THE CONNECTION BETWEEN BODY REPRESENTATION AND TACTILE SENSATION THRESHOLDS

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ABSTRACT

In order to accurately interpret tactile information, the brain needs to have an accurate representation of the body to which to refer the sensations. Despite this, body representation has only recently been incorporated into the study of tactile perception. The effect of body representation on tactile thresholds was explored in two different ways. First, tendon vibration illusions were used to investigate whether distortions of body representation affect tactile sensations. Tactile acuity and sensitivity were increased when perceived size of the arm and waist were altered. Secondly, masking was used to investigate whether stimulation to one part of the body representation alters thresholds at other sites. Effects of contralateral masking on the arms was found, along with spatial tuning of this effect. Masking through the body was also demonstrated by measuring the effect of a masking stimulus on the back on the tactile sensitivity of the corresponding point on the front.

ACKNOWLEDGMENTS

I would like to thank my supervisor Dr. Laurence Harris for his guidance, support and encouragement. I would also like to thank my lab mates for their support.

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CHAPTER 1:

General Introduction

Our body is unique, fundamental, and essential for every task that we perform in day-to-day life. Knowledge about body posture, body position, body size, and body structure are required to extract the basic properties that we use to create perceptions of our body as a rather special physical object. We also rely on our body to provide essential context to the interpretation and processing of stimuli, such as visual, auditory, vestibular, or tactile information, from our complex sensory systems. Recently emerging studies have shown that much processing of sensory information is done with reference to a representation of the body. For example, interpreting stereopsis requires a knowledge of how far apart the eyes are and how high they are above the ground (ref Ian's 3 vol book on Seeing in Depth), interpreting interaural timing differences requires a knowledge of the distance between the ears (ref any sound localization paper) and information about the position and movement of the head. The connection between body and interpreting sensory information is particularly obvious for the tactile sense because interpreting tactile information requires knowledge not only of which areas of skin are exposed to pressure but also the configuration of the body and hence the location of that patch of skin in space and relative to other body parts. To know that we are holding a pen, for example, requires knowledge not just of the pressure points but also the organization of the fingers involved in the grip. This thesis takes this body-sensory integration one step further. Before we can discuss how the body representation might be involved in perception we need to introduce some terms.

1.1. Body Representation

Body representation involves the notion that there is a neural representation of the body in the brain to which other senses and motor acts can be related. Sensory inputs from all the different body parts combine into such a global, multisensory body representation (Serino & Haggard, 2010). The idea that there is a body representation in the brain originates from clinical observations. Famous studies done by Head and Holmes (1911) based on neurological patients who suffered damage in the parietal region of their brains found that these patients could detect touch but not identify on which part of the body they had been touched. It was as if they no longer knew about the layouts of their own bodies. Further investigations by Head and Holmes suggested that there were at least two representations, one that coded the proportions and lay out of the body (this being the one missing in patient who could not tell where they were touched). Head named this the "body schema" (Head & Holmes, 1911). At a later stage information about the posture was added to create a postural schema. The later enables the coding of the spatial location of a touch relative to other body parts. For example, if the arm is raised then a touch on the hand is at a different point in space from if the same touch is experienced with the arm in some other posture. Curiously, the body schema does not seem to be limited to the physical boundaries of the body but can incorporate things temporarily attached to the body, such as a tool or even clothes. A quote from Head and Holmes classic 1911 paper indicates that body representation is far removed from the signals in the somatosensory cortex: "Anything which participates in the conscious movement of our bodies is added to the model of ourselves and becomes part of these schemata: a woman's power of localization may extend to the feather in her hat."

