Report

Phantom Tactile Sensations Modulated by Body Position

Jared Medina[1],* and Brenda Rapp[2],*
[1]Department of Neurology and Center for Cognitive
  Neuroscience
University of Pennsylvania
Philadelphia, PA 19104
USA
[2]Department of Cognitive Science
Johns Hopkins University
Baltimore, MD 21218
USA

Summary

Bilateral activation of somatosensory areas after unilateral stimulation [1–6] is assumed to be mediated by crosshemispheric connections [7–11]. Despite evidence of bilateral activity in response to unilateral stimulation, neurologically intact humans do not experience bilateral percepts when stimulated on one side of the body. This may be due to active suppression of ipsilateral neural activity [12, 13] by inhibitory mechanisms whose functioning is poorly understood. We describe an individual with left fronto-parietal damage who experiences bilateral sensations in response to unilateral tactile stimulation—a rarely reported condition known as synchiria (previously described in visual [14], auditory [15], and somatosensory modalities [16–19]). Presumably, the phantom sensations result from normal bilateral crosshemispheric activation, combined with a failure of inhibitory mechanisms to prevent bilateral perceptual experiences. Disruption of these mechanisms provides a valuable opportunity to examine their internal functioning. We find that the synchiria rate is affected by hand position relative to multiple reference frames. Specifically, synchiria decreases as the hands move from right (contralesional) to left (ipsilesional) space in trunk- and head-centered reference frames and disappears when the hands are crossed. These findings provide novel evidence that mechanisms that inhibit bilateral percepts operate in multiple reference frames [20–27].

Results

Case Report

DLE was a 71-year-old left-handed male engineer who suffered a left middle cerebral artery infarct 3 years before this investigation. The CVA resulted in written and spoken language production deficits and right hemiparesis affecting both upper and lower limbs. MRI revealed damage to the entire inferior frontal gyrus, insula, and much of the precentral gyrus, sparing the superior frontal gyrus, a significant portion of the middle frontal gyrus, and the medial surface of the frontal lobe. In the parietal lobe, there was severe damage to the postcentral gyrus, the supramarginal gyrus, and the anterior portion of the angular gyrus, sparing the superior region of the postcentral gyrus, the medial surface of the parietal lobe, the superior parietal lobule, and the posterior angular gyrus. The occipital lobe was spared, and damage to the temporal lobe was restricted to the posterior/superior portions of the superior temporal gyrus. There was left thalamic damage, principally affecting the lateral, anterior portion (see Figure S1 available online for MRI images).

Basic Evaluation: Mislocalization, Synchiria, and Extinction

In two evaluation tasks, stimulation was always a light touch with a flat, rubber cylinder (5 mm diameter). In task 1, stimulation was presented to the dorsal surface of the distal segment of the middle finger; in task 2, designed to gather more detailed localization information, stimulation was presented to 1 of 22 locations covering the dorsal hand surface (see Supplemental Data). Trials were unilateral (left- or right-hand stimulation only) or bilateral; task 1 additionally included "no-stimulation" trials. Stimuli were presented to DLE (eyes closed) with hands flat on the table on either side of his body midline, and he reported stimulation location (eyes open). In task 1, he indicated whether stimulation had occurred on the right hand, left hand, both hands, or neither; in task 2, he indicated the specific location of stimulation (see Supplemental Data for additional methodological details).

Three significant abnormalities were identified. First, on unilateral-right hand trials, although DLE was highly accurate in detecting the presence of right-hand stimulation (98%, 131/134), he was highly inaccurate in his perception of its location, producing a mean displacement of localization judgments of 34.8 mm along the y axis (running distal-proximal through the stimulation point) and 29.7 mm along the x axis (perpendicular to the y axis through the stimulation point). In fact, virtually all right-hand stimuli were perceived as originating on the third and fourth fingers (see Figure S2C). This contrasted with relatively accurate localization of left-hand (ipsilesional) stimulation (mean displacement of 9.8 mm along the y axis and 1.5 mm along the x axis). Second, on unilateral-left-hand trials, always reported stimulation to the left hand (134/134), but he also reported synchiric, phantom sensations on the right hand for a total of 50% of synchiric trials (67/134). Synchiria was also reported subsequent to unilateral-left-side stimulation of other skin surfaces: (forearm, 77%; biceps, 66%; chest under breastbone, 50%; cheek, 69%; thigh, 76%; ankle, 60%). No synchiria was reported in visual or auditory modalities. Third, on bilateral stimulation trials, although left-hand stimulation was reported with 100% accuracy (178/178), right-hand stimulation was not reported on 28% of trials (49/178). The failure to perceive the contralesional stimulus under bilateral stimulation conditions is referred to as "extinction." It is worth noting that extinction rates are likely to have been underestimated because at least some apparently "correct" responses on bilateral trials may have been based on "illusory" right-hand sensations. Experiments 1–3 will support and expand upon this interpretation.

