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LAST BUT NOT LEAST

How many arms make a pair? Perceptual illusion of having an additional limb

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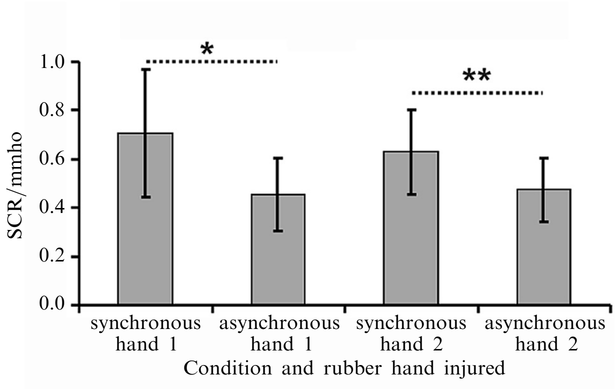
Abstract. What are the natural constraints for the human body representation? Here I report a perceptual illusion where healthy individuals experience having two right arms, with both sensing touches applied to them. This effect reveals how visual and tactile signals from the body are integrated in a probabilistic fashion, resulting in a single limb being represented at two locations at the same time, giving rise to a perceptual duplication of this limb. This is an important observation because it suggests that even the gross morphology that we experience of ourselves is a construct resulting from dynamic and integrative processes in the perceptual systems.

An organism's body plan refers to the symmetry and the number of segments and limbs of the body. It is current wisdom that the body plan imposes fundamental constraints on the neuronal representations of the body (Brugger et al 2000; Melzack 1990). However, the way we perceive ourselves depends on the integration and interpretation of noisy and sometimes ambiguous multisensory signals from the body. The resulting bodily percepts can differ from the actual state of the physical body, as is the case in a number of well-known body illusions (Botvinick and Cohen 1998; Lackner 1988). Most of these involve people experiencing illusory displacement of limbs or changes in the perceived size and shape of body parts. Illusions that violate the human body plan are rarer, but these are potentially interesting for what they could tell us about the natural constraints of human body representation. In Aristotle's illusion, for example, people sometimes experience two noses when touching their nose with their fingers crossed (Benedetti 1985). Similarly, Caske (1977) described how some participants felt multiple limbs during a procedure of biceps tendon vibration. However, these were anecdotal reports, and no experimental evidence for changes in body representation that specifically reflected the additional limbs or noses was presented.

Here, I report a novel version of the rubber hand illusion (Botvinick and Cohen 1998) where healthy individuals experience having two right arms, with both sensing touches applied to them. In the experiments the participant's real right hand was hidden under a table, while two realistic life-sized right rubber hands were placed on the table in front of the participant in full view (figure 1a). These model hands were placed side by side (10 cm apart), 10 cm above the real hand, so that they both resembled the person's right arm. The experimenter used a specially designed double paintbrush (consisting of two small paintbrushes attached to a single holder) and a regular paintbrush to stroke the two rubber hands and the participant's hidden hand on the corresponding sites, synchronising the timing of the brushing. After 2 min of brushing, the majority of people tested reported sensing the paintbrushes on both rubber hands, ie they had two spatially distinct sensations of being touched, one on 'each'. People also often described how both rubber hands felt like their own right hand at the same time.

To provide objective quantitative evidence for this effect, an experiment was conducted with twenty naive participants (eight males and twelve females, aged between 21 and 31 years; mean age ($\pm$SD) 25.1 ± 3 years) with the skin-conductance response (SCR) measured when the rubber hands were 'hurt' (see figure legend for details).