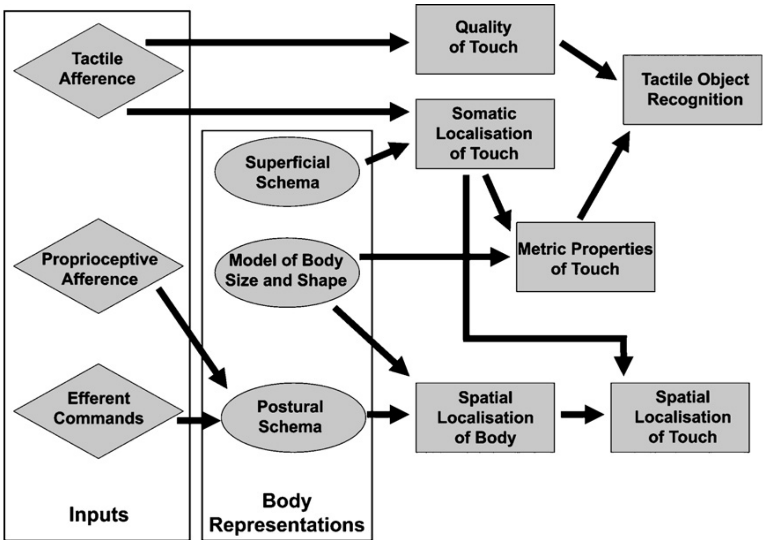
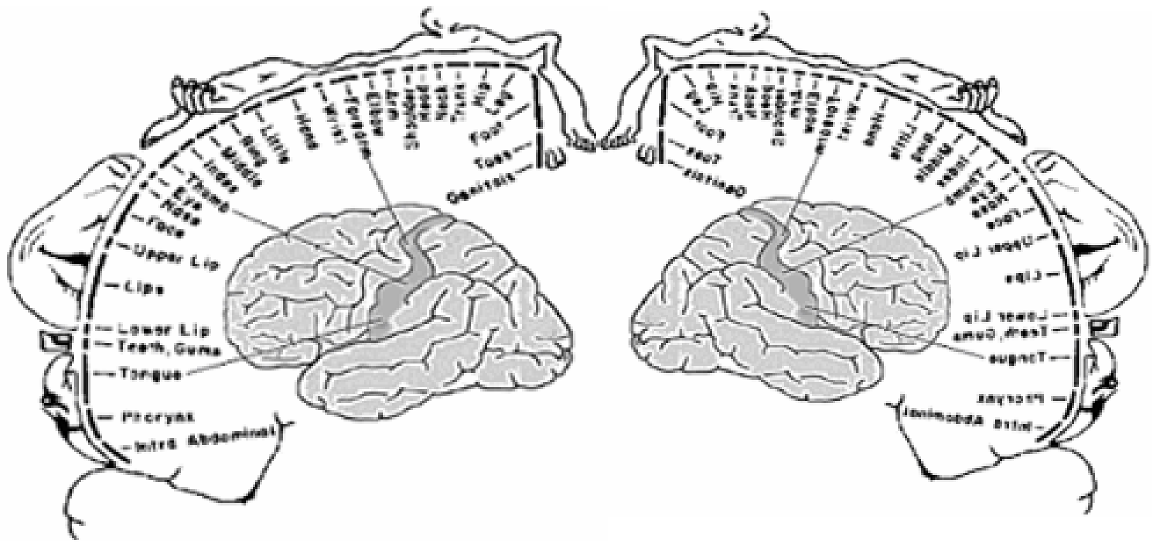


Figure 1. A model of somato-perceptual information processing which highlights the role of body representations in the construction of somatic percepts. Inputs are depicted as diamond shapes, body representations as ovals, and perceptual processes as rectangles. My thesis concentrates on the effects of the model of body size and shape on the "metric properties of touch". Taken from *Longo, Azañón, & Haggard (2010*)

In order to characterize different body representations, body schema, postural schema and body image are the typical classifications used (Kammers, van der Ham, & Dijkerman, 2006). Body image is a psychological construct that can often have little to do with a person's actual body. This thesis does not directly address this concept. Figure 1 represents a useful summary of the interplay between the different sensory inputs and the body representations to which they contribute. Here the term "body schema" (used with considerable confusion in the literature) has been replaced by "model of body size and shape”. This representation derives from the well-known heavily distorted representation of the body in the primary somatosensory cortex (Figure 2). The distortions there, first demonstrated by the pioneering work of Penfield (Penfield & Boldrey, 1937) are caused by the uneven distribution of touch receptors over the body surface. The fingertips, for example, are much more heavily innervated than the back and therefore get a larger representation in this early cortical map. The model of the body needs to adjust for such variations in order to represent the metric properties of touch because otherwise a touch on the finger tip of the same magnitude as one on the back would be perceived as stronger because of the greater number of nerve fibres activated. Similarly distances may otherwise be misrepresented as many receptive fields would separate two touches quite close together on the finger tips, but only a few for the same separation of touches on the back. My thesis looks at the interplay between “the body of body size and shape” and the metric properties of touch.



