



Spatial aspects of bodily self-consciousness

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ABSTRACT

Visual, somatosensory, and perspectival cues normally provide congruent information about where the self is experienced. Separating those cues by virtual reality techniques, recent studies found that self-location was systematically biased to where a visual–tactile event was seen. Here we developed a novel, repeatable and implicit measure of self-location to compare and extend previous protocols. We investigated illusory self-location and associated phenomenological aspects in a lying body position that facilitates clinically observed abnormal self-location (as on out-of-body experiences). The results confirm that the self is located to where touch is seen. This leads to either predictable lowering or elevation of self-localization, and the latter was accompanied by sensations of floating, as during out-of-body experiences. Using a novel measurement we show that the unitary and localized character of the self can be experimentally separated from both the origin of the visual perspective and the location of the seen body, which is compatible with clinical data.

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1. Introduction

In our daily life body and self are unified at one single location in space. What are the crucial sensory cues the brain takes into account in the creation of this apparently stable and embodied self-representation? Do we localize our self according to where we feel our body to be (somatosensory cues), where we see our body to be (visual cues) or at the origin of our visual perspective? The empirical study of bodily self-consciousness has proven difficult, because the body is always there (James, 1890) and never a discrete object of perception. Thus Edmund Husserl (1952) noticed that “I do not have the possibility of distancing myself from my body, nor it from me...”. Visual, vestibular and somatosensory cues normally provide congruent information about self-location and their spatial dissociation is far from methodologically trivial, making it difficult to experimentally investigate their relative contribution to bodily self-representation.

Data from neurological patients may be useful here as neurological interference enables the study of instances of spatially dissociated bodily representations (e.g. Blanke, Ortigue, Landis, & Seeck, 2002; Devinsky, Feldmann, Burrowes, & Bromfield, 1989). In certain pathological conditions as during an out-of-body experience the self can be localized at the origin of the visual perspective even though this location is different from the seen location of one’s body (Blanke, Landis, Spinelli, & Seeck, 2004). In other neurological cases, the self can be experienced as being at the location of the felt body, although this location does not correspond to that of the origin of visual perspective or the seen body (De Ridder, Van Laere, Dupont, Menovsky, & Van de Heyning, 2007). Furthermore, patients with heautoscopy may experience two rapidly alternating per-

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spectives, leaving them often confused about where their self is localized (Blanke et al., 2004; Brugger, Agosti, Regard, Wieser, & Landis, 1994).

Based on these neurological observations several recent studies on bodily self-consciousness have extended self-observations made in the 19th century by Stratton (1899). Systematic studies were necessary due to the small sample sizes of clinical studies, the difficulties in generalizing these findings to normal functions, and other methodological concerns. By exposing participants to conflicting multisensory cues by means of mirrors or simple virtual reality devices these authors developed experimental strategies to manipulate the spatial unity between body and self in healthy subjects (Altschuler & Ramachandran, 2007; Ehrsson, 2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Mizumoto & Ishikawa, 2005).

In Lenggenhager et al. (2007), a protocol similar to that used in the rubber hand illusion (Botvinick & Cohen, 1998) was extended to the full body (Fig. 1A). The participant's back (that was stroked by the experimenter) was recorded and projected synchronously or not to a head mounted display (HMD) that the participant was wearing. When participants saw their body in front of themselves, being stroked synchronously with their own back, they felt as if the virtual body was their own (subjective ratings gathered by questionnaire), and mislocalized themselves towards it—i.e. towards the front. In Ehrsson (2007), a similar set-up was used but the subjects were stroked on their chests (hidden from the cameras' view) and saw the stroking in front of the camera, which in the synchronous condition induced the experience of being at the position of the camera—i.e. behind their body (as confirmed by questionnaires and psychophysiological responses to threat; Fig. 1B).

These two studies suggest that with only slightly different manipulations of how the stroking is applied and projected onto the HMD, aspects of bodily self-consciousness can be shifted in a predictable fashion in opposite directions (Fig. 1A and B). They revealed visual capture by showing that the visual information about stroking dominated over tactile information leading to erroneous self-localization to the position where the touch was seen (Meyer, 2008). This may correspond with either (1) the location of the seen body (Lenggenhager et al., 2007), or (2) with the origin of the visual perspective (Ehrsson, 2007). Accordingly, these data also suggest that self-localization can be experimentally separated from the origin of the visual perspective as well as from the location of the seen body which is compatible with clinical data (Blanke et al., 2004; De Ridder et al., 2007).

