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RESEARCH ARTICLE

Long-range tactile masking occurs in the postural body schema

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Abstract Long-range tactile masking has been reported between mirror symmetric body locations. 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. Do such effects occur before or after posture is added to the body schema? Here, we address this question by exploring the effect of arm position on long-range tactile masking. The influence of arm position was investigated using different positions of both the test and masking arms. Tactile sensitivity was measured on one forearm, while vibrotactile-masking stimulation was applied to the opposite arm or to a control site on the shoulder. No difference was found in sensitivity when test arm position was varied. Physical contact between the arms significantly increased the effectiveness of a masking stimulus applied to the other arm. Long-range masking between the arms was strongest when the arms were held parallel to each other and was abolished if the position of either the test arm or the masking arm was moved from this position. Modulation of the effectiveness of masking by the position of both the test and masking arms suggests that these effects occur after posture information is added to the body's representation in the brain.

Keywords Masking · Somatosensory sensitivity · Long-range tactile masking · Tactile detection thresholds · Body representation

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Introduction

The representation of the body in the brain can be explored by using tactile masking to reveal details of which parts are connected to others. Masking is when the presence of one stimulus affects the perception of another stimulus. In the case of tactile masking, a stimulus at one location on the body surface alters the perception of touch at another location. Classic masking effects have been shown in which tactile sensitivity is affected when one touch is close to another on the body surface (von Békésy 1967) which reveal details of peripheral interactions such as lateral inhibition. However, longer-range effects between points quite separate on the body have also been demonstrated. Long-range tactile masking can be used to explore the representation of the body in the brain.

Long-range tactile masking has been reported between mirror symmetric points on the hand and arm (that is, touch at a particular point on one limb has effects specifically at that same point on the other limb, Sherrick 1964; Braun et al. 2005; Tamè et al. 2011; D'Amour and Harris 2014a) and between the front and back of the body (D'Amour and Harris 2014b). These studies reveal unexpected connections between distantly separated parts of the body suggesting a nonlinear arrangement of the body representation. Long-range reciprocal inhibitory pathways have been demonstrated between tactile maps in the somatosensory cortices (Reed et al. 2011; Tamè et al. 2015) which may provide a neurophysiological explanation of these long-range interactive effects. Taken together, these findings suggest a general principle of contralateral inhibition between corresponding points on each side of the body that may serve to enhance the ability to distinguish touches on the two halves of the body. At what functional stage in the representation process might these connections emerge? The pioneering work of

Head and Holmes (Head and Holmes 1911) suggested that a superficial body schema (a representation of the body in the brain) is first created in a canonical position with posture being added later to form what they called the postural schema. Their seminal study has since obtained substantial support (Shuler et al. 2001; Azañón and Soto-Faraco 2008; Schntz-Bosbach et al. 2009; Azañón et al. 2010a, b). The present experiment investigates whether long-range masking effects occur at the level of the superficial body schema or after postural information has been added to form a postural schema.

To interpret tactile information about objects explored by touch, it is necessary to integrate tactile information with knowledge about how the touching surfaces are arranged in space. That is, it is necessary to integrate tactile and posture information. Many studies have shown the importance that body posture plays in tactile processing. Tactile discrimination and identification of fingers and hands are influenced by body posture (Riemer et al. 2010). Long-range contralateral masking also seems to depend on the how limbs are arranged: for example, contralateral masking from one fingertip to another is disrupted if one hand is palm up and the other palm down (Tamè et al. 2011). However, such studies have generally concentrated on the hands.

