Correspondence

Contraction of body representation induced by proprioceptive conflict

Matthew R. Longo[1,*], Marjolein P.M. Kammers[1,2,*], Hiroaki Gomi[3], Manos Tsakiris[4], and Patrick Haggard[1]

Our body is not only an extended object in external space, but also the basis of our sense of self. Proprioceptive signals from muscle spindle organs, specifying body position, play a key role in this unique dual quality of body representation, as they define a ‘here’ or set of locations, where ‘I’ am located [1]. Position information from muscle spindles can be manipulated by vibrating the muscle tendon, generating illusions of position and movement [2]. For example, biceps vibration generates illusions of elbow extension, while triceps vibration generates illusions of flexion. Here we report that proprioceptive *conflict* induced by simultaneous vibration of antagonistic biceps and triceps muscle tendons alters representation of the body in a way qualitatively different from single vibrations. Rather than relocation or movement, this incoherent conflict of location produces perceived telescoping of the arm towards the elbow. Loss of coherent information about body position in space seems to produce *contraction* of the body representation itself. Our result suggests that basic sensory signals about body posture also play an essential role in representing the self as an extended object in space.

In Experiment 1, we applied 100 Hz vibration to participants’ immobilised right forearm. In the ‘biceps alone’ condition, one vibrator stimulated the biceps tendon, proximal to the elbow. In the ‘dual tendon’ condition, identical vibration was applied to both biceps and triceps tendons simultaneously. In the ‘dual off tendon’ condition, vibrators were placed on the dorsal and volar forearm, distal to the elbow.

During vibration, participants made two types of judgment about the stimulated right arm. To ensure that tendon vibration induced proprioceptive illusions, we asked participants to match the position of their vibrated right arm with their left [2]. To investigate changes in perceived body extension in space, we asked participants to point with their left index finger to either their right index finger, or an elastic ring around the right forearm. A vertical Plexiglas surface prevented the arms touching (Figure 1).

When participants matched elbow angles, biceps vibration alone produced expected illusions of elbow extension: the right arm was perceived as lower than it was (Figure 1). Crucially, we also found no matching bias in the dual tendon condition, consistent with previous findings showing no net illusion of movement following vibration of antagonistic muscle tendons [3]. Simultaneous vibration of antagonistic muscle tendons produced equal and opposite effects, which were not interpreted as overall proprioception biases in joint angle.

Simultaneous vibration of both muscle tendons did, however, produce significant biases in *pointing* to body locations (Figure 1), with responses becoming more proximal. This telescoping effect was found both for pointing to the right fingertip, and to the elastic ring

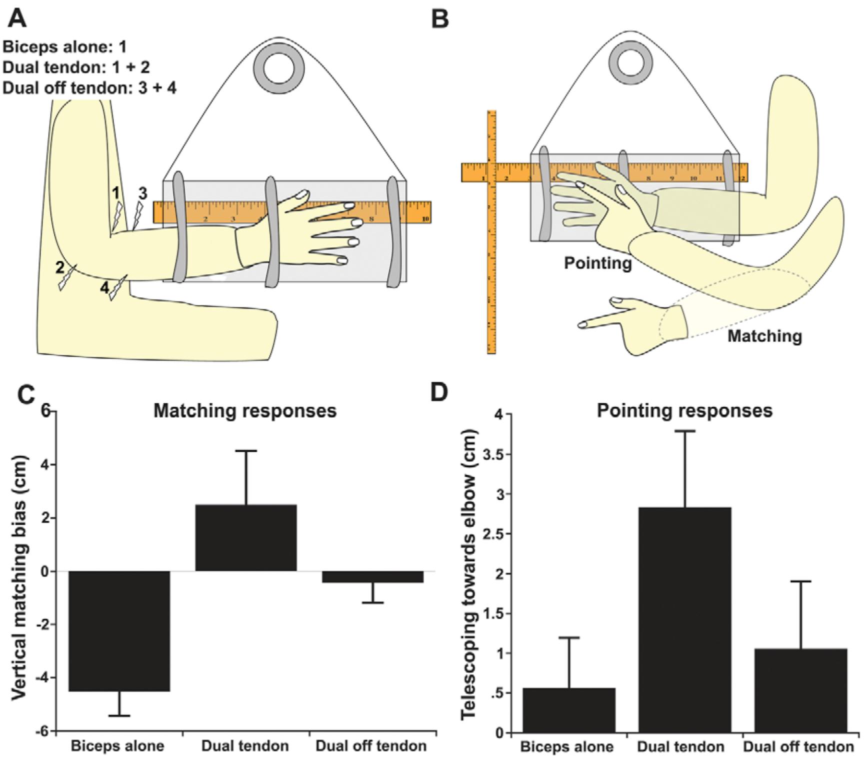

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Figure 1. Experimental setup and results.

