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Visual Enhancing of Tactile Perception in the Posterior Parietal Cortex

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Abstract

■ The visual modality typically dominates over our other senses. Here we show that after inducing an extreme conflict in the left hand between vision of touch (present) and the feeling of touch (absent), sensitivity to touch increases for several minutes after the conflict. Transcranial magnetic stimulation of the posterior parietal cortex after this conflict not only eliminated the enduring visual enhancement of touch, but also impaired normal tactile perception. This latter finding demonstrates a direct role of the parietal lobe in modulating tactile perception as a result of the conflict between these senses. These results provide evidence for visual-to-tactile perceptual modulation and demonstrate effects of illusory vision of touch on touch perception through a long-lasting modulatory process in the posterior parietal cortex. ■

INTRODUCTION

Common sense suggests that vision is our dominant sensory modality. For example, when we are confronted with a loud sound or feel a slight sensation on our unseen arm, we typically orient our eyes to the source of the information to determine what produced it. Visual dominance has also been reported experimentally for more than a century (Sekiyama, Miyauchi, Imaruoka, Egusa, & Tashiro, 2000; Rossetti, Koga, & Mano, 1993; Posner, Nissen, & Klein, 1976; Pick & Hay, 1964; Rock & Victor, 1964; Rock, Mack, Adams, & Hill, 1965; Harris, 1963; Gibson, 1933; Stratton, 1897). In the first of these studies in the late 1800s, Stratton (1897) elegantly described in a case report experiment conducted on himself that gradual changes in the other senses could result as a consequence of altered visual input. In particular, he showed proprioceptive and auditory adaptation to upside-down vision when inverting lenses were worn for extended periods. Since then, others have shown similar types of effects using prisms (Sekiyama et al., 2000; Rossetti et al., 1993; Pick & Hay, 1964; Harris, 1963; Gibson, 1933) and other types of distortive lenses (Rock & Victor, 1964; Rock et al., 1965).

Of particular relevance, it has been shown that vision captures touch when there is concurrent conflicting information between these two sensory modalities. In one study, for example, Rock & Victor (1964), using a minifying lens demonstrated that when subjects feel an object that is visually minified by the lens, the feel of the object, demonstrated by a subsequent selection task, corresponds with what was seen rather than what was actually felt (but see van Beers, Wolpert, & Haggard, 2002; Ernst, Banks, & Bulthoff, 2000; Ernst & Banks, 2002). Whether such a conflict between the sensory modalities, however, could result in a lasting alteration of touch sensitivity in an attempt to resolve the conflict has never been shown. We therefore induced an extreme conflict between vision of touch and sensation of touch using mirrors (see Figure 1) and measured after exposure to this conflict situation whether tactile sensitivity had changed.

To determine the neural basis for any modulatory effects, transcranial magnetic stimulation (TMS) was used to transiently interfere with signals in the posterior parietal and frontal cortices. Since recent studies have demonstrated that the posterior parietal cortex is involved not only in multisensory processing (Andersen, Snyder, Bradley, & Xing, 1997), but also for coding correspondence between vision and somatosensory information regarding one's own body parts (Graziano, Cooke, & Taylor, 2000), this region was an ideal candidate for investigation. Any changes in sensitivity to touch as a result of the visual information providing illusory feedback of tactile sensations may result from lasting modulations of the posterior parietal cortex.

RESULTS

In the critical conditions of all experiments, subjects viewed their right hands being brushed while looking leftwards at a mirror reflection of their right hands for 2.5 min (see Figure 1). Some subjects spontaneously reported that they knew that their left hand was not

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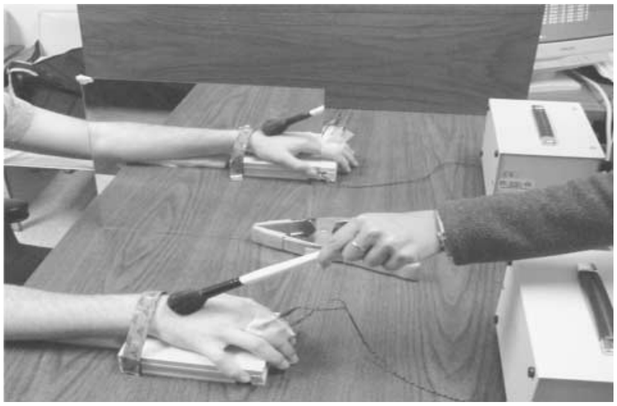

