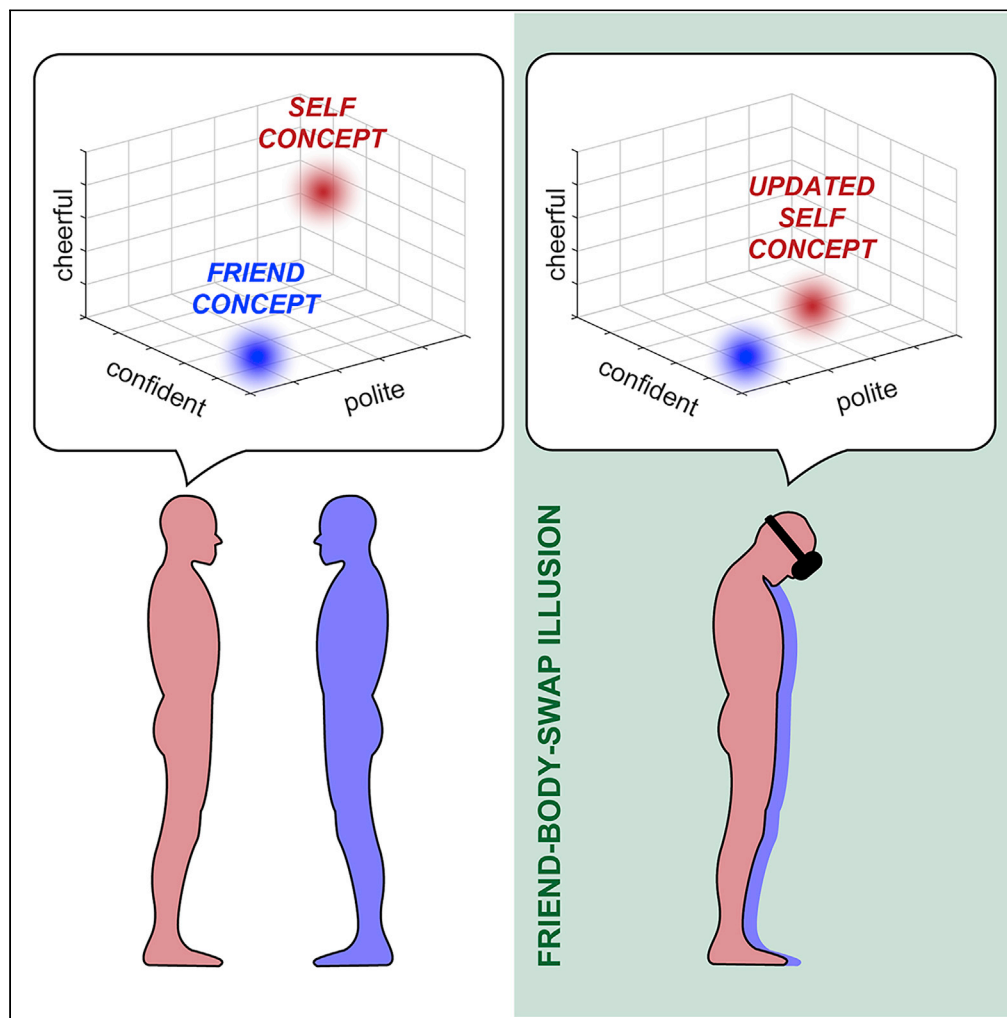


Article

# Perception of Our Own Body Influences Self-Concept and Self-Incoherence Impairs Episodic Memory



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**HIGHLIGHTS**

We used the perceptual illusion that pairs of friends swapped bodies with each other

Each participant rated their own and their friend's personality characteristics

During the illusion, beliefs about the self and about the friend became more similar

This self-concept updating was beneficial for the ongoing memory encoding

Article

# Perception of Our Own Body Influences Self-Concept and Self-Incoherence Impairs Episodic Memory

Pawel Tacikowski,<sup>1,2,4,\*</sup> Marieke L. Weijs,<sup>1,3</sup> and H. Henrik Ehrsson<sup>1</sup>

## SUMMARY

**How does our body affect the way we think about our personality? We addressed this question by eliciting the perceptual illusion that pairs of friends swapped bodies with each other. We found that during the illusion, the participants rated their own personality characteristics more similarly to the way they previously rated their friend's personality, and this flexible adjustment of self-concept to the "new" bodily self was related to the strength of illusory ownership of the friend's body. Moreover, a subsequent memory test showed that personality traits rated during the friend-body-swap illusion were generally remembered worse than traits rated during the control conditions; importantly, however, this impairment of episodic recognition memory was reduced for the participants who considerably adjusted their self-concept during the illusory body swapping. These findings demonstrate that our beliefs about own personality are dynamically shaped by the perception of our body and that coherence between the bodily and conceptual self-representations is important for the normal encoding of episodic memories.**

## INTRODUCTION

What makes us who we are? Is it the body we wake up in every morning and use as a "vehicle" through our daily activities, or is it a collection of thoughts and beliefs that we have about ourselves as individuals with certain skills, traits, and social identity? If it is a combination of the two, then how would a unified sense of self emerge from such a fusion of conscious beliefs and bodily perceptual experience? For example, would our sense of who we are change if one day our mind woke up inside the body of our best friend? These questions relate to one of the most fundamental problems in psychology and neuroscience: how we come to perceive a coherent sense of self. In addition to general relevance to all of us as thinking individuals, mechanisms of self-unity are important for the treatment of psychiatric disorders in which a sense of self is fragmented, such as in depersonalization disorder or schizophrenia.

One major element of the mental representation of ourselves is the *self-concept*: the multiple beliefs that we have about our own personality (Baumeister, 1998; Oyserman et al., 2012). These beliefs have a multi-dimensional structure that is unique for each person, and self-concept is commonly regarded as a "reference point" that organizes our experience, guides our complex behaviors, and helps to predict future situations (Baumeister, 1998; Oyserman et al., 2012; Swann, 1997). Owing to its robust representation in our memory system, self-concept also facilitates the encoding of new information; for example, trait adjectives rated in relation to the self are remembered better than traits encoded in other semantic contexts, the so-called self-reference effect (Rogers et al., 1977; Sui and Humphreys, 2015; Symons and Johnson, 1997). A second main component of our self-representation is the *bodily self*, that is, a sense of being distinct from the outside world and centered within a body that feels like our own (Blanke et al., 2015; Brugger and Lenggenhager, 2014; Ehrsson, 2020, 2012). Remarkably, experimental manipulations of visuotactile synchrony induce perceptual illusions that fake limbs (Botvinick and Cohen, 1998; Ehrsson et al., 2004; Tsakiris and Haggard, 2005) or even entire artificial bodies (Petkova et al., 2011; Petkova and Ehrsson, 2008) viewed from a natural first-person perspective become part of the bodily self, which demonstrates that the representation of our own body is highly flexible and that multisensory integration mechanisms play a key role in attributing ownership to our body (Ehrsson, 2012, 2020; Kilteni et al., 2015; for studies on self-recognition of bodies and faces viewed at a distance from a third-person perspective, see also Lenggenhager et al., 2007; Tsakiris, 2008; Aspell et al., 2009; Preston et al., 2015). Research has also shown that such experimentally induced changes of the bodily self have specific cognitive, emotional, and behavioral consequences; for

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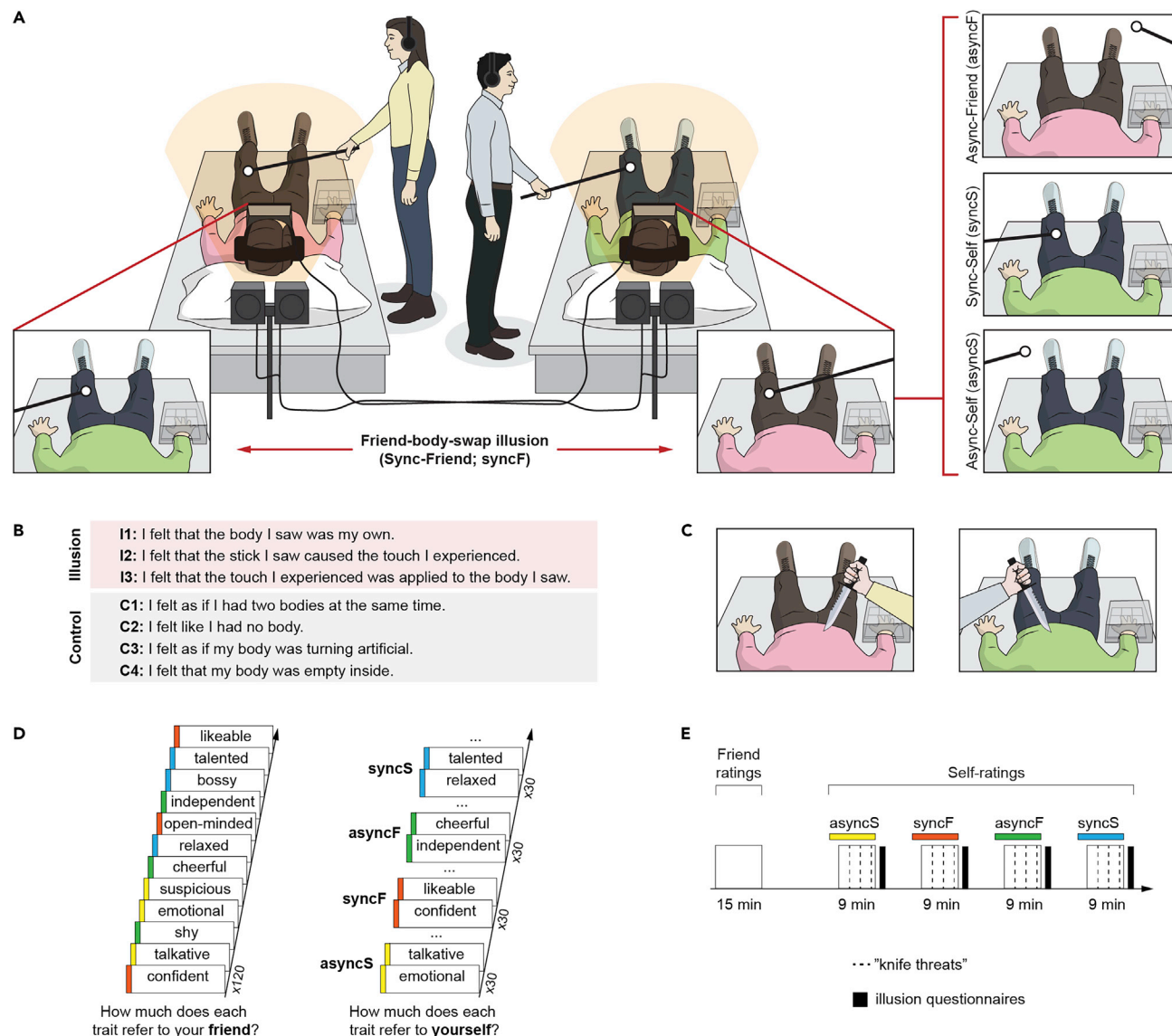
example, attitudes toward a racial group change after the illusory embodiment of a member of that group (Maister et al., 2013; Peck et al., 2013), emotional feelings of social fear (Guterstam et al., 2015a) and body dissatisfaction (Preston and Ehrsson, 2016) can be modulated by full-body ownership illusions, and the recognition of one's own face (Sforza et al., 2010; Tajadura-Jimenez et al., 2012; Tsakiris, 2008), the style of one's own behavior (Yee et al., 2009), and implicit associations with the past self (Banakou et al., 2013) are flexibly shaped by the ongoing perception of one's own body. Importantly, experimental disruptions of a sense of the bodily self through an induction of an out-of-body illusion (Bergouignan et al., 2014) or by making the body invisible (Bréchet et al., 2019) also impair the ongoing encoding of episodic memories. What remains unknown, however, is whether the bodily self dynamically shapes multiple beliefs that constitute the conscious self-concept, and if so, what the function of this shaping is for episodic memory.

Here, we induced the perceptual illusion that pairs of friends “swapped” bodies with each other to test the hypothesis that self-concept is flexibly adjusted to the ongoing perception of one's own body and that this adjustment is beneficial for the ongoing encoding of episodic information. Based on neurocognitive models of the human self (Apps and Tsakiris, 2014; Tsakiris, 2017), evidence from social psychology (Campbell et al., 1996; Festinger, 1957; Hirsh and Kang, 2016), and studies on individuals with depersonalization disorder or schizoprenia who feel “detached” from their body (Giesbrecht et al., 2010; Postmes et al., 2014; Sierra and David, 2011), we reasoned that coherence of self-representation is functionally advantageous, whereas self-incoherence is associated with cognitive, emotional, and behavioral deficits. We theorized that this would make sense because for our self-representation to be informative in the ever-changing world, it needs to be accurate and up to date with regard to the current sensory, social, and cultural context. Thus, illusory ownership of the friend's body in our paradigm should lead to updating of the participants' beliefs about their own personality so that they become more similar to beliefs about the friend's personality. Moreover, the mismatch between the bodily and conceptual self-representations experienced during the “friend-body-swap illusion” should impair the ongoing encoding of episodic information, in line with earlier work (Bergouignan et al., 2014). Importantly, however, reinstating a coherent sense of self should reduce this memory impairment.

