

Bodily Illusions Modulate Tactile Perception

Frédérique de Vignemont,^{1,3,*} Henrik H. Ehrsson,² and Patrick Haggard¹

¹Institute of Cognitive Neuroscience and Department of Psychology

²Wellcome Department of Cognitive Neurology and Functional Imaging Laboratory

University College London

17 Queen Square

London WC1N3 AR

United Kingdom

Summary

Touch differs from other exteroceptive senses in that the body itself forms part of the tactile percept. Interactions between proprioception and touch provide a powerful way to investigate the implicit body representation underlying touch. Here, we demonstrate that an intrinsic primary quality of a tactile object, for example its size, is directly affected by the perceived size of the body part touching it. We elicited proprioceptive illusions that the left index finger was either elongating or shrinking by vibrating the biceps or triceps tendon of the right arm while subjects grasped the tip of their left index finger. Subjects estimated the distance between two simultaneous tactile contacts on the left finger during tendon vibration. We found that tactile distances feel bigger when the touched body part feels elongated. Control tests showed that the modulation of touch was linked to the perceived index-finger size induced by tendon vibration. Vibrations that did not produce proprioceptive illusion had no effect on touch. Our results show that the perception of tactile objects is referenced to an implicit body representation and that proprioception contributes to this body representation. We also provide, for the first time, a quantitative, implicit measure of distortions of body size.

Results and Discussion

The sense of touch differs from other senses in that the body itself seems to form part of the content of tactile percepts. Katz (1925) suggested that touch always has both exteroceptive and interoceptive aspects. Proprioception and touch might thus be expected to interact because proprioception is clearly interoceptive and dedicated to representing the body. Moreover, the neural systems subserving proprioception and touch are closely linked [1–3]. However, the interoceptive aspect of touch has never been clearly quantified [4, 5]. Here, we demonstrate that proprioception can bias exteroceptive judgments about tactile stimuli. Previous attempts to study the relation between proprioception and touch

have focused on active touch [6, 7]. However, changes in tactile sensations during action could reflect either proprioception-touch or efferent-touch interactions, and so they cannot provide unambiguous evidence for a direct link between proprioception and touch. Other studies have shown that tactile stimuli are remapped into external space on the basis of proprioceptive inputs [8–10]. In these studies, it is the proprioceptively coded external spatial location of the stimulus, rather than the proprioceptive representation of the body per se, that influences tactile processing. We suggest here that proprioception also directly influences touch. Put another way, tactile perception of an external stimulus is mediated by the proprioceptive representation of the body part that is touched. To manipulate the proprioceptive representation of the body, we used a classical perceptual illusion [11]. In this illusion, the subject experiences an illusory elongation or shrinking of a body part. We used this illusion to investigate whether perceived changes in finger size would affect the tactile perception of an object in contact with the finger. We predicted that the subjects would feel the object to grow in size as the finger feels elongated.

Blindfolded subjects held the tip of their left index finger with their right index finger and thumb. At the same time, we vibrated (~90 Hz) the tendons of either the biceps or the triceps muscles of the right arm suspended by a hoist, which elicited a kinaesthetic illusion of passive extension or flexion of the right elbow, respectively (Figure 1). Because the subjects' hands were in direct contact, they felt the illusion that the left index finger was elongated when biceps vibration elicited illusory extension of the right arm. Likewise, the subjects felt that their left index finger shrank when we vibrated the triceps, causing illusory flexion of the right arm. In the control condition, subjects had their arms and hands in the same position as in the illusion conditions, but vibration was now applied to the skin beside the tendon. This provided tactile, postural, and acoustic inputs similar to those of the other two conditions, but no kinaesthetic illusion. As soon as subjects reported feeling the illusory elbow movement in the biceps and triceps conditions, we applied a test tactile stimulus to subjects' left index finger and a reference tactile stimulus to the forehead in a randomized order. Test and reference stimuli consisted of two simultaneous contacts from a line of four miniature solenoids. The active solenoids were selected at random on each trial so that subjects experienced tactile distances of 15, 30, or 45 mm on the finger and the forehead. In half of the trials, the tactile distance on the index finger differed from the forehead distance by ±15 mm, whereas in the other half, there was no difference. We asked the subjects to judge which of the two tactile distances felt greater (finger or forehead). Vibration was maintained continuously until the subject had completed a block of 20 tactile judgments. Each condition was composed of 20 test + reference sets of tactile stimuli and was repeated twice according to a counterbalanced order. The duration of the vibration depended on the subject's re-

*Correspondence: fvignemont@isc.cnrs.fr

³Present address: Institut de Sciences Cognitives, 67 boulevard Pinel, 69675 Bron cedex, France.

