A) Virtual reality is used to show participants the filming of a mannequin being brushed while they are also being brushed (in this case, the belly is being brushed). B) In the synchronous condition, when the filming is presented in real-time and the somatosensory and visual information about the brush strokes are simultaneous, participants perceive their self inside the mannequin's body as opposed to their own. C) In the asynchronous

condition, when a delay between the visual and the somatosensory information is introduced, participants experience their self inside their own body as opposed to the mannequin's.

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