Touch improvement at the hand transfers to the face

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The hand–face border is one of the most prominent features of the primate somatosensory cortex. A reduction of somatosensory input, following amputation or anesthesia, induces perceptual changes across this border that are explained by plastic competitive mechanisms [1–4]. Whether cross-border plasticity can be induced by learning processes relying on increased somatosensory input has been unclear. Here we report that training-independent learning [5] improves tactile perception, not only at the stimulated index finger, but also at the unstimulated face. These findings demonstrate that learning-induced tactile improvement can cross the hand–face border, suggesting that facilitation-based plasticity may operate in the healthy human brain.

Perceptual improvement can be induced by protracted training but also by brief training-independent learning through repetitive somatosensory stimulation (RSS) [5–7]. Applied to the index finger, RSS reliably improves tactile acuity at this finger [6,7], presumably via functional reorganization within somatosensory cortices [6]. Prior investigations concluded that RSS-induced changes were local, as no changes were found either at the adjacent or homologous fingers [7]. To investigate the possible spread of learning-induced changes across the hand–face border we applied RSS to the right index fingertip of healthy participants and tested tactile acuity at the unstimulated face. In experiment 1, two-point discrimination thresholds were assessed using force-controlled devices at the right (stimulated) and left (control) index fingertips (right/left-D2) and above the right and left upper-lip (right/left-Lip) in two groups of 15 participants before and after a three-hour period during which the RSS device was either ON (RSS_{Exp1}) or OFF ($Control_{Exp1}$) (Figure S1).

To ensure our RSS protocol replicated the well-established finger-specific improvement of tactile acuity, fingertip thresholds were submitted to a rmANOVA. The triple interaction ($F_{(1,28)} = 5.90$, $P = 0.022$) revealed a significant decrease in right-D2 threshold after RSS in the RSS_{Exp1} group (Bonferroni-corrected: $P_{Bonf} = 0.002$), but no changes at left-D2 in this group or at either finger in the $Control_{Exp1}$ group (P-values > 0.9) (Figure 1A). This acuity gain (–15.26% ±3.85) is consistent with previous work (–15.6% on average; Supplemental Results in the Supplemental Information).

A double interaction from the same analysis on the lip data ($F_{(1,28)} = 7.37$, $P = 0.011$) revealed significantly lowered thresholds only in the RSS_{Exp1} group ($P_{Bonf} = 0.002$; $P > 0.9$ in $Control_{Exp1}$ group) (Figure 1A). This indicates a transfer of the RSS-induced behavioural effect across the hand–face border, likely arising from a spread of plastic changes from the right-D2 somatosensory representation [6] into the face region through horizontal intracortical connections. Although limited in number, these cross-border connections undergo Hebbian-based plastic changes [8] and are the most likely substrate for the interactions observed between the hand and face [2,3].

Notably, tactile improvement was side-specific at the fingers, but not at the lips, making transcallosal transfer unlikely. Instead, given the bilateral representation of the lips within the primary somatosensory cortex [9], the bilateral improvement observed at the lips may arise from transfer of right-D2's representational changes [6] to the neighbouring lips region within the left somatosensory cortices. To test this model of side-specificity, in experiment 2 (Supplemental Information) we measured two-point discrimination thresholds not only at the fingers and lips, but also at the cheeks (represented more