Figure 1. In the baseline conditions, subjects passively viewed their left hand or a mirror reflection of the right hand while tactile detection rates were measured. In the visual adaptation and conflict conditions, subjects first viewed the mirror reflection of their right hand being brushed with either a small or large brush. In these conflict conditions, there was a strong visual impression that the left hand was being brushed, but no tactile stimulation was delivered to the left hand. Many subjects spontaneously reported feeling something on their left hand in these conditions, even though they were aware that there was no brushing on the left hand. Following 2.5 min of this conflict, tactile detection rates on the left hand were measured.

being brushed, but nonetheless felt sensations on their left hand due to the visual input. Following the 2.5 min of adaptation in these conflict conditions, comprising approximately 125 brush strokes delivered to the right hand, tactile sensitivity was measured in the left, never-touched hand of the subjects.

Experiment 1: Tactile Modulations from Vision

In both of the critical visual–tactile conflict conditions (large brush and small brush), there was a large change in sensitivity to touch on the never-brushed left hand. Because of this perceptual conflict, tactile sensitivity was altered such that the detection rate of a near-threshold stimulus measured after conflict exposure was consistently increased. As can be seen in Figure 2, there were clear differences between the four conditions of this experiment ($p < .01$). Detection rates for the two baseline conditions, where subjects passively viewed their real left hands or a virtual image (mirror reflection) of their right hands while detection rates were measured, did not significantly differ from one another. Hence, detection rates were stable throughout the experiment and comparable whether subjects looked at the real or virtual image of their hand. Detection rates for conditions in which the subjects had previously received strokes with either a small brush or with a large brush on the right hand, and therefore "saw" but did not feel anything on their left hand, were both significantly greater than the baseline conditions ($p < .05$ for any of the conflict vs. baseline comparisons). Although we expected to find a larger increase in tactile perception with the larger brush, since there was a larger conflict between vision and touch, the two conflict conditions with different size brushes did not significantly differ from each other. The false alarm rate was extremely low in this experiment (mean rate of 1.8%, with 8 of the 12 subjects having no false alarms for any of the conditions).

Experiment 2: Replication and Control

It could be argued that the visual enhancement effects may be due to the brushing independent of the conflict, or some other nonspecific effect. For example, changes in sensation of the right hand due to the brushing may have altered tactile perception in the left hand or subjects may have been more alert after the 2.5 min of brushing. In fact, a recent study has shown that numbing of the right hand with anesthesia can increase sensitivity on the left hand (Werhahn, Mortensen, Van Boven, Zeuner, & Cohen, 2002). The brushing of the right hand may therefore have reduced sensitivity on the right hand, thereby leading to an increase in sensitivity of the left hand, regardless of whether or not a visual–tactile conflict was experienced. To rule out this effect and other potential nonspecific effects, and to replicate the basic findings from the previous experiment, we ran a control experiment in which subjects either simply viewed their real left hand while being brushed on the right or experienced the visual–tactile conflict as before in the critical conditions. Only the large brush was used in this and all subsequent experiments since the previous experiment showed that brush size did not matter. As can be seen in Figure 3, we found that only the visual–tactile conflict condition significantly increased detection rates for the left hand as compared to the two baseline conditions (both $ps < .01$). Detection rates after the control condition with brushing of the right hand while viewing the real left hand showed no differences between the two baseline conditions (both $ps > .2$),

