

and interpret the neurophysiology. The development of the honeybee as a model genetical system may also permit another line of entry into understanding between brain structures and behaviour. One day we may be able to knock out individual components of spatial behaviour and observe the results.

We know now that an insect such as an ant or bee has a variety of spatial memories that are acquired at different rates and offer different advantages and disadvantages. These ensembles provide both complementarity and redundancy, permitting reliable navigation while guiding the acquisition of new memories and allowing behaviour flexible enough to adapt to changes in surroundings, resource distribution or requirements. Understanding better how insects use spatial memories will help elucidate what their relatively small brains are capable of. Discovering their limitations may help explain the evolution of our own larger and more complex brains.

Further reading

- Collett, M., and Collett, T.S. (2006). Insect navigation: no map at the end of the trail? *Curr. Biol.* 16, 48–51.
- Collett, M., and Collett, T.S. (2007). Spatial aspects of foraging in ants and bees. *Cold Spring Harbor Monograph Series* 49, 467.
- Collett, M., and Collett, T.S. (2009). Local and global navigational coordinate systems in desert ants. *J. Exp. Biol.* 212, 901.
- Collett, T.S., and Kelber, A. (1988). The retrieval of visuo-spatial memories by honeybees. *J. Comp. Physiol. A- Sens. Neural Behav. Physiol.* 163, 145–150.
- Collett, T.S., Collett, M., and Wehner, R. (2001). The guidance of desert ants by extended landmarks. *J. Exp. Biol.* 204, 1635–1639.
- Dyer, F.C., and Dickinson, J.A. (1994). Development of sun compensation by honeybees: how partially experienced bees estimate the sun's course. *Proc. Natl. Acad. Sci. USA* 91, 4471–4474.
- Hironaka, M., Filippi, L., Nomakuchi, S., Horiguchi, H., and Hariyama, T. (2007). Hierarchical use of chemical marking and path integration in the homing trip of a subsocial shield bug. *Anim. Behav.* 73, 739–745.
- Lehrer, M., and Collett, T.S. (1994). Approaching and departing bees learn different cues to the distance of a landmark. *J. Comp. Physiol. A- Sens. Neural Behav. Physiol.* 175, 171–177.
- Poulet, J.F.A., and Hedwig, B. (2005). Auditory orientation in crickets: Pattern recognition controls reactive steering. *Proc. Natl. Acad. Sci. USA* 102, 15665–15669.
- Wehner, R., and Srinivasan, M.V. (2003). Path integration in insects. In *The Neurobiology of Spatial Behaviour*, K.J. Jeffery, ed. (Oxford: Oxford University Press), pp. 9–30.
- Zeil, J., Boeddeker, N., Hemmi, J.M., and Sturzl, W. (2007). Going wild: toward an ecology of visual information processing. *Cold Spring Harbor Monograph Series* 49, 381.

School of Psychology, University of Exeter,
Exeter EX4 4QG, UK.
E-mail: M.Collett@exeter.ac.uk

Correspondence

Feeling numbness for someone else's finger

Sebastian Dieguez¹,
Manuel R. Mercier¹, Nate Newby^{1,2},
and Olaf Blanke^{1,3}

The experience that our body and its parts belong to us and are not those of other people is a key aspect of the 'self' called body ownership [1]. In six experiments, we have investigated body ownership and its neurophysiology using a tactile illusion [2,3] that disrupts body ownership and tactile sensation robustly, repeatedly, and with no particular apparatus by inducing an illusory feeling of numbness for another person's finger — the 'numbness illusion' (NI). Our results show that the NI does not depend primarily on visual or motor signals, but on tactile inputs modulating activity in primary somatosensory cortex.

The NI arises when one person holds the palm of one hand against another person's opposite palm and strokes with his other hand the two joined index fingers (Figure 1A) [2,3]. In study 1, we documented the NI by asking participants to rate the intensity of experienced numbness and other items (see Supplemental data available on-line) and manipulated the Stroker (by varying whether stroking of the two index fingers was done by the participant or experimenter) and Synchrony (by touching both fingers at the same or at alternating times). The NI depended on Synchrony, but only during self-stroking ($F(1,13) = 21.96$; $p < 0.001$; Figure 1B), being strongest during synchronous self-stroking. This suggests that the NI depends on the temporal synchrony between visual, somatosensory, and motor signals. In study 2, we tested whether visual signals modulate the NI and further investigated its phenomenology. We confirmed that the NI depends on synchrony and stroking (see Supplemental data) and found that the subject's view (direct versus occluded view of the hands) did not affect the NI (view: $F(1,16) = 0.62$; $p = 0.44$; Stroker x Synchrony x

View interaction: $F(1,16) = 2.21$; $p = 0.08$). Other feelings including body ownership also showed strong ratings only during synchronous self-stroking (see Supplemental data), confirming that the NI is accompanied by a disruption of body ownership. Study 2 suggests the NI arises from synchronous somatosensory and motor signals resulting from one's right thumb touching one's left index finger and one's right index finger touching the other person's index finger, while one's left fingertips are in static contact with the other person's fingertips (Figure 1A).