## RESULTS

Pairs of friends participated in this study simultaneously ( $N = 66$ ). During the main friend-body-swap illusion condition (“synchronous-friend”; syncF), both friends lay on beds, and through head-mounted displays (HMDs), they saw live recordings from cameras placed just above the other person's head, that is, from the perspective from which one normally looks at one's own body. At the same time, the experimenters applied synchronous touches to both participants on the corresponding body parts (Figure 1A; Video S1). A match between touches felt on one's actual body, which was out of view, and touches seen on the friend's body, which was displayed in the HMDs, should induce the perceptual illusion that the friend's body is one's own (Guterstam et al., 2015a; Petkova et al., 2011; Petkova and Ehrsson, 2008; van der Hoort et al., 2011). In contrast, asynchronous visuotactile stimulation in the “asynchronous-friend” (asyncF) condition, implemented by delaying the display in HMDs by three seconds, should reduce the illusion and serve as a well-matched control (i.e., the same visual input but no ownership of the friend's body). The “synchronous-self” (syncS) condition was a baseline built into our design; during this condition, the participants saw their own body and experienced no visuotactile delay, similar to everyday life. Finally, the “asynchronous-self” (asyncS) condition controlled for any potential effects of asynchronous visuotactile stimulation itself. The strength of the full-body ownership illusion was assessed by a questionnaire administered after each condition (Figure 1B) in which the participants rated the strength of three perceptual experiences associated with the illusion (e.g., “I felt that the body I saw was my own”) and four conceivable experiences that were not directly related to our experimental manipulation (e.g., “I felt that my body was empty inside”); the latter control items accounted for potential effects of suggestibility or task compliance (Guterstam et al., 2015a; Petkova et al., 2011; Petkova and Ehrsson, 2008; van der Hoort et al., 2011). The illusion was also assessed by skin conductance responses measured when the friend's or one's own real body was “threatened” with a mock knife (Figure 1C); this measure was intended to provide objective physiological evidence that the full-body ownership illusion was successfully induced (Guterstam et al., 2015a; Petkova et al., 2011; Petkova and Ehrsson, 2008; van der Hoort et al., 2011).

With regard to our main hypotheses, the participants performed two personality rating tasks (Figure 1D). The first friend-rating task was conducted before the four full-body illusion conditions and did not involve any body perception manipulations. During this task, the participants sat in front of computers and rated



**Figure 1. Procedure**

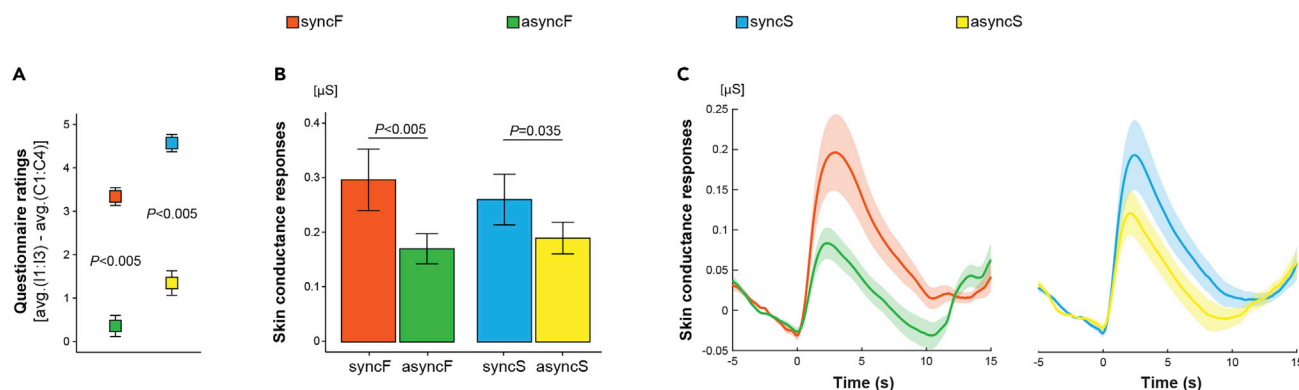
(A) **Induction of the friend-body-swap illusion and visuotactile stimulation in the control conditions.** The participants—a pair of friends (pink and green jumpers)—lay on two beds and wore two sets of head-mounted displays (HMDs). The recordings shown in the HMDs came from two digital cameras placed just above and behind each participant’s head. This created high-quality 3D movies of either the friend’s body (syncF, asyncF) or one’s own body (syncS, asyncS) shown from a first-person perspective. At the same time, the experimenters applied strokes to the participants’ bodies; the location, onset, and duration of each stroke were precisely controlled by audio cues heard by the experimenters. In the synchronous conditions, the touches seen in the HMDs and the touches felt on one’s actual body were matched, whereas in the asynchronous conditions, the displays were delayed 3 s, creating a visuotactile mismatch.

(B) **Illusion questionnaire.** After each condition, the participants rated illusion (I1:I3) and control (C1:C4) statements on a 7-point scale (–3 “strongly disagree”; +3 “strongly agree”).

(C) **Knife threats.** Genuine ownership of the friend’s body should be associated with increased physiological stress responses when this body is physically threatened. Thus, during each condition, we simultaneously “attacked” both participants’ bodies with mock knives and measured skin conductance responses during these events.

(D) **Friend rating and self-rating tasks.** At the beginning of the study, before any body perception manipulation was applied, the participants listened to 120 trait adjectives and rated how well each trait described their friend (1 “not at all”; 9 “very much”). The same traits were then randomly assigned to the four full-body illusion conditions, and *during* each condition, the participants rated how well each trait described themselves.

(E) **Timeline.** Condition order was randomized across participants. The break between friend- and self-rating tasks was ~10 min; during this time, the full-body illusion setup was prepared.



**Figure 2. Synchronous Visuotactile Stimulation in syncF Successfully Induced the Friend-Body-Swap Illusion, Whereas Asynchronous Stimulation in asyncS Reduced Ownership of One's Own Actual Body**

(A) Illusion scores were significantly higher in the synchronous than in the asynchronous conditions ( $p < 0.005$ ). Plot shows means  $\pm$  SE.

(B) Knife threats that occurred during the synchronous conditions triggered significantly stronger skin conductance responses than knife threats during the asynchronous conditions ( $p < 0.005$ ). Bar plot shows means  $\pm$  SE.

(C) Time courses of the skin conductance signal during knife threat events plotted for descriptive purposes. To take into account typical physiological variability of response latencies, we time-locked each response to its onset (time "0"; see [Transparent Methods](#)). Solid lines are averages of all trials, and shaded areas correspond to SE. For the detailed statistical results behind this figure, see [Tables S1](#) and [S2](#); for individual data points, [Figure S1](#); and for full questionnaire results, [Tables S3](#) and [S4](#) and [Figure S2](#).

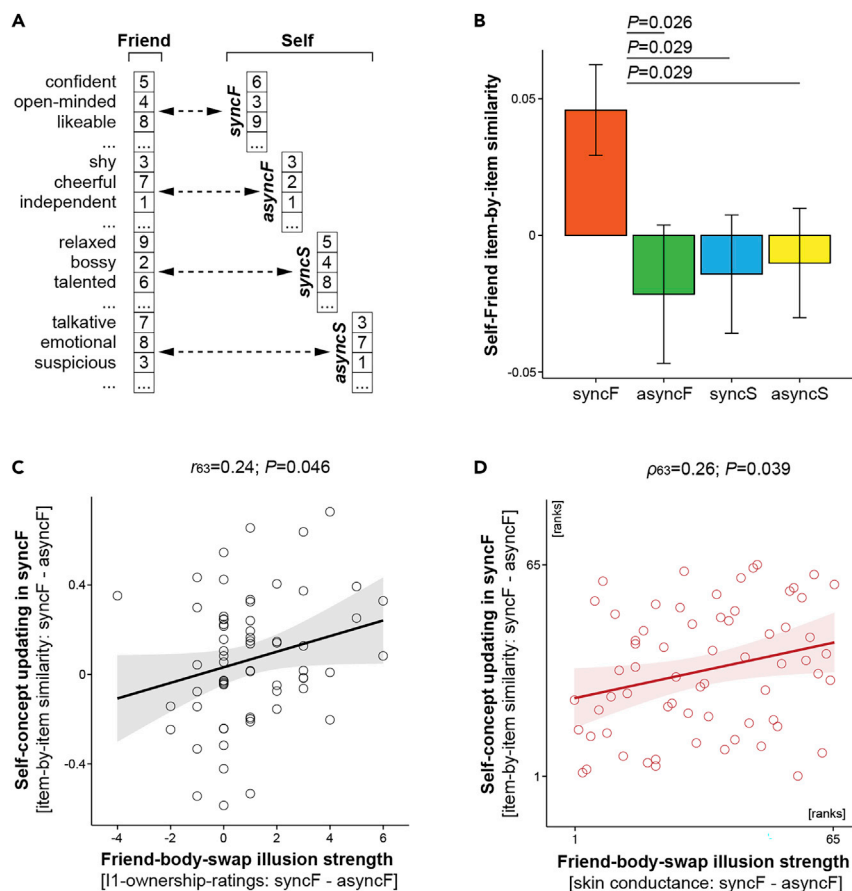
how well each of the 120 trait characteristics described the friend ([Data S1](#)). In the following self-rating task, the same traits were randomly assigned to the four full-body illusion conditions (30 traits per condition), and during each condition, the participants rated how well each trait described themselves. Ratings from these two tasks allowed us to measure how similar the participants' beliefs about their own and the friend's personalities were during different embodiment contexts ([Figure 1E](#)). Because the friend ratings in the present paradigm were "fixed" (i.e., they were collected before the four full-body illusion conditions) and because the assignment of traits to different conditions was random, an increase in similarity between self-ratings and friend ratings in a given condition, compared with other conditions, suggests an adjustment of beliefs about one's own personality to beliefs about the friend's personality in that condition ("updating of self-concept") and not the other way around.

### Eliciting the Friend-Body-Swap Illusion

We first checked whether the friend-body-swap illusion was successfully induced. To this end, for each participant, we calculated "illusion scores" as differences between the average illusion (I1:I3) and control (C1:C4) ratings from the illusion questionnaire. These scores provided an overall estimate of the full-body illusion strength above potential suggestibility or task-compliance effects (see earlier). As expected, we found that in the synchronous conditions, the illusion scores were significantly ( $p < 0.005$ ) higher than in the asynchronous conditions ([Figures 2A](#) and [S1A](#); for detailed statistical results, see [Tables S1](#) and [S2](#)). Moreover, and in agreement with the above results for the illusion scores, all three individual illusion statements in the syncF condition were associated with positive ratings (median  $\geq +2$ ) that were significantly ( $p < 0.005$ ) higher than in the asyncF condition, which means that the majority of participants affirmed both illusory ownership and sensing touch on the friend's body in the syncF condition ([Tables S3](#) and [S4](#); [Figure S2](#)). Furthermore, and importantly, knife threats that occurred during the synchronous conditions evoked stronger skin conductance responses than knife threats during the asynchronous conditions ([Figures 2B, 2C](#), and [S1B](#) and [S2](#)). It is also worth noting that there was no significant modulation of the friend-body-swap illusion strength by closeness of friendship, friendship duration, participants' sex, condition order, or baseline self-friend similarity in syncS ([Figure S5](#)). Thus, both the questionnaire and skin conductance data show that the friend-body-swap illusion was successfully induced in the syncF condition and that visuotactile asynchrony in asyncS weakened the ownership of one's actual body.

### Friend-Body-Swap-Induced Updating of Self-Concept

To test our first main hypothesis that the bodily self dynamically shapes the content of self-concept, for each participant in each condition, we calculated cosine similarity between self-ratings and friend ratings