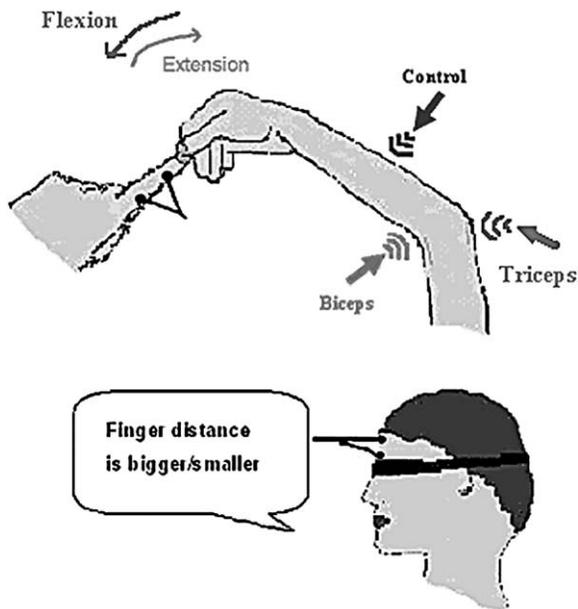


Figure 1. Experimental Setup

Blindfolded subjects held their left index finger with their right arm. Vibration was applied to the right arm on either the biceps tendon, the triceps tendon, or a nearby control location that did not stimulate the tendon. The biceps vibration induced a subjective extension of the right arm and, consequently, a subjective elongation of the left index finger. The triceps vibration induced a subjective flexion of the right arm and, consequently, a subjective shrinking of the left index. The control vibration did not induce any illusion. While being vibrated, subjects were touched successively on the left index finger and on the forehead with two pairs of miniature solenoids. Subjects judged whether the distance between the solenoids felt bigger or smaller on the index finger or the forehead. They received no feedback during the task.

response time, but it usually lasted ~ 120 s. After each period of vibration, the subjects pointed with their right hand toward one of a range of pictures of the index finger, indicating the one corresponding to the perceived size of their own finger. Each picture showed a prototypical whole hand with the index finger selectively elongated or shrunk. The index-finger size varied across pictures; it was 2/7, 3/7, 4/7, 5/7, 6/7, 1, 8/7, 9/7, or 10/7 of the width of the pictured hand. (We did not show pictures corresponding to the real sizes of subjects' hands because of the large visual-array size required.)

We included only the subjects who experienced proprioceptive illusion by vibration of the right-arm elbow tendons ($n = 10$). For a further 20 subjects, no clear illusion of elbow extension could be elicited, and testing was discontinued. However, all ten subjects who felt their arm moving also felt their finger changing size. Subjects first performed the tactile judgment task in a pretest baseline condition. They then performed the same task during each of three different vibration conditions (biceps, triceps, and control) repeated twice. Finally, they repeated the task with no vibration as a posttest.