The mislocalization and extinction of stimulation to the right hand are consistent with damage to basic mechanisms of somatosensory representation and/or attention. The synchiric

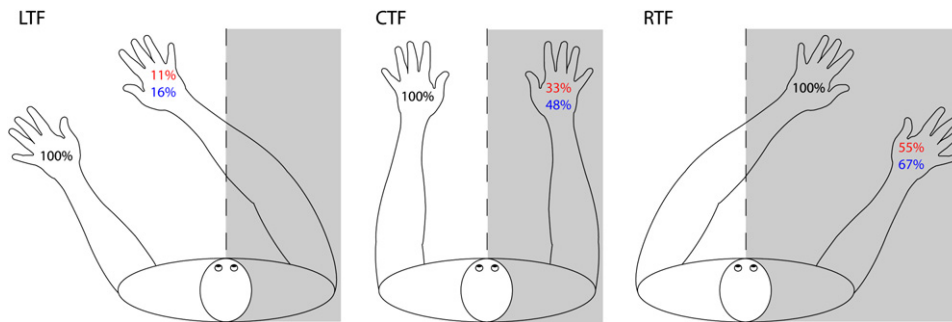*Correspondence: jared.medina@uphs.upenn.edu (J.M.), brapp1@jhu.edu (B.R.)

Figure 1. Results from Unilateral-Left and Bilateral Stimulation Trials in Experiment 1

Percent of correct responses for the left hand on unilateral-left trials (black), percent of synchiric responses on the right hand on unilateral-left trials (red), and percent of correct responses on bilateral stimulation trials (blue). Gray shading indicates contralesional space relative to the trunk midline. In the center-trunk-field condition (CTF), the left hand was positioned to the left of the trunk midline, the right hand was positioned at the symmetrical location on the right of the trunk midline, and the middle finger of each hand was positioned ∼20 cm from the trunk midline. In the left-trunk-field condition (LTF), both hands were positioned ∼30 cm left of their position in CTF condition, such that both hands were to the left of the trunk midline. In the right-trunk-field condition (RTF), hands were positioned ∼30 cm to the right of their position in CTF condition, such that both hands were to the right of the trunk midline. The head was always aligned with the trunk midline. Stimulation: 14 blocks in LTF and RTF, 10 blocks in CTF.

phenomena suggest disruption to inhibitory mechanisms concerned with at least some aspects of interhemispheric activation. We examined the frame(s) of reference within which these inhibitory mechanisms operate by evaluating whether the rate of synchiric experiences was modulated by the position of the hands relative to the trunk midline (experiment 1), head midline (experiment 2), and the position of the right hand relative to the left hand (experiment 3). Stimulation and testing conditions were as described above for task 1, where stimulation was limited to the dorsal segment of the middle finger.

Experiment 1: Trunk-Midline Reference Frame
Stimuli were presented with hands in three positions relative to the trunk midline (see Figure 1). For unilateral-right and no-stimulation trials, results are combined over all three trunk-field conditions because there were no significant differences between them, yielding the following accuracy levels: unilateral-right, 89% (338/380) and no-stimulation trials, 92% (199/216). In contrast, on unilateral-left stimulation trials, synchiric errors decreased as DLE's hands moved from right to left with respect to the trunk midline (see Figure 1). Specifically, DLE experienced synchiric phantoms on 55% (77/140) of trials when his hands were positioned to the right of the trunk midline (RTF) and on only 11% (15/140) of trials when his hands were positioned to the left of the trunk midline (LTF) (LTF versus center-trunk field [CTF], $\chi^2 = 18.1$, p < 0.001; LTF versus RTF, $\chi^2 = 62.2$, p < 0.001; CTF versus RTF, $\chi^2 = 11.4$, p < 0.001).