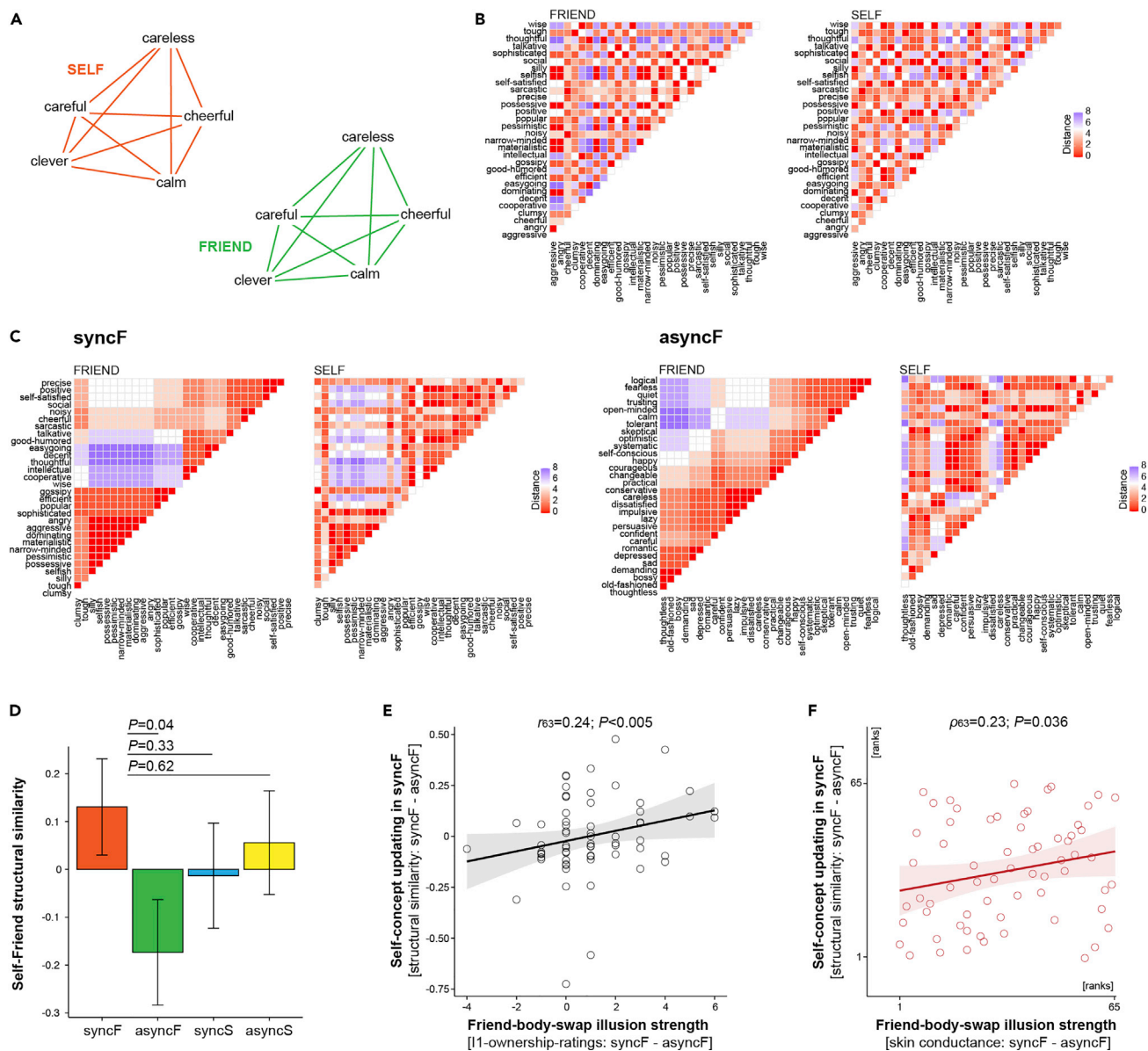
**Figure 3. Illusory Ownership of the Friend's Body in syncF Was Related to Updating of Beliefs About One's Own Personality So That They Became More Similar to Beliefs about the Friend**

(A) For each participant in each condition, we calculated similarity scores between the self-ratings and friend ratings of the same traits.

(B–D) (B) During the friend-body-swap illusion, the participants rated their own personality characteristics more similarly to the way they previously rated the friend's personality (means  $\pm$  SE; for individual data points, see Figure S3A). This dynamic adjustment of self-concept to the "new" bodily self was enhanced for the participants who experienced strong illusory ownership of the friend's body, as indicated by the questionnaire (C) and skin conductance (D) measures.

of the same personality characteristics (Figure 3A; Transparent Methods). Cosine similarity is a common metric of resemblance between arrays of different text items that ranges from 1 (identical) to  $-1$  (dissimilar). To account for the overall degree of similarity between the way the participants viewed themselves and their friends, which could obviously vary across participants, we "centered" similarity scores from each condition on the average of scores from all conditions for a given participant. We found that during the friend-body-swap illusion, the participants rated themselves more similarly to the way they previously rated the friend (Figures 3B and S3A; syncF vs. asyncF:  $b = 0.07$ ;  $SE = 0.03$ ;  $t = 2.24$ ;  $p = 0.026$ ; syncF vs. syncS:  $b = 0.06$ ;  $SE = 0.03$ ;  $t = 2.22$ ;  $p = 0.029$ ; syncF vs. asyncS:  $b = 0.06$ ;  $SE = 0.03$ ;  $t = 2.21$ ;  $p = 0.029$ ; linear mixed-models [LMMs]; two-sided;  $N = 65$ ). Moreover, the stronger the ownership of the friend's body during syncF, the higher the similarity between self-ratings and friend ratings in this condition. This significant correlation was present for the questionnaire and skin conductance measures of the illusion (Figures 3C and 3D, respectively;  $r_{63} = 0.24$ ;  $p = 0.046$ ; Pearson correlation; two-sided;  $\rho_{63} = 0.26$ ;  $p = 0.039$ ; Spearman correlation; two-sided;  $N = 65$ ). Control analyses further excluded the possibility that increased similarity between beliefs about one's own and the friend's personalities in syncF was driven by more negative self-evaluations in this condition, a concern related to the possibility that "self-enhancement bias" (Brown, 1986) was reduced by illusory ownership of the friend's body (Figure S6). Collectively, the above results support our first main hypothesis and show that the perception of one's own body dynamically shapes multiple conscious beliefs that constitute the self-concept.





**Figure 4. The Friend-Body-Swap Illusion Also Reconfigured the Multidimensional Structure of Self-Concept and Made It More Similar to the Structure of Friend-Concept**

(A) A schematic illustration of “structural similarity.” Graphs represent ratings of five example personality traits provided with regard to the self (red) and the friend (green). Pairs of traits that are closer to each other were rated more similarly than traits that are farther apart. Structural similarity corresponds to resemblance between shapes of the whole graphs rather than between individual traits.

(B) For each participant in each condition, we calculated two distance matrixes: one between friend ratings (left) and the other between self-ratings (right). Both matrixes are based on the same traits (i.e., only the ones that were presented during a given condition). These unique “barcodes” of the participant’s beliefs about one’s own and friend’s personalities correspond to distances between the ratings of each trait in relation to all other traits. For group analyses, we calculated a correlation between the self-matrix and the friend-matrix for each participant in each condition.

(C) Data from the syncF and asyncF conditions from a representative participant who experienced a strong friend-body-swap illusion (11-ownership-ratings: syncF - asyncF = 4). For display purposes, trait adjectives are sorted according to the hierarchical clustering algorithm applied to friend ratings (“template”). Without sorting, the heatmaps in syncF would have looked like (B) (same data). Importantly, in the syncF condition, the main clusters of similar (low distance; red) and dissimilar (high distance; blue) ratings are largely preserved between the self- and friend-matrixes, resulting in high overall self-to-friend similarity (Spearman’s rho = 0.54). In contrast, in the asyncF condition, the structure of clusters is very different between the self- and friend-matrixes, resulting in low overall self-to-friend similarity (Spearman’s rho = 0.12).

**Figure 4. Continued**

(D) At the group level, structural similarity between self- and friend-ratings was higher in the syncF than in the asyncF condition ( $N = 65$ ; means  $\pm$  SE). (E and F) The stronger the illusion of owning the friend's body—as measured by the illusion questionnaire ownership ratings (E) and threat-evoked skin conductance responses (F)—the greater the structural similarity between ratings of one's own and the friend's personalities in the syncF condition.

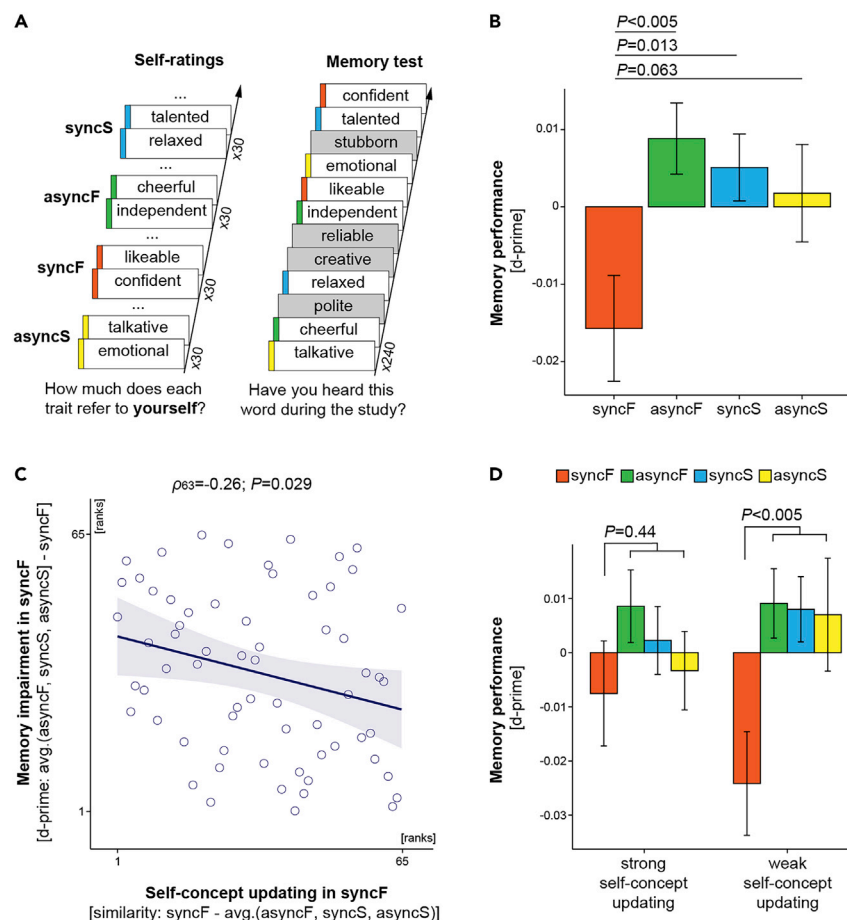
**Structural Reconfiguration of Self-Concept**

In a complementary post hoc approach, we next examined whether the illusion also reconfigured the multidimensional structure of self-concept and made it more similar to that of a friend-concept (Figure 4A). To this end, for each participant in each condition, we calculated the Euclidean distances between the ratings of every trait in relation to all other traits and compared how similar these distance matrixes were across beliefs about one's own and the friend's personalities in different conditions (Figure 4B). Please note that structural similarity as defined above is largely independent from the item-by-item similarity reported in the previous paragraph; for instance, a standard correlation between  $X [1\ 2\ 3\ 4\ 5]$  and  $Y [5\ 4\ 3\ 2\ 1]$  is  $-1$ , whereas the similarity of item relationships within  $X$  and  $Y$  is 1. We found that structural similarity between self-ratings and friend ratings was higher in the syncF than in the asyncF condition (Figures 4C and 4D; syncF vs. asyncF:  $b = 0.3$ ;  $SE = 0.15$ ;  $t = 2.05$ ;  $p = 0.04$ ; syncF vs. syncS:  $b = 0.14$ ;  $SE = 0.15$ ;  $t = 0.97$ ;  $p = 0.33$ ; syncF vs. asyncS:  $b = 0.07$ ;  $SE = 0.15$ ;  $t = 0.51$ ;  $p = 0.62$ ; LMMs; two-sided;  $N = 65$ ). Furthermore, the stronger the friend-body-swap illusion, the higher the structural similarity between self-ratings and friend ratings in syncF; this significant relationship was present for the questionnaire and skin conductance measures of the illusion (Figures 4E and 4F, respectively;  $r_{63} = 0.24$ ;  $p < 0.005$ ; Pearson correlation; one-sided;  $\rho_{63} = 0.23$ ;  $p = 0.036$ ; Spearman correlations; one-sided;  $N = 65$ ; see also Figure S4). It is noteworthy that the above analyses were performed on complex datasets, which makes it highly unlikely that the results were driven by the participants' conscious strategy or task compliance (see Limitations). Instead, the above findings provide complementary evidence that the moment-to-moment perception of one's own body reconfigures the multidimensional structure of beliefs about one's own personality.

**Self-Concept Updating and Episodic Recognition Memory**

Moving to our second main hypothesis, we tested whether reinstating a coherent self-representation across the bodily and conceptual levels is beneficial for the ongoing encoding of episodic information. To this end, we asked the same participants to complete a memory task that was conducted immediately after the four full-body illusion conditions. During this task, the participants sat in front of computers (without experiencing any body-perception manipulation) and listened to the same trait adjectives as before that were now intermixed with 120 new trait characteristics (Data S1 and S2). The task was to indicate whether a given word had already occurred in the study (Figure 5A). Because the participants did not know about this memory test beforehand (i.e., memorizing traits was not explicitly required in the preceding personality rating part), it probed implicit (incidental) episodic recognition memory during the different full-body illusion conditions (Symons and Johnson, 1997). This paradigm is well suited for the current study because (1) it measures encoding of information in relation to the self-concept and (2) it complements the more explicit personality-ratings data. We found that memory performance for words encoded during the friend-body-swap illusion was generally reduced (Figure 5B; syncF vs. asyncF:  $b = -0.02$ ;  $SE = 0.01$ ;  $t = -3$ ;  $p < 0.005$ ; syncF vs. syncS:  $b = -0.02$ ;  $SE = 0.01$ ;  $t = -2.59$ ;  $p = 0.013$ ; syncF vs. asyncS:  $b = -0.02$ ;  $SE = 0.01$ ;  $t = -1.89$ ;  $p = 0.063$ ; LMMs; two-sided;  $N = 65$ ). This was expected because the illusion of owning the friend's body should create a conflict between the bodily self and the self-concept and thus reduce overall self-coherence (Bergouignan et al., 2014; Bréchet et al., 2019). Importantly, however, high similarity between self-ratings and friend ratings during syncF was related to less impaired memory encoding in this condition (Figure 5C;  $\rho_{63} = -0.26$ ;  $p = 0.029$ ; Spearman correlation; two-sided). Analogously, among the participants who indicated high self-to-friend similarity during the friend-body-swap illusion, there was no significant difference between memory performance in syncF and other conditions (Figure 5D; memory: avg. (asyncF, syncS, asyncF) – syncF;  $t_{32} = 0.77$ ;  $p = 0.44$ ;  $N = 33$ ; one-sample t test; two-sided). In contrast, the participants who showed weaker self-to-friend similarity during the illusion had significantly reduced recognition memory for traits encoded during the syncF condition (Figure 5D; memory: avg. (asyncF, syncS, asyncF) – syncF;  $t_{31} = 2.52$ ;  $p < 0.005$ ;  $N = 32$ ; one-sample t test; two-sided). Control analyses indicated that these two subgroups of participants did not differ significantly with regard to potential confounding factors (Table S5). These results suggest that maintaining a coherent representation of ourselves across the bodily and conceptual levels is important for normal encoding of episodic information, whereas self-representation incoherence that is not compensated by self-concept updating impairs this encoding.