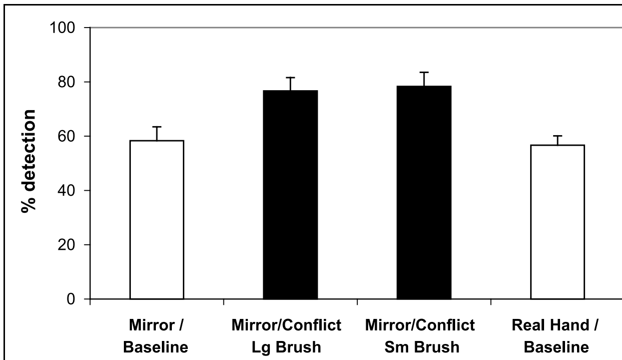

Figure 2. Results from the first behavioral experiment. The proportion of detected tactile pulses was significantly increased following the visual experience of touch (78% detection for both brushes) as compared to the two baseline conditions (58% detection during passive mirror viewing vs. 57% detection during passive real-hand viewing). Error bars represent standard errors of the mean.

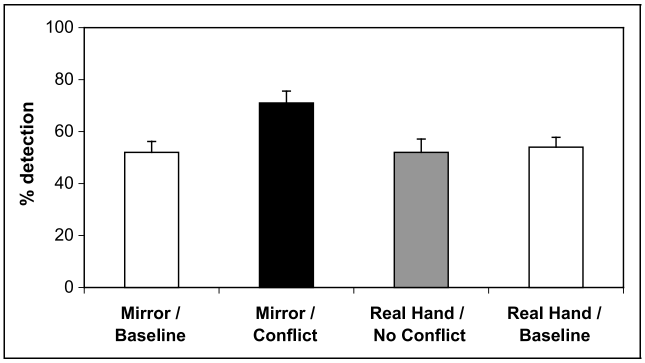

Figure 3. Results from the control experiment. The proportion of detected tactile pulses was significantly increased following the visual experience of touch (71% detection) as compared to the control condition in which brushing occurred, but there was no conflict between vision and touch (52% detection), as well as the two baseline conditions (52% detection during passive mirror viewing vs. 54% detection during passive real-hand viewing). Error bars represent standard errors of the mean.

ruling out any effects due to the brushing on the right hand. As in the previous experiment, the false alarm rate was low (mean rate of 6.9%, with 8 of the 16 subjects having no false alarms for any of the conditions).[1]

Experiment 3: Time Course Experiment

We next asked how long this alteration in touch perception would last. After a baseline block followed by the 2.5 min of exposure to the visual–tactile conflict, detection rates were measured in seven sequential blocks. Figure 4 shows that this effect lasted 3.7 min on average across the new subjects tested in this experiment. Only in the first three blocks of 25 trials each after

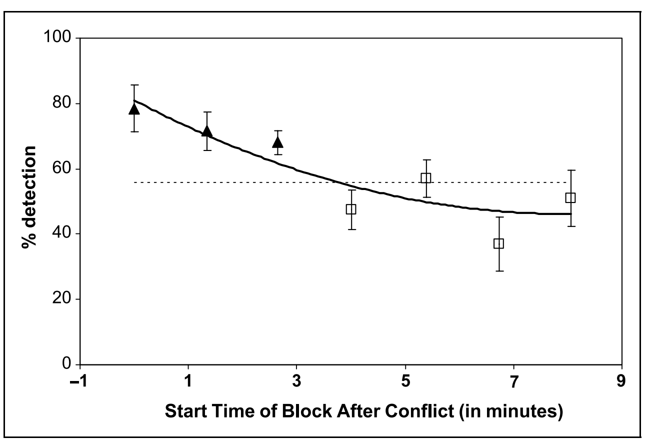

Figure 4. The time course of the alterations in tactile sensitivity. The baseline rate (dotted line) was measured at the start of the experiment. Subsequently, seven blocks of trials were sequentially run and average performance across subjects is plotted as a function of time (solid line). Detection rates returned to baseline levels approximately 3.7 min after experiencing the visual conflict. Solid triangles represent blocks with significantly increased ($p < .05$) detection rates over baseline. Error bars represent standard errors of the mean.

the intersensory conflict was there a significant modulation in tactile detection. Following the 3.7 min of alterations, detection rates returned to the baseline rate as measured at the beginning of this experiment. Again, as in the previous experiments, the mean false alarm rate was low (4.5%), with 2 of the 10 subjects not producing any false alarms for any of the conditions.

