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RESEARCH ARTICLE

Contralateral tactile masking between forearms

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Abstract Masking effects have been demonstrated in which tactile sensitivity is affected when one touch is close to another on the body surface. Such effects are likely a result of local lateral inhibitory circuits that sharpen the spatial tuning of a given tactile receptor. Mutually inhibitory pathways have also been demonstrated between cortical tactile maps of the two halves of the body. Occasional reports have indicated that touches on one hand or forearm can affect tactile sensitivity at contralateral locations. Here, we measure the spatial tuning and effect of posture on this contralateral masking effect. Tactile sensitivity was measured on one forearm, while vibrotactile masking stimulation was applied to the opposite arm. Results were compared to sensitivity while vibrotactile stimulation was applied to a control site on the right shoulder. Sensitivity on the forearm was reduced by over 3 dB when the arms were touching and by 0.52 dB when they were held parallel. The masking effect depended on the position of the masking stimulus. Its effectiveness fell off by 1 STD when the stimulus was 29 % of arm length from the corresponding contralateral point. This long-range inhibitory effect in the tactile system suggests a surprisingly intimate relationship between the two sides of the body.

Keywords Long-range masking · Somatosensory sensitivity · Tactile detection thresholds · QUEST · Somatosensory psychophysics · Cross-body tactile inhibition

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Introduction

If I touch you on the arm and ask you to report what happened, you are most likely to report that you were touched on the arm. It is very unlikely that you would include mention of which arm. It seems that at some level the representation of the body is more concerned about body regions (arm, leg, torso) than in distinguishing sides of body. This is supported by the properties of cells in the somatosensory cortex and beyond which show responses to touch on either side of the body (Iwamura et al. 2002). Phenomena such as lateral inhibition sharpen spatial localization on a given area of skin. It is possible that long-range inhibition across the body may serve to similarly enhance spatial localization on the much larger scale of discriminating the location of touches in terms of side of the body.

The influence of one tactile stimulus on the perception of another has historically revealed details of the arrangement of the peripheral somatosensory system. In his classic seminal work, Georg von Békésy (1967) used the masking effects of systematically separated stimuli to uncover and quantify lateral inhibition in the somatosensory system and to explore the size of the receptive fields of tactile receptors distributed over the body surface. Lateral inhibition and central summation effectively sharpen the localization of vibrotactile stimulation and improve tactile two-point resolution and detection (Carmon 1968; Levin and Benton 1973). In addition to interactions between adjacent points on the body surface, superficially similar long-range tactile masking effects have been reported between mirror-symmetric points on the hand and arm (Sherrick 1964; Braun et al. 2005; Tamè et al. 2011). Although behavioural studies have concentrated on the effects of a touch on one hand or arm on the other hand or arm, mutual inhibitory pathways have been demonstrated between all points of the tactile map in the somatosensory cortices (Reed et al. 2011). This suggests a general principle of contralateral inhibition between corresponding points on each side of the body that may serve to enhance distinguishing touches on the two halves of the body. In addition, Tamé et al. (2011) made the intriguing discovery that the effectiveness of the cross-body masking effect depended on the limbs being aligned: contralateral masking from one finger tip to another was disrupted if one hand was palm up and the other palm down. To explore the matching of "corresponding points" across the body, here we measure the spatial tuning of the masking effect on the forearm. To look at the effect of posture, we measured contralateral masking between the forearms with the arms in two configurations.

Methods

Participants

Ten participants took part in Experiment 1 (four females, mean age 29.7 years, SD = 11.3 years), and 19 individuals participated in Experiment 2 (ten females, mean age 24 years, SD = 5.0 years). They were recruited from the York University Undergraduate Research Participant Pool and received credit for taking part in the experiments. All experiments were approved by the York Ethics Board, and all participants signed informed consent forms. All experiments were performed in accordance with the Treaty of Helsinki.

Stimuli

Detection stimulus

The stimulus that the participants were asked to detect was a pulse for 100 ms of 250-Hz vibration of variable intensity controlled by a 64-bit sound card. Stimuli were presented by C2 tactors (Audio Research, California) applied to dorsal surface of the middle of the left forearm halfway between the inner angle of the elbow and the wrist crease (Fig. 1). The tactor was held in place by a surgical bandage wrapped loosely several times around the arm.

