

A fraction of dynamic loci (178 loci, table S2) show species-specific differences, whereas the conserved gene pair was interrupted in the three strains of one species by genes absent from the three strains of the other species. These loci would include sites where differences arose while the *Escherichia* and *Salmonella* lineages were diverging. Other dynamic loci (e.g., those where only a single strain shows a difference) would have arisen only after recombination had effectively ceased between the two lineages. Genes adjacent to species-specific loci are 6.2% older than genes adjacent to other dynamic loci ($P < 10^{-2}$ by randomization; gray bars in Fig. 3); thus, species-specific genes are not randomly distributed but are found preferentially in the older regions, indicating that the incipient *Escherichia* and *Salmonella* lineages continued to participate in recombination at loci unlinked to lineage-specific genes.

In contrast to the rapid formation of eukaryotic species boundaries, the ~70-My time frame over which genetic isolation evolved between *Escherichia* and *Salmonella* represents a temporal fragmentation of speciation. Because separate lineages arise within populations that continue to recombine at some loci for tens of millions of years, relationships among species inferred from few loci may underestimate their underlying complexity. Taxa may show different relationships depending on the genes compared. Long

periods of partial genetic isolation allow extant, named species (such as *E. coli*) to contain multiple nascent species. Although one can observe recombination at some genes within *E. coli* as a whole, strains also have niche-specific loci that may act as genetic progenitors for the creation of new species. That is, it may not be possible to make a clear distinction between intraspecific and interspecific variability (26), and clearly defined species cannot represent newly formed lineages. Therefore, the species concept proposed by Dykhuizen and Green [in which gene phylogenies are congruent among representatives of different species but are incongruent among members of the same species (5)] works to delineate long-established species but fails to recognize incipient species.

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27. This work was supported by grant GM078092 from the NIH. We thank B. Siegler Retchless and H. Hendrickson for helpful discussions and comments on the manuscript.

Supporting Online Material

www.sciencemag.org/cgi/content/full/317/5841/1093/DC1
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9 May 2007; accepted 27 July 2007
10.1126/science.1144876

Video Ergo Sum: Manipulating Bodily Self-Consciousness

Bigna Lenggenhager,¹ Tej Tadi,¹ Thomas Metzinger,^{2,3} Olaf Blanke^{1,4*}

Humans normally experience the conscious self as localized within their bodily borders. This spatial unity may break down in certain neurological conditions such as out-of-body experiences, leading to a striking disturbance of bodily self-consciousness. On the basis of these clinical data, we designed an experiment that uses conflicting visual-somatosensory input in virtual reality to disrupt the spatial unity between the self and the body. We found that during multisensory conflict, participants felt as if a virtual body seen in front of them was their own body and mislocalized themselves toward the virtual body, to a position outside their bodily borders. Our results indicate that spatial unity and bodily self-consciousness can be studied experimentally and are based on multisensory and cognitive processing of bodily information.

Ever since William James categorized different aspects of self-consciousness at the end of the 19th century, these aspects have been continuously refined and expanded,

including many different sensory, emotional, or cognitive layers. This has led to an excess of definitions, in the absence of a widely accepted model of self-consciousness that is based on empirical neurobiological data (1). More recent philosophical and neurological theories converge on the relevance of bodily self-consciousness (i.e., the nonconceptual and prereflective processing and representation of body-related information) as one promising approach for the development of a comprehensive neurobiological model of self-consciousness (1–4).

We investigated bodily self-consciousness experimentally, and we now describe an illusion during which healthy participants experienced a virtual body as if it were their own and localized their “selves” outside of their body borders at a different position in space. We modified the so-called “rubber-hand illusion” (RHI), during which synchronous stroking of a seen fake hand and one’s own unseen hand causes the fake hand to be attributed to one’s body (to “feel like it is my hand”; misattribution). Under such conditions of multisensory conflict, vision typically dominates over proprioception and touch (5). Several studies have demonstrated that the RHI also induces a mislocalization of one’s hand toward the fake hand, which is often referred to as “proprioceptive drift” (6–8). Brain-imaging studies associated the RHI mainly with the activation of the multisensory premotor cortex, posterior parietal areas (7), and right posterior insula (9); these areas have also been implicated in the integration of visual and somatosensory signals in nonhuman primates (10). These experimental findings corroborate anecdotal clinical data in neurological patients with right temporo-parietal damage leading to somatoparaphrenia, during which patients misattribute their own hand or foot as belonging to another person (11). The data on the RHI shows that important subglobal aspects of bodily experience, such as self-attribution and self-localization

¹Laboratory of Cognitive Neuroscience, Ecole Polytechnique Fédérale de Lausanne, Station 15, 1015 Lausanne, Switzerland.

