

Keeping the world a constant size: object constancy in human touch

Marisa Taylor-Clarke¹, Pamela Jacobsen² & Patrick Haggard¹

The perceived size of objects touching different regions of skin varies across the body surface by much less than is predicted from variations in tactile receptor density. Here we show that altering the visual experience of the body alters perceived tactile distances. We propose that the brain attempts to preserve tactile size constancy by rescaling the primary, distorted body-surface representation into object-centered space according to visual experience of the body.

In an illusion originally reported by Weber, two points that are moved over the body surface are felt to converge when they pass from a region of high acuity to low acuity, for example from lip to forehead¹. We quantified Weber's illusion by asking blindfolded subjects to judge which of two tactile distances felt greater (Fig. 1). Subjects perceived a given distance on the index finger as greater than the same distance on the forearm (77% of trials, $P < 0.001$), middle finger (63%, $P < 0.01$) or back (70%, $P < 0.001$). Subjects also perceived a given distance as greater on the face than on the back (80%, $P < 0.001$). By contrast, subjects perceived no difference between identical distances presented to skin regions with similar densities of receptors and cortical representations (index finger versus face, $P = 0.585$; left forearm versus right forearm, $P = 0.62$).

These results demonstrate a failure to maintain perceptual constancy and confirm Weber's original reports. The classical explanation of varying densities of tactile receptors across body parts has not been challenged. The explanation is unsatisfactory, however, because the illusion is much smaller than are the differences in receptor density or cortical extent, as measured by tactile acuity² and functional neuroimaging³. For example, variations of 340% in tactile acuity² produce only variations of 30% (ref. 4) in perception of tactile distance across the same body parts. Instead, we suggest that judging tactile distance requires a rescaling of neural signals, from a distorted, primary representation based on receptor density, to an object-centered space⁵. This rescaling requires a representation of the physical size of the stimulated body part. Weber's illusion reflects failure to completely rescale tactile information from skin regions with varying cortical extents according to their true size.

In experiment 2, we investigated this rescaling process by distorting the visual experience of the body and measuring the subsequent changes in tactile size estimation. We found that purely visual experience of the body influenced judgments about tactile distance without altering tactile acuity. Eight new subjects participated (age 20.8 ± 1.6 years (mean \pm s.d.); six females) in blindfolded pre-test, visual training and blindfolded post-test phases. At pre-test, we measured two-point discrimination thresholds and tactile distance perception on the index finger and the forearm⁶, as in experiment 1 (Fig. 1). As above, we found that there was a bias to judge a given distance as bigger on the index finger than on the forearm (81%, $P < 0.001$). During visual training, subjects viewed their hand as reduced and their forearm as increased for 1 h, and received no tactile stimulation during this period (Fig. 2). Visual stimuli were projected onto the distorted hand and arm simultaneously during viewing. In a visual analogue of tactile distance perception, subjects judged a distance between two dots projected on the enlarged arm to be smaller than the same distance projected on the shrunken hand in 75% of trials. The post-test repeated the pre-test measures.

At post-test, the bias in tactile distance perception was significantly reduced to 74% ($t_7 = 2.58$, $P = 0.018$; one-tailed t -test) (Fig. 3), corresponding to a modulation of 1.63 mm. Tests of intercept coefficients of logistic regressions fitted to the data of each subject confirmed modulation of the illusion ($t_7 = 2.38$, $P = 0.024$; one-tailed t -test). Changes in tactile acuity between pre-test and post-test were nonsignificant for both the finger ($P = 0.65$) and the forearm ($P = 0.59$) and were in the wrong direction for explaining the tactile distance results. Therefore, primary somatosensory representation was apparently unaffected by distorted vision and cannot account for altered tactile distance perception.

In a control experiment (experiment 3), we excluded the possibility that undistorted visual information might modulate tactile distance judgments. Four new subjects (age 20.3 ± 2.2 years; two females) repeated experiment 2, but with undistorted vision of hand and arm. The change in tactile distance perception from pre-test to post-test was now nonsignificant ($P = 0.85$) and was opposite in direction to that induced by distorted vision. These effects of distorted vision on tactile distance perception were replicated and extended in a fourth experiment (Supplementary Note online), in which subjects viewed an enlarged video-image of their hand for 5 min and did not make explicit visual size judgments (Supplementary Fig. 1 online).