Masking stimulus

The masking stimulus was provided by a Magic Wand (Hitachi, Japan) vibrator applied to the skin. The head of this vibrator is spherical with a diameter of about 4 cm. It was applied lightly to the skin making a contact zone of about 1 cm^2. Masking vibration was 83 Hz with the device set on "low". This provided a certain level of background sound that was constant throughout the duration of all the trials in the experiments. In Experiment 1, the masking stimulus was applied at one of two sites on the right arm (Fig. 1a), either at the point corresponding to the test site on the other arm or on the shoulder (as a control). For Experiment 2, the masking stimulus was applied at one of five sites equally spaced along the dorsal (outside) surface of the right arm (Fig. 1b), a control position (on the front of the shoulder), halfway up the upper arm (halfway between the outer angle of the elbow and the top of the shoulder), on the outside part of the elbow, halfway along the forearm at the point (corresponding to the test site on the other arm), and on the wrist (level with the ulna process). Since arm length varied between participants, vibration sites are described in percentage of arm length. The experimenter applied the masking stimulus by hand. For a given experimental block of 20 trials, the masking stimulus was left on throughout each block.

Procedure

Participants sat in a chair with their left arm on a table with a tactor on the middle of their left forearm (see above). The experimenter applied the masking stimulus to the pre-chosen body site and left it running in place while a block of 20 trials was conducted. Using a 2AFC paradigm, participants were presented with two 1-s periods marked by three beeps (5, 3 and 5 kHz; duration 100 ms) and identified in which period the touch was present. Stimulus intensity was controlled by a QUEST psychometric procedure (Watson

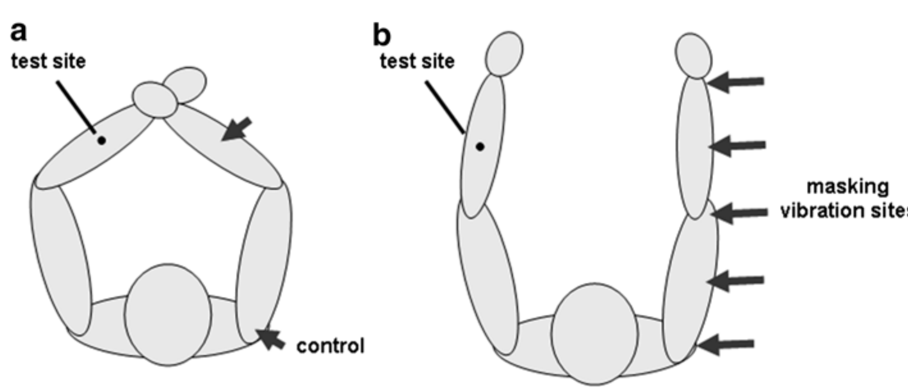

Fig. 1 Showing the sites of masking (*arrows*) and test stimuli (*dots*) for two arm positions. **a** For Experiment 1, the right hand was resting lightly on the left wrist. Only two masking sites were used. **b** For Experiment 2, the arms were held parallel to each other. For this experiment, there were five equally spaced masking sites. The test site was the same in both experiments

and Pelli 1983) running in MATLAB (version 2011b) on a PC. Each block of 20 trials was repeated twice for each masking condition, for a total of 40 trials for each condition. Each block took about 40 s. Participants wore a blindfold throughout the experiment.

For Experiment 1, participants rested their right hand lightly on top of the left wrist throughout the experiment (Fig. 1a). Two conditions were tested—a control condition, with the masking stimulus placed on the right shoulder, and a masking condition, with the masking stimulus placed on the middle of the right forearm at the point corresponding to the location of the test site on the left arm. Thus, the experiment consisted of four blocks, with masking sites alternating between blocks. Participants reported in which period the stimulus occurred using foot pedals (Yamaha, FC5: left for first period, right for second period).

For Experiment 2, the right arm was positioned parallel to the left arm (Fig. 1b) with the right elbow resting on a cushion. Again, the experiment was conducted in a block design with two blocks per masking site run in a pseudorandom sequence for a total of ten blocks. The ordering of the five conditions was chosen for each subject using a Latin square and repeated twice in the same order.

Data analysis

The QUEST program returned an estimate of the threshold value. To visualize and confirm this, the participant's decision (correct or incorrect, 1 or 0) was plotted against the intensity used for each trial and fitted with a cumulative Gaussian (Eq. 1) using the curve fitting toolbox in MATLAB.

$$\text{Percent correct} = 0.50 + 0.50/(1 + \exp(-(x - x_0)/b)) \tag{1}$$

where x_0 is the 75 % threshold value, x is the intensity tested, and b is the standard deviation. Statistical analyses were conducted on these values.

Out of the 19 participants used in Experiment 2, four participants' data had to be discarded because the QUEST was unable to find a reliable threshold value within 40 trials. Thresholds were converted to decibels relative to the "control" threshold measured when the masking stimulus was applied to the right shoulder using Eq. 2.

$$\text{dB} = 10 \times \log_{10}(\text{threshold/control threshold}) \tag{2}$$

Results

Experiment 1 (hands touching)

A paired-samples t test was conducted to determine whether the control condition differed from the masking condition. A significant effect was found, $t(9) = -3.585$, $p = 0.007$ (0.0035 one-tailed), with a 3.34 dB ± .97 increase in tactile detection threshold when the masking stimulus was applied. This is shown graphically in Fig. 2.