A

B

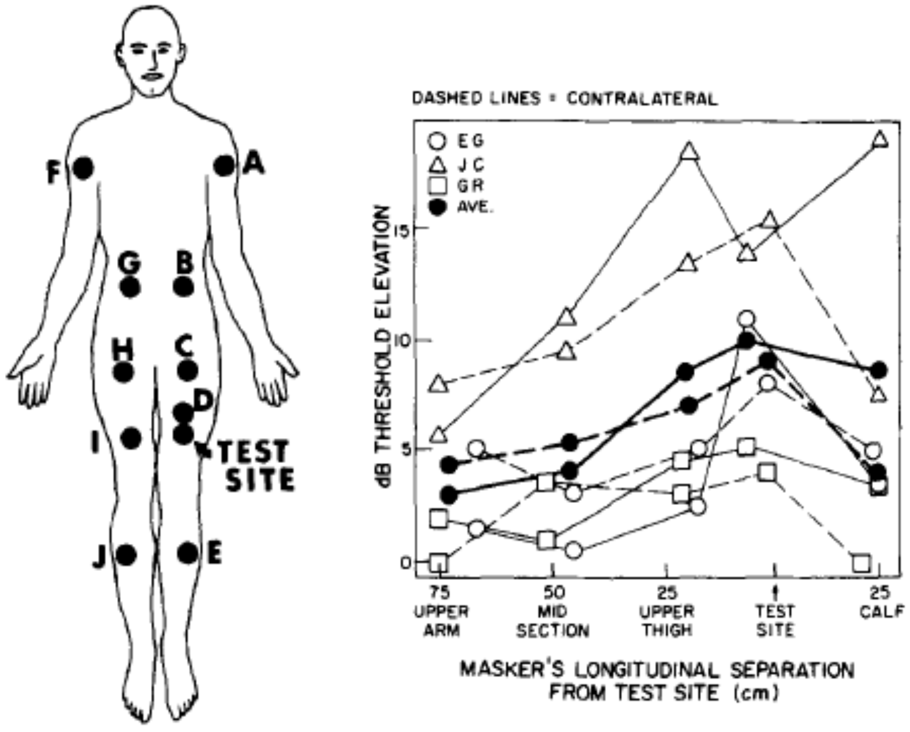
Figure 2. The map of the body in the somatosensory cortex. A. Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. Taken from *Penfield & Boldrey, 1937.* B. Distorted homunculus. Areas with more nerve fibres get more space in this map resulting in the familiarly distorted homunculus.

1.2. Tactile Perception and Body Representation

Many studies have focused on the effects that body representation has on visual and tactile perception. Altering the perception of the body in various ways impacts how we perceive stimuli, ourselves, and the world. The classic Pinocchio illusion has been used to alter the perceived length of a body part. The way that this illusion works is by using tendon vibration to alter the perceived position of the arm and therefore anything that the hand is holding, such as the tip of the nose. Lackner (Lackner, 1988) showed that the perception of changing limb size can also occur as a result of mislocalizing limbs using tendon vibration. de Vignemont, Ehrsson, & Haggard (2005) used this illusion to demonstrate that altering perceived arm length affects tactile distance perception on the distorted body part. However, up until the novel studies reported in this thesis, only subjective tactile perception tasks have been used in previous studies. If the “body model” of Figure 1 corrects for receptor densities in order to produce accurate and consistent perceived metrics of touch, it follows that alterations of this mapping process by changing the perceived size of a body part may disrupt this correction process. Such changes may be revealed in the perceived metrics of touch at the most basic level: detection and discrimination of pressure.