The goal of this study was to explore whether long-range masking effects occur before or after postural information has been added to the body representation by investigating the influence of various arm positions. In our previous study, (D'Amour and Harris 2014a), we found a difference in the strength of the masking effect when the arms were together or separate, but it was not clear whether it was caused from actual skin contact or arm position. The first goal of the current study was therefore to answer this question by testing contralateral masking when the hands were touching and when they were extremely close but not touching. To systematically examine the role of body posture on long-range tactile masking, the effect of masking was tested with different positions of both the test and masking arms. We also measured sensitivity thresholds in different arm positions during control vibration to rule out the possibility of arm position modulating sensory thresholds directly. The study consisted of ten conditions designed to test four specific hypotheses. Hypothesis 1: the relative position of the arms will not alter sensitivity to vibrotactile stimulation. Hypothesis 2: the strength of the between-arms masking effect will be stronger when the two arms are touching compared to when they are in the same relative positions but not touching. Hypotheses 3: the position of the test arm will affect the strength of the between-arms masking effect. Hypothesis 4: the position of the masking arm will affect the strength of the between-arms masking effect.

Methods

Participants

Seventeen participants took part in the study (eleven females, mean age 20.8 years, SD ± 3.8 years). They were recruited from the York University Undergraduate Research Participant Pool and received course credit for taking part in the study. The study was approved by the York Ethics Board, and all participants signed informed consent forms. The study was performed in accordance with the 1964 Declaration of Helsinki.

Stimuli

Test stimulus

The tactile stimulus was a 100-ms pulse of 250-Hz vibration of variable intensity controlled by a 64-bit sound card played through a C2 tactor (Audio Research, California). The tactor was applied to the dorsal surface of the middle of the left forearm, half way between the inner angle of the elbow and the wrist crease. 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 right arm. The frequency of vibration was approximately 83 Hz (device set on "low"). The head of the vibrator is spherical, and by holding it lightly against the skin, the contact area was about 1 cm^2 of skin although the vibration would have spread over a larger area. The vibrator produced a certain level of background sound (a buzzing noise) that was constant throughout the duration of all the trials in the experiment. The masking stimulus was applied at one of two sites on the right arm, either at the point corresponding to the test site on the other arm, or on the shoulder as a control site (see inserts to Fig. 1). The vibrator was held in place by the experimenter, and continuous vibration was applied throughout each block of trials.

Experimental design

To explore the effect of arm position on masking, both test arm and masking arm positions were varied systematically to provide ten conditions. The test site was always the same on the left forearm, and the testing procedure for measuring thresholds at this site for each condition was identical. The analysis then compared various conditions to test the four hypotheses described in the introduction.