Direct comparison of the two studies however is hampered by the fact that different body positions (standing vs. sitting), different questionnaire items, and different behavioral measurements (drift vs. emotional response) were employed. Here we re-investigated both experimental procedures using a novel, implicit measurement of self-location which requires participants to mentally imagine a ball dropping from their hand to the ground, and estimate its falling time. Importantly, this

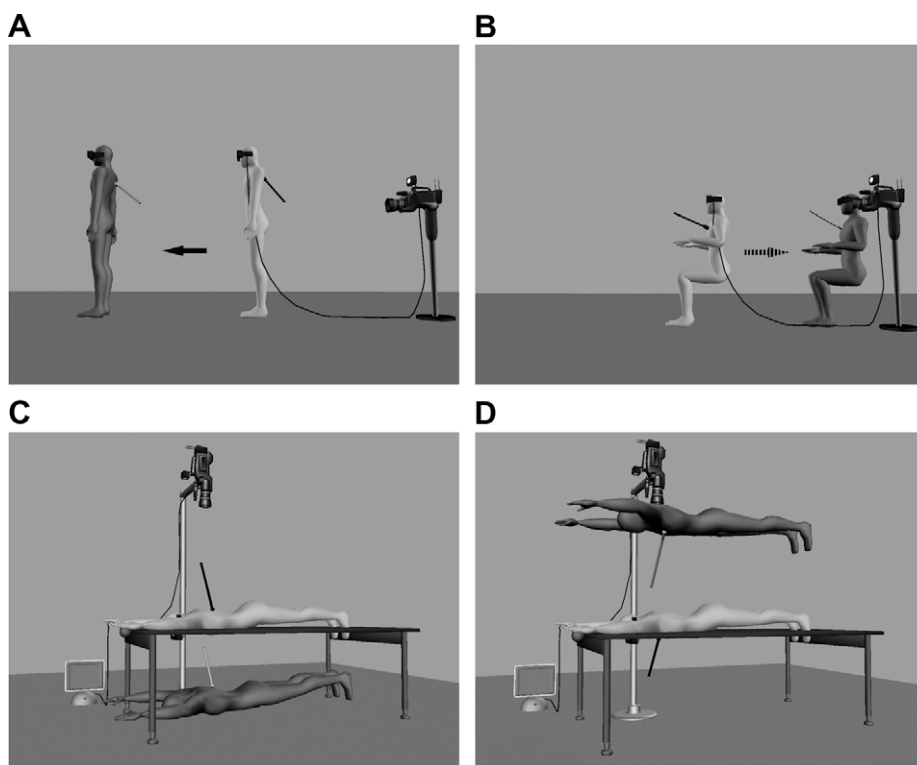


Fig. 1. Experimental set-up previously used in (A) Lenggenhager et al. (2007) and (B) Ehrsson (2007) as well as the (C) back stroking or (D) chest stroking used in the present study. In all set-ups the subject is filmed from the back and sees the recorded scene on a HMD that he is wearing. The light body indicates where the subjects' real body is located, the dark body the hypothesized location of the perceived self. Arrows indicate the direction of change in self-localization.

measurement allows the collection of repeated measurements, which was not the case for methods used in previous studies. We hypothesized that during synchronous back stroking visual capture would lead to a downward shift in self-localization, while synchronous chest stroking would evoke an upward shift in self-localization (Fig. 1C and D). For the first time additional baseline conditions (without stroking) were used, to address the question where the self is localized in the most basic conflict of visual perspective and visual information about body location, without any additional information about touch (Blanke, Metzinger, & Lenggenhager, 2008). Furthermore we extended the previously employed questionnaires to investigate more explicitly the changes in visual perspective, in spatial unity between the self and the body, and in feelings of elevation and floating as classically associated with out-of-body experiences. Since out-of-body experiences most frequently occur in a prone body position (Arzy, Thut, Mohr, Michel, & Blanke, 2006; Blanke et al., 2004), we adapted both experimental procedures to this position.

2. Materials and methods

Twenty-one healthy, naïve and male right-handers (aged 24.2 years \pm 6.3 *SD*) participated. They all gave written informed consent. The protocol was performed in accordance with the ethical standards of the Declaration of Helsinki.