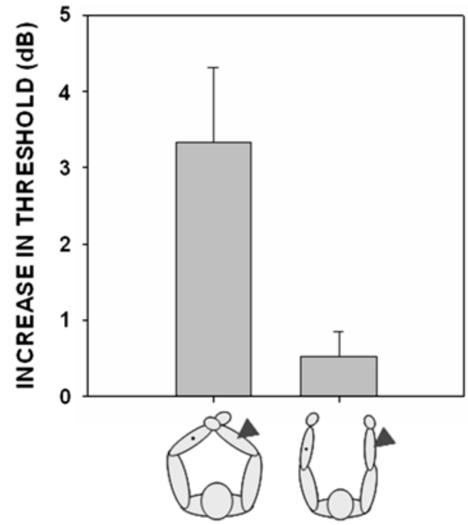

Fig. 2 The effect of arm position on the increase in tactile threshold at a site on the left forearm (*dot*) caused by the application of a masking stimulus (*triangles*) at the corresponding point on the opposite arm. The *left bar* is with the right hand resting lightly on the left wrist (Experiment 1), and the *right bar* is with the arms held parallel (Experiment 2). Threshold elevation is expressed in decibels relative to the control condition with vibrotactile stimulation applied to the shoulder. *Error bars* are standard errors

Experiment 2 (hands separate)

A paired-samples t test was conducted between the thresholds measured with the masking stimulus at the control site and at the corresponding site on the other arm while the arms were held parallel. A significant difference was found, $t(14) = -1.752$, $p = 0.05$ (one-tailed), with a 0.52 dB ± .33 increase in threshold compared to when the masking stimulus was applied to the shoulder. Tactile detection thresholds measured on the dorsal surface of the left forearm were systematically affected by the position of the masking stimuli applied to the right arm. This variation is shown in Fig. 3 in which threshold elevation (relative to masking stimulus applied to the shoulder) is plotted as a function of masking stimulus location (expressed as percentage of arm length). A best-fit Gaussian through the means has a peak at 64 % arm length (test site was at 75 %) with a standard deviation of 29 %.

Experiment 1 versus Experiment 2: effect of arm location

To determine whether arm position had an effect on the extent of masking, an independent-samples t test (corrected

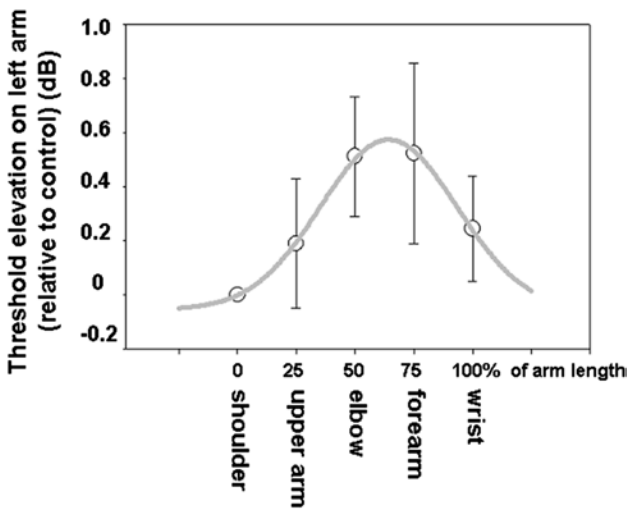

Fig. 3 Thresholds on the left forearm as a function of masking stimulus location on the right arm. All thresholds are expressed in decibels relative to the control thresholds obtained when the vibrotactile stimulus was applied to the right shoulder. The control is plotted as zero on the graph. The peak and width of the best-fit Gaussian curve (*solid line*) are 64 % and ±29 % of arm length, respectively. *Error bars* are standard errors

using Levene's test for equality of variances) was conducted on the threshold elevations in Experiments 1 and 2 when the masking stimulus was on the corresponding point of the other arm. This revealed that when the arms were in contact, tactile detection thresholds were significantly higher (masking was more effective) than when the arms were separated, $t(9.872) = 4.335$, $p = 0.002$, with a mean difference of 2.81 dB ± 1.02. This is shown in Fig. 2.

Discussion

We have demonstrated contralateral masking between one forearm and the other with a spatial tuning (standard deviation) of about 29 % of arm length. The masking effect was considerably stronger if the arms were touching compared with if they were parallel (3.3 dB compared with 0.52 dB).