Experiment 4: Cortical Localization of the Visual-to-Tactile Modulation

To localize the neural contributions to these adaptation effects, we used single-pulse TMS to transiently disrupt neural functioning (Hallett, 2000; Jahanshahi & Rothwell, 2000; Pascual-Leone, Walsh, & Rothwell, 2000). Tactile detection rates were measured during the baseline trials or after the visual–tactile conflict with TMS pulses delivered 50 msec prior to the tactile stimulus (Seyal, Masuoka, & Browne, 1992; Seyal, Ro, & Rafal, 1995; Cohen, Bandinelli, Sato, Kufta, & Hallett, 1991). TMS was given over the parietal or frontal control site (see Figure 5) either while subjects only looked at their right hand in the mirror (baseline TMS conditions) or

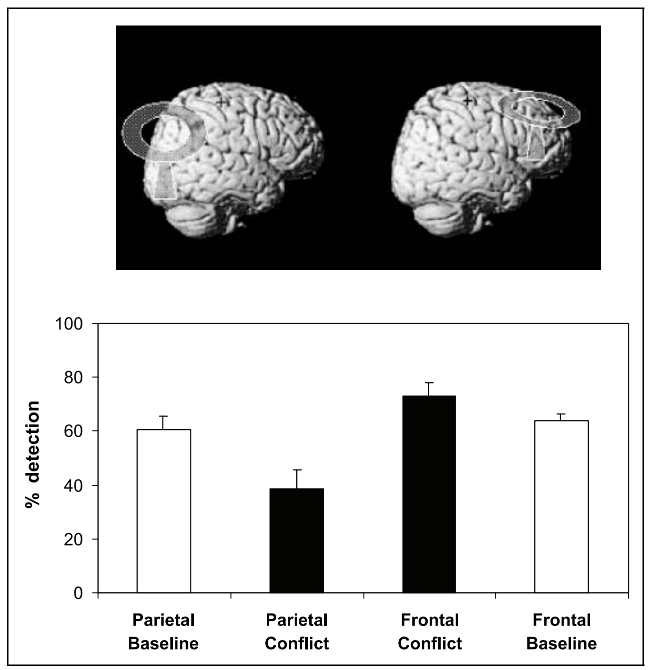

Figure 5. Top: The hand area of the motor cortex (cross) was first localized with a focal figure-eight coil. For the posterior parietal cortex block, with TMS over area 5 and the intraparietal region, the anterior-most edge of the circular coil was positioned over the cortex 3 cm posterior and 2 cm lateral to the hand area. For the control TMS site, the posterior-most portion of the coil was held over the cortex 3 cm anterior to the hand area. The coil size and positions were drawn to scale on the Montreal Neurological Institute template MRI using some functions of SPM99 (London, UK). Bottom: TMS over the posterior parietal region not only eliminated the visual enhancement effect, but also significantly altered tactile perception below baseline levels when the enhancement signal was disrupted. Error bars represent standard errors of the mean.

after 2.5 min of the intersensory conflict via the brushes and mirror. The graph on the bottom of Figure 5 shows that after the intersensory conflict, stimulation of the posterior parietal cortex eliminated the visual enhancement effect and even decreased tactile sensitivity below baseline levels. Tactile sensitivity was systematically lower in this condition as compared to all other conditions (all ps $< .05$). The significant difference between the parietal baseline TMS and the parietal conflict TMS conditions demonstrates that TMS of the parietal lobe after the conflict did not simply reduce overall tactile detection rates, but rather that parietal TMS modulated signals that were representing changes in tactile perception as a result of the visually induced conflict. The difference between the two frontal TMS conditions was not significant. However, detection in the frontal conflict condition was significantly higher than the parietal baseline condition ($p < .05$) and the difference between the parietal baseline and frontal baseline was not significant ($p > .20$). Therefore, the nonsignificant difference between the frontal conditions is likely due to a slight increase in detection in the frontal baseline condition. Also note that the detection rates in the frontal conflict condition were comparable to the previous experiments. The mean false alarm rate in this experiment was 20.6%, with two of the eight subjects not producing any false alarms. Although the false alarm rates were higher in this experiment, there were no statistical differences in false alarm rates between any of the conditions. Thus, the TMS results demonstrate that the visual enhancement of touch requires signals from the posterior parietal cortex.