2.1. Materials

The participants were placed in a prone position on a table (1 m height; Fig. 1C and D). They wore a HMD (i-glasses; 800 \times 600 resolution, 25.6°/17.1° field of view) that was covered by a black mask to occlude peripheral vision. A camera (JVC 5) with a special object lens (Virtual FX 3D converter) to render the recorded image in 3D was attached to an aluminum structure placed 2 m above the participant. This enabled the participants to view an interlaced video of their own body as though below them in stereoscopic 3D. The table contained an opening (32 \times 16 cm) at the level of the participants' chests, to allow chest stroking, and a second opening (32 \times 22 cm) to enable a comfortable placement of the head in a horizontal position. In their left hands participants held a ball (16 \times 12 \times 14 cm) and in their right hands a response button device. These two objects were outside of the camera's (respectively, the participants') field of view. E-Prime (Psychology Software Tools Inc., Pittsburgh, PA, USA) was used to record the participants' responses.

2.2. Procedure

The experiment included four randomly presented experimental conditions. Participants were stroked with a wooden stick either on their backs (Lenggenhager et al., 2007) or on the chests (Ehrsson, 2007). In both conditions the participants saw the movie of themselves either online (enabling synchrony between the seen and the felt stroking) or replayed (creating asynchrony between the seen and the felt stroking). Each condition lasted 3 min. During the first 2 min participants passively observed the stroking, then participants were asked to perform several times the mental ball dropping task (see below). A training session ensured that participants were familiar with the task.

Two baseline conditions where no stroking was applied were tested before and after the experiment. Participants were either blindfolded (HMD off, baseline condition 1) or saw their body through the HMD (HMD on, baseline condition 2).

2.3. Measurements

2.3.1. Mental ball dropping

In order to assess participants' implicit self-location in space they were asked to imagine dropping the ball that they were holding in their hand (mental ball dropping task, MBD). They were instructed to indicate with a first button press when they imagined releasing the ball from their hand, and with a second button press when the ball would hit the ground (cf. paradigm used to investigate internal models of object trajectories, (e.g. Indovina et al., 2005). The difference between the two button presses was measured (in milliseconds). Ten auditory cues during the third minute of stroking told subjects to each time do a MBD task.

2.3.2. Questionnaire

After each experimental condition, participants described the experience (open question) and filled out a 12-item questionnaire (based on Ehrsson, 2007; based on Lenggenhager et al., 2007; see Table 1). The questions were randomly ordered and answered on a continuous scale between 0 and 10. Two out of the 12 items were control questions to check for susceptibility and were excluded from further analysis.

2.4. Data processing

For performance in the MBD, a repeated measurement 2 \times 2 ANOVA with within-factors Typ of Stroking (back/front) and Synchrony (synchronous/asynchronous) was calculated. For the questionnaire data, an additional within-factor Question (1–10) was included in the first analysis. Fisher's Least Significant Difference (LSD) analysis was used for post-hoc comparisons.

Table 1
Main and interaction effects of the questionnaire scores (*significant effects ($p < .05$)).

Questions	Type	Synch	Type Synch*
Q1. How strong was the feeling that the rod you saw was directly touching you?	0.02*	0.00*	0.16
Q2. How strong was the feeling that you were located at some distance behind the visual image of the body that you saw?	0.04*	0.07	0.17
Q3. How strong was the feeling that you were looking at someone else?	0.41	0.53	0.02*
Q4. How strong was the feeling that you had more than one body?	0.80	0.21	0.86
Q5. How strong was the feeling that you were drifting downwards or upwards?	0.29	0.81	0.16
Q6. How strongly did you feel the touch simultaneously at two locations in space?	0.89	0.43	0.59
Q7. How strong was the feeling that the visual image of the body you saw was really you?	0.08	0.01*	0.05
Q8. How strong was the feeling that the touch you felt was where you saw the stroking?	0.03*	0.00*	0.02*
Q9. How strong was the feeling to float in air?	0.10	0.46	0.07
Q10. How strong was the feeling that you were dissociated from your body (as if your self and your body were in different locations)?	0.96	0.06	0.59

Response times smaller than 100 ms or bigger than 3000 ms were excluded. One participant was excluded because 55% of his data was in this range (compared with 6% in the other subjects). Results were analyzed using Statistica 6.1 (StatSoft Inc., Tulsa, USA); $p < .05$ is considered as significant, $p < .1$ as a trend. Baseline conditions were analyzed with t -tests before and after the stroking period.