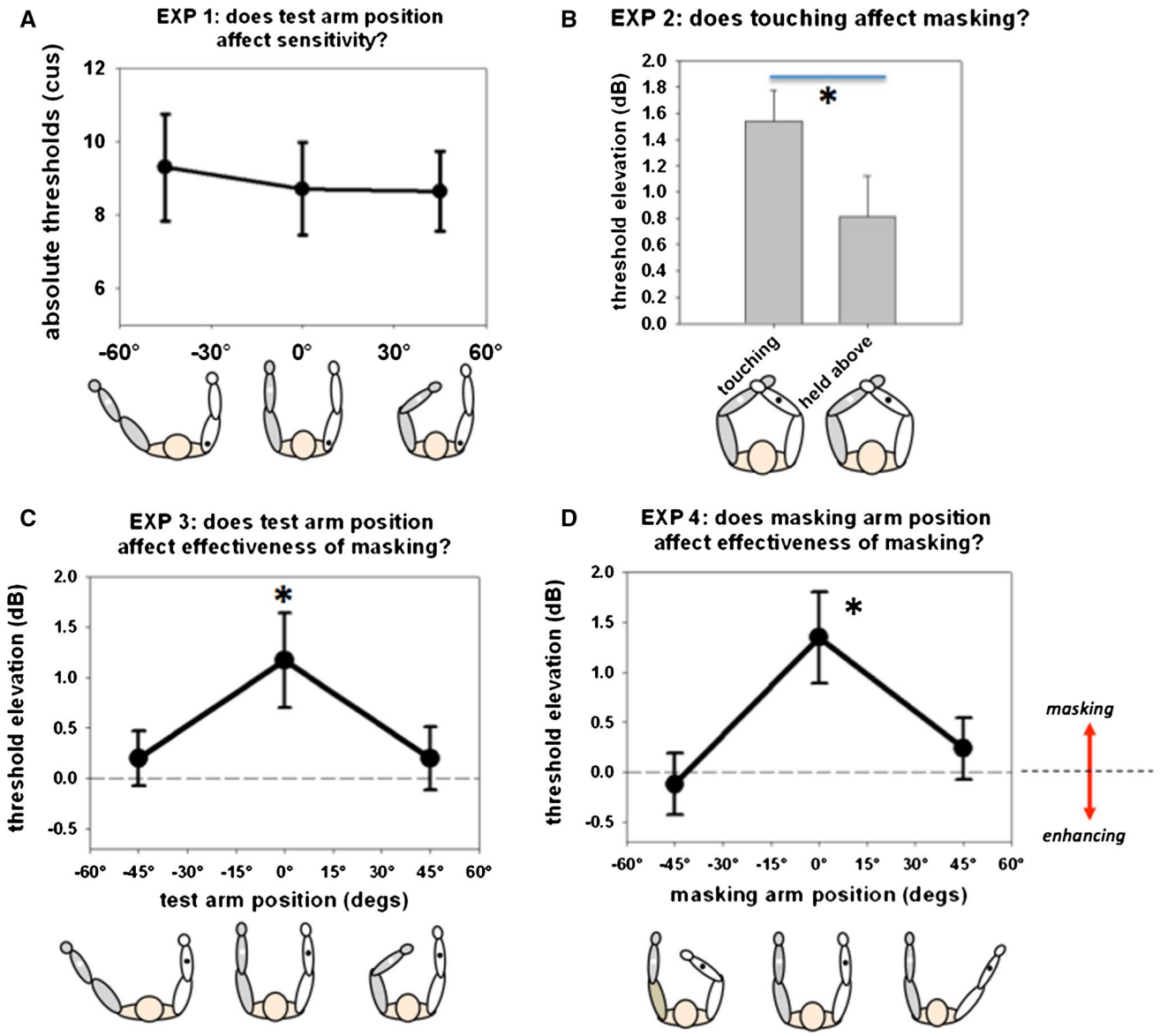

Fig. 1 Effect of arm position on long-range tactile masking. The test arm (left arm) is shown in *grey*, and the masking arm (right arm) is shown in *white*. The test site is shown as a *white dot*, and the probe site is shown as a *black dot*. **a** The sensitivity of the test arm was unaffected by its position. Control stimulation was applied on the shoulder (*black dot*) during these measurements. **b** Comparison between the effect of masking when the arms were touching and when they were separated vertically by 2 cm. The *asterisk* indicates that the increases were different from each other with $p < .05$. **c** The effect of test arm (grey arm) position and **d** masking arm (white arm) position on the effectiveness of inter-arm masking. The test (*white dot*) and masking stimuli (*black dot*) were positioned on corresponding points on the two arms. *Asterisks* indicate increases that were significantly different from 0. Standard errors are shown

The effect of test arm position on thresholds (hypothesis 1) was investigated by comparing three conditions—test arm (left arm, shown in grey in the figure) positioned to the left, straight ahead, and to the right while control vibration was applied to the shoulder (Fig. 1a). The effect of touching on between-arms masking (hypothesis 2) was investigated by comparing two conditions—one with the hands touching and a second with the arms in the same position but with the right hand held 2 cm above the left hand while applying the masking stimulus to the corresponding site on the right arm (Fig. 1b). To explore the effect of arm position on masking, both test arm and masking arm positions were varied. The effect of test arm position (hypothesis 3) was investigated with two conditions—the test arm (left arm) was positioned to the left and to the right (Fig. 1c). The effect of masking arm position on the strength of the between-arms masking effect (hypothesis 4) was explored by testing two conditions—the masking arm was positioned

to the left and to the right (Fig. 1d). To compare differences in positions, thresholds were also measured in one condition—when both arms were straight out and parallel to each other. Thus there were a total of ten arm configurations tested.