Study 3 revealed that somatosensory cues from the static fingertips are crucial, as numbness intensity was significantly reduced when both hands were separated by an empty space (Supplemental data). As previous data revealed the importance of motor signals for body ownership [4], we tested whether these are crucial for the NI (study 4). Attaching tight rubber bands to the joined fingers (Figure 1C), we compared the NI in *passive* and *active* conditions and the self-synchronous condition. NI ratings differed across conditions ($F(2,28) = 24.8$; $p < 0.001$) and were significantly smaller in the active ($p < 0.001$), but not the passive condition ($p = 0.29$; Supplemental data). This is compatible with the foremost importance of tactile cues (see also study 5; Supplemental data) because the NI was strong as long as participants felt their own fingers touching and being touched (independent of who was moving them). We suggest that the NI arises as a result of somatosensory predictions and lack of anticipated somatosensory stimulation [5] on the illusory owned finger due to tactile information from the touching index finger and thumb, as well as from the touched index finger (double-touch), the spatial and temporal congruency of these signals, the contact with the other person's hand, and the similarity in shape and texture of the other person's finger.

Predicting that somatosensory cortex is involved in the NI, we recorded somatosensory evoked potentials (SEPs) to left median nerve stimulation during the experimental conditions of study 1. SEPs at electrode C4 (over somatosensory cortex contralateral to the electrically stimulated median nerve) revealed