²Philosophical Seminar, Johannes Gutenberg-Universität Mainz, 55099 Mainz, Germany. ³Frankfurt Institute for Advanced Studies, Johann Wolfgang Goethe-Universität, 60438 Frankfurt am Main, Germany. ⁴Department of Neurology, University Hospital, 1214 Geneva, Switzerland.

*To whom correspondence should be addressed. E-mail: olaf.blanke@epfl.ch

of body parts, can be manipulated experimentally (12).

Yet, the fundamental sense of selfhood (2, 13, 14) that is associated with bodily self-consciousness (but not with cognitive or emotional layers of self-consciousness) is experienced as the transparent content of a single, coherent whole-body representation, rather than as multiple representations of separate body parts. Accordingly, the latter have been referred to as the sense of body-part ownership, whereas whole-body representations or global ownership are directly associated with the sense of selfhood (2). Studies on the RHI and somatoparaphrenia thus investigated only body-part ownership or the attribution and

localization of a body part with respect to the global bodily self; i.e., a part-to-whole relationship. Thus, these studies did not experimentally manipulate selfhood per se.

To manipulate attribution and localization of the entire body and to study selfhood, we designed an experiment based on clinical data in neurological patients with out-of-body experiences. These data suggest that the spatial unity between self and body may be disrupted (15–17), leading in some cases to the striking experience that the global self is localized at an extracorporeal position (15, 17). The aim of the present experiments was to induce out-of-body experiences in healthy participants to investigate selfhood. We hypothesized that, under adequate

experimental conditions, participants would experience a visually presented body as if it were their own, inducing a drift of the subjectively experienced bodily self to a position outside one's bodily borders. Evidence for this conjecture stems not just from out-of-body experiences, but also from early anecdotal mirror-induced whole-body illusions (18) and the phenomenon of "presence" in virtual-reality environments (19, 20).

We applied virtual reality to examine the possible induction of out-of-body experiences by using multisensory conflict. In the first experiment, participants viewed the backs of their bodies filmed from a distance of 2 m and projected onto a three-dimensional (3D)–video head-mounted display (HMD) (Fig. 1A). The participants' backs were stroked for 1 min, either synchronously or asynchronously with respect to the virtually seen body. Global self-attribution of the virtual character was measured by a questionnaire that was adapted from the RHI (6). Global self-localization was measured by passively displacing the blind-folded participants immediately after the stroking and asking them to return to their initial position (21).

As predicted, participants showed a drift toward the virtual body (anterior-posterior axis) in the synchronous condition [24.1 ± 9.0 cm (mean \pm SEM)]. This position differed significantly from the initial position ($P = 0.02$, Student's t test = 2.67) (21). In the asynchronous condition, the drift was smaller ($12. \pm 8.5$ cm) and no longer significant ($P = 0.17$, $t = 1.45$) (Fig. 2A). No significant drift was measured along the left-to-right axis (fig. S1). Global illusory self-localization was corroborated by high-self-attribution scores on the three relevant questionnaire items (Q1 to Q3) (21) also showing significant differences between synchronous and asynchronous conditions (all P values < 0.001) (Fig. 2B). Participants reported varied feelings of "weirdness" or "strangeness," and some found the experiment irritating. None of the participants reported sensations of overt disembodiment or a change in visuospatial perspective.