Procedure

Blindfolded participants sat in a chair with their left elbow resting on a table and the right arm resting on a cushioned armrest. The participants' arms were configured for one of the ten conditions. Using a 2AFC paradigm, participants were presented with two 1-s periods for each trial, delineated by three auditory beeps (5, 3 and 5 kHz; duration 100 ms). They identified in which period a touch was presented on their left (test) arm using foot pedals (Yamaha, FC5: left for first period, right for second period). Stimulus intensity was controlled by a QUEST adaptive staircase psychometric procedure (Watson and Pelli 1983) running in MATLAB (version 2011b) on a PC to hone in on the threshold values (details below). The whole study consisted of ten conditions and was run in a single session. Each condition had 40 trials, which was divided into two blocks of 20 trials (each block took less than 2 min). Block order was determined by a Latin square and counterbalanced across participants.

Data analysis

The QUEST program returned an estimate of the threshold value. The QUEST algorithm assumes the observer's psychometric function follows a Weibull distribution and adaptively determines the next stimulus intensity to be presented on the basis of the participant's response to the previous trials. As the experiment goes on, knowledge on the observer's psychometric accumulates and each new value tested (based on the mean of an accumulating probability density function—see Watson and Pelli 1983 for details) becomes progressively more accurate.

Firstly, we examined participants' data for each condition to validate the accuracy and efficiency of the QUEST procedure and to check the QUEST's performance in order to determine whether reliable thresholds were obtained within 40 trials. To do this, we plotted the intensity values for the 40 trials that the QUEST tested to visualize whether the QUEST had converged on a reliable threshold value. If the data for the last 20 trials were stable, the QUEST was deemed to have converged. If not the data were flagged as unreliable.

Secondly, the participant's decision for each trial (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.

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

where x is the intensity, x_0 is the 75 % threshold value, and b is the standard deviation. The threshold value obtained was compared with the QUEST threshold value. If the two threshold values were substantially different (differed by more than 10 %), the data were flagged as unreliable.

Thresholds were measured in arbitrary units. The aim of these experiments was to compare thresholds obtained under different conditions. Therefore, the data to be used to test hypotheses 2–4 were expressed in decibels. In order to convert thresholds to decibels, it was necessary to determine a control threshold from the three control conditions where vibration was applied to the right shoulder with the test arm in the three tested configurations (Fig. 1a). The control thresholds were obtained from the conditions used to test hypothesis 1 (which were not converted into decibels but used as the control values to convert all the other data). Since no difference was found between these conditions (see results), the three thresholds were combined into a single control threshold for each participant. Only the control data that met the above two criteria were included in the average. Each control value was used to convert all that participant's data into decibels using Eq. 2.

$$\text{dB} = 10 * \log_{10}(\text{threshold}/\text{control threshold}) \quad (2)$$

After conversion to dB, two further criteria were applied. First, the data were put into SPSS and descriptive statistics were run including testing dispersion, distribution, normality, and boxplots. Data from these analyses that were shown on the boxplots to be outliers were flagged. Secondly, data that were more than ±2 standard deviations from the mean were also flagged.

Data that had been flagged more than once were considered to have failed to meet our criteria and were discarded. If a participant had data in only one condition that needed to be discarded, we removed that participant's data only from the analysis of the hypothesis for which those data were relevant (for example, in "testing hypothesis 3", if a participant's data were considered an outlier for one of the three relevant conditions, we removed all three conditions, but not all 10 conditions). Since most of the participants did not perform optimally in all 10 conditions, this was a way to maximize the use of the data collected instead of just completely removing all the data from a participant if they performed poorly in just one or two conditions.