### Figure 5. Strong Updating of Self-Concept during the Friend-Body-Swap Illusion (syncF) Was Related to Less Impaired Recognition Memory of Personality Traits That Occurred during This Condition

(A) A schematic illustration of the memory task (orange, green, blue, and yellow bars represent items rated during syncF, asyncF, syncS, and asyncS, respectively; gray boxes represent new items).

(B) Memory performance for words encoded during the friend-body-swap illusion was generally reduced (means  $\pm$  SE). For all subjects' individual data points, see [Figure S3B](#).

(C) Strong updating of the self-concept toward the friend-concept during the friend-body-swap illusion was related to less impaired memory performance in syncF.

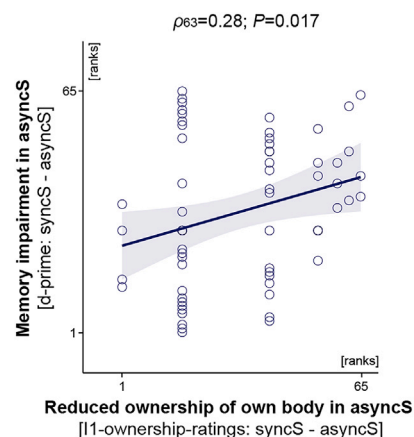
(D) Analogously, among the participants who showed strong updating of self-concept during syncF ( $\geq$  median "similarity updating score"; syncF - avg. (asyncF, syncS, asyncS);  $N = 33$ ), there was no significant difference between memory performance in syncF and in other conditions. In turn, the participants who showed weaker self-concept updating during syncF ( $<$  median "similarity updating score";  $N = 32$ ) remembered significantly fewer items from the syncF than from the control conditions (means  $\pm$  SE). Please note that the median split was performed mainly for display purposes and to complement the main analyses shown in (B) and (C).

### Memory Performance in asyncS

Finally, we tested whether memory encoding was also impaired by another type of self-incoherence, namely, by reduced ownership of one's own actual body in the asyncS condition (see syncS vs. asyncS; [Figure 2](#)). Indeed, we found that the participants who felt strong disownership of their real body in view during asyncS remembered fewer trait adjectives from this condition than from the syncS baseline condition ([Figure 6](#);  $\rho_{63} = 0.28$ ;  $p = 0.017$ ; Spearman correlation; two-sided;  $N = 65$ ). This result suggests that incoherence of the bodily self evoked by the disintegration of visual and somatosensory signals also impairs ongoing memory encoding.

### DISCUSSION

The present study examined the hypotheses that (1) the perception of one's own body (bodily self) dynamically shapes beliefs about one's own personality (self-concept) and (2) coherence between these two



**Figure 6. Reduced Ownership of One’s Own Actual Body in asyncS Was Associated with More Impaired Recognition Memory of Traits That Were Rated during This Condition**

components of self-representation is important for normal memory encoding. With regard to the first hypothesis, we found that even a brief experience of illusory ownership of the friend’s body changed the content and structure of multiple beliefs about one’s own personality and made them more similar to beliefs about the friend’s personality. This finding extends previous knowledge in several important ways. First, it challenges a common assumption that self-concept is relatively fixed over time and emphasizes the role of the body in the continuous construction of our sense of who we are; this role has been largely neglected in past social psychology research (Baumeister, 1998; Oyserman et al., 2012; Swann, 1997). Second, this result shows that perceptual aspects of the bodily self dynamically shape *multiple, abstract* beliefs that constitute our *conscious* self-concept rather than only selected aspects of self-representation that are perceptual, body-related, or implicit (Banakou et al., 2013; Sforza et al., 2010; Tajadura-Jimenez et al., 2012; Tsakiris, 2008; Yee et al., 2009). Third, this finding clarifies that the illusory ownership of another person’s body not only modifies attitudes toward this person or toward a social group to which this person belongs (Maister et al., 2014, 2013; Paladino et al., 2010; Peck et al., 2013) but also, and perhaps predominantly, modifies beliefs about the self. Taken together, our results highlight the importance of the sense of one’s own body as a foundation of social identity and self-concept.

With regard to possible cognitive mechanisms of this body-related updating of self-concept, embodied cognition theories propose that all concepts are grounded in sensorimotor representations (Barsalou, 2008); thus, a change in the representation of one’s own body affects the content of self-concept. In turn, predictive processing theories suggest that, if the low-level perceptual representation of one’s own body creates a conflict further up in the processing hierarchy, this conflict is resolved by updating higher-order beliefs about the self (Apps and Tsakiris, 2014; Tsakiris, 2017). Other studies have proposed that (1) illusory ownership of someone else’s body involves making inferences about one’s own attributes, e.g., “I am polite because the person whose body I have is polite” (Yee et al., 2009); (2) that the illusion allows new associations to be formed within the “self-image network” (Bedder et al., 2019); (3) that “owning” another person’s body primes the concept of that person in the structure of knowledge (Peña et al., 2009); or (4) that body experiences of this kind increase the perceived physical similarity between the self and the other, which consequently increases the perceived conceptual similarity (Maister et al., 2014). What the present study adds to this complex discussion is the demonstration that self-concept updating is not a result of deliberate inference because the participants were not aware that their self-ratings became more similar to their friend ratings in the syncF condition (see further). Furthermore, the effect could not simply be explained by priming because the friend concept was likely “activated” even by looking at the friend’s body during the asyncF condition. Instead, we found that the adjustment of self-concept toward the friend concept was tightly linked to the perceived strength of the illusory ownership of the friend’s body (Figures 3C and 3D), which suggests that it was the multisensory experience of “having” the friend’s body that drove the plastic changes of self-concept. As a novel hypothesis, we propose that (1) the brain represents self-concept as a convex region in the multidimensional space of different traits, skills, group-identities, etc. (Bellmund et al., 2018; Gärdenfors, 2004) and (2) because the illusion of having someone else’s body greatly

modifies the default way one experiences the self, this illusion leads to “remapping” of the self-concept in the above-mentioned multidimensional space. We speculate that at the neural level, this remapping is implemented by functional interactions between the multisensory fronto-parietal areas that represent perceptual aspects of the bodily self (Ehrsson et al., 2004; Petkova et al., 2011), the medial prefrontal region that is involved in the self-concept representation (Heatherton et al., 2006; Tacikowski et al., 2017), and the hippocampal-retrosplenial system that is related to spatial navigation, episodic memory, and translating between allocentric and egocentric mental perspectives (Andersen et al., 2007; Bergouignan et al., 2014; Burgess et al., 2001; Byrne et al., 2007; Eichenbaum, 2000; Guterstam et al., 2015b; Nyberg et al., 1996). Future neuroimaging and intracranial electrophysiology studies should investigate whether and, if so, how the multivariate representation of self-concept in the prefrontal cortex is “remapped” during illusory ownership of a familiar other’s body.

Our second main finding is that the flexible adjustment of self-concept to the “new” bodily self is beneficial for the ongoing encoding of episodic information, whereas incoherence between the bodily and conceptual self-representations is associated with impaired memory processes. This finding is different from earlier experiments on out-of-body illusions (Bergouignan et al., 2014) and manipulations of the visual appearance of the body (Bréchet et al., 2019) that showed impaired encoding of episodic memories due to a disrupted sense of the bodily self (see further below). The present results establish that coherent self-representation across different levels—here, conceptual and bodily—plays an important role in normal mnemonic processing. Importantly, this finding cannot be explained by differences in the to-be-encoded material because traits in the present study were randomly assigned to different conditions. Furthermore, a context mismatch between the encoding and retrieval phases (Godden and Baddeley, 1975) cannot explain this finding because (1) memory performance in the most context-matching condition (syncS) was not higher than in all context-mismatching conditions (syncF, asyncF, asyncS) and (2) contextual cues related to visuotactile stimulation, the type of body in view, body position, etc., were all precisely controlled in our factorial experimental design. Finally, this finding cannot be explained by the possibility that the participants were just distracted during the friend-body-swap illusion and consequently missed some of the items in this condition because (1) all traits included in the memory dataset were associated with a button press in the preceding self-reference task; therefore, they were noticed and rated with similar task demands (i.e., the same instructions in all conditions) and (2) behavioral performance (i.e., reaction times and misses) did not differ significantly between conditions (see [Transparent Methods](#)). Instead, the present results suggest that coherence between different levels of self-representation is important for normal memory encoding, which advances our understanding of the fundamental relationship between the sense of self and memory. Regarding a possible mechanism, we speculate that a fragmented sense of self impairs the hippocampal binding mechanism during memory encoding (Andersen et al., 2007; Bergouignan et al., 2014; Eichenbaum, 2000; Nyberg et al., 1996) and makes it more difficult for this brain structure to integrate sensory and semantic information into coherent representations for long-term storage.

Two additional observations deserve brief discussion. First, visuotactile asynchrony in the asyncS condition reduced ownership of one’s own actual body, which extends previous work that found such effects only for a single limb (Gentile et al., 2013; Kannape et al., 2019; Reader and Ehrsson, 2019) or when viewing oneself from a distance (Ehrsson, 2007; Guterstam et al., 2015b; Guterstam and Ehrsson, 2012). This result provides further support for multisensory models of full-body ownership (Ehrsson, 2020, 2012; Kilteni et al., 2015) by generalizing the temporal congruence principle—previously established in studies using mannequins (Petkova and Ehrsson, 2008), computer-simulated avatars (Slater et al., 2009), and unknown others (Preston and Ehrsson, 2014; Tacikowski et al., 2020)—to the case of one’s real body viewed from a natural first-person perspective. Second, this reduced ownership of one’s entire body was related to impaired memory performance, which goes beyond previous studies that found memory deficits (1) when the participants adopted a third-person perspective on their own body and changed self-location (Bergouignan et al., 2014) or (2) when the body was removed from view altogether (Bréchet et al., 2019). Evidently, a sense of reduced ownership of one’s real body in view, even when it is observed from a first-person perspective, is sufficient to disrupt normal memory encoding. Interestingly, this disruption resembles the memory deficits of patients with depersonalization disorder who feel “detached” from their body (Giesbrecht et al., 2010; Sierra and David, 2011), which suggests that the current “full-body disownership illusion” could perhaps serve as an experimental model of memory impairments in this disorder. More generally, our memory findings during asyncS support the idea that reduced coherence of the multisensory representation of one’s own body interrupts the hippocampal binding mechanisms engaged in episodic memory (Bergouignan et al., 2014).

In sum, we used a friend-body-swap illusion paradigm to show how self-concept is dynamically updated by changes in the bodily self and how the resulting increase in self-coherence facilitates memory encoding. These results advance our understanding of the basic link between the bodily self and self-concept as well as our understanding of the functional role of this connection. Moreover, the body-perception-induced fluidity of self-concept that we report here could have important implications for applied psychology; for example, it can be used as a therapeutic tool to promote more positive views of oneself in depression or to develop a deeper understanding between people by allowing them to literally experience the world from another person's perspective.

### Limitations of the Study

A general concern with studies that use subjective ratings as a dependent variable, as we did, is how to rule out cognitive biases, task compliance, or suggestibility effects. In our opinion, such confounding factors cannot explain the current results for the following reasons. First, updating of the self-concept during syncF was related to increased skin-conductance responses, which are controlled largely automatically by the sympathetic nervous system (Dawson et al., 2000). Second, "producing" the structural similarity result would have been extremely difficult for the participants because it would have required them to maintain a mental overview of eight 30-by-30-item matrixes, be aware of the expected pattern of results, be able to quickly adjust their responses accordingly, and be able to simultaneously control their physiological reactions because the structural similarity finding was also related to enhanced skin-conductance responses. Third, memory results could not have been driven by cognitive bias because at the time of memory encoding, the participants did not know that a memory test would subsequently take place. Finally, we interviewed all the participants after the study, and none of the participants guessed the expected pattern of results (see [Transparent Methods](#)). Thus, even though illusory ownership of the friend's body updated the *explicit* content of people's self-concept, our findings suggest that this process of updating was largely *implicit*, which supports our main conclusions.

It is important to clarify that our memory task assessed episodic recognition memory, that is, whether the participants remembered encountering specific items during the preceding study session or not. Although this task is largely immune to the participants' possible conscious strategies (see earlier) and is relevant to the current research question (i.e., memory of items related to the self-concept is measured), task performance can be based on a feeling of familiarity even without a conscious recollection of how or when a particular item was encoded. Thus, we cannot determine whether the present findings can be generalized to other aspects of episodic memory, such as vividness or location at a specific time and place. Future studies should investigate this important question.

### Resource Availability

#### Lead Contact

Further information and requests for resources should be directed to the Lead Contact, Pawel Tacikowski ([pawel.tacikowski@ki.se](mailto:pawel.tacikowski@ki.se)).