With regard to bilateral stimulation trials, if, as suggested above, left-hand stimulation often produces a synchiric rather than a veridical percept on the right side, then, as conditions favoring the generation of synchiric percepts change, accuracy on bilateral stimulation trials should also change. Specifically, as synchiria decreases, apparent accuracy on bilateral stimulation trials should also decrease. This prediction was confirmed (Figure 1) because DLE's apparent accuracy on bilateral trials with hands in the left-trunk field (where synchiria was at its lowest rate) was only 16% (22/140) compared to 67% (94/140) with hands in the right-trunk field (where synchiria was at its highest rate) (LTF versus CTF, $\chi^2 = 29.4$, p < 0.001; LTF versus RTF, $\chi^2 = 75.6$, p < 0.001; CTF versus RTF, $\chi^2 = 8.85$, p = 0.003). This provides clear confirmation of the hypothesis that right-sided percepts on bilateral stimulation trials were often synchiric phantoms.

The coupling of head and trunk midlines in this experiment makes it impossible to determine whether the relevant reference frame was based on the trunk or head midline or both. Additional data from experiment 2 were used to resolve this question.

Experiment 2: Head Midline Frame of Reference
Stimuli were presented with hands in three positions relative to the head midline (see Figure 2). Again, for unilateral-right and no-stimulation trials, results were combined over all three trunk-field conditions because there were no significant differences between them, yielding the following accuracy levels: unilateral-right, 96% (153/160) and no-stimulation trials, 95% (91/96). On unilateral-left trials, the rate of synchiric errors was determined by the position of the hands relative to the head midline. Figure 2 indicates that DLE reported fewer synchiric percepts on trials in which his hands were to the left of his head midline (LHF, 8% [5/60]) compared to trials on which hands straddled the head midline (CHF, 28% [11/40], $\chi^2 = 6.56$, p = 0.01) or when they were positioned in right-head field (RHF, 38% [23/60], $\chi^2 = 15.1$, p < 0.001). These results provide clear evidence of the involvement of a head-based reference frame.

If we consider data from both experiments 1 and 2, we can uncouple head and trunk midlines to determine whether, in addition to a head-based frame of reference, there was also involvement of a trunk-based reference frame. To do so, we compared accuracy between RHF trials in experiment 2 (with hands in center-trunk space and right-head space) and the RTF trials from experiment 1 (with hands in right-trunk space and right-head space) (see Figures 1 and 2). In these two conditions, hand position relative to head is constant (hands to the right of head), and hand position relative to the trunk midline changes (hands at the center or to the right of the trunk midline). If position of the hands relative to the trunk midline is relevant, there should be significantly more synchiric errors in the right-trunk-field condition compared to the right-head-field condition. Consistent with this prediction, DLE made significantly more synchiric errors in the right-trunk field (55%) versus right-head field (38%) condition (RTF versus RHF, $\chi^2 = 4.67$, p < 0.031). The combined results of experiments 1 and 2, therefore, reveal the influence of both head- and trunk-centered reference frames on synchiric perception.
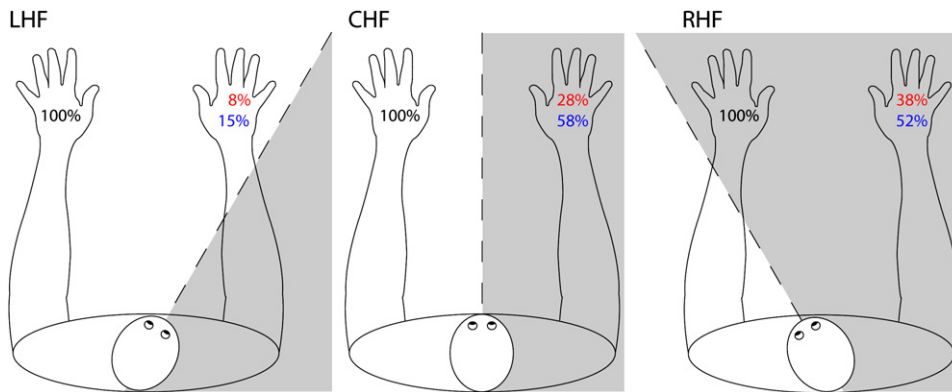
Figure 2. Results from Unilateral-Left and Bilateral Stimulation Trials in Experiment 2

Percent of correct responses for the left hand on unilateral-left trials (black), percent of synchiric responses on the right hand on unilateral-left trials (red), and percent of correct responses (including right-hand responses) on bilateral stimulation trials (blue). Gray shading indicates contralesional space relative to the head midline. DLE's hands and trunk remained in the same position with trunk facing forward and hands ~20 cm to the right or left of the trunk midline. In the left-head field condition (LHF), the head was turned ~30° to the right of the trunk midline such that both hands were on the left side of the head midline. In the right-head field condition (RHF), the head was turned ~30° to the left of the trunk midline such that both hands were positioned to the right of the head midline. Stimulation: four blocks in the CHF, six blocks each in LHF and RHF.