Because the direction of the illusion in each condition

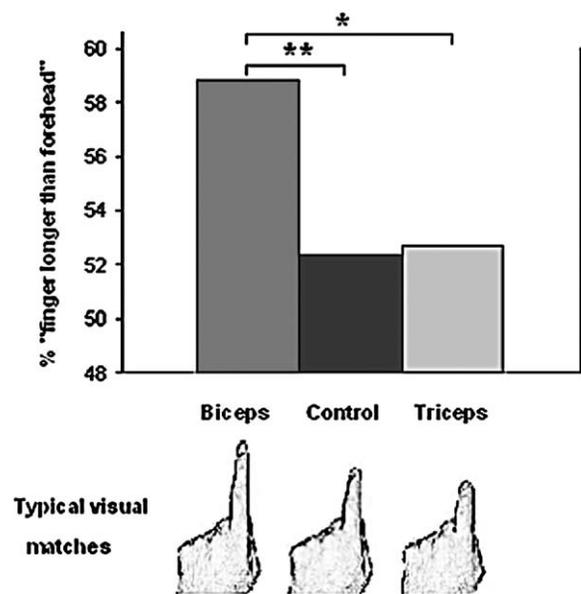


Figure 2. Results

Probability that the stimulus separation on the finger felt greater than on the forehead (the actual lengths were on average equal on the two body parts). Subjects were more likely to rate the finger stimulus as larger than the forehead stimulus during biceps vibration than either control or triceps vibration. Tactile distance judgments during triceps vibration did not differ from control. The abscissa displays finger drawings closest to the mean choice; these drawings were used to describe their subjective feeling of finger distortion.

was predicted in advance, we used one-tailed statistical tests throughout. First, we quantified the phenomenology of the kinaesthetic illusion with visual templates. Subjects selected significantly smaller visual matches to their index finger after triceps vibration than control (ratio of 0.53 versus 0.74 of the width of the viewed hand, $t_9 = 3.713$, $p = 0.005$) and significantly larger matches after biceps tendon vibration than control (ratio of 1.07 versus 0.74 of the width of the viewed hand, $t_9 = 7.282$, $p \leq 0.001$). This demonstrated that the kinaesthetic elbow-movement illusions induced by tendon vibration caused a change in perceived finger length, as expected. The illusion had a rapid onset and was persistent: On debriefing, subjects reported that the bodily illusions caused by the tendon vibration began shortly after vibration onset and lasted throughout the block (~ 120 s).

We investigated the effects of the illusion on exteroceptive touch by calculating the probability that the distance between dual tactile stimuli on the finger felt greater than on the forehead. Subjects more frequently rated the finger stimulus as larger than the forehead stimulus during biceps vibration (59%) than during control (52%) or triceps vibration (53%; $t_9 = 3.39$ and 1.89, respectively, both $p < 0.05$). Tactile distance judgments during triceps vibration did not differ from control (Figure 2 and Table 1). Finally, we confirmed that the tactile judgment bias was an online effect of the bodily illusion by measuring tactile distance perception in pretest and posttest blocks before and after the vibration condi-

Table 1. Percentage of ‘Finger Distance Longer than Forehead Distance’ Judgments in Each Condition

	Pretest	Biceps Tendon Vibration	Triceps Tendon Vibration	Control Vibration Not Affecting Tendons	Posttest
Mean	52.25	58.5	51.25	51.75	53
Standard deviation across subjects	8.2	7.28	10.75	7.17	6.43

tions. Pretest and posttest scores did not differ significantly from each other, nor from the control condition of vibrating just away from the tendon without eliciting bodily illusion (all $p > 0.4$). Thus, the key finding was that a tactile distance feels bigger when the stimulated body part feels temporarily elongated because of altered proprioceptive input at another body part.

Perceived distortions in the size and shape of body parts have been reported after various pathological conditions [12], during local anesthesia of a limb [13, 14], or after various experimental manipulations, such as tendon vibration, in healthy subjects [11, 15–17]. However, most of these studies assessed the illusion only by explicit, direct measures, such as verbal or graphic report. They have not addressed the effects of somatic illusions on other sensory modalities or on perception of external stimuli.

In contrast, our study provides the first body-size illusion measures that are both quantitative and implicit. It shows that *internal*, proprioceptive perception of the body can directly influence the perception of an *external* tactile object. We propose that perception of tactile objects is referenced to body representation, which derives at least partly from perception. Changes in proprioceptive signals about the posture of one body part can imply a change in the size of a second body part if the two are in contact. In our study, vibration inducing illusion of elbow extension produced illusory elongation of the finger. We show that this change in perceived finger length in turn affected tactile object perception at that body surface. The body surface can be described as a tactile field. We suggest that this field accommodates the perceived size of the body part. Exteroceptive judgments of tactile distance are made with respect to this body-referenced tactile field. In vision, stretching the retina reduces spatial resolution in the visual field, increasing the size of the retinal image and making visual objects appear larger [18]. Similarly, inducing “stretching” of the tactile field at the level of the central neural representations makes objects feel bigger. Thus, one cannot modify the representation of bodily surface without also modifying exteroceptive tactile perception. Our results thus demonstrate that body-part size is represented coherently with proprioception and that the body surface is represented coherently with body-part size. This coherence implies a well-formed, integrated, implicit model of the body, or body schema, in the brain. We show that this schema underlies and mediates tactile perception, even though our phenomenal experience of touch is dominated by the exteroceptive component [4].