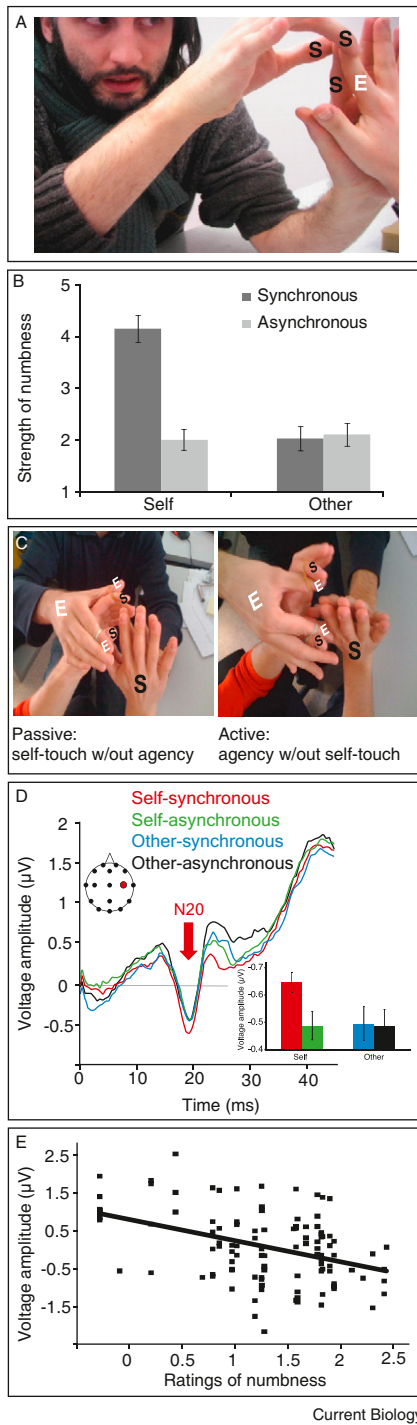


Figure 1. The numbness illusion. (A) Procedure to induce the numbness illusion (NI). The person on the left (Subject, indicated by black 'S') strokes his own left index finger with his right thumb, as well as the other person's (Experimenter, indicated by white 'E') index finger synchronously. When doing this people often report a feeling of 'numbness' (note that the illusion can be performed with eyes closed as well). (B) The intensity of the NI depends on synchrony, there is no illusion if another person does the stroking and numbness is rated strongest during synchronous self-stroking. A Likert scale was used ranging from 1 (complete disagreement) to 7 (complete agreement). Dark bars indicate the synchronous stroking conditions and light bars the asynchronous stroking conditions; error bars are SEM. The person carrying out the stroking is indicated (Self/Subject; Other/Experimenter). (C) In study 4, subjects rated the NI in the self-synchronous condition (as in studies 1 and 2; Figure 1A) and in two conditions using tight rubber bands to attach the joined fingers of the subject and the experimenter. In the *passive* condition (left), subjects held the palm of their left hand against the experimenter's opposite palm and the experimenter moved the subject's stroking fingers over the two joined index fingers to apply the touches. In the *active* condition (right), subjects moved the experimenter's stroking fingers to apply the touches (therefore not feeling any self-touch). If motor signals are critical to the NI the *active* condition should yield ratings comparable or higher than those in the self-synchronous condition, and the *passive* condition should diminish or abolish the sensation of numbness. On the other hand, if tactile cues are critical to the NI, the opposite should occur. Subject and Experimenter are indicated as in Figure 1A. (D) During this illusion, the amplitude of the N20 component of somatosensory evoked potentials (recorded at electrode C4 contralateral to the stimulated left median nerve) was found to depend on synchrony only during self-stroking. Grand average somatosensory evoked potential recordings at electrode C4 (see left upper inset for C4 scalp location – red dot) for the four experimental conditions are shown. The amplitude of the N20 component in the four experimental conditions is shown in the small inserted plot (same color-code as in the larger plot; values of the grand average are plotted; note that the polarity of the potentials is inverted in this plot for ease of comparison with Figure 1B; error bars are SEM). (E) Analysis of the N20 amplitude at C4 for each single rating epoch (plotted as standardized z scores) correlated significantly and negatively with the subjective ratings of numbness only during the self-synchronous condition.

a condition-dependent amplitude modulation 20 ms after stimulus onset (N20; Figure 1D). Only the N20 amplitude depended on synchrony, but only during self-stroking, being strongest during synchronous self-stroking ($F(1,8) = 86.94$; $p < 0.001$). Moreover, the N20 amplitude for single rating epochs correlated

negatively with NI intensity during synchronous self-stroking (Figure 1E; $r = -0.40$; $p < 0.001$), but not the other conditions (Supplemental data) showing that variations in repeated NI judgments are correlated with activity changes in S1 [6]. This suggests that the NI leads to an activity enhancement in S1, compatible with

data showing N20 enhancement following hand deafferentation [7,8].

In conclusion, our results show that double touch and early activity in S1 are crucial mechanisms underlying numbness and ownership for another person's finger, extending other methods based on tactile conflicts [9]. Our simple procedure may also be useful to understand peripheral and central mechanisms leading to numbness in neurology [10].

Supplemental Data

Supplemental data are available at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01917-4](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01917-4).

Acknowledgments

We thank Safa Mohanna, Amalia Londono and Par Halje for their assistance. The authors declare no competing financial interests.

References

- Gallagher, S. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends Cognit. Sci.* 4, 14–21.
- Boulware, J.T. (1951). Numbness, body-image, and the Japanese illusion. *Science* 114, 584–585.
- Arnold, H.L. (1952). Japanese Illusion. *Science* 115, 577.
- Tsakiris, M., Prabhu, G., and Haggard, P. (2006). Having a body versus moving your body: how agency structures body-ownership. *Conscious. Cogn.* 15, 423–432.
- Blakemore, S.J., Frith, C.D., and Wolpert, D.M. (1999). Spatio-temporal prediction modulates the perception of self-produced stimuli. *J. Cogn. Neurosci.* 11, 551–559.
- Allison, T., McCarthy, G., Wood, C.C., Darcey, T.D., Spencer, D.D., and Williamson, P.D. (1989). Human cortical potentials evoked by stimulation of the median nerve. I. Cytoarchitectonic areas generating short-latency activity. *J. Neurophysiol.* 62, 694–710.
- Tinazzi, M., Zanette, G., Polo, A., Volpato, D., Manganotti, P., Bonato, C., Testoni, R. and Fiaschi, A. (1997). Transient deafferentation in humans induces rapid modulation of primary sensory cortex not associated with subcortical changes: a somatosensory evoked potential study. *Neurosci. Lett.* 223, 21–24.
- Werhahn, K.J., Mortensen, J., Van Boven, R.W., Zeuner, K.E., and Cohen, L.G. (2002). Enhanced tactile spatial acuity and cortical processing during acute hand deafferentation. *Nat. Neurosci.* 5, 936–938.
- Ehrsson, H.H., Holmes, N.P., and Passingham, R.E. (2005). Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. *J. Neurosci.* 25, 10564–10573.
- Chaudhry, V. (2001). Numbness or tingling. In *The Primary Care Physician's Guide to Common Psychiatric and Neurologic Problems*, P. R. Slavney and O. Hurko, eds. (Baltimore: The John Hopkins University Press), pp. 156–170.

¹Laboratory of Cognitive Neuroscience, Ecole Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland. ²Wyle/NASA Johnson Space Center, Houston, TX, 77058, USA. ³Department of Neurology, University Hospital, Geneva, Switzerland. E-mail: olaf.blanke@epfl.ch