3. Results

3.1. Questionnaire

The $2 \times 2 \times 10$ ANOVA revealed a significant three-way interaction between question, Type of Stroking and Synchrony ($F_{(11,209)} = 3.5$; $p < .001$, $\eta^2 = 0.78$). Separate 2×2 ANOVAs with the factors of Type of Stroking and Synchrony were therefore calculated for each question. Table 1 summarizes all main and interaction effects. All significant effects as well as trends are plotted with mean and standard error in Fig. 2. The relevant questions were clustered according to their inter-item

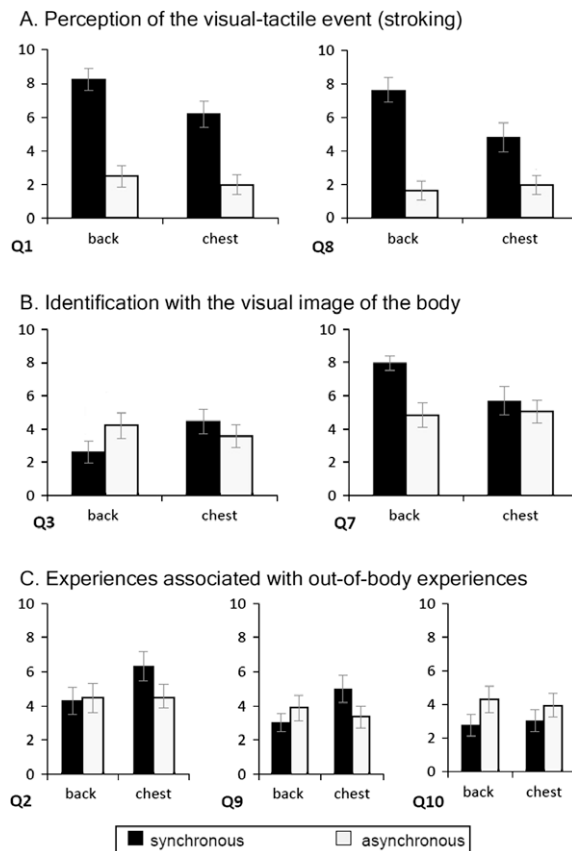


Fig. 2. Results of the questions that showed a trend or a significant effect in the ANOVA. Means and standard errors are plotted.

correlation and content (and for the sake of clarity) into three different aspects: (A) perception of the visual–tactile event (Q1, Q8), (B) identification with the visual virtual body (Q7, Q3), and (C) experiences associated with out-of-body experiences (Q2, Q9, Q10). The inter-item correlation (Pearson's correlation) for the mean score over all conditions for these questions is shown in Table 2, bold r -values indicate highly significant correlations ($p < .01$).

The main effect of Synchrony in the 2×2 ANOVA showed that during both synchronous (as compared to the asynchronous) stroking there was a stronger impression that the stroking was felt where it was seen (Q1, Q8), suggesting as hypothesized a fusion of the visual and the tactile information about the stroking. This “feeling of the touch where it is seen” in the synchronous conditions (in the back and chest stroking) tended to be associated with a feeling of being dissociated from the body (“as if the self and the body were in different locations”) as revealed by the trend of Synchrony for Q10.

As suggested by the Fisher's post-hoc analysis, identification with the visual virtual body was highest during synchronous back stroking (Q7; as compared to back asynchronous $p = .002$, chest synchronous $p = .02$, chest asynchronous $p = .003$) while the feeling of looking at someone else was on the contrary stronger during synchronous chest than synchronous back stroking (Q3; $p = .02$). Vestibular sensations were mainly found in the synchronous chest condition (Q9) and significantly less in the synchronous back condition ($p = .05$) and tended to be less in the asynchronous chest stroking ($p = .09$). See Fig. 2 and Table 1 for further details.

3.2. Mental ball dropping

During back stroking, participants' MBD time was shorter in the synchronous condition (mean \pm standard error, 736.1 ± 47.5 ms) than in the asynchronous condition (832.6 ± 56.1 ms) or in the synchronous chest stroking condition (791.7 ± 41.7 ms, Fig. 3). No difference was found between synchronous and asynchronous chest stroking conditions (819.5 ± 48.7 ms; Fig. 3A). Statistical analysis showed a significant main effect of Synchrony ($F_{(1,19)} = 6.9$; $p = .02$, $\eta^2 = 0.27$) and a trend for the Typ of Stroking \times Synchrony interaction ($F_{(1,19)} = 3.5$; $p = .08$, $\eta^2 = 0.16$). Post-hoc analyses revealed a significant difference between synchronous and asynchronous stroking for the back stroking ($p = .002$) but not for the chest stroking ($p = .30$). The two synchronous stroking conditions differed significantly ($p = .045$) while the asynchronous conditions did not ($p = .62$).