#### Materials Availability

All trait-stimuli are listed in the [Data S1](#) and [S2](#). For the illustration of the experimental setup, please see the [Video S1](#). Captions are provided in the Supplemental Information file.

#### Data and Code Availability

Data underlying the study cannot be made publicly available owing to ethical concerns regarding participant privacy. We do not have ethics approval to make the raw data from individual subjects publicly available. The code is available from the Lead Contact on request.

## METHODS

All methods can be found in the accompanying [Transparent Methods supplemental file](#).

## SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.isci.2020.101429>.

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## AUTHOR CONTRIBUTIONS

P.T. and H.H.E. designed the study. P.T. and M.L.W. collected and analyzed the data. P.T. and H.H.E. wrote the manuscript. All authors provided revisions and approved the final version of the manuscript for submission.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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## **Supplemental Information**

### **Perception of Our Own Body Influences Self-Concept and Self-Incoherence Impairs Episodic Memory**

**Pawel Tacikowski, Marieke L. Weijs, and H. Henrik Ehrsson**

**This document includes the following:**

Transparent Methods

Supplementary References

Supplementary Figures S1-S7

Supplementary Tables S1-S5

Captions for Data S1, Data S2, and Video S1

## **Transparent Methods**

**Participants:** Sixty-six healthy volunteers participated in the study (42 females; 64 right-handed; mean age:  $26 \pm 5$  years). The sample size was chosen based on similar previous studies (Banakou et al., 2013; Peck et al., 2018). We recruited pairs of friends (same-sex) who knew each other for at least 6 months (mean: 3.5 years). All participants had normal or corrected-to-normal vision, normal hearing, and no history of neurological or psychiatric illness. One participant was excluded from the analyses of similarity and memory data because he did not follow the instructions. All participants provided written informed consent, and the study was approved by the Regional Ethical Review Board of Stockholm (since 2019, the Swedish Ethical Review Authority).

**Procedure:** Pairs of friends participated in the experiment simultaneously. First, we administered the Inclusion of Other in the Self (IOS) scale (Aron et al., 1992) and the short version of the Network of Relationships Inventory (NRI): Behavioral Systems Version (Furman and Buhrmester, 2009); these questionnaires assessed different aspects of friendship and were used in the control analyses (Fig. S5 and Table S5). Next, the participants practiced how to use a numeric keypad without looking at it; this skill was required in the following self-rating task (see further). During this practice, a cardboard box covered the participant's hand and the keypad, and the task was to press a key that corresponded to a number presented on the screen (20 trials). All participants completed this practice without problems. Then, the friend-rating part was conducted during which the participants sat in front of separate computers (no body perception manipulation applied) and rated 120 trait characteristics in relation to the friend (Fig. 1D; for details, see the "Friend- and self-reference tasks" section). In the following self-rating part, the same 120 trait characteristics were randomly assigned to the syncF, asyncF, syncS, and asyncS conditions (30 traits in each) and rated by the participants in relation to the self (Fig. 1D). The two friends did not see each other's

responses in either the friend- or the self-rating task. The full-body illusion conditions started with an induction phase (45 s), followed by spoken instructions and the self-rating task. During each condition, when both participants provided 10, 20, and 30 self-ratings, respectively, we simultaneously “threatened” both participants with mock knives and measured skin conductance responses during these events (Fig. 1C and 1E). Each condition lasted ~ 9 min, and the order of conditions was randomized. During breaks between conditions, the participants took off the Head Mounted Displays (HMDs) and filled out the illusion questionnaire (Fig. 1B and 1E). After the four conditions, the participants completed the last memory task while sitting in front of computers again without any body perception manipulation (Fig. 5A). Finally, a short debriefing was performed with each participant separately in which we asked for feedback and assessed naivety (“What result do you think we expect in this study?”; “Have you used any special strategy in any of the tasks, and if so, what was it?”; “Do you have any other comments or feedback?”). No participant guessed the purpose of the study or reported the hypothesized pattern of results.

***Full-body illusion paradigm and visuotactile stimulation:*** The participants laid down on two beds and wore HMDs (Oculus Rift, Melo Park, CA, USA). The participants’ necks were supported with pillows, and their heads were tilted forward (~45°), as if the participants were looking directly at their feet. Each set of HMDs was connected to two digital cameras (Grasshopper3, FLIR, Ludwigsburg, Germany) placed parallel to each other (~7 cm apart), directly behind, and above the participants’ heads (Fig. 1A). This setup allowed us to present true stereoscopic, high-quality videos of the participant’s own body (syncS, asyncS) or the friend’s body (syncF, asyncF) recorded from a first-person perspective. During the synchronous conditions, recordings were displayed with a negligible delay (setup’s intrinsic delay: <100 ms). In contrast, a 3 s delay was introduced in the asynchronous conditions. In each condition, the participants received the same number of



touches on three body locations (upper legs and lower abdomen; ~13 touches per minute). Strokes were applied with white Styrofoam balls (10 cm diameter) attached to the end of thin rods. The order of touches was pseudorandom (not more than 2 consecutive touches to the same body part). The duration of each stroke was 1 s, and the interval between subsequent strokes was 2, 3, or 4 s. Each touch covered ~25 cm of the participant's body. To ensure synchrony between the two experimenters, they practiced the procedure beforehand, and during the study, they both listened to the same audio cues indicating the onset, duration, and location of each stroke. The participants did not hear these cues because they were played through the experimenters' headphones. The participants performed the self-rating task while receiving visuotactile stimulation. The stroking sequence was paused after 10, 20, and 30 completed ratings; during these pauses, the experimenters simultaneously "attacked" both participants with mock knives (see "Skin conductance responses" below). We instructed the participants to relax and move as little as possible during each condition. The participant's right hand was covered with a cardboard box to eliminate visual feedback from finger movements during the self-rating task.

***Illusion questionnaire:*** After each condition, a questionnaire was administered to quantify the strength of the full-body illusion. Illusion and control statements were adapted from (Petkova and Ehrsson, 2008), and the participants indicated how much they agreed or disagreed with each statement (Fig. 1B; -3 "strongly disagree", +3 "strongly agree"). The illusion items concerned body ownership (I1) and referral of touch (I2, I3), which are considered to be the two core elements of the multisensory full-body illusion (Ehrsson, 2012; Kilteni et al., 2015), whereas control items (C1:C4) assessed any potential effects of suggestibility or task compliance. The L1 statement ("I felt that I was located on the other bed") was added for exploratory purposes to probe possible changes in self-location (Guterstam et al., 2015) during the friend-body swap condition. The order

of statements was pseudorandom: C1, I1, C2, I2, C3, C4, I3, I4, L1. Ratings of individual statements were analyzed with pairwise Wilcoxon signed-rank tests (two-sided), and *P*-values were corrected for multiple comparisons (Benjamini-Hochberg method; FDR).

***Skin conductance responses:*** Data were recorded with the Biopac System (MP150, Goleta, CA, USA; sampling rate: 100 Hz). AcqKnowledge® software (Version 3.9.1.6, Biopac) was used to process the data. Two electrodes with electrode paste (Biopac, Goleta, USA) were placed on the participant's left index and left middle fingers (distal phalanges). We threatened the body by making a stabbing motion and stopping the knife just above the abdomen (Fig. 1C). Each knife threat lasted ~ 2 s. Before the study, we showed the “knives” to the participants to prevent extreme emotional stress in line with good ethical practice. Three threat events occurred in each condition when both participants rated 10, 20, and 30 items (Fig. 1E). The timings of threat events were marked in the recording file by the experimenters by pressing a key on a laptop immediately after the threat was presented.

***Friend- and self-reference tasks:*** Trait adjectives were selected from (Anderson, 1968). We chose items that were comprehensible by nonnative English speakers and that showed the highest variability of ratings in the pilot study (N=10). Presentation® software (version 16.4, Neurobehavioral Systems, Inc., Berkeley, CA, USA) was used to present all stimuli and record responses. All items were presented through headphones worn by the participants. Responses were given by a key press on a numeric keypad (“How much does this trait refer to your friend/yourself?”; 1 “not at all”; 9 “very much”). Each item was preceded by a “fixation beep” (200 ms). Trait item duration was on average  $0.8 \pm 0.1$  s. After hearing each trait, the participants had a maximum of 6 s to provide a rating. The intertrial interval was 1, 1.5, or 2 s. The participants

rated the same 120 trait adjectives in the friend- and self-reference tasks (30 traits in syncF, asyncF, syncS, and asyncS; see also the main text and Data S1).

**Memory task:** In the recognition memory task, 120 “old” items (the same as in the friend- and self-rating tasks) were randomly intermixed with 120 “new” trait adjectives (Fig. 5A; Data S1 and S2). The participants used the left and right mouse keys to indicate whether they had already heard a given word during the experiment. Key assignment was counterbalanced between the participants. Stimulus length was on average  $0.7 \pm 0.1$  s. After each word, the participants had a maximum of 2.5 s to give a response. After each response, the participants received feedback (“correct”, “incorrect”, or “too long”). The interval between trials varied (1, 1.5, or 2 s).

**Analysis of illusion questionnaires:** To assess the overall strength of the full-body illusion and to eliminate potential suggestibility or task-compliance effects, we calculated “illusion scores” as differences between the average illusion (I1:I3) and control (C1:C4) ratings for each participant in each condition (van der Hoort et al., 2017, 2011). These illusion scores were analyzed with the linear mixed model:  $\text{score} \sim 1 + \text{synchrony} + \text{body} + 1|\text{id}$  (Tables S1 and S2). The factors of “body” and “synchrony” had two levels each (self vs. friend and synchronous vs. asynchronous, respectively), and both of these factors were the fixed effects in the model. The “1|id” refers to the random intercept, which accounted for general variability between the participants. Follow-up tests (syncF vs. asyncF and syncS vs. asyncS) used the following linear mixed models:  $\text{score} \sim 1 + \text{condition} + 1|\text{id}$ . For the results of individual statements, see Fig. S2 and Tables S3 and S4.

**Analysis of skin conductance responses:** The amplitude of each response was identified as the difference between the maximum and minimum conductance values in the 0-6 s period after a knife threat. Skin conductance values were square-root-transformed, in line with common practice (Dawson et al., 2000). Data were analyzed with the following linear mixed model:  $\text{response} \sim 1 +$

synchrony + repetition + 1|id (Table S1 and S2). The fixed effect of repetition (values from 1 to 12) indicated which knife threat a given event was during the course of the experiment. It is well established that skin conductance responses decrease with subsequent threats (Dawson et al., 2000), and we found this habituation effect as well ( $b=0.7$ ;  $SE=0.05$ ;  $t=14.8$ ;  $P<0.005$ ; Fig. S7A). Notably, a transformed repetition number ( $1/n$ ) substantially improved the fit of the linear model to the data ( $\chi^2_1=58.6$ ;  $P<0.001$ ; Fig. S7B). For the analyses presented in Fig. 3D and Fig. 4F, we extracted residuals from the following model,  $\text{response} \sim 1 + \text{repetition}$ , and calculated the difference between average responses in the syncF and asyncF conditions for each participant. In this way, we reduced the confounding habituation effect (see earlier) and measured the physiological friend-body-swap illusion more directly. For purely descriptive purposes, we further displayed the time courses of skin conductance responses (Fig. 2C). To do so, we performed the following steps: (i) we extracted data segments between -10 to 20 s around each knife threat marker; (ii) we manually selected a response onset in each segment (for “no response” trials where the difference between baseline and peak was  $< 0.05 \mu\text{S}$ , the “response onset” was set to the marker time); (iii) we removed a linear trend from the signal (“detrend” MATLAB function) and baseline corrected each segment (subtracted the average value from the -5 to 0 s period before the response onset); and (iv) we averaged all trials from each condition. By time-locking each response to its onset, we accounted for typical physiological variability with regard to latencies of skin conductance responses (Dawson et al., 2000).

***Analysis of self- and friend-ratings:*** The number of personality traits that were rated both with regard to the self and the friend (i.e., traits that were used to calculate the self-to-friend similarity) was on average 29.2 per condition (min. 20 out of 30 possible traits), which shows that there were enough data points to assess multiple aspects of one’s own and the friend’s personalities in each

of the four conditions (Fig. S7D). We also checked whether personality ratings showed desired variability (i.e., cosine similarity would not have been very meaningful if the participants used only one or two different ratings to describe their own and their friend’s personalities). We found that in almost all (99.7%) condition-specific datasets, the participants used five or more different rating-values, which indicates that our choice of the similarity measure was appropriate (Fig. S7C). To account for the fact that some traits (e.g., aggressive) are generally likely to be rated low whereas other traits (e.g., nice) are generally likely to be rated high, we ran a linear mixed-model with a random intercept of trait-type (rating  $\sim 1|\text{trait}$ ). This preprocessing step essentially set different “baselines” for different traits and thus made the remaining variability in ratings more relevant to our actual experimental manipulation. It is noteworthy that (i) the key findings of the present study were replicated when we used raw ratings instead and (ii) that the abovementioned preprocessing step did not bias our subsequent analyses because it was run on all friend ratings and self-ratings from all conditions combined. Residuals from the “rating  $\sim 1|\text{trait}$ ” model were then used to calculate cosine similarity between friend ratings (FR) and self-ratings (SR) for each participant in each condition ( $i$  in the formula refers to each trait in a given dataset).

$$\text{cosine similarity} = \frac{\sum_{i=1}^n \text{FR}_i \text{SR}_i}{\sqrt{\sum_{i=1}^n \text{FR}_i^2} \sqrt{\sum_{i=1}^n \text{SR}_i^2}}$$

To account for general between-subject differences in the degree of similarity between self-ratings and friend ratings, similarity scores from each condition were corrected in the following way: similarity score from a given condition = score from this condition – average of scores from all conditions for a given participant. Structural similarity data were preprocessed in the same way as above, but the similarity between the “self” and “friend” distance matrixes in each condition was calculated with the Spearman correlation test. For pairwise comparisons at the group level (syncF



vs. asyncF; syncF vs. syncS; syncF vs. asyncS), z-scored data were analyzed with the following linear mixed model:  $\text{similarity} \sim 1 + \text{condition} + 1|\text{id}$ . The analyses presented in Figs. 4E, 4F, and S4 were conducted on raw Spearman correlation coefficients.