The human sense of touch represents external objects through a highly distorted representation of the body surface⁷. These distortions

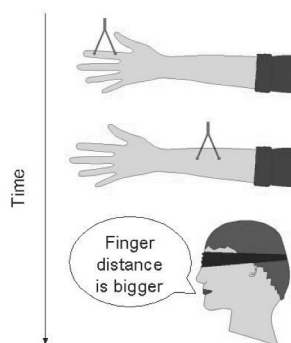


Figure 1 Tactile distance perception task. In experiment 1, 11 subjects (aged 20–56 years, five males) were touched successively on two body parts with two small spheres. Informed, written consent was obtained from all subjects in each experiment. Here, the finger and forearm condition is shown. Eight new subjects (aged 22–56 years, four males) were also tested on the left and right forearms. The distance between the two spheres was 45 mm (20 trials) or 55 mm (20 trials) in experimental trials. In 24 'catch' trials, the index finger distance differed from the forearm distance by ± 10 mm. Subjects judged whether the distance between the spheres felt bigger or smaller on the first or the second body part touched and received no feedback during the task.

¹Institute of Cognitive Neuroscience and Department of Psychology, University College London, 17 Queen Square, London WC1N 3AR, UK. ²Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, UK. Correspondence should be addressed to P.H. (p.haggard@ucl.ac.uk).

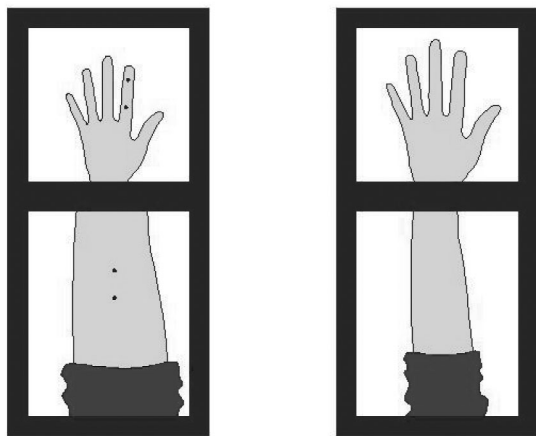


Figure 2 Distorted and undistorted views of the arm in experiments 2 and 3. Left, the image that subjects viewed in the visual training phase in experiment 2. Using a video camera coupled with magnifying and reducing mirrors, subjects viewed their hand reduced to half its size and their forearm increased to double its size on a screen for 1 h, while performing a visual analogue of the tactile distance perception task with no feedback. Right, the undistorted image that subjects viewed in experiment 3.

allow improved representation of crucial sensorimotor body parts such as fingers, but they raise the problem of maintaining perceptual constancy. We have shown that tactile inputs are rescaled according to the visually specified physical size of body parts to achieve tactile object constancy. The finger is small relative to the arm, but it has a larger representation in somatosensory cortex. To preserve size constancy, primary distorted cortical representations must be transformed into object-centered space by secondary rescaling processes. Weber's illusion arises because the gain of rescaling is lower than is veridically required. We have further shown that rescaling is adaptive and driven by visual experience of our own bodies. Other sensory modalities could also contribute to the rescaling process. But visual information about the size of body parts may be particularly important, because no proprioceptive receptor can signal this dimension directly.

Visual object constancy has been studied widely⁸, but the brain's computational mechanisms of tactile object constancy have been largely ignored. Early visual representations are hierarchically processed to recognize perceptual objects⁹. Rescaling for cortical overrepresentation of the fovea or for disproportions of the body-surface map is part of the interpretative process of transforming receptor-centered representations into object-centered representations. Visual constancies provide more examples in which magnitudes of an interpreted perceptual dimension can be dissociated from the underlying primary receptor information, akin to our tactile result. Thus, although relative disparity thresholds are a linear function of retinal angle, a given change in disparity is interpreted as a small change in depth at near distances and a large change at far distances. Changes in perceived magnitude that do not derive from changes in threshold imply a secondary, postreceptor scaling process.