1.3. Tactile Masking

Masking is where a tactile stimulus at one location on the body surface alters the perception of a touch at another location. This is a technique pioneered by von Bekesy (v. Békésy, 1967) to reveal location interactions, especially lateral inhibition, between areas of skin that are adjacent on the body surface. However, longer-range effects between points quite separate on the body have been demonstrated. Tactile masking can be used to explore the representation of the body in the brain. Masking is when the presence of one stimulus affects the perception of another stimulus. Masking is a classic technique that has been used in visual, auditory, and tactile research, usually when the stimuli are close together to reveal local interactions. Long-range tactile masking has been reported between mirror symmetric points on the hand and arm (Braun, Hess, Burkhardt, Wühle, & Preissl, 2005; Sherrick, 1964) indicating a puzzling interplay between areas of the skin that are quite distant from each other. Figure 3 shows some of these effects.



A B

Figure 3. Tactile Masking. From Gilson (1969), showing the effect of stimulating at one site on detection thresholds measured at remote sites.

Such studies would seem to indicate some kind of linkage between remote areas of the body that may reveal details of the way the “model of body size” is arranged in the representation.

Mutually inhibitory pathways have been demonstrated between tactile maps in the somatosensory cortices (Reed, Qi, & Kaas, 2011) that might underlie such observations. A summary of some of these bilateral receptive fields is given in Figure 4. Long-range tactile masking and the extensive receptive fields that may underlie them 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.

I explored the generality of these findings by investigating both left/right and front/back long-range tactile masking on the arms and trunk.

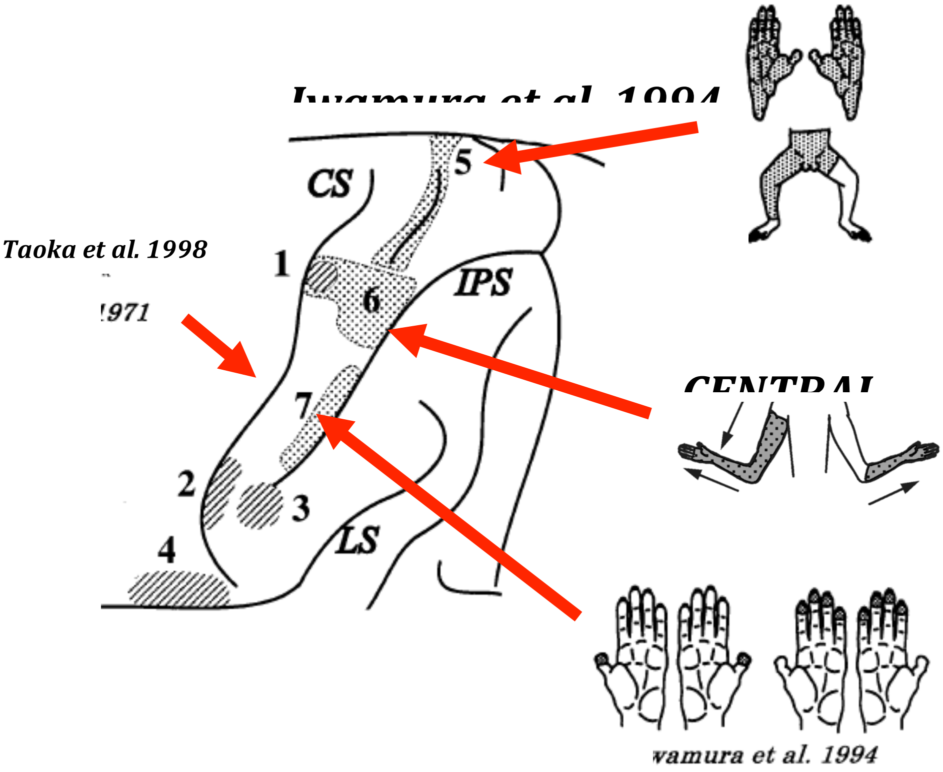


Figure 4. Bilateral receptive fields. Showing the receptive fields of some neurons found at the border between the somatosensory and parietal cortices that may represent the neural basis of long-range tactile masking.