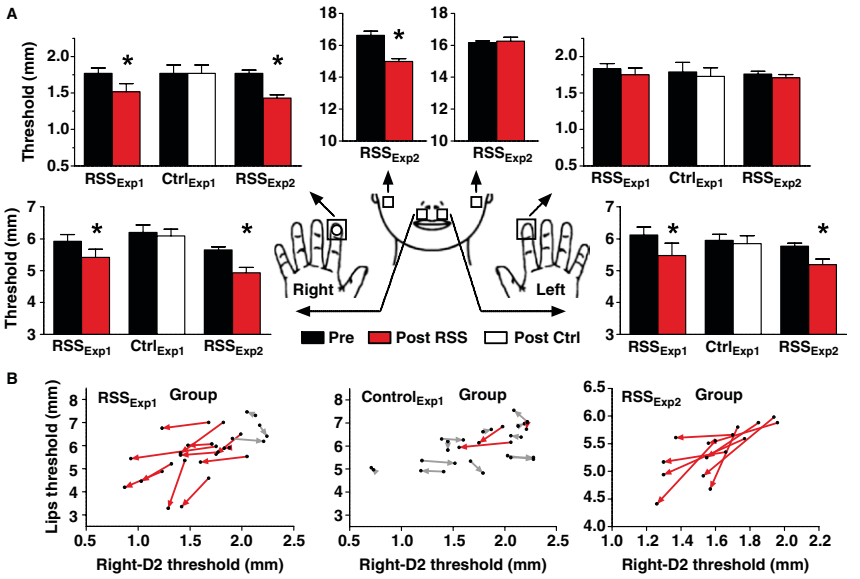

Figure 1. Improvement of touch acuity transfers from the finger to the face.
(A) Mean two-point discrimination threshold pre (black) and post the procedure applied to the right-D2 (RSS: red; Control: white), assessed at right/left-D2, right/left-Lip and right/left-Cheek (mean ± SEM; see also Figures S1 & S2). Repeated measures ANOVAs on data from the fingers, lips, and cheeks followed by Bonferroni-corrected post-hoc tests revealed significant threshold decreases (*$P_{Bonf} < 0.05$) at right-D2, both sides of the upper-lip, and right-Cheek in the RSS groups only (Supplemental Results). (B) Vectors showing the consistent relationship between threshold changes at the lips and right-D2 for each participant in the RSS_{Exp1} (left panel), $Control_{Exp1}$ (central panel) and RSS_{Exp2} (right panel) groups. The starting and ending points of vectors respectively represent pre- and post-session thresholds. Red vectors indicate parallel threshold decreases at both right-D2 and lips, whereas grey vectors illustrate other combinations of threshold changes (see also Figure S1).

contralaterally [9]), before and after RSS (RSS_{Exp2} group). In addition to replicating the significant threshold decreases at both upper-lips ($F_{(1,7)} = 18.25$, $P = 0.004$) and at the right- ($F_{(1,7)} = 36.56$, $P_{Bonf} < 0.001$) but not left-D2 ($P > 0.9$; Figure 1A), a side-specific effect was also found for the cheek ($F_{(1,7)} = 21.32$, $P < 0.001$), with a significant improvement at the right-Cheek only ($P_{Bonf} = 0.005$; Figure 1A), thus supporting our model.

D-prime analyses confirmed sensitivity gains for right-D2, right-Cheek and both upper-lips (RSS_{Exp1}: all P_{Bonf}-values ≤ 0.027, RSS_{Exp2}: all P_{Bonf}-values ≤ 0.045), with no slackening of participants' response criterion in either experiment (Supplemental Table S1). Furthermore, the stable pattern observed in the equally-sized $Control_{Exp1}$ group, whose baseline thresholds were similar to those of the RSS_{Exp1} group (P-values ≥ 0.8), rules out unspecific contributions of training or attention.

Threshold decreases at the left- and right-Lip were correlated with each other ($r = 0.57$, $P = 0.026$), but not with right-D2 threshold decrease (P-values ≥ 0.4; Supplemental Results). However, 12/15 RSS_{Exp1} participants and all RSS_{Exp2} participants had decreased thresholds at both the right-D2 and lips, whereas this was true for only 3/15 $Control_{Exp1}$ participants (Figure 1B). Interestingly, all RSS_{Exp2} participants also exhibited acuity gains at both the right-D2 and right-Cheek, which tended to correlate ($r = 0.70$, $P = 0.051$). Averaging across experiments, the mean threshold at the lips and right-Cheek decreased respectively by 10.8% (±2.8) and 9.8% (±3.6), which represent 62.4% and 56.6% of the improvement observed at right-D2 (Figure S1C).

The distribution of threshold changes combined with the high proportion of transfer strengthens the hypothesis of a large and robust spread of plastic changes across the hand–face border. Consistent with the intra-hemispheric shift of right-D2's representation following RSS [6], the correlation between gains at both upper-lips and the side-specificity at other body parts support the intra-hemispheric hypothesis. Since there is currently no evidence that RSS effects transfer to other fingers [7], our findings further imply that training-independent perceptual improvement transfers across the hand–face border, without necessarily transferring within the hand. This may be surprising given the position of the thumb's representation (between that of the index and face [10]), but is consistent with results showing that the thumb's cortical representation is unchanged after RSS of the right-D2 [6]. This might be due to differences in remote and local circuit properties [8], with long-range facilitatory connections allowing hand–face transfer and shorter-range lateral inhibition preventing inter-finger transfer.

The cross-border perceptual improvements reported here provide evidence that passively increasing input to a body part can positively affect touch perception at cortically close, but physically distant body-parts, and thus reveal a novel perceptual learning phenomenon whereby improvement transfers across the hand–face border. To date, the theoretical framework within which hand–face border crossings have been interpreted has been one of 'competition' [1–4], whereby the face cortical area invades the deprived territory after permanent or transient removal of hand afferent inputs [3,4]. Although the present findings might rely on the same connections, the functional context (increased input) and subsequent consequences (acuity gain at non-contiguous body parts) indicate the need to extend the framework of cross-border plasticity beyond 'competition', which might apply to specific conditions of dramatically reduced afferent inputs, to generate new models of cortical plasticity that also account for 'facilitation' based forms of cross-border plasticity.

Supplemental Information

Supplemental Information includes supplemental results, experimental procedures, two figures and one table, and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.07.021.

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