**Analysis of memory data:** Only “old” traits that were rated in the self- and friend-reference tasks (i.e., traits followed by a button press) were included in the analysis of memory data (n=7593 out of 7800). In this way, we ensured (i) that similarity and memory datasets were fully compatible (Fig. 5C) and (ii) that all traits had been heard and noticed during stimulus encoding. Behavioral performance during the self-reference task did not differ significantly between conditions, which further indicates that all conditions were associated with similar attentional engagement (number of “misses”: syncF vs. asyncF;  $t_{64}=-0.74$ ;  $P=0.46$ ;  $\text{BF}_{01}=5.67$ ; syncF vs. syncS;  $t_{64}=-1.37$ ;  $P=0.18$ ;  $\text{BF}_{01}=3.03$ ; syncF vs. asyncS;  $t_{64}=0.78$ ;  $P=0.44$ ;  $\text{BF}_{01}=5.49$ ; reaction times: syncF vs. asyncF;  $t_{64}=-1.2$ ;  $P=0.24$ ;  $\text{BF}_{01}=3.72$ ; syncF vs. syncS;  $t_{64}=0.76$ ;  $P=0.45$ ;  $\text{BF}_{01}=5.57$ ; syncF vs. asyncS;  $t_{64}=1.55$ ;  $P=0.13$ ;  $\text{BF}_{01}=2.37$ ; paired t-tests; two-sided; N=65). All “new” traits were included in the analysis of memory data (n=7800). For the main analysis, we calculated “d-primes” for each participant in each condition separately. These indexes assessed how well the participants were able to discriminate between the “new” and “old” items in an unbiased way (Wickens, 2002). The average d-prime from all participants and all conditions combined was  $2.51 \pm 0.07$ , which is well above the chance level ( $t_{64}=35.03$ ;  $P<0.005$ ; one-sided). This shows that, in general, the participants performed very well in discriminating between the old and new words. D-primes from each condition were corrected in the following way:  $\text{d-prime from a given condition} = \text{d-prime from this condition} - \text{average of d-primes from all conditions for a given participant}$ . This correction accounted for the between-subject variability in the overall memory capacity. For planned comparisons (syncF vs. asyncF, syncF vs. syncS, and syncF vs. asyncS), we used the

following linear mixed model:  $d\text{-prime} \sim 1 + \text{condition} + 1|id$ . Furthermore, the “criterion” values did not differ significantly between the four conditions (syncF:  $-0.623 \pm 0.025$ ; syncS:  $-0.633 \pm 0.025$ ; asyncF:  $-0.634 \pm 0.026$ ; asyncS:  $-0.631 \pm 0.026$ ;  $F_{3,256}=0.038$ ;  $P=0.99$ ).

**General statistical information:** All analyses were performed in RStudio and R software (Version 3.3.3, The R Foundation for Statistical Computing, <https://www.r-project.org>). Linear mixed models were estimated using the “lme4” package. For analyses that focused specifically on the effect of illusory ownership of the friend’s body, which can only vary between the syncF and asyncF conditions, we used similarity indexes from the same two conditions (Fig. 3C, 3D, 4E, 4F). In turn, for the analysis that tested how the updating of self-concept during syncF affects memory performance in this condition (Fig. 5C), we used the difference between syncF versus all control conditions because this index captures what is unique to syncF also compared to the conditions with one’s own body. Model selection was performed with the “lmerTest” package (the “step” function; Table S1). *P*-values for the F-tests were based on Satterthwaite’s approximation to degrees of freedom as implemented by the “lmerTest” package (Table S2). *P*-values for all correlations and planned pairwise tests were obtained with the bootstrapping technique (“boot” package; 10000 simulations). D-primes were calculated with the “psycho” package and Bayes factors with the “BayesFactor” package ( $r=0.707$ ). For hierarchical clustering (Fig. 4C), we used the “hclust” R function.

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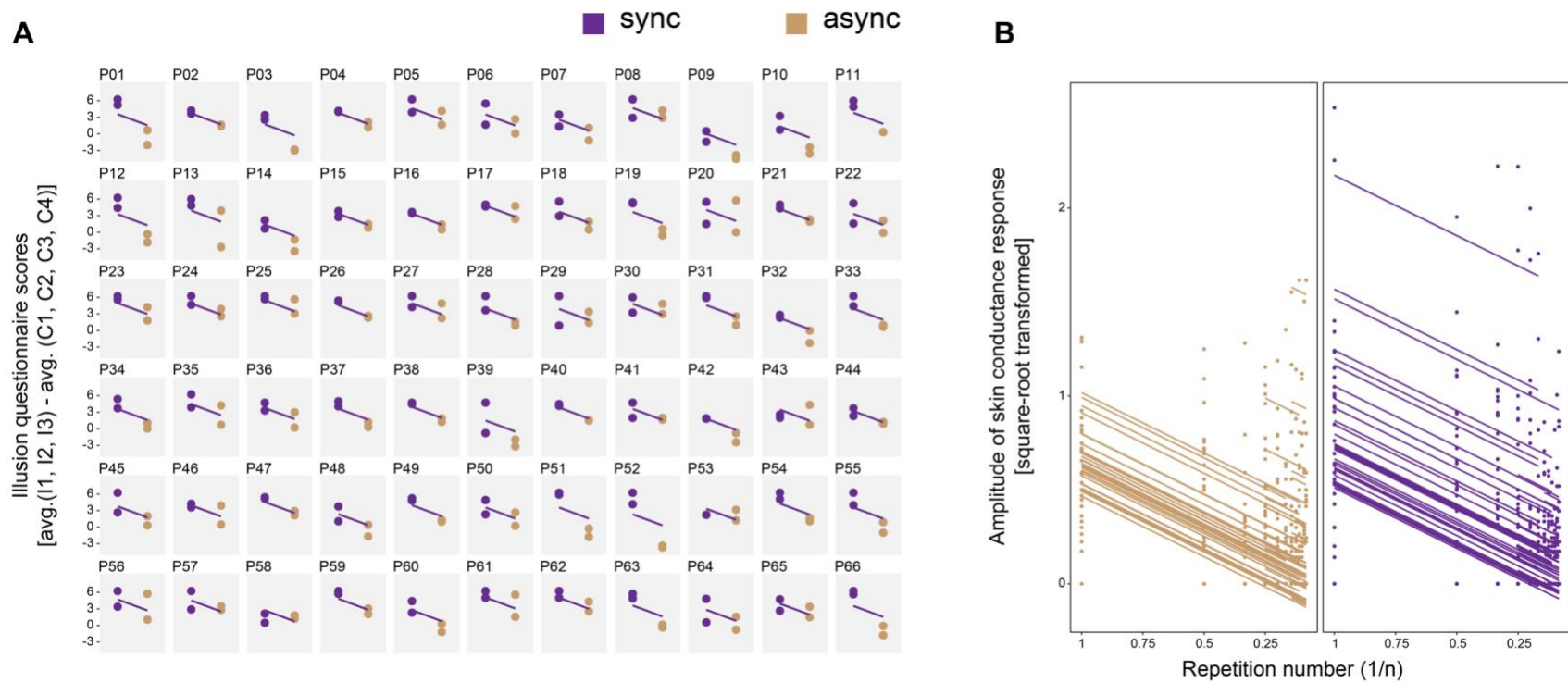
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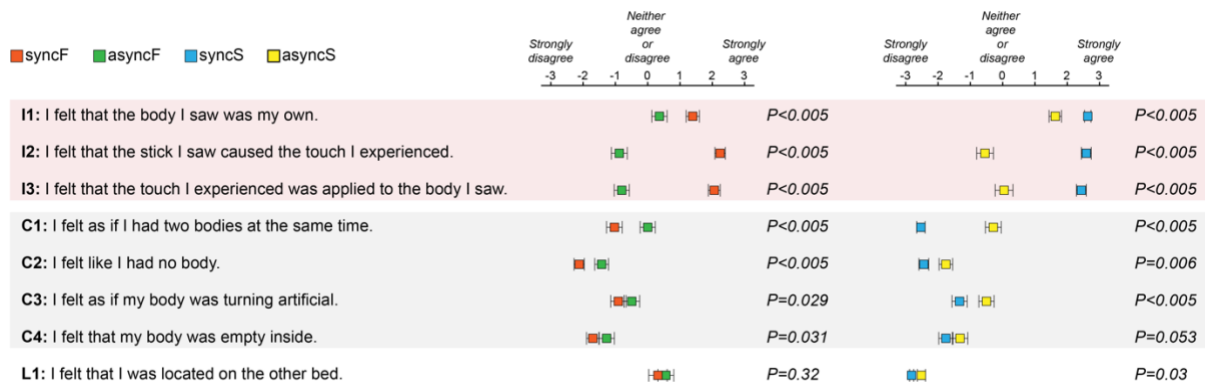
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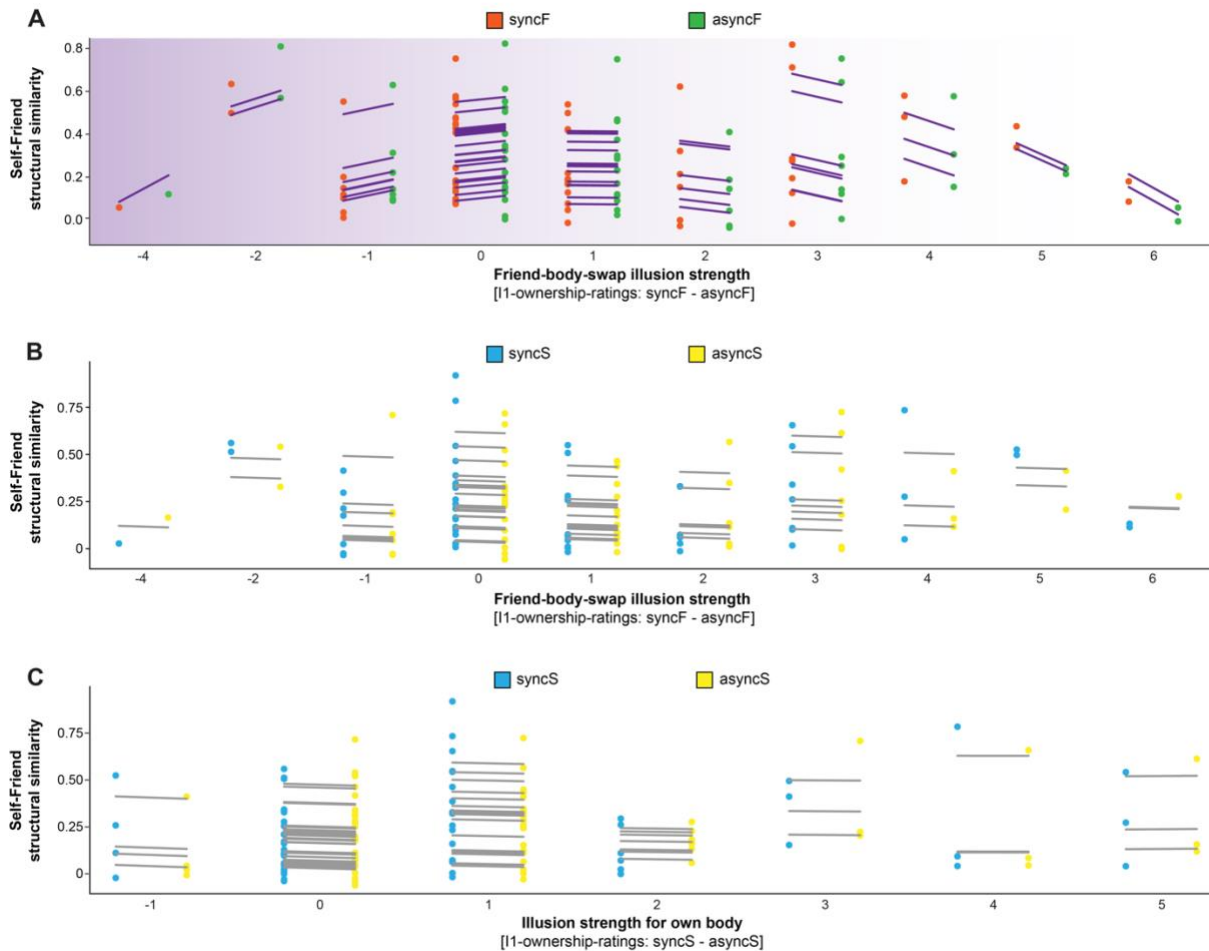
**Fig. S1. (A) Illusion questionnaire scores. Related to Fig. 2.** Each panel shows data from one participant, where each point corresponds to an illusion score from one condition. The lines represent the model's predictions of the main effect of synchrony. For most participants, the illusion scores were higher in the synchronous than the asynchronous conditions. **(B) Skin conductance responses.** Each line corresponds to the model's prediction of the main effect of repetition for one participant. Points correspond to skin conductance responses in individual knife threat trials. Skin conductance responses during the synchronous conditions (right panel) were generally higher than during the asynchronous conditions (left panel).