In a second study, we examined whether this illusion depends on cognitive knowledge about bodies and whether the drift toward the virtual body was not due to a general motor bias to overshoot the target position. With the use of a constant time delay in asynchronous conditions, we either presented the participant's own body (as in study I) (Fig. 1A), a fake body (Fig. 1B), or an object (Fig. 1C) being stroked synchronously or not. Compared to a motor-control condition [no visual scene was shown (21)], we found a significant drift toward the virtual own body ($P = 0.02$, $t = 2.78$) and the fake body ($P = 0.01$, $t = 3.02$) (21). This drift was weaker and no longer significant in the case with a non-corporeal object ($P = 0.07$, $t = 1.95$) and absent when the stroking was asynchronous (all P values > 0.11) (Fig. 3). There was no drift in further control conditions or for the left-to-right axis (21). Yet, self-attribution differed between

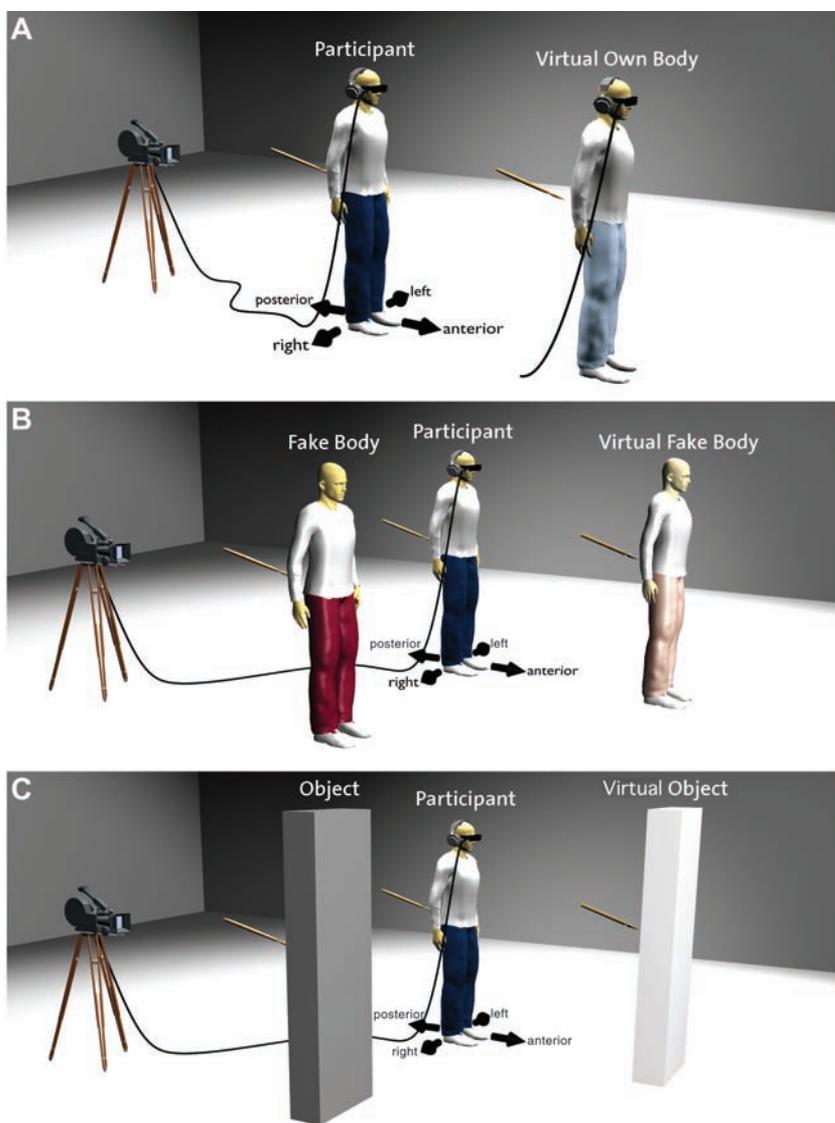


Fig. 1. (A) Participant (dark blue trousers) sees through a HMD his own virtual body (light blue trousers) in 3D, standing 2 m in front of him and being stroked synchronously or asynchronously at the participant's back. In other conditions (study II), the participant sees either (B) a virtual fake body (light red trousers) or (C) a virtual noncorporeal object (light gray) being stroked synchronously or asynchronously at the back. Dark colors indicate the actual location of the physical body or object, whereas light colors represent the virtual body or object seen on the HMD. [Illustration by M. Boyer]