3.3. Baseline

t -Tests found no significant difference between pre- and post-experimental measurements for the ‘HMD off condition’ ($p = .44$), but a significant difference for the ‘HMD on condition’ ($p = .02$), with longer estimation times in the post-experi-

Table 2

Inter-item correlations (Pearson's correlation) of all questions that showed a significant effect or a trend in the 2×2 ANOVA. Highly significant r^2 -values ($p < .01$) are shown in bold.

	Q1	Q2	Q3	Q7	Q8	Q9	Q10
Q2	-0.03						
Q3	-0.33	0.28					
Q7	0.23	-0.45	-0.78				
Q8	0.68	-0.11	-0.13	0.14			
Q9	-0.23	0.62	0.19	-0.26	0.07		
Q10	-0.37	0.66	0.62	-0.55	-0.26		0.47

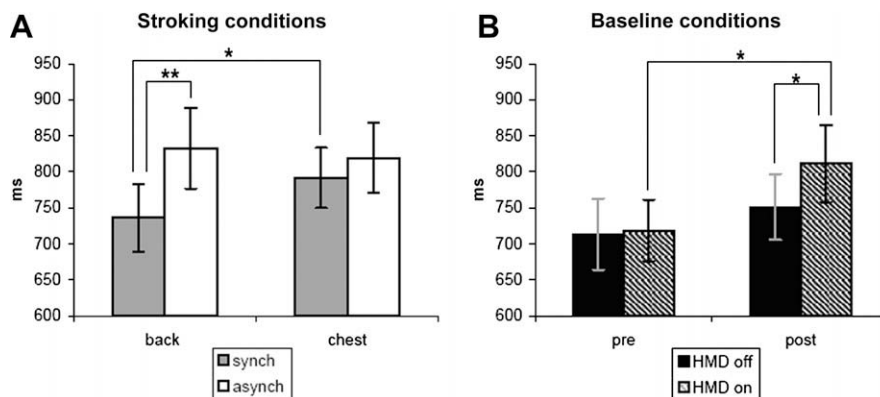


Fig. 3. Mental ball dropping times (mean \pm standard error) for (A) synchronous and asynchronous back and chest stroking as well as for (B) the pre- and post-experimental baseline conditions.

mental condition. This was also reflected in a significant difference ($p = .049$) between HMD on and off conditions after the experiment (see Fig. 3B).

4. Discussion

The data from the implicit, and repeated measurement of self-location (MBD) and from the questionnaire corroborate and extend previous findings showing that global bodily self-consciousness can be systematically manipulated through conflicting multisensory inputs in healthy subjects. Three main conclusions can be drawn from our data. First, confirming previous data, synchronous back stroking (compared to asynchronous stroking) led to increased self-identification and illusory touch on the seen body. Synchronous chest stroking led to opposite effects: decreased self-identification and illusory touch sensation on the seen body. Second, the present data show that synchrony between visual and tactile information about the stroking may systematically change bodily self-consciousness, leading in the prone body position to predictable and implicitly measurable upward and downward drifts in self-localization. Third, the present set-up rendered the induced illusory perceptions more comparable to related clinical conditions such as out-of-body experiences (Blanke et al., 2004), which both original studies were inspired by. This seems especially relevant since the subjective elevated self-location in the present study were combined with a floating sensation, suggesting a modulation of vestibular sensations.