Comparison with previous reports

Ipsilateral tactile masking has been extensively investigated since von Békésy using electrical stimulation (Uttal 1960; Schmid 1961), pressure (Abramsky et al. 1971) and vibrotactile stimulation (Sherrick 1964; Gilson 1969). Contralateral tactile masking, in contrast, has been regarded mostly as a curiosity, and there has been little investigation since the 1960s when it was established that the effect shared temporal tuning properties with its ipsilateral cousin (Halliday and Mingay 1961; Schmid 1961; Sherrick 1964; Bird 1964; Abramsky et al. 1971). When a stimulus is present on corresponding points on both sides of the body, sensitivity (Gilson 1969; Snyder 1977) and discrimination performance (Harris et al. 2001) are reduced and the ability to locate near-threshold stimuli applied to fingers of the other hand is also degraded (Schweizer et al. 2000; Braun et al. 2005). Perhaps, contralateral masking is an epiphenomenon of the body's representation in the brain: some aspects of body representation appear to be more concerned with body regions rather than body sides although studies until now have been largely restricted to looking at the hands (Harris and Diamond 2000; Braun et al. 2005).

One study has looked at the spatial properties of contralateral masking using a test probe on the thigh. The effect of a contralateral mask seems to falls off with longitudinal distance from the test site (Gilson 1969) although Gilson interpreted this as more of a temporal phenomenon. His unexpected observation that ipsilateral and contralateral masks were equally effective for the thigh (whereas ipsilateral masking is much more effective than contralateral masking for arm and hand studies, see above) led him to suggest that the neural organization of the thigh region might be different from the upper limbs. Our study is the first to look at the spatial tuning of the masking effect on the forearm. We found a large spatial spread of effect of ±29 % of the arm length: much larger than the underlying cutaneous receptive fields. What could such a large spatial spread correspond to?

Neural basis of contralateral masking

Early studies of the somatosensory cortex found cells in S1 that were responsive to stimuli from either side of the body (Mountcastle and Powell 1959). These were thought to be largely a "midline" phenomenon and were relatively rare. However, at the cortical sites of higher body maps, many cells have been found that are responsive to stimuli from either side of the body and that have receptive fields on the arm and hand (Iwamura et al. 1993, 1994; Taoka et al. 1998). Moreover, imaging studies in humans have shown overlap between activity evoked by ipsilateral and contralateral stimulation in both S1 and S11 (Noachtar et al. 1997; Tamè et al. 2012). The bilateral cells on the forearm have very large receptive fields, often covering the whole forearm (Taoka et al. 1998). These cells then provide a signal that an arm was touched but do not distinguish which arm.

Mutually inhibitory pathways have been demonstrated between tactile maps in area 3b of the somatosensory cortices for the hand region (Reed et al. 2011) that might underlie the phenomenon of contralateral masking reported here. These connections have been postulated as being particularly significant during bimanual manipulations, but the callosal anatomy (Killackey et al. 1983; Taoka et al. 2000) suggests that this might be a general principle reflecting the somatosensory organization of all regions of the body (Alliusi et al. 1965).

Effects of posture

Intriguingly, Tamè et al. (2011) showed that contralateral masking (quantified by an interference task) was essentially abolished if the hands did not have the same orientation. Here, we indicate a dramatic effect of posture. We take this variation with posture to indicate that the enhanced discrimination of which arm was stimulated is only useful if the two arms are in some particular orientation. When the two arms are in differing postures, they are likely to be involved in some exploratory task during which such "lateral inhibition" may perhaps be less useful. Another possibility why the masking was more effective when the hands were close could be due to the physical contact of the arms (c.f., Frings and Spence 2013; Gallace and Spence 2011; Haggard et al. 2006). The contribution of posture to this contralateral masking effect will be the subject of a future study aimed at discovering the "optimal" relative arm positions needed for maximum contralateral inhibition, whether the position effectiveness depends on the position of only the masking arm or both, and whether skin contact has an effect.

Conclusions

Ipsilateral masking reveals principles of lateral inhibition that are essential for enhancing detection and discrimination under natural circumstances. We postulate that contralateral inhibition represents a mechanism that achieves the same aim but on a much cruder scale. Whereas ipsilateral inhibition enhances spatial perception at the scale of the area of skin on which the touch is felt, we postulate that contralateral inhibition may enhance spatial perception at the level of which side of the body is stimulated. By reducing sensitivity on the side of the body opposite to a touch, a comparison between the two sides would be enhanced, just as a comparison between two adjacent skin regions is enhanced by local inhibitory circuits. The consequences for the hand during bimanual manipulation may be to aid tactile proprioceptive integration by helping distinguish the hand of origin of a tactile sensation. Although this seems unlikely to be as significant for other parts of the body that are rarely touched at the same time, it may assist orientation and generally enhance the body's representation in the brain.

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