the bodily conditions and the object condition. The first two questions of the questionnaire (Q1 and Q2) were answered positively in all of the synchronous conditions (own body, fake body, and object) and were significantly different and answered negatively in the asynchronous conditions ($P < 0.01$, $t > 2.56$). However, the third question (Q3: "It felt as if the virtual character was my body") led to different results. Whereas in both bodily conditions (own body and fake body) the result was the same as in Q1 and Q2 ($P < 0.05$, $t > 2.40$), this was not the case in the object condition where participants gave negative scores in the synchronous condition, revealing no significant difference between synchronous and asynchronous stroking ($P > 0.05$, $t = 1.55$) (fig. S2). This suggests that Q3 is important to evaluate self-identification with virtual bodily and nonbodily characters, whereas the first two questions seem more related to the feeling and location of touch.

With the use of virtual reality and multisensory conflict, we induced an illusion that makes it possible to quantify selfhood by manipulating attribution and localization of the entire body. Our results show that humans systematically experience a virtual body as if it were their own when visually presented in their anterior extrapersonal space and stroked synchronously. This finding was corroborated by the participants' mislocalization of their own bodies to a position outside their bodies, showing that self-attribution and localization of the entire body rely, at least partly, on similar visual-somatosensory integrative mechanisms to those of body parts (6–8). Although research of visual-somatosensory integration has mostly investigated directly visible body parts, comparable interactions have also been found for body parts that humans cannot see directly, such as the back (22). The overall pattern of the data from studies I and II suggests that, under appropriate conditions of multisensory conflict between visual signals conveying information about a virtual body (on a HMD) and tactile, proprioceptive, and vestibular signals conveying information from the participant's body, visual capture is still present. There were also

differences between both studies. Asynchrony in study II was more predictable (21), and the relation between felt and seen events might have been perceived as stronger, leading to larger drifts in the asynchronous conditions in study II. This might have led to the diminished effect of synchrony on the drift in the own-body condition, which is compatible with higher questionnaire scores for the asynchronous conditions from study II as compared with those from study I (Q1 to Q3) (Fig. 2C and fig. S2A) (21).

By manipulating visual input in the RHI, controversial data have been reported concerning the influence of cognitive constraints on multisensory integration, self-localization, and self-attribution. Whereas some authors argue that multisensory correlation is a sufficient condition for self-attribution (23), others argue for additional cognitive constraints in terms of higher-level knowledge about the body (8). We found evidence for higher-level knowledge by revealing in study II a weaker drift toward the object as compared with the fake-body condition, as well as a selective effect of synchrony in the fake-body condition. Because the fake-body and object conditions are completely comparable concerning the experimental setup (21), and given the pattern of results, we suggest that in order to investigate the influence of cognitive knowledge on self-localization, the comparison between the fake-body and object conditions is more relevant than that between the own-body and object conditions. These effects on illusory self-localization were corroborated by illusory self-attribution. When asked whether it felt as if the virtual character or object was their body (Q3), participants self-identified with both bodily stimuli but not with the object during synchronous stroking. Collectively, these findings speak in favor of bottom-up mechanisms as well as cognitive constraint (8), rejecting a pure Bayesian account (23) for self-attribution and self-localization of the entire body.

Illusory self-localization to a position outside one's body shows that bodily self-consciousness and selfhood can be dissociated from one's physical body position. This finding differs from

the RHI, in which this aspect of selfhood remained constant and only the attribution and localization of the stimulated hand was manipulated. Does illusory self-localization to a position outside one's body mean that we have experimentally induced full-blown out-of-body experiences? Out-of-body experiences are characterized by a disembodiment of the self to an extracorporeal location, an extracorporeal visuospatial perspective, and the sight of one's own body from this self-location. Because the present illusion was neither associated with overt disembodiment nor with a change in visuospatial perspective, we argue that we have induced only some aspects of out-of-body experiences or rather the closely related experience of heautoscopy that has also been observed in neurological patients (15–17). During heautoscopy, patients either constantly or intermittently experience as if they were seeing from and were localized at the position of an illusory body, their physical body, or at an intermediate position (15, 24). Such patients may also see themselves from behind (17) and often identify with the illusory body and partly transfer selfhood to the illusory body, even if visual bodily detail is lacking (17). Yet, they never report the overt disembodiment that is the most characteristic feature of out-of-body experiences (25, 26). Because our healthy participants did not report feelings of overt disembodiment, the present data suggest that other mechanisms in addition to conflicting visual-somatosensory information, such as visual-vestibular disintegration, are involved in generating full-blown out-of-body experiences and a more complete transfer of selfhood to an illusory body. These findings are compatible with clinical data (15, 17). Damage to or electrical stimulation of the temporo-parietal junction may lead to out-of-body experiences and heautoscopy (15, 27), and healthy participants activate the same region when employing extracorporeal self-locations in mental imagery (28, 29). Although other important aspects of self-consciousness are likely to involve additional brain areas such as the amygdala and the right frontal cortex (3) as well as multisensory areas in premotor and parietal cortices [representing both