We propose that rescaling may be particularly important for touch, because primary somatosensory cortical representation is highly plastic¹⁰, varying with tactile experience¹¹ and bodily changes¹². Secondary interpretative processes must adjust for these changes, if tactile input is to be useful for object-oriented actions. For example, altered afferent input after local anesthesia or cooling also causes large changes in the perceived size of body parts¹³. Secondary rescaling processes could reduce the effect of such variations on tactile object perception.

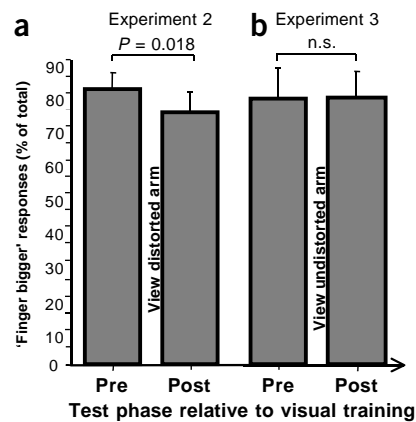


Figure 3 Viewing the body influences tactile distance perception. (a) Results of experiment 2. In the pre-test tactile distance perception task, subjects perceived the distance between tactile stimuli on the finger as greater than the same distance on the forearm in 81% of trials. In the post-test task, this bias was reduced to 74%. (b) Results of experiment 3. There was no reduction in the bias to perceive identical distances as greater on the finger than on the forearm.

The physiological mechanism underlying the present effect is unclear. Our results showing that unaltered acuity is coupled with altered size estimation imply an involvement of secondary, interpretative brain regions, rather than primary cortex. Parietal cortex contains bimodal neurons that respond to visual stimuli in the space around the tactile receptive field¹⁴. The visual receptive field typically moves when the hand moves¹⁴ and extends when the hand is effectively extended by tool use¹⁵. The effect of such changes on the tactile response is not known; however, those neurons receive the appropriate inputs and show the appropriate rapid plasticity to adjust tactile processing in the manner reported here.

Note: Supplementary information is available on the Nature Neuroscience website.

ACKNOWLEDGMENTS

Supported by the Engineering and Physical Sciences Research Council (M.T.C.), and a Leverhulme Trust research fellowship (P.H.). We thank J. Woodhouse, S. Kennett and D. Wolpert for advice and support.

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

Received 10 November 2003; accepted 27 January 2004

Published online at <http://www.nature.com/natureneuroscience/>

- Weber, E.H. *The Sense of Touch* (H.E. Ross & D.J. Murray, trans.) (Academic, London, UK, 1978).
- Weinstein, S. in *The Skin Senses* (ed Kenshalo, D.R.) 195–218 (Thomas, Springfield, IL, 1968).
- Kurth, R. *et al. NeuroReport* **11**, 1487–1491 (2000).
- Green, B.G. *Percept. Psychophys.* **31**, 315–323 (1982).
- Paillard, J., Michel, F. & Stelmach, G. *Arch. Neurol.* **40**, 548–451 (1983).
- Kennett, S., Taylor-Clarke, M. & Haggard, P. *Curr. Biol.* **11**, 1188–1191 (2001).
- Penfield, W. & Rasmussen, T. *The Cerebral Cortex of Man: a Clinical Study of Localization of Function* (Macmillan, Oxford, UK, 1950).
- Boring, E.G. *Am. J. Psychol.* **77**, 494–498 (1964).
- Marr, D. *Vision* (W.H. Freeman, San Francisco, CA, 1982).
- Calford, M.B. *Neuroscience* **111**, 709–738 (2002).
- Recanzone, G.H., Merzenich, M.M., Jenkins, W.M., Grajski, K.A. & Dinse, H.R. *J. Neurophysiol.* **67**, 1031–1056 (1992).
- Ramachandran, V.S. & Rogers-Ramachandran, D. *Arch. Neurol.* **57**, 317–320 (2000).
- Gandevia, S.C. & Phegan, C.M.L. *J. Physiol. (Lond.)* **514**, 609–616 (1999).
- Graziano, M.S.A. *Proc. Natl. Acad. Sci. USA* **96**, 10418–10421 (1999).
- Iriki, A., Tanaka, M. & Iwamura, Y. *NeuroReport* **7**, 2325–2330 (1996).