DISCUSSION

Taken together, these results provide evidence for visual dominance over somatosensation, whereby tactile sensitivity is increased for several minutes following visual experience of unfelt touches. They further demonstrate that visual adaptation under such a peculiar conflict situation between vision and touch can alter tactile sensitivity through the posterior parietal cortex. Our results are in line with several recent investigations showing multisensory interactions (Maravita, Spence, Sergent, & Driver, 2002; Pavani, Spence, & Driver, 2000; Shams, Kamitani, & Shimojo, 2000; Driver & Spence, 1998). They are also in line with results demonstrating that viewing a body part that is being touched can enhance tactile detection and perception (Taylor-Clarke, Kennett, & Haggard, 2002; Kennett, Taylor-Clarke, & Haggard, 2001; Tipper et al., 1998, 2001; Rorden, Heutink, Greenfield, & Robertson, 1999; Halligan, Hunt, Marshall, & Wade, 1996). Our results, however, extend these findings considerably by showing that the visual system can induce lasting changes in sensitivity of tactile perception of a body part that has *never* been touched and the neural basis for such effects. The findings of posterior parietal cortex modulating tactile perception after adaptation demonstrate a role of the parietal lobe in maintaining an altered representation.

The boosting of tactile sensitivity as a result of the conflict between vision and touch is likely to have been due to a modulation of the somatosensory system by the visual system in an attempt to provide congruency between these two sensory modalities. Since seen touches were not felt in the critical conditions, an increase in the gain of tactile sensitivity would be a reasonable way to resolve the conflict based on the illusory visual input; by increasing the gain of touch, one might then congruently feel what is seen to be making contact with one's skin. The TMS results demonstrate that the parietal cortex is involved with such a modulatory process, suggesting that in addition to multisensory and motor processes as well as attention, the parietal lobes may also be involved with long-term processes that modify sensation and perception.[2]

An alternative account for these results is that the effects may be due to an increase in attention due to the conflict, which consequently enhances tactile detection. The parietal cortex involvement would be consistent with such an account since this region has been shown to be involved with shifting and orienting attention (e.g., Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Colby & Goldberg, 1999; Posner, Walker, Friedrich, & Rafal, 1984; Posner, Walker, Friedrich, & Rafal, 1987; Bushnell, Goldberg, & Robinson, 1981). This attentional explanation is unlikely for several reasons. First, the modulatory effects lasted nearly 4 min, an interval much longer than would be expected based on an attentional orienting account, which has been shown to be more transient in nature (e.g., Egly, Rafal, Henik, & Berger, in press; Corbetta et al., 2000; Posner et al., 1984). Furthermore, because the task required only the simple detection of touch on the left hand after the conflict, subjects most likely allocated full attentional resources to this detection task in all conditions. Finally, if TMS of the parietal cortex modulated attention rather than a somatosensory gain increasing signal, the baseline parietal TMS condition should have also produced significantly lower detection rates in comparison to the frontal baseline condition. Since this was not the case, an attentional biasing account does not seem very likely.

These lasting effects of vision on touch also suggest that such situations of conflict may be useful in the rehabilitation of patients with somatosensory deficits, similar to the rehabilitative effects on movement with visually induced conflicts through mirrors (Sathian, Greenspan, & Wolf, 2000; Altschuler et al., 1999; Ramachandran & Hirstein, 1998). For example, after inducing this type of visual–tactile conflict on a regular basis, lasting changes to touch perception through the visual modality may be observed. We are currently exploring the cortical boundaries of these adaptation effects, especially in more posterior regions (Zangaladze, Epstein, Grafton, & Sathian, 1999), to determine the extent and nature of cortical sparing from a stroke that would be necessary for these adaptation and potentially rehabilitative effects to take place.