Statistical analyses were conducted on these values. Repeated measures analysis of variances (ANOVAs), with alpha set at $p < .05$, and paired sample t tests using Bonferroni corrections were used for data analysis. Planned comparisons were used to test a priori hypotheses.

Results

Testing hypothesis 1: Does arm position affect absolute detection thresholds?

Figure 1a shows the effect of test arm position on sensitivity with control stimulation applied on the shoulder. A repeated measures analysis of variance (ANOVA) was conducted to determine whether any change in tactile detection thresholds occurred between the three arm positions. No main effect was found, $F(1.450, 23.194) = .428$, $p = .656$, $\eta_\rho^2 = .026$, thus confirming that sensitivity was not affected by position of the arm during control vibration.

Testing hypothesis 2: Does touching matter?

Comparison between the amount of masking found when the arms were touching and when they were separated by 2 cm is shown in Fig. 1b. Both conditions were significantly different from zero: hands touching $t(14) = 6.605$, $p < .001$, two-tailed, hands above $t(14) = 2.619$, $p = .02$, two-tailed. A paired sample t test revealed that skin contact had a significant effect on the extent of masking, $t(14) = 2.875$, $p = .012$, two-tailed. Tactile thresholds increased by .73 dB ± .25 when the hands were touching compared to when the right hand was held 2 cm above the left hand.

Testing hypothesis 3: Effect of test arm position

The effect of test arm position on contralateral masking from the right arm is shown in Fig. 1c. The only significant threshold increase was when the hands were parallel $t(9) = 2.492$, $p = .043$, two-tailed. A repeated measures ANOVA was conducted and a significant main effect of test arm position, $F(1.254, 11.286) = 4.781$, $p = .044$, $\eta_\rho^2 = .347$ was found (corrected with Greenhouse-Geisser correction). Planned comparisons revealed significant effects for thresholds to decrease when the test arm was moved to the left, $t(9) = -2.280$, $p = .049$, two-tailed (MD = −.967, SE = .424) and right $t(9) = -2.270$, $p = .049$, two-tailed (MD = −.968, SE = .427) compared to when it was straight out and parallel with the masking arm.

Testing hypothesis 4: Effect of masking arm position

Threshold increases, expressed in decibels relative to the control thresholds, are plotted in Fig. 1d as a function of masking arm position. The only significant threshold increase was when the hands were parallel, $t(10) = 2.946$, $p = .015$, two-tailed. To investigate the effect of masking arm position on the effectiveness of masking, a repeated measures ANOVA was performed revealing a main effect of masking arm position, $F(2, 20) = 3.877$, $p = .038$, $\eta_\rho^2 = .279$, meaning that the position of the masking arm has an effect on contralateral masking of stimuli on the left arm. A similar effect of reduced thresholds was observed when the masking arm was positioned left, $t(10) = -2.551$, $p = .029$, two-tailed (MD = −1.465, SE = .574) and right, $t(10) = -1.834$, $p = .096$, two-tailed (MD = −1.109, SE = .604) compared to when it was straight.

Discussion

The goal of the present study was to examine the effect of arm position on contralateral tactile masking. We demonstrated that varying the position of either the test arm or the masking arm to take them out of the parallel position strongly reduced the contralateral masking effect. We also showed that physical contact between the arms significantly increased the effectiveness of a masking stimulus applied to the other arm.

The effect of arm position

Displacing either the test or masking arm from the aligned configuration broke the masking effect. This suggests that long-range tactile masking affects the representation of the body in the brain at a point after posture information has been added. Whether this was because the arms were not lined up with the canonical representation (Wolpert et al. 1998; Tsakiris and Haggard 2005; Costantini and Haggard 2007; Corradi-Dell'Acqua et al. 2009; Longo et al. 2010) or just not lined up with each other is an open experimental question. However, if the arms were to be aligned with them both arranged at, say, 45° to the left, it would produce a confound as one arm would necessarily need to cross the midline making this a hard hypothesis to test. The increase shown in Fig. 1b when the arms were both bent inwards slightly is more compatible with the canonical alignment requirement because in this case the arms were not aligned with each other but were instead in a posture that could potentially correspond to an internal canonical position.