4.1. Phenomenological aspects

Participants perceived the synchronously seen and the felt stroking as a single event, i.e. perceived the tactile stimulus at the location where they see it (Q1, Q8) which confirms previous questionnaire data (Ehrsson, 2007; Lenggenhager et al., 2007). This is in accordance with visual capture, a mechanism that has also been described to be important in the rubber hand illusion (Botvinick & Cohen, 1998) and may be associated with changes in receptive fields of bimodal neurons (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). Interestingly, subjective self-localization also drifted to where touch was perceived (illusory), leading in the chest as well as in the back stroking to slightly higher sensations of dissociation between the self and the body (Q10) in the synchronous conditions. During synchronous back stroking the location of perceived touch coincided with the location of the seen body and was accompanied with increased self-identification with the seen body (Q7, Q3). The opposite was found for the synchronous chest stroking: participants felt that they were localized at the origin of visual perspective which was rather associated with decreased self-identification with the seen body as well as the feeling of looking at someone else (Ehrsson, 2007). Furthermore the question on vestibular sensations revealed that in the synchronous chest stroking the sensation of floating was stronger than in the back stroking. Even if this result is based on a trend only and has rather to be taken as preliminary, previous work has shown the importance of vestibular (otolith) signals in abnormal self-location (Blanke et al., 2002, 2004) and vestibular cues may interfere with body and self-representation (Le Chapelain, Beis, Paysant, & Andre, 2001; Lenggenhager, Lopez, & Blanke, 2008; Lopez, Halje, & Blanke, 2008; Sang, Jauregui-Renaud, Green, Bronstein, & Gresty, 2006). Minimized vestibular sensory updating due to the motionless and prone body position of the participants may have further contributed to the occurrence of such vestibular sensations highlighting their potential relevance for bodily self-consciousness.

Interestingly in the asynchronous conditions, the pattern described above reversed for both stroking types and the stroking was no longer perceived where it was seen but where it was felt. This suggests that during asynchronous conditions the somatosensory body representation (or somatosensory capture) prevails. Philosopher René Descartes and more recently many others have argued that the bodily self is mainly based on somatosensory signals, since it is the most reliable sense in distinguishing between self and the external world. The present data concord with previous work on visual capture showing that this is only true under certain conditions (Haggard, Taylor-Clarke, & Kennett, 2003). Nevertheless, it seems that the self is—at least in the present experimental set-up—always localized where touch is subjectively perceived (even if this perception is wrong), independently of the visual perspective or the visual information about the body. We speculate that—although cognitive and conceptual mechanisms are important aspects of self-consciousness (Gallagher, 2000; Blanke & Metzinger, *in press*; Zahavi, 2005)—the present investigation was able to utilize conflicting multisensory inputs for the manipulation of crucial aspects of bodily self-consciousness that may be a foundation of higher-level, cognitive and conceptual, aspects of self-consciousness (Gallagher, 2000; Blanke & Metzinger, *in press*).

4.2. Implicit self-localization

These predictable changes in self-localization were—at least partly—confirmed by a novel implicit behavioral measure. As expected, during back stroking the MBD revealed significantly shorter estimated times when subjects were stroked synchronously as compared to asynchronously. This suggests that participants mislocalized their self to a position closer to the seen body, in this case at a lower position, replicating previous findings in the standing position, but using a different measure and body position (Lenggenhager et al., 2007). The synchronous back stroking condition also led to shorter estimation times than the synchronous chest stroking, which we predicted based on the results of Ehrsson (2007). However, we did not find the expected difference between synchronous and asynchronous chest stroking. This might be for a number of reasons: (1) methodological concerns, (2) differences in contradicting sensory information (3) gravitational effects (4) perspectival

habituation effects, and (5) the hypothesis that explicit (questionnaire) and implicit (MBD) variables may not measure the same aspects of bodily self-consciousness.