A recent study showed that perception of the distance between two tactile stimuli was influenced by distorted *visual* experience of body parts [19]. In that

study, however, vision of the body and tactile perception occurred in separate phases of the experiment. There, offline visual experience of the body provided an external scale that recalibrated subsequent tactile distance judgment. However, in that study, it is unclear whether the distorted visual feedback actually induced a change in the perceived size of the hand. Furthermore, it is unclear whether this external scale could also be provided by visual experience of other objects, instead of the body. Thus, the external visual recalibration of touch might reflect a general process of cross-modal scaling rather than a specific link to a dynamic body schema [20]. In contrast, the present study shows that judgments about tactile objects are processed with reference to an *instantaneous* representation of one’s own body.

The link between proprioception and touch was asymmetric in relation to the direction of the finger-length changes. Illusory shrinkage of the finger had no effect on tactile judgments. Why did the tactile distance not feel smaller when the finger was felt to be shrinking? This finding suggests an anisotropy of the body surface: The tactile body surface would be capable of expanding but not shrinking. Ontogenetic development tends in the direction of growing and cannot normally be reversed. When people actually lose a whole body part, they may keep on feeling their phantom limb [16]. Furthermore, when a body part is anaesthetized and receives no afferent input, it feels bigger [13]. Although the neuroscience literature emphasizes the plasticity of the body schema, it mainly describes cases of bodily extension, notably through tools, and body part addition [20–22]. Yet, in some psychiatric pathologies, patients can suffer from delusions of excessive body size (macrosomatognosia) and delusions of reduced body size (microsomatognosia) [23]. Interestingly, some studies suggest that microsomatognosia is less frequent than macrosomatognosia and usually applies to the whole body rather than to single body parts [24–26]. The effects of somatic illusions on the perceived size of body parts may differ from delusions of the size of the body as a whole [27]. In addition to an online body schema, the brain may contain a long-term body image that specifies the shape and the size of the limbs and that can slowly evolve through development until the body reaches its adult size [28, 29]. We speculate that judgments of tactile distance may be mediated by a weighted combination of at least two body representations: an online body schema (as in the present experiment) and a long-term body image. Confronted with an implausible body experience of a shrinking finger, the interpretation of tactile distance may switch from an online body schema to a long-term body image.

What neuronal mechanisms could underlie the pre-

sent rescaling of the tactile body surface? Tactile and proprioceptive signals are processed in separate areas of the primary somatosensory cortex, with tactile signals dominating in areas 3b and 1 and proprioceptive inputs in area 3a [30–34]. Moreover, macrogeometric properties such as the shape and the size of external objects are computed in higher-order somatosensory areas [35] rather than in the primary somatosensory cortex. In contrast, interactions between touch and proprioception may be mediated by higher-order somatosensory areas in the posterior parietal cortex. For example, tactile and proprioceptive signals converge in area 5 and in the intraparietal cortex [36, 37]. Thus, we speculate that the modulation of the perceived tactile distance in the present experiment may arise in higher-order somatosensory areas in the posterior parietal cortex.

In summary, we show that the experience of body-size distortion affects tactile object perception. This demonstrates a close connection between tactile perception of the external world and the sense of one's own body. It also demonstrates a remarkable coherence and plasticity of the body schema. An illusory finger elongation that altered input to the biceps tendon has the direct result of illusory elbow extension. It also transfers indirectly to an illusion of finger length, and beyond that, it biases macrogeometric exteroceptive touch. These results are consistent with online integrative neural processes acting to maintain a coherent body representation. They also show how such body representations are used to calibrate perception of the external world. Interestingly, these processes are anisotropic, in that they preserve overall bodily coherence when a body part extends, but not when it contracts. Our study also provides the first implicit quantitative measure of the effects of bodily illusions induced by tendon vibration.

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