METHODS

All experiments were conducted using an Intel (Santa Clara, CA) Pentium III PC with custom software. Two Grass (West Warwick, RI) SD9 stimulators, driven by the parallel port of the computer, were used to deliver the tactile pulses. A mirror measuring 30.5 × 30.5 cm was positioned slightly to the left of the midsagittal plane of a subject, with the reflective side to the right. Two custom-made wooden blocks (16 × 12 cm) with a Velcro strap were used to minimize movement of the hands. Two brushes of different sizes were used in Experiment 1. The smaller brush (Staedtler, Chatsworth, CA, model 841 Pony, size 2) measured 17 cm in length, including a 1-cm-long brush tip, and was 0.2 cm wide at the brush tip. The larger brush (Winsor & Newton, Middlesex, UK, series 340, size 6) measured 24.5 cm in length, including a 4.5-cm brush tip, and was 1.8 cm wide at the brush tip. The larger brush was used for all of the remaining experiments.

In all experiments, following informed consent, each subject was seated on a chair in front of a table. The subject's middle fingers were treated with electrode preparation pads (70% isopropyl alcohol and pumice) and ring electrodes (NeuroSupplies, Waterford, CT, model E502) were then taped to each middle finger. After attaching the ring electrodes to the middle fingers, the subjects were asked to comfortably position their forearms on either side of a mirror so that while looking left at the reflective side of the mirror, it looked and felt as though the subjects were seeing their left hands through the mirror (see Figure 1). When this position was achieved, the subject was asked to tap each hand five times synchronously and simultaneously to provide a further impression that the viewed, mirror-reflected right hand was identical in visual nature to the real left hand. To make the visual information reflected by the mirror nearly identical to that seen without it, vertically oriented wooden plates were located on either side of the edge of the table.

The electrodes were then connected to two stimulators on each side of the mirror, opposite the subject. The threshold intensity for detecting a 0.3-msec electrical pulse delivered to the left middle finger was then established. To determine threshold, the experimenter applied electrical impulses to the left hand while having the subject view this hand. The subject was asked to report whether something was felt on the left hand. When the detection rate was between 40% and 60% out of 10 trials, this intensity was used as the threshold intensity throughout the experiment for that given subject. All subjects were neurologically unimpaired and had normal touch and normal or corrected-to-normal vision.

Experiment 1

In this first main behavioral experiment, each of the 12 subjects participated in one experimental session with four conditions. During the first and last blocks, while viewing the real left or reflected right hand, counterbalanced in order across subjects, 25 baseline tactile detection trials were collected. A 250-msec tone (500 Hz) was presented to start each trial, and on a random 80% of the trials, a near threshold electrical pulse was delivered to the middle finger of the left hand. The remaining 20% of the trials were catch trials in which no electrical pulse was delivered. This lower proportion of catch trials was used to ensure that we obtained enough experimental trials in as short a time as possible because we were uncertain of the duration of the effects. The task was to simply report by saying "yes" or "no" as to whether the electrical pulse was felt. The two main conditions of this experiment were the conflict conditions, where subjects first viewed a mirror reflection of their right hand being brushed with either a small or a big brush before detection rates were measured. Following the visual–tactile conflict, detection rates were measured as in the baseline trials with a near-threshold pulse delivered to the middle finger of the never-touched left hand. The order of these two middle conditions was also counterbalanced across subjects. A 2.5-min break was given after each experimental block/condition to recover from the adaptation of the preceding condition. Although Experiment 3 showed that this break should have been closer to 4 min, the order of the conditions was counterbalanced, thereby equalizing any carryover effects from one condition to the next.

Experiment 2

Sixteen new subjects participated in the replication and control experiment. For this control experiment, each subject completed four conditions, including the mirror viewing and real-hand viewing baseline conditions, which were identical to the baseline conditions in the first experiment. The conflict condition was also identical to the large brush condition of the previous experiment, with detection rates measured after the visual–tactile conflict. The remaining control condition was included to determine whether any differences in touch may have been due to the brushing of the right hand alone rather than the conflict between vision and touch. Therefore, in this control condition, subjects viewed their real left hand while their unseen right hand was brushed for 2.5 min. Detection rates were then measured after this control condition. Five-minute breaks were given between conditions and the order of the baselines and the conflict/no conflict conditions was counterbalanced.