**Fig. S2. Illusion questionnaire results for individual items. Related to Fig. 2A.** Plots show means $\pm$ SE. For medians and ranges, see Tables S3 and S4. Data for each statement were analyzed by pairwise comparisons (Wilcoxon signed-rank tests;  $P$ -values were FDR-corrected;  $N=66$ ). Notably, the ratings of individual illusion statements (I1-I3) were significantly higher in the synchronous condition than in the corresponding asynchronous condition (syncF vs. asyncF and syncS vs. asyncS). Some control statements showed significant differences between the synchronous and asynchronous conditions as well, but in those cases, the ratings from synchronous conditions indicated stronger disagreement (i.e., ratings below zero) than the already low ratings from asynchronous conditions.

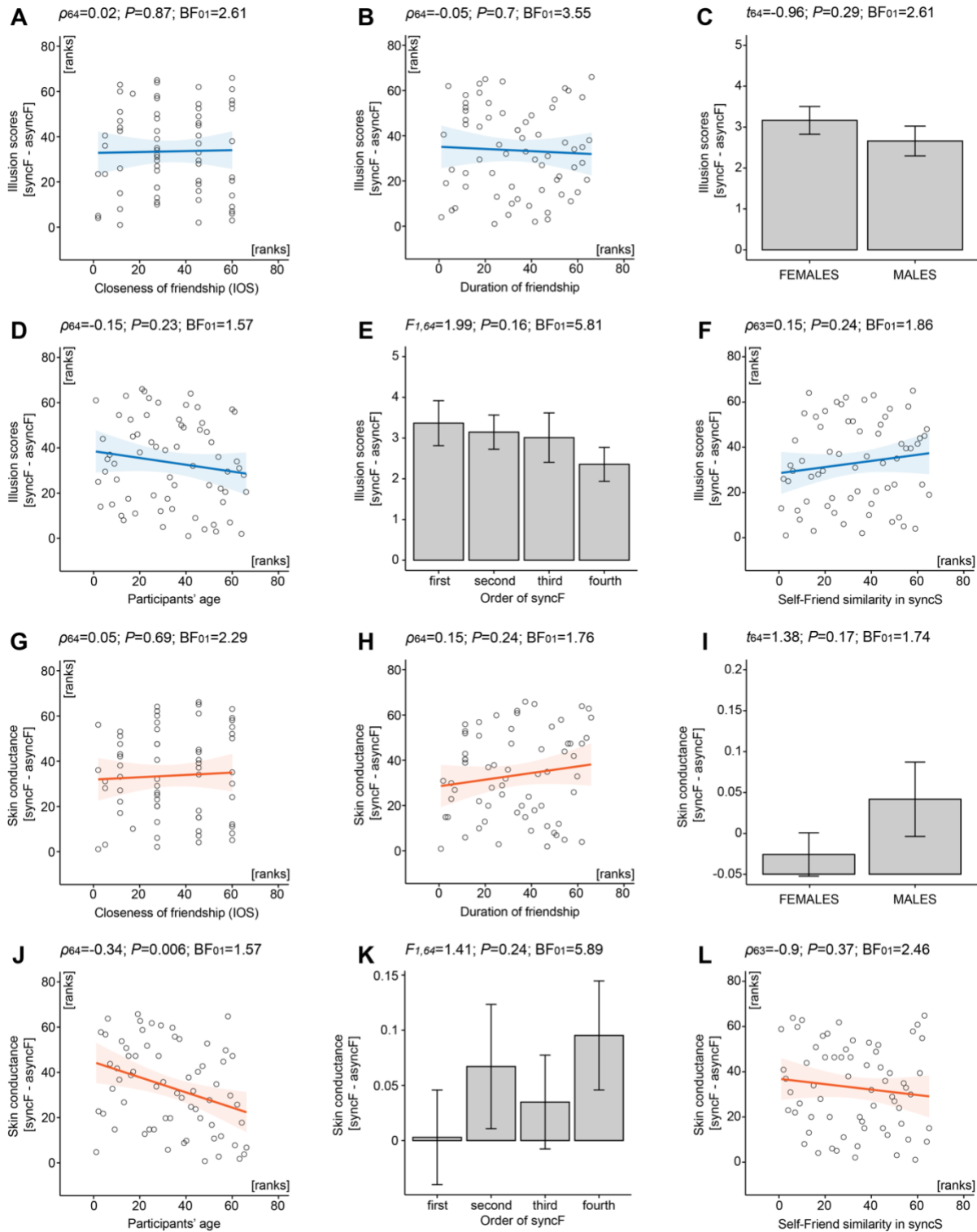


**Fig. S3. (A) Item-by-item similarity data. Related to Fig. 3B.** Each panel shows data from one participant, where each point represents the degree of similarity between self-ratings and friend ratings from one condition. The green, blue, and yellow lines represent the models' predictions of the following differences: syncF vs. asyncF, syncF vs. syncS, syncF vs. asyncS, respectively. Self-ratings and friend ratings were usually more similar in the syncF than in the other conditions. **(B) D-prime indexes of episodic recognition memory. Related to Fig. 5B.** The display convention is analogous to panel A, but each point represents a d-prime value from a given condition (see the legend). Trait adjectives encountered during the syncF condition were generally remembered worse than traits encountered in the other conditions.



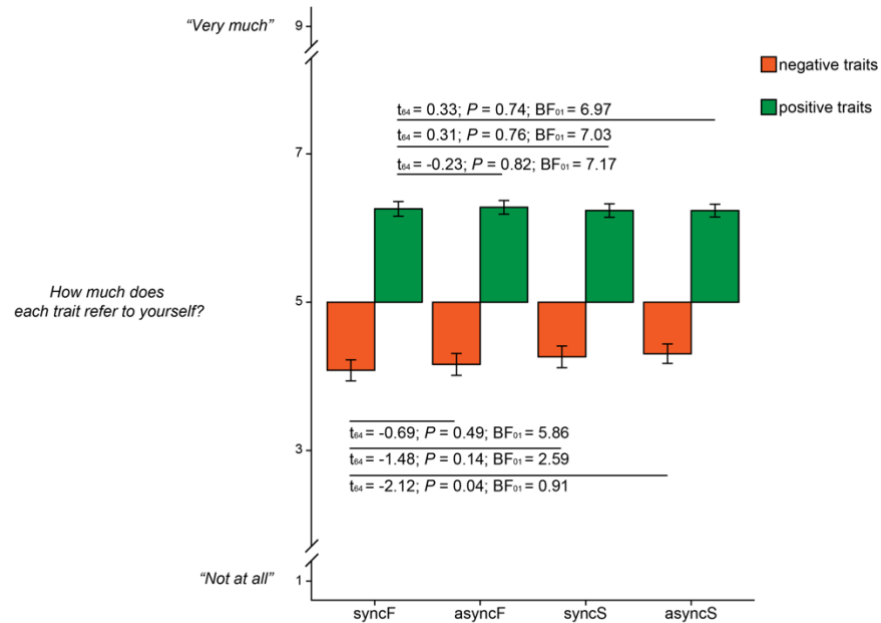
**Fig. S4. Additional analyses of structural similarity data. Related to Fig. 4.** (A) Strong illusory ownership of the friend’s body during syncF was related to increased structural similarity in the syncF condition compared to the asyncF condition, suggesting that the “new” bodily self updated beliefs about the participant’s own personality so that they became more similar to beliefs about the friend’s personality [condition  $\times$  ownership:  $F_{1,65}=4.01$ ;  $P=0.047$ ; LMM: similarity  $\sim$  condition  $\times$  ownership + (1|id); two-sided; N=65]. (B) A control analysis showed that there was no significant relationship between the friend-body-swap illusion strength and the degree of structural similarity in the syncS and asyncS conditions, which indicates that the effect shown on panel A was specific to syncF [condition  $\times$  ownership:  $F_{1,65}=0.001$ ;  $P=0.99$ ; LMM: similarity  $\sim$  condition  $\times$  ownership + (1|id); two-sided; N=65]. (C) Another control analysis demonstrated that there was no significant relationship between ownership of one’s own actual body in syncS and the degree of self-friend similarity in syncS versus asyncS, which suggests that our main finding (panel A) was related to illusory ownership of the friend’s body specifically and not to body ownership more generally [condition  $\times$  ownership:  $F_{1,65}=0.03$ ;  $P=0.87$ ; LMM: similarity  $\sim$  condition  $\times$  ownership + (1|id); two-sided; N=65]. Individual lines in each plot represent the models’ predictions of the main effect of condition at different levels of body ownership. Each dot indicates structural similarity for one participant in one condition.



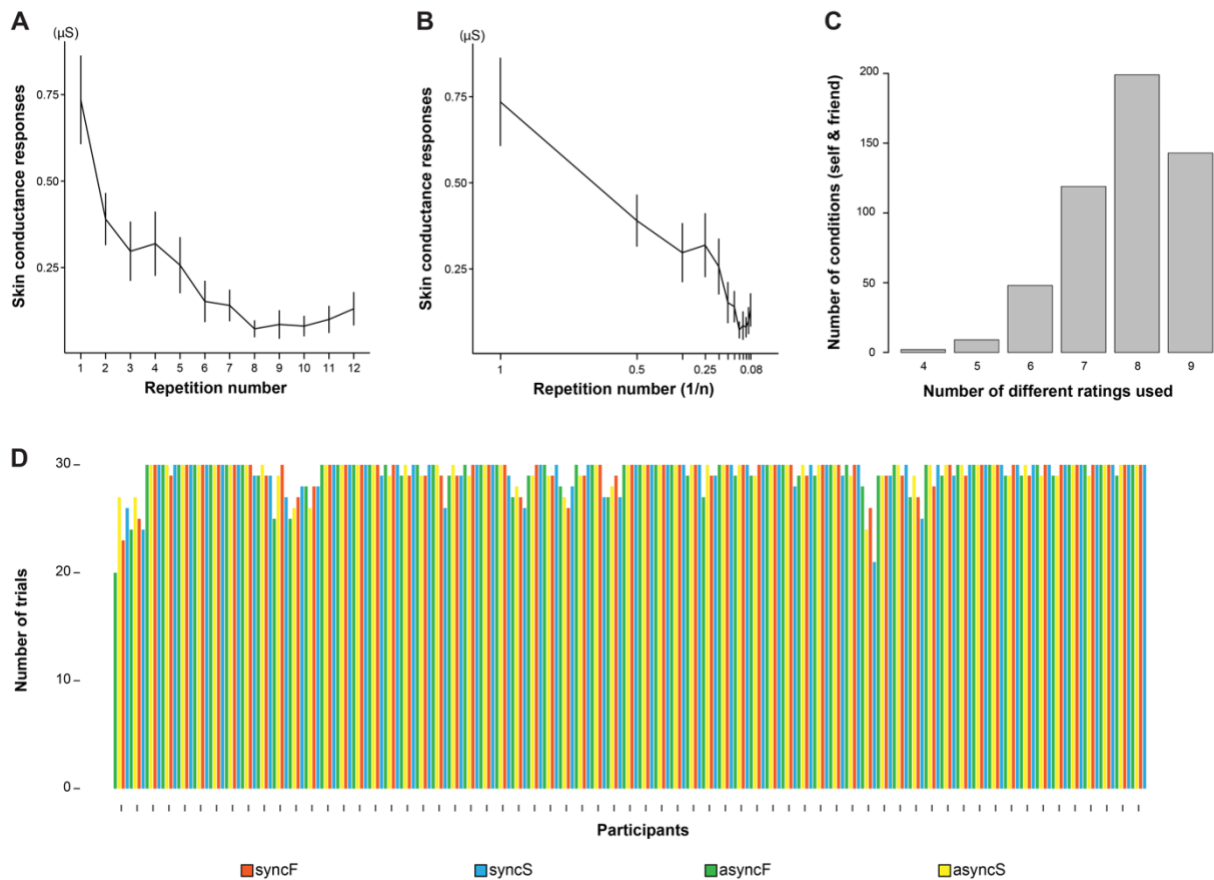


**Fig. S5. Control analyses of potential confounding factors that could affect the strength of the friend-body-swap illusion. Related to Fig. 2.** There was no significant relationship between illusion scores in the syncF condition and closeness of friendship (IOS; Inclusion of Other in the Self scale) (A), duration of friendship (B), participants' sex (C), participants' age (D), condition

order (**E**), or similarity between ratings of one's own and the friend's personalities in the syncS baseline condition (**F**). A similar pattern of results was present for the skin conductance measure of the friend-body-swap illusion (**G-L**). Please note that the participant's age correlated significantly with skin conductance responses (**J**) but not with illusion scores (**D**); thus, future studies are needed to determine whether age consistently modulates the strength of full-body illusions. To analyze continuous variables, we used Spearman's correlation tests. The effect of participants' sex was assessed with an independent-samples *t*-test. Condition order was analyzed with a one-way between-subjects ANOVA. Bayes factors ( $BF_{01}$ ) indicate support for the null hypothesis. All *P*-values are two-sided. Bar plots correspond to means $\pm$ SE.