Firstly, it may be that the synchronous chest condition was 'less synchronous', since delivering synchronous input is technically more demanding in this condition. Yet, our questionnaire results (especially Q1) would argue against this explanation, since participants strongly felt that the seen stick was touching them directly. Secondly, it might be that the chest stroking feels in the prone body position less natural since participants get conflicting sensory information: they are lying on their chest, but nevertheless receive tactile stimulation on the chest through the table opening. This is not the case during back stroking conditions. Although this may be a contributing factor in the chest stroking conditions that we cannot exclude, it does not explain why the participants localized themselves (according to the MBD) under synchronous as well as asynchronous conditions rather at the position of the visual perspective (see below). Third, an influence of gravity-related processing on self-location as estimated in the prone body position, especially for the chest stroking conditions, cannot be excluded. Thus, the constant direction of gravity (downwards) can be assumed to counteract directional effects that we predicted in the (synchronous) chest stroking conditions (upwards), especially as such gravitational effects have been observed to influence the perceived motion of objects (e.g. Hubbard, 1990) as well as MBD estimation times under different experimental conditions (e.g. Indovina et al., 2005). Furthermore out-of-body experiences, that include mostly a self-elevation in the direction opposite to gravity, have previously been linked to a lack of detection of gravity through disturbed vestibular/otolith processing (e.g. Blanke et al., 2004). Yet, findings from mental own body transformation, a task that has been closely linked to OBEs (Blanke et al., 2005) suggest a rather small influence of gravitational constraints (Creem, Wraga, & Proffitt, 2001), so that further careful studies seem necessary to elucidate effects of gravity on self-location. A forth and in our opinion plausible alternative explanation is that a fast habituation effect for the elevated perspective (even without stroking) may have occurred and lessened potential effects of the chest synchronous stroking. The data of the baseline measured in the present study suggests that participants localized their self at the location where the body is seen, when first exposed to this multisensory conflicting situation (compare Blanke et al., 2008). This can be seen in similar MBD times during the pre-experimental baseline as during synchronous back stroking condition, in which participants felt to be located at the position of the seen body. However, after the experiment (that lasted for ~1 h), participants showed longer MBD times suggesting that they now localized their self at a more elevated position and thus closer to the origin of the visual perspective. These data corroborate much earlier self-observations by Stratton (1899) who described that self-localization may change over time between where the body is seen, felt, and at the origin of visual first perspective. Thus, if in all experimental conditions the participants show a drift in self-location from the visual body towards the visual perspective of the camera, the synchronous chest stroking condition may not be able to further elevate the perceived self-location spatially, but may still strengthen the vividness of the feeling of being there. This would be compatible with the values of MBD and questionnaire scores in our chest stroking conditions. These findings do not contradict previous findings by Ehrsson (2007) since the experimental procedure and conditions, as well as body position and video-recordings were different. Moreover, Ehrsson (2007) did not quantify self-location spatially e.g. with proprioceptive drift (self-location) or the MBD time, but via an emotional reaction to a threat (electrodermal skin response; implicit measurement), which could be correlated with the vividness of the feeling of being there (explicit measurement). Future research should investigate whether and how these different behavioral proxies of bodily self-consciousness relate to each other and how different aspects of bodily self-consciousness (such as self-location and self-identification) are associated with each other. For the rubber hand illusion several studies found differences between the explicit and implicit measurements (e.g. Armel & Ramachandran, 2003; Kammers et al., 2008), but only recently a psychometrical study has addressed this question explicitly (Longo, Schuur, Kammers, Tsakiris, & Haggard, 2008). Latter authors suggested that "embodiment" during the RHI is not a single perceptual experience but can be broken down into different components of which only certain dimensions (quantified by questionnaire scores (explicit measurement)) predict the amount of proprioceptive drift (implicit measurement). This might be the fifth reason why different results were obtained for data from the questionnaire and from the MBD.

5. Conclusion

Recent philosophical and neurological theories converge on the relevance of bodily processes in self-consciousness (e.g. Gallagher, 2005). Studying the role of various bodily cues in self-representations in a rigorous scientific set-up is important to further evolve these theories. Here we investigated where participants experience and localize their self, given conflicting information about the seen and the felt body as well as the visual perspective. The data suggest that participants localize their self where they perceive to be touched, even if this tactile perception is mislocalized through visual capture, leading in the present set-up to predictable up- or downwards shifts in self-location. The former was associated with feeling of floating as typically found in neurologically caused cases of disturbed self-location. Disentangling the contribution of different bodily cues to self-location may help to better understand normal and abnormal embodiment and self-consciousness.