(A) Experimental setup: Participants sat with their right forearm supported in a sling, pressed against a Plexiglas surface. (B) Dependent measures: For matching responses, participants used left arm to mirror the perceived position of their stimulated right arm. For pointing responses, participants pointed with their left index finger along the Plexiglas to the perceived location of (1) the tip of their right index finger, and (2) the location of an elastic ring around their right forearm. (C) Results from matching responses: A significant downward bias was found in the biceps only condition, $t(7) = -4.94$, $p < 0.005$, but not in the dual tendon or dual off tendon conditions, $t(7) = 1.24, -0.58$, respectively. This bias in the biceps only condition was significantly larger than in either of the other conditions, $t(7) = 2.99, 4.50$, respectively, both $p < 0.05$. (D) Results from pointing responses: Significant telescoping was observed in the dual tendon condition compared to the biceps only and dual off tendon conditions for pointing responses both to the fingertip, $t(7) = 4.50, 3.60$, p’s < 0.01, and the forearm (elastic band), $t(7) = 3.24, 10.51$, p’s < 0.01 (averaged in this figure).

on the right forearm. Importantly, pointing errors were consistently directed *towards* the elbow, and therefore cannot be explained by fluctuating proprioceptive sensations of rotation in either direction *around* the elbow, or by uncertainty over elbow angle itself. Further, we found no change in proprioceptive bias across the six trials of each block (see Supplemental data available on-line), suggesting that the illusion was a rapid result of absent position information, rather than a progressive proprioceptive drift over time.

Experiment 2 replicated the overall telescoping effect using a purely passive perceptual judgment task. The participant's left finger was passively moved along the Plexiglas until the participant reported it matched the target position. Direction of passive movement was counterbalanced. In the dual tendon condition clear telescoping was observed for the fingertip. Matching the forearm band produced shifts in the same direction, though non-significant (see Supplemental data). An additional no vibration condition produced results similar to dual off-tendon vibration (Figure 1), showing that the presence of vibration itself cannot account for the found results.

Experiment 3 investigated whether the telescoping effect could reflect perceived shoulder rotation backwards. We measured shoulder versus elbow angles with protractors while participants matched right arm posture with the left arm. There were no differences in matched joint angle across conditions. Thus, the telescoping effects of experiments 1 and 2 do not reflect perceived *movement* of the whole arm; rather, conflicting proprioceptive information about elbow angle led to perceived *shrinkage*, or telescoping, of the hand and forearm distal to the vibration

Previous reports demonstrated rapid readjustment of body representation following novel proprioceptive input [4,5]. In contrast, the present *conflicts* in proprioceptive information cannot be resolved by simple readjustment of any somatosensory signal or body representation. Instead, conflicts produced a contraction of the represented body, as if the limb itself were attenuated or entirely deleted from the body representation. Our result is consistent with several neurological findings. Whereas amputees with phantom limbs often perceive telescoping of the arm into the stump [6], paraplegics, whose limbs are physically intact but deafferented, do not report similar effects [7]. Telescoping may therefore reflect conflict between pre-established body image and visual information. This conflict occurs following amputation, but not paraplegia, because paraplegics' vision of their intact limb matches their premorbid body image. Furthermore, acute deafferentation also changes perceived size of body parts in healthy volunteers [8]. We suggest that the present results are mediated by posterior parietal areas known to mediate telescoping [5,6] and to be sensitive to perceptual conflict [9].

We previously suggested that perceived body-part location was distinct from other aspects of bodily self-consciousness [10]. These results suggest that sense of body-part location may be a functional prerequisite to other aspects of embodiment. Previous studies noted dramatic somatosensory plasticity with augmented and/or task-relevant sensory inputs. Other studies showed that the level of afferent input influences higher-order cognitive body representations such as body part size [8]. Our results suggest that it is not only the level of afferent signals, but also their overall spatial coherence, that influences body representation. Specifically, the perceived size of a limb shrinks rapidly when there are conflicting proprioceptive signals about limb position compared to every other condition. Sustained coherent afferent input about body part location appears to be essential for maintaining a cognitive representation of the body as an extended spatial object, suggesting that 'I' indeed depends on 'here' [1].

Supplemental Data

Supplemental data are available at http://www.cell.com/current-biology/supplemental/S0960-9822(09)01409-2

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[1]Institute of Cognitive Neuroscience, University College London, UK. [2]Helmholtz Research Institute, Utrecht University, The Netherlands. [3]NTT Communication Science Laboratories, Nippon Telegraph and Telephone Co., Kanagawa, Japan. [4]Department of Psychology, Royal Holloway, University of London, UK.
*The first two authors contributed equally to this research.
E-mail: p.haggard@ucl.ac.uk