On bilateral trials, we observed the same pattern as was reported in experiment 1 (Figure 2) with lower "accuracy" under conditions of low synchiria, such that accuracy was lower when hands were placed to the left relative to the head midline (15% accuracy [9/60]) than when they were straddling the head midline (58% accuracy [23/40]) or placed to the right of the head midline (52% accuracy [31/60]) (LHF versus CHF, χ^2 = 19.9, p < 0.001 and LHF versus RHF, χ^2 = 18.2, p < 0.001). Furthermore, with regard to the question of the role of both head- and trunk-based reference frames, we found that, on bilateral trials, DLE was significantly more accurate under RHF versus RTF conditions when hands were always to the right of the head midline but varied with respect to trunk midline (RTF versus RHF, χ^2 = 4.29, p < 0.038).

Experiment 3: Limb-Relative Frame of Reference
Previous work has reported that tactile extinction rates may be modulated by crossing of the hands [22, 23, 28]—a manipulation that always positions the right hand to the left of the left hand in a limb-relative reference frame. Given that results from experiments 1 and 2 indicate the sensitivity of DLE's synchiric percepts to right-left hand positioning, we examined the possible modulation of the synchiric effect by relative hand position by using the same trunk-field conditions as in experiment 1, except that DLE's hands were crossed in all conditions. Furthermore, to determine whether hand crossing per se affected synchiric perception or whether effects were restricted to the crossed limbs, we included blocks of hand-crossed trials in which the upper (uncrossed) arms were stimulated.

As indicated in Figure 3, when DLE's arms were crossed and stimulation was delivered to the finger, DLE demonstrated no synchiria, being 100% (140/140) accurate on every unilateral-left trial, regardless of the position of the crossed hands relative to the trunk midline. With regard to the upper-arm stimulation, DLE reported synchiric phantoms on his right
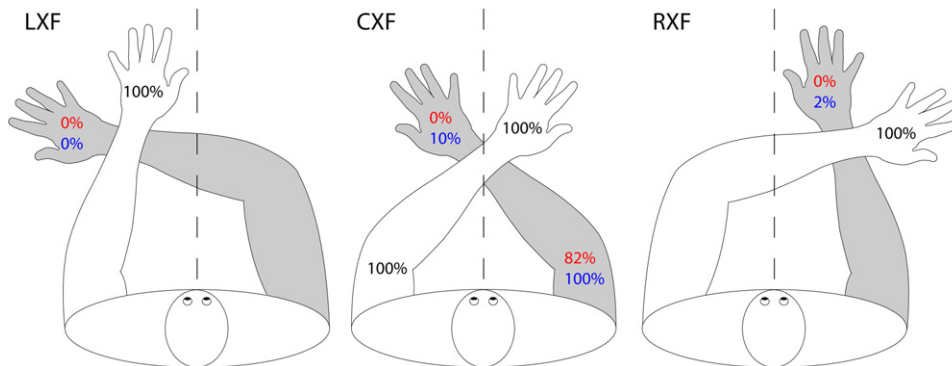

Figure 3. Results from Unilateral-Left and Bilateral Stimulation Trials in Experiment 3