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References

- Altschuler, E. L., & Ramachandran, V. S. (2007). A simple method to stand outside oneself. *Perception*, 36(4), 632–634.
- Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: Evidence from skin conductance response. *Proceedings. Biological Sciences/The Royal Society*, 270(1523), 1499–1506.
- Arzy, S., Thut, G., Mohr, C., Michel, C. M., & Blanke, O. (2006). Neural basis of embodiment: Distinct contributions of temporoparietal junction and extrastriate body area. *Journal of Neuroscience*, 26(31), 8074–8081.
- Blanke, O., Landis, T., Spinelli, L., & Seeck, M. (2004). Out-of-body experience and autoscopia of neurological origin. *Brain*, 127(Pt. 2), 243–258.
- Blanke, O., & Metzinger, T. (in press). Full body illusions and the minimal phenomenal self. *Trend in Cognitive Science*, 13 (1).
- Blanke, O., Mohr, C., Michel, C. M., Pascual-Leone, A., Brugger, P., Seeck, M., et al. (2005). Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. *Journal of Neuroscience*, 25(3), 550–557.
- Blanke, O., Metzinger, T., & Lenggenhager, B. (2008). How does the brain localize the self. *Science, E-letters*. Available from: <<http://www.sciencemag.org/cgi/eletters/317/5841/1096>>.
- Blanke, O., Ortigue, S., Landis, T., & Seeck, M. (2002). Stimulating illusory own-body perceptions. *Nature*, 419(6904), 269–270.
- Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature*, 391(6669), 756.
- Brugger, P., Agosti, R., Regard, M., Wieser, H. G., & Landis, T. (1994). Heautoscopy, epilepsy, and suicide. *Journal of Neurology, Neurosurgery, and Psychiatry*, 57(7), 838–839.
- Creem, S. H., Wraga, M., & Proffitt, D. R. (2001). Imagining physically impossible self-rotations: Geometry is more important than gravity. *Cognition*, 81(1), 41–64.
- De Ridder, D., Van Laere, K., Dupont, P., Menovsky, T., & Van de Heyning, P. (2007). Visualizing out-of-body experience in the brain. *The New England Journal of Medicine*, 357(18), 1829–1833.
- Devinsky, O., Feldmann, E., Burrowes, K., & Bromfield, E. (1989). Autoscopy phenomena with seizures. *Archives of Neurology*, 46(10), 1080–1088.
- Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. *Science*, 317(5841), 1048.
- Gallagher, S. (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends in Cognitive Sciences*, 4, 14–21.
- Gallagher, S. (2005). *How the body shapes the mind*. Oxford: Oxford University Press.
- Haggard, P., Taylor-Clarke, M., & Kennett, S. (2003). Tactile perception, cortical representation and the bodily self. *Current Biology*, 13(5), R170–R173.
- Hubbard, T. L. (1990). Cognitive representation of linear motion: Possible direction and gravity effects in judged displacement. *Memory & Cognition*, 18(3), 299–309.
- Husserl, E. (1952). *Ideen zu einer reinen Phänomenologie und phänomenologischer Philosophie*. Zweites Buch: Phänomenologische Untersuchungen zur Konstitution. The Hague: Martin Nijhoff.
- Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E., & Lacquaniti, F. (2005). Representation of visual gravitational motion in the human vestibular cortex. *Science*, 308(5720), 416–419.
- James, W. (1890). *The principles of psychology* (2). London: Macmillan.
- Kammers, M. P., Verhagen, L., Dijkerman, H. C., Hogendoorn, H., De Vignemont, F., & Schutter, D. J. (2008). Is this hand for real? Attenuation of the rubber hand illusion by transcranial magnetic stimulation over the inferior parietal lobule. *Journal of Cognitive Neuroscience*.
- Le Chapelain, L., Beis, J. M., Paysant, J., & Andre, J. M. (2001). Vestibular caloric stimulation evokes phantom limb illusions in patients with paraplegia. *Spinal Cord*, 39(2), 85–87.
- Lenggenhager, B., Lopez, C., & Blanke, O. (2008). Influence of galvanic vestibular stimulation on egocentric and object-based mental transformations. *Experimental Brain Research*, 184(2), 211–221.
- Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video ergo sum: Manipulating bodily self-consciousness. *Science*, 317(5841), 1096–1099.
- Longo, M. R., Schuur, F., Kammers, M. P., Tsakiris, M., & Haggard, P. (2008). What is embodiment? A psychometric approach. *Cognition*, 107(3), 978–998.
- Lopez, C., Halje, P., & Blanke, O. (2008). Body ownership and embodiment: Vestibular and multisensory mechanisms. *Neurophysiologie Clinique*, 38(3), 149–161.
- Meyer, K. (2008). How does the brain localize the self. *Science E-letters*. Available from: <<http://www.sciencemag.org/cgi/eletters/317/5841/1096#10767>>.
- Mizumoto, M., & Ishikawa, M. (2005). Immunity to error through misidentification and the bodily illusion experiment. *Journal of Consciousness Studies*, 12(7), 3–19.
- Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981). Afferent properties of periarculate neurons in macaque monkeys. I. Somatosensory responses. *Behavioural Brain Research*, 2(2), 125–146.
- Sang, F. Y., Jauregui-Renaud, K., Green, D. A., Bronstein, A. M., & Gresty, M. A. (2006). Depersonalisation/derealisation symptoms in vestibular disease. *Journal of Neurology, Neurosurgery, and Psychiatry*, 77(6), 760–766.
- Stratton, G. M. (1899). The spatial harmony of touch and sight. *Mind*, 8, 492–505.
- Zahavi, D. (2005). *Subjectivity and selfhood: Investigating the first-person perspective*. Cambridge: MIT Press.