Experiment 3

Ten new subjects participated in this experiment, which was similar to the first experiment, except that only one baseline condition was run at the start of the experiment. Subjects passively viewed the mirror reflection of their right hand in this baseline condition and detection rates were measured. This procedure was then followed by the brush-stroking procedure for 2.5 min. Detection rates were subsequently measured in seven subsequent and sequential blocks of 25 trials each, with 20 detection trials and 5 catch trials.

Experiment 4

Eight subjects who did not participate in any of the behavioral experiments were run in the TMS experiment. The procedures were identical to the first behavioral experiment except for the following changes. TMS was delivered with a Cadwell MES-10 (Kennewick, WA). The hand area of the right motor cortex was first localized with a focal figure-eight coil, with each component of the figure-eight measuring 4.5 cm. A 9-cm focal point circular TMS coil was then used for the experiment at an intensity 10% above the motor threshold obtained with this coil. In all conditions, TMS was delivered on each trial 50 msec prior to the near-threshold tactile stimulus. Baseline detection rates were measured while TMS was delivered over the right parietal or right frontal cortex at the beginning and end of this experiment. Only the large brush was used to induce conflict between vision and touch for the middle two blocks in this experiment, after which detection rates were measured with TMS over the right parietal or right frontal cortex. The order of the first and last blocks as well as the middle two blocks was counterbalanced across subjects, with 2.5-min breaks given between each block.

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Notes

1. One might still argue that the tactile enhancements may simply be due to observations of the hand being brushed, regardless of the conflict, or from passively viewing a mirror reflection of the hand for extended periods. The results from another control experiment with 8 new subjects, in which brushing of both hands was administered while subjects either looked at the real left hand or the mirror reflection of the right hand, however, showed no significant differences between any of the bilateral brushing versus baseline conditions (all ps $>$ .10). The false alarm rate was very low in this control experiment, with a mean of 2.8% across subjects and 5 out of 8 subjects having no false alarms for any of the conditions. This experiment rules out any such alternative interpretations since most of the conditions in this experiment provide identical parameters for the different conditions as the previous experiment without inducing a conflict between vision and touch.

2. As noted by an anonymous reviewer, it is possible, since we used the detection of an electrical pulse as our dependent measure, that the visual–tactile conflict induced an enhancement in skin conductance rather than a direct change in tactile perception. This change in the skin conductance response (SCR) may have then been indirectly responsible for the increased detection rates that we measured. Although the results of the time course and TMS experiments would argue against this explanation, as the effects were longer lasting than changes in the SCR and the brain areas involved with generating the SCR are unlikely to be specific to the parietal cortex (for a review, see Dawson, Schell, & Filion, 2000), we nonetheless conducted a further control experiment to rule this out. In this control experiment, we measured two-point tactile discrimination in 12 new subjects either in a baseline control condition or after the visual–tactile conflict condition as induced with a mirror. The order of these conditions was counterbalanced and 10 trials were collected in each condition. We also directly measured the SCR in 10 of the subjects of this experiment using a Grass-Astromed (West Warwick, RI) P122 amplifier attached to an SCA1 unit, which was connected to a data acquisition card for digitization (CyberResearch, Branford, CT). The SCR was continuously sampled at 2 Hz for 4 min. Two-point discrimination measured on the dorsum of the left hand was significantly better after the conflict condition (16.0 mm) as compared to the baseline condition (18.1 mm) ($p < .025$). Furthermore, the SCR was not any different between these two conditions ($p > .20$). Therefore, the effects we measured in these experiments cannot be due to a less specific change in skin conductance because (1) we showed enhanced tactile perception in a discrimination task that should not depend on the SCR and (2) there were no changes in the SCR after the visual–tactile conflict. These results directly rule out an explanation based on skin conductance.

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