Percent of correct responses for the left hand on unilateral-left trials (black), percent of synchiric responses on the right hand on unilateral-left trials (red), and percent of correct responses (including right-hand stimulation) on bilateral stimulation trials (blue). Gray shading indicates the contralesional arm. Hands were crossed ~8 cm above the wrist joint and placed on the table, with trunk and head aligned with one another in the forward-facing position. In the crossed-center body field modulation (CXF), crossed hands straddled the body midline. In the crossed-left (LXF) and crossed-right (RXF) body field conditions, both hands were crossed, and the midpoint between hands was 30 cm to the left or right of the body midline. Stimulation: five blocks of trials each in LXF and RXF, eight blocks in CXF. In CXF: four blocks with stimulation to the dorsal surface of the distal segment of the middle finger(s), four blocks with stimulation to the dorsal surface of the uncrossed upper forearms.
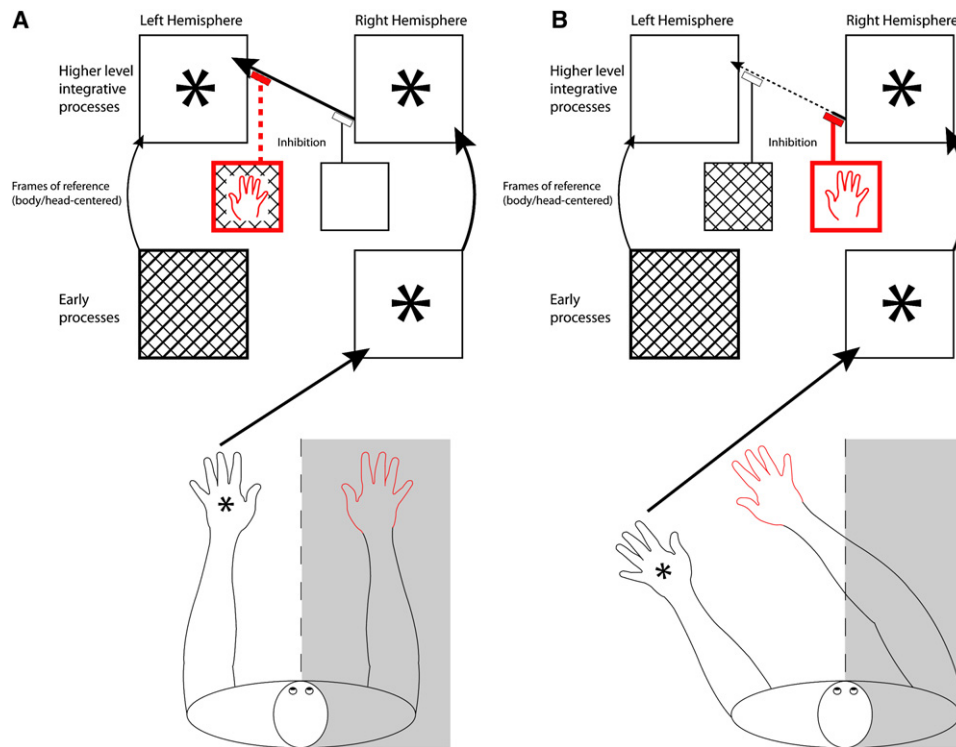
Figure 4. Shift in Hemispheric Control of Inhibition of Bilateral Percepts under Conditions of Left-Hand Stimulation

A schematic of somatosensory processes under conditions of left-hand stimulation when the right hand is in contralesional (A) compared to ipsilesional (B) space relative to the trunk midline. Note that we include only the mechanisms and connectivity required to highlight the shift in hemispheric control that takes place under these circumstances. In each hemisphere, the lower large box represents early cortical somatosensory processes, and the upper large box represents higher-level integrative processes involved in body image and tactile awareness. The small boxes represent left and right hemisphere mechanisms involved in frame of reference representation and processing; these contribute to the inhibition of bilateral percepts from crosshemispheric transmission of somatosensory information (as indicated by flat-topped arrows). Note that, for clarity, only one reference frame mechanism is shown (trunk or head centered), although we propose that at least three separate mechanisms (trunk centered, head centered, and limb relative) operate in a similar manner. Crosshatched boxes and dashed lines indicate damaged mechanisms; we assume that DLE has damage to early left-hemisphere somatosensory processes and inhibitory processes, but that at least some higher-level processes are spared. Asterisk indicates a stimulus. Thick red arrows and outlining indicate the critical aspects of processing related to the unstimulated right hand. Thick black arrows and outlining indicate critical aspects of processing related to the stimulated left hand.

(A) DLE's unstimulated right hand is in right space relative to trunk and head midlines. This information is represented in the contralateral (and damaged) left hemisphere. Under those conditions, the inhibitory mechanisms responsible for inhibiting the bilateral percept are likely to fail, and a synchiric phantom sensation on the right hand will be experienced.

(B) The right hand is in left space relative to head and body midlines. This information is represented in the contralateral (and intact) right hemisphere, resulting in the successful inhibition of the spurious bilateral percept.