(a)



(b)

Figure 1. (a) The set-up with the participant looking at two identical cosmetic right-hand prostheses being stroked in synchrony with touches applied to the hidden right hand (placed below the table between the model hands). (b) Physiological evidence for the illusion of having two right arms (see text). Error bars denote standard error of the mean. The skin conductance responses (SCR) were recorded and stored with a Biopac MP150 system (Biopac Inc., Goleta, USA), and analysed with Biopac's software Acqknowledge 3.9.1. Two electrodes were attached to the pulps of the index and middle fingers of the participants' left hand with Biopac's isotonic recording electrode gel (Gel 101). The recording procedures followed published guidelines. The synchronous and asynchronous condition was repeated six times in a balanced randomised design for every participant. The trials took the form of 60 – 120 s of synchronous or asynchronous brushing (~60 brushstrokes per minute; each stroke was 3 – 4 cm long and applied on the second or third digit), whereupon the first (left in figure) or second rubber hand was stabbed, immediately, above the knuckle of the index finger with a stainless steel needle attached to a syringe. Each of the two right rubber hands was stabbed three times a piece in total, once per trial. Each 'injuring procedure' took about 3 s. Great care was taken to move the needle in the same way from trial to trial. The SCR was identified as a peak in the conductance that occurs up to 3 s after the needle hit the rubber hand. We computed the magnitude of the SCR for each condition by using the data from all trials and all participants.

The SCR is a measure of ownership that reflects fear and anxiety when an owned body part is under physical threat (Armel and Ramachandran 2003). After a period of synchronous or asynchronous brushing of the real and rubber hands, lasting for 60 – 120 s, a needle was stabbed in one rubber hand or the other (see figure legend). The asynchronous stimulation does not elicit the illusion and served as control for unspecific emotional responses associated with seeing the rubber hand injured. The analysis of the SCR data showed that there was a significantly greater response when the stabbing took place immediately after the synchronous condition than when it occurred straight after the control condition (figure 1b) [$p = 0.0315$, main effect illusion stimulation, $F_{1,19} = 5.391$, using a repeated-measures General Linear Model as implemented in SPSS 15.0 (SPSS Inc., Chicago, USA)]. This effect was significant for both rubber hands ($p = 0.034$, paired one-tailed t-test, rubber hand one; $p = 0.006$, paired one-tailed t-test, rubber hand two), and the effect was equally strong (no significant interaction between hand and stimulation; $p = 0.33$, $F_{1,19} = 0.33$; $p = 0.53$ paired two-tailed t-test between synchronous stimulation of hand one and hand two).

These results show that the participants' perceptual and emotional systems treated both rubber hands as parts of their own bodies.

The present illusion seems to violate fundamental assumptions of the human body representation. It is hard to explain the duplication-hand illusion with a traditional model where the location of the upper limb is computed by the weighted average of visual, tactile, and proprioceptive signals (Welch and Warren 1986). The illusory duplication of the single touch applied to the real hand into two separate touches on two owned right arms is better explained in a probabilistic framework (Deneve and Pouget 2004), where the brain is estimating the most probable location of the arm allowing for biphasic probability distributions (Ma et al 2006). In this framework, the result of the multisensory integration process would be that there are two equally probable locations of the right arm. The perceptual consequence of this is the experience of having two right arms. Neurons in the premotor and posterior parietal cortex that integrate visual, tactile, and proprioceptive signals from near-personal space (Graziano et al 1997) could be mediating the referral of touch in the rubber hand illusion (Ehrsson et al 2004). One can speculate that, in the present arm-duplication illusion, these neurons split into two sub-populations, with each population mediating the visuo-tactile binding in coordinates centred on one of the two rubber hands. Thus, each brushstroke applied to the hidden real hand is sensed as two separate tactile events occurring on the two rubber hands being stroked by the double brush. This made the participants experience that both rubber hands belonged to their body, which, in itself, is compelling evidence that the sensation of being touched is a strong factor in producing a feeling of body ownership.

A prediction of this model is that the sense of ownership of each of the two rubber hands should add up to the total feeling of ownership experienced when a single artificial hand is presented. I have carried out pilot experiments suggesting that the illusion is indeed stronger and more prevalent when a single rubber hand is used, and that the ownership of each hand becomes systematically weaker the more rubber hands are presented (two or three). This relationship should be quantified in future experiments.

In conclusion, the present experiments reveal that the central body representation is substantially more dynamic and plastic than commonly assumed, even allowing healthy individuals to feel and see supernumerary limbs.

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