Many aspects of tactile perception are affected by posture, with many studies showing profound effects when body posture is crossed. Having the fingers interleaved caused a decrease in direction discrimination performance compared to when fingers are in the normal anatomical posture (Zampini et al. 2005). These results match other findings showing impaired performance in tactile temporal order judgment (TOJ) tasks when hands are crossed over the midline (Yamamoto and Kitazawa 2001; Shore et al. 2002; Craig 2003; Craig and Belser 2006). When the hands are placed in the normal anatomical posture, better

performance is almost always observed. Other studies have shown improved performance in tactile TOJ tasks when the hands are placed far apart rather than close together (Shore et al. 2005; Gallace and Spence 2005). These results provide support for the idea that the representation of vibrotactile stimuli used to make tactile TOJs is not purely somatotopic. Posture information is also taken into account when tactile information is used to create tactile apparent motion (Harrar et al. 2008).

Since we have shown that the effect of masking is modulated by posture, we conclude that the effect occurs not at the level of the primary somatosensory cortex (SI), but at the level of the postural schema (after posture information has been added to the representation in the brain). Neurons as early as the secondary somatosensory cortex (SII) are modulated by posture (Fitzgerald et al. 2004); however, it is not until the superior parietal lobule (SPL) that full limb posture is encoded (Sakata et al. 1973; Parkinson et al. 2010). We postulate that this may be the site where these long-distance masking effects are modulated.

Why might tactile masking be modulated by arm position?

The functional significance of why touches on one part of the body may have effects on thresholds on remote sites is not obvious. It may serve a function of highlighting or "pulling out" a stimulus in the same way as local lateral inhibition is known to do in so many aspects of sensory processing (von Békésy 1967). Or it may be related to a developmental process (Simpson 1990). Intriguingly it may be connected to a well-known tactile interaction between remote sites that forms the basis of acupuncture (see Leung 2012 for a review) although it is unclear whether the position of the limbs has any modulatory influence there. We feel that the modulating effect of posture is unlikely to be functional but perhaps provides a clue as to the level in the brain at which this intriguing phenomenon appears.

The effect of touching

We have demonstrated that physical contact between the arms enhances the masking effect between them (Fig. 1b). We do not know whether this is due to possible physical transmission of the vibrations from the other arm when the arms are touching, or whether the arms are treated more as a unit when the arms are physically connected (Haggard et al. 2006; Gallace and Spence 2011; Frings and Spence 2013). Frings and Spence (Frings and Spence 2013) showed, using negative tactile priming, that if the arms were made into a unit by holding the hands together, this enhanced negative priming. They also repeated the same experiment except that the participants wore gloves. Removing skin contact by wearing gloves was enough to break the formation of a common unit and remove the transfer of negative priming.

Touching hands thus seems to create a fused "arm unit" with strong connections between each side supported by the close ties between the arms indicated by across-the-body masking (D'Amour and Harris 2014a) and bilateral neurophysiological responses even at the level of S1 (Iwamura et al. 1994; Taoka et al. 1998, 2000; Iwamura et al. 2002; Nihashi et al. 2005; Braun et al. 2005; Hlushchuk and Hari 2006; Fabri et al. 2006; Tamè et al. 2012, 2015).

Conclusions

Contralateral long-range tactile masking has been known since the 1960s. However, it seems to have been regarded as a curiosity without a conceptual framework for interpretation. These are the first experiments to demonstrate that this phenomenon is dependent on arm position and our data represent a challenge for interpreting the structure of the body representation in the brain. The representation may look as strange and counterintuitive as the original horribly distorted homunculi drawn by Mrs. Cantlie to illustrate Wilder Penfield's discovery of the body's representation in the somatosensory cortex (Schott 1993).

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