(contralesional) upper arm on 83% (33/40) of trials on which the left upper arm was stimulated (unilateral-left hand versus unilateral-left-forearm stimulation trials in the CXF: $\chi^2 = 56.2$, p < 0.001).

Given the dramatic reduction of synchiric percepts with the hand-crossing manipulation, as well as the evidence from the previous two experiments that accuracy on bilateral trials is based, at least in part, on illusory synchiric percepts, we would predict very poor accuracy on bilateral crossed-hands stimulation trials. As indicated in Figure 3, DLE averaged 4% (5/140) correct on bilateral stimulation trials, with all but one of the responses consisting of extinction of the stimulus presented to the right hand.

Discussion

The primary and novel empirical finding of this research is that the degrees of right-hand synchiria and extinction are modulated by the position of the right hand as defined by multiple reference frames. In addition, we have reported disruption of localization, but not awareness of unilateral-right-hand stimulation. To provide an account for these findings, we propose a schematic functional architecture of somatosensory processing and posit-specific disruptions (Figure 4). All of the assumptions we make in this proposal have independent motivation, discussed earlier in this paper. Here, we bring them together in a way that allows us to provide an account of our findings. We acknowledge that, given the still relatively scarce findings in this area, other architectures are likely to also be consistent with the current evidence. Finally, note that we refer primarily to functional processing mechanisms, making only general reference to their neural substrates, because the lesion evidence does not allow fine-grained conclusions in this regard.

The finding that DLE can accurately detect, but not localize, stimuli presented to his contralesional (right) hand is explained by assuming that detection and localization of right-hand stimulation rely on damaged left-hemisphere somatosensory

substrates in SI and SII (indicated in Figure 4 as "early processes"). The remaining limited substrates may be sufficient to support detection accuracy (of above threshold stimuli) but insufficient for precise localization, producing gross distortions in the perception of stimulus location, as was proposed by Rapp et al. [29]. Furthermore, it is plausible that this damage also makes DLE susceptible to extinction of right-hand percepts under conditions of bilateral stimulation.

Given previous evidence indicating bilateral activity in response to unilateral stimulation at a number of levels of the somatosensory system (including but not limited to superior and posterior regions of parietal cortex [5, 6, 30], depicted in Figure 4 as "higher-level integrative processes"), we assume that the synchiric percepts experienced by DLE result, at least in part, from a failure to appropriately inhibit this bilateral activity. On the basis of our findings, we propose that these inhibitory mechanisms operate in a number of reference frames (trunk centered, head centered, and limb relative). Furthermore, we propose that hemispheric control of inhibition is driven by the location of the hands as defined by these frames of reference, such that the hemisphere contralateral to the relative location of the unstimulated hand drives the inhibitory processes. As a result, when the right hand is in on the right side (as defined by a given reference frame), it relies on the contralateral-left hemisphere inhibitory processes to suppress spurious percepts. In DLE's case, under these conditions, the damaged left hemisphere cannot carry out its inhibitory functions and synchiric, right-hand phantoms are experienced (see Figure 4A). In contrast, when the right hand is in left space, intact right-hemisphere inhibitory processes are utilized and are able to more successfully suppress the synchiric percepts (see Figure 4B). When the hands are crossed, the right hand is always on the left side in limb-relative space and, therefore, the intact right-hemisphere inhibitory mechanisms are engaged; this results in virtually no synchiric experiences and reveals the full extent of the extinction of right-hand percepts under conditions of bilateral stimulation. We make no specific claims regarding inputs to these inhibitory mechanisms other than they are multiple and represent limb location in multiple frames of reference [25].

It is generally assumed that higher levels of somatosensory processing and representation produce a unified body image percept that allows us to move through space and interact with the world. Such a representation is developed on the basis of rich and complex computations that constantly integrate and update information from a variety of intra- and interhemispheric sources regarding the organism's somatosensory haptic, proprioceptive, and other sensory experiences. The results of this investigation contribute to our understanding of this complex process by providing evidence for existing claims that unilateral stimulation results in bilateral activation and that crosshemispheric inhibitory mechanisms may be involved in preventing bilateral percepts. Furthermore, this research provides novel evidence that the hemispheric control of these inhibitory processes is determined by the position of a limb in one or more frames of reference that define tactile locations relative to head and trunk midlines as well as the position of the hands relative to one another.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and two figures and can be found with this article online at http://www.current-biology.com/supplemental/S0960-9822(08)01537-6.

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