**Fig. S6. Control analyses showed that increased similarity between ratings of one’s own and friend’s personalities in syncF was not associated with generally more negative ratings of one’s own personality in this condition. Related to Fig. 3.** One could argue that uncertainty about one’s own body, presumably induced by the friend-body-swap illusion, could reduce the general tendency to evaluate oneself more positively than others (“self-enhancement bias”). Such a potential reduction of the self-enhancement bias could by itself increase the similarity between ratings of one’s own and the friend’s personalities. To test this possibility, we asked five independent raters to indicate whether each trait from the experiment was positive, negative, or neutral in their opinion. If the majority of raters indicated the same category, a given trait was assigned to this category (“ties” were assigned to the neutral category). This procedure resulted in 61 traits classified as positive, 38 traits classified as negative, and 21 traits classified as neutral. We found that self-ratings of negative traits did not increase significantly in syncF as compared to other conditions (i.e., self-views did not become more negative) and self-ratings of positive traits did not significantly decrease in syncF as compared to other conditions (self-views did not become less positive). These results speak against the possibility that illusory ownership of the friend’s body reduced the self-enhancement bias and instead support our main interpretation that the illusion dynamically updated the multidimensional content of self-concept. Pairwise comparisons used paired t-tests (two-sided). Bayes factors (BF<sub>01</sub>) indicate support for the null hypothesis. Bar plots correspond to means±SE.



**Fig. S7. Data quality checks. Related to Fig. 2-6.** (A) Skin conductance responses decreased exponentially with subsequent knife threats (means $\pm$ SE; data combined from all conditions and all participants). (B) The transformed repetition number ( $1/n$ ) “linearized” this decrease and provided a substantially better fit of the linear mixed model to the data ( $\chi^2_{21}=58.6$ ;  $P<0.001$ ). (C) In almost all single-condition datasets (99.7%), the participants used 5 or more different values to rate their own or their friend’s personality, which validates our choice of similarity measures. (D) The number of traits rated with regard to one’s own and the friend’s personalities (i.e., only these traits were used to calculate the self-to-friend similarity) was sufficiently high to assess multiple aspects of one’s own and the friend’s personalities (i.e., min. 20 out of 30 possible traits per condition; mean = 29.2).

**Table S1.** Model selection<sup>^</sup>. Related to Fig. 2.

|     | <b>full model</b>                | <b>df</b> | <b>AIC</b> | <b>selected model</b>        | <b>df</b> | <b>AIC</b> |
|-----|----------------------------------|-----------|------------|------------------------------|-----------|------------|
| IQS | score ~ sync × body + (1 id)     | 6         | 1049       | score ~ sync + body + (1 id) | 5         | 1047       |
| SCR | scr ~ sync × body + rep + (1 id) | 7         | 20         | scr ~ sync + rep + (1 id)    | 5         | 16         |

<sup>^</sup> – For model selection, we used the “lmerTest” package (“step” function). All models included fixed and random intercepts. Models including interactions also included main effects; for example, “sync×body” is equivalent to “1 + sync + body + sync×body”.

**Abbreviations:** **AIC** – Akaike information criterion; **body** – factor with two levels: own body vs. friend’s body; **df** – degrees of freedom; **id** – participants; **IQS** – illusion questionnaire scores (avg. (I1+I2+I3) – avg. (C1+C2+C3+C4); **rep** – SCR repetition number; **SCR** – skin-conductance responses; **sync** – factor with two levels: synchronous vs. asynchronous.

**Table S2.** Statistical analysis of illusion questionnaire scores and skin conductance responses. Related to Fig. 2.

|     | <b>Model</b>                                | <b>Effect</b> | <b>dfN</b> | <b>dfD</b> | <b>F</b> | <b>P</b> |
|-----|---|---------------|------------|------------|----------|----------|
| IQS | score ~ sync + body + (1 id)                | sync          | 1          | 198        | 296.43   | <0.005   |
|     |   | body          | 1          | 198        | 37.91    | <0.005   |
|     | syncF vs. asyncF: score ~ sync + (1 ID)     | sync          | 1          | 66         | 140.61   | <0.005   |
|     | syncS vs. asyncS: score ~ sync + (1 ID)     | sync          | 1          | 66         | 138.52   | <0.005   |
| SCR | scr ~ sync + rep + (1 ID)                   | sync          | 1          | 726        | 9.00     | <0.005   |
|     |   | rep           | 1          | 726        | 459.48   | <0.005   |
|     | syncF vs. asyncF: scr ~ sync + rep + (1 ID) | sync          | 1          | 330        | 10.41    | <0.005   |
|     |   | rep           | 1          | 344        | 134.66   | <0.005   |
|     | syncS vs. asyncS: scr ~ sync + rep + (1 ID) | sync          | 1          | 330        | 4.49     | 0.035    |
|     |   | rep           | 1          | 346        | 54.60    | <0.005   |

**Abbreviations:** **asyncF** – synchronous-Friend condition; **asyncS** – synchronous-Self condition; **body** – factor with two levels: own body vs. friend’s body; **dfN** – degrees of freedom in the numerator; **dfD** – degrees of freedom in the denominator; **F** – F-ratio; **id** – participants; **IQS** – illusion questionnaire scores (avg. (I1+I2+I3) – avg. (C1+C2+C3+C4); **P** – P-value; **rep** – SCR repetition number; **SCR** – skin-conductance responses; **sync** – factor with two levels: synchronous vs. asynchronous; **syncF** – synchronous-Friend condition; **syncS** – synchronous-Self condition.

**Table S3.** Questionnaire results for individual items in the syncF and asyncF conditions. Related to Fig. 2A and S2.

| Items:  | syncF |      |      |      |      |     | asyncF |      |      |      |     |     | Z <sup>^</sup> | P <sup>^^</sup> |
|---|-------|------|------|------|------|-----|--------|------|------|------|-----|-----|----------------|-----------------|
|   | min   | Q1   | Q2   | M    | Q3   | max | min    | Q1   | Q2   | M    | Q3  | max |                |                 |
| <b>I1:</b> It felt as if the body I saw was my own body.                  | -3.0  | 1.0  | 2.0  | 1.4  | 2.0  | 3.0 | -3.0   | -1.0 | 1.0  | 0.4  | 2.0 | 3.0 | 3.99           | <0.005          |
| <b>I2:</b> It felt as if the stick I saw caused the touch I experienced.  | -3.0  | 2.0  | 3.0  | 2.2  | 3.0  | 3.0 | -3.0   | -3.0 | -2.0 | -0.9 | 1.0 | 3.0 | 6.49           | <0.005          |
| <b>I3:</b> It seemed that the touch I felt was applied to the body I saw. | -3.0  | 2.0  | 3.0  | 2.1  | 3.0  | 3.0 | -3.0   | -2.8 | -1.0 | -0.8 | 1.0 | 3.0 | 6.49           | <0.005          |
| <b>C1:</b> It felt as if I had two bodies at the same time.               | -3.0  | -3.0 | -2.0 | -1.0 | 1.0  | 3.0 | -3.0   | -1.0 | 1.0  | 0.0  | 1.8 | 3.0 | -3.84          | <0.005          |
| <b>C2:</b> It felt like I had no body.                                    | -3.0  | -3.0 | -3.0 | -2.1 | -1.3 | 1.0 | -3.0   | -3.0 | -2.0 | -1.4 | 0.0 | 2.0 | -3.22          | <0.005          |
| <b>C3:</b> It felt as if my body was turning artificial.                  | -3.0  | -3.0 | -1.0 | -0.9 | 1.0  | 3.0 | -3.0   | -2.0 | 0.0  | -0.5 | 1.0 | 3.0 | -2.29          | 0.029           |
| <b>C4:</b> It felt as if my body was empty inside.                        | -3.0  | -3.0 | -2.0 | -1.7 | -1.0 | 2.0 | -3.0   | -3.0 | -2.0 | -1.3 | 0.8 | 3.0 | -2.21          | 0.031           |
| <b>L1:</b> It felt as if I was located on the other bed.                  | -3.0  | -2.0 | 1.0  | 0.3  | 2.0  | 3.0 | -3.0   | -1.0 | 1.0  | 0.6  | 2.0 | 3.0 | -0.99          | 0.322           |

Please note that the illusion statements (I1-I3) in syncF were affirmed by most participants (Q2/median  $\geq +2$ ), whereas the control statements (C1-C4) were typically rejected with negative median rating scores. (^) Wilcoxon signed-rank tests (N=66). (^^) FDR-corrected *P*-values (two-sided). **Abbreviations:** M – mean; Q1-Q3 – quartiles.

**Table S4.** Questionnaire results for individual items in the syncS and asyncS conditions. Related to Fig. 2A and S2.

| Items:  | syncS |      |      |      |      |     | asyncS |      |      |      |      |     | Z <sup>^</sup> | P <sup>^^</sup> |
|---|-------|------|------|------|------|-----|--------|------|------|------|------|-----|----------------|-----------------|
|   | min   | Q1   | Q2   | M    | Q3   | max | min    | Q1   | Q2   | M    | Q3   | max |                |                 |
| <b>I1:</b> It felt as if the body I saw was my own body.                  | -2.0  | 2.3  | 3.0  | 2.6  | 3.0  | 3.0 | -2.0   | 1.0  | 2.0  | 1.6  | 3.0  | 3.0 | 4.83           | <0.005          |
| <b>I2:</b> It felt as if the stick I saw caused the touch I experienced.  | -3.0  | 3.0  | 3.0  | 2.6  | 3.0  | 3.0 | -3.0   | -3.0 | -1.0 | -0.5 | 1.0  | 3.0 | 6.48           | <0.005          |
| <b>I3:</b> It seemed that the touch I felt was applied to the body I saw. | -3.0  | 2.0  | 3.0  | 2.4  | 3.0  | 3.0 | -3.0   | -2.0 | 0.0  | 0.0  | 2.0  | 3.0 | 5.87           | <0.005          |
| <b>C1:</b> It felt as if I had two bodies at the same time.               | -3.0  | -3.0 | -3.0 | -2.5 | -2.3 | 2.0 | -3.0   | -2.0 | 0.0  | -0.3 | 1.0  | 3.0 | -6.17          | <0.005          |
| <b>C2:</b> It felt like I had no body.                                    | -3.0  | -3.0 | -3.0 | -2.4 | -3.0 | 3.0 | -3.0   | -3.0 | -3.0 | -1.8 | 0.0  | 2.0 | -2.83          | 0.006           |
| <b>C3:</b> It felt as if my body was turning artificial.                  | -3.0  | -3.0 | -2.0 | -1.3 | 0.8  | 3.0 | -3.0   | -2.0 | 0.0  | -0.5 | 1.0  | 3.0 | -3.28          | <0.005          |
| <b>C4:</b> It felt as if my body was empty inside.                        | -3.0  | -3.0 | -3.0 | -1.8 | -1.0 | 3.0 | -3.0   | -3.0 | -2.0 | -1.3 | 0.0  | 3.0 | -1.94          | 0.053           |
| <b>L1:</b> It felt as if I was located on the other bed.                  | -3.0  | -3.0 | -3.0 | -2.8 | -3.0 | 0.0 | -3.0   | -3.0 | -3.0 | -2.5 | -3.0 | 1.0 | -2.19          | 0.033           |

Please note that the illusion statements (I1-I3) in syncS were affirmed by most participants (Q2/median  $\geq +2$ ), whereas the control statements (C1-C4) were typically rejected with negative median rating scores. (^) Wilcoxon signed-rank tests (N=66). (^^) FDR-corrected *P*-values (two-sided). **Abbreviations:** M – mean value; Q1-Q3 – quartiles.

**Table S5.** Control analyses for the participants who showed strong vs. weak updating of self-concept in syncF. Related to Fig. 5D.

|   | <b>Strong updating</b> | <b>Weak updating</b> | <b>Chi / t</b> | <b>P</b> | <b>BF<sub>01</sub></b> |
|---|------------------------|----------------------|----------------|----------|------------------------|
| <b>N</b>                                    | 33                     | 32                   |                |          |                        |
| <b>female</b>                               | 20                     | 22                   | 0.18           | 0.67     | 2.77                   |
| <b>age (years)</b>                          | 25 ± 1                 | 27 ± 1               | -1.35          | 0.18     | 1.82                   |
| <b>friendship (months)</b>                  | 45 ± 8                 | 42 ± 6               | 0.31           | 0.76     | 3.79                   |
| <b>IOS</b>                                  | 5.3 ± 0.2              | 5.3 ± 0.3            | 0.02           | 0.98     | 3.94                   |
| <b>NRI (support)</b>                        | 3.4 ± 0.1              | 3.3 ± 0.1            | 0.81           | 0.42     | 2.99                   |
| <b>NRI (negative)</b>                       | 1.5 ± 0.1              | 1.4 ± 0.1            | 0.9            | 0.37     | 2.79                   |
| <b>control scores (avg. C1:C4 in syncF)</b> | -1.2 ± 0.2             | -1.6 ± 0.2           | 1.22           | 0.23     | 2.09                   |

Values are counts or means ± SE. The proportion of females was tested with the equality of proportions chi-square test. The remaining variables were tested with two-sample t-tests (two-sided). Bayes factors report evidence for the null hypothesis (BF<sub>01</sub>). **Abbreviations:** IOS – Inclusion of Other in the Self Scale; NRI – the Network of Relationships Inventory.