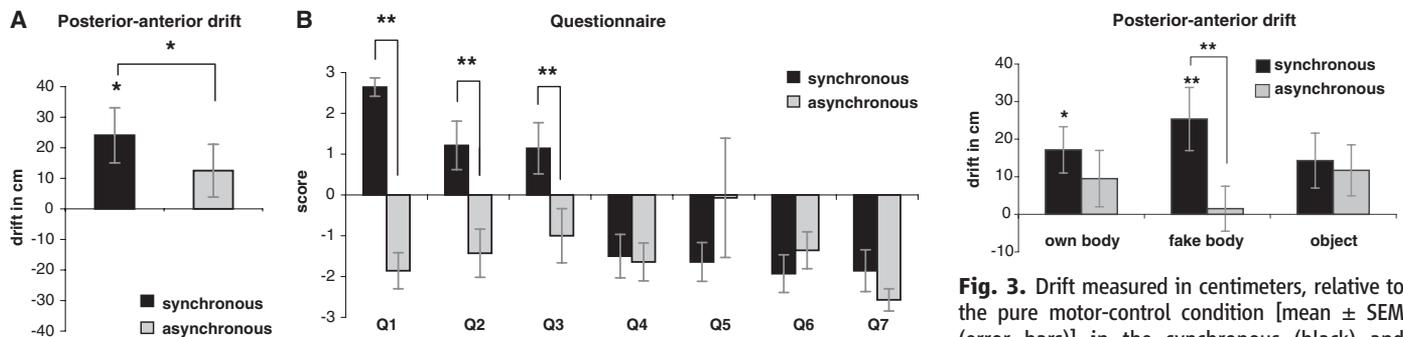


Fig. 2. (A) Drift measured in centimeters [mean \pm SEM (error bars)] in the synchronous (black) and asynchronous stroking conditions (gray) on the posterior-anterior axis. Participants showed a significantly stronger drift in the direction of the virtual body in the synchronous condition. $*P < 0.05$. (B) Score (mean \pm SEM) on the "self-attribution questionnaire" as adapted from (6). $**P < 0.01$.

Fig. 3. Drift measured in centimeters, relative to the pure motor-control condition [mean \pm SEM (error bars)] in the synchronous (black) and asynchronous stroking conditions (gray) for the different experiments: own body, object, and fake body. Only posterior-anterior drift is shown. $*P < 0.05$, $**P < 0.01$.

the seen and felt positions of one's arm (10) and correlating with the RHI (7)], we speculate that humans' daily experience of an embodied self and selfhood, as well as the illusion reported here, relies on brain mechanisms at the temporo-parietal junction. Experimentally creating illusions of the globalized, multisensory awareness of selfhood in a controlled manner with virtual-reality technology opens a new avenue for the investigation of the neurobiological, functional, and representational aspects of embodied self-consciousness. Further research should include the entire spectrum of disturbed global own-body perceptions, ranging from autoscopic hallucinations and heautoscopy to full-blown disembodied states such as out-of-body experiences.

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30. This work was supported by the Cogito Foundation, the Fondation de Famille Sandoz, the Fondation Odier, and the Swiss National Science Foundation. We thank S. Arzy, A. Burrack, S. Dieguez, and W. Singer for their helpful comments on a previous version of the manuscript and M. Boyer for the illustrations in Fig. 1.

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Materials and Methods

SOM Text

Figs. S1 to S2

Table S1

References

4 April 2007; accepted 19 July 2007

10.1126/science.1143439