1.4. The Current Studies

This thesis explores how body representation affects basic tactile sensation using two approaches. First, I asked how altering body representation might affect tactile acuity and sensitivity thresholds. To test this, perceived arm and waist size were altered using tendon vibration illusions and tactile thresholds were measured. These experiments are described in Chapter 2. My hypothesis is that altering the perceived size of the body will have direct consequences on the ability to detect pressure on the body and on tactile acuity. Second, I considered how vibration applied to one part of the body might affect tactile sensitivity thresholds at other sites. Such effects can tell us about how closely related components of the body's representation in the brain are linked. I used two experimental designs to answer this question: in Chapter 3, I examined contralateral masking between the forearms to explore whether the two sides of the body (that are initially processed separately with information from each half of the body going to the contralateral somatosensory cortex) are connected. My hypothesis was that corresponding points on the two sides of the body may be connected in some special way such that stimulation of one side would inhibit the detectability of touches on the corresponding point on the other side of the body. In Chapter 4, I consider how the back and front of the body may be connected. There is considerable evidence that body representation may have a visual component. If so, might unseen parts of the body be linked to visible parts? I investigated this by looking for signs of connection that might be revealed by tactile masking, through the body, between the front and the back of the trunk. My hypothesis was that I might find similar long-range masking effects between the front and back of the body that would suggest that those regions might be connected in the representation of the body in the brain.

CHAPTER 2:

Bodily Illusions Disrupt Tactile Sensations

The body of this text has been submitted to the *Journal of Experimental Psychology: Human Perception and Performance.* I have added sections 2.1.1., 2.6.2., 2.6.3., and 2.6.4. for this thesis.

2.1. Introduction

We perceive tactile sensations with reference to a central body representation that is built up from multisensory experience. Visual, proprioceptive, and tactile information are integrated to provide direct and indirect cues about body size and shape. The brain maintains but is also required to plastically adjust and update this internal body representation in response to changes in body shape during growth and development. The consequences of altered body representation on sensory perception have frequently been used as an indirect way of examining the nature and extent of this plasticity. Artificially altering body representation using various techniques may have serious consequences on many aspects of tactile perception. Surprisingly, the effects on fundamental sensations (as opposed to the perception that they can give rise to) such as tactile acuity and sensitivity are unknown.

Visually modifying the perceived size of the body, for example by viewing the body through a magnifying lens, is known to impact tactile perception (Kennett, Taylor-Clarke, & Haggard, 2001), tactile distance perception (Taylor-Clarke, Jacobsen, & Haggard, 2004), tactile size perception (Longo & Sadibolova, 2013), haptic perception (Bruno & Bertamini, 2010), pain perception (Mancini, Longo, Kammers, & Haggard, 2011; Moseley, Parsons, & Spence, 2008), the perceived size of objects and their perceived distance from the observer (van der Hoort, Guterstam, & Ehrsson, 2011), the rubber hand illusion (Pavani & Zampini, 2007), and motor control, such as grasping (Marino, Stucchi, Nava, Haggard, & Maravita, 2010). Even non-informative vision can improve tactile perception by generally enhancing somatosensory processing (Haggard, Christakou, & Serino, 2007; Kennett et al., 2001; Longo, Pernigo, & Haggard, 2011). Together, these observations suggest that visually changing perceived body size can alter the mental representation of the body and that these changes affect tactile perception. Distorting perceived body size and shape visually (Bruno & Bertamini, 2010; Marino et al., 2010; Moseley et al., 2008; Taylor-Clarke et al., 2004), proprioceptively (de Vignemont, Ehrsson, & Haggard, 2005; Lackner, 1988; Longo & Kammers, 2009) or with cutaneous anaesthesia (Gandevia & Phegan, 1999) provides further evidence of the complex relationship between tactile perception and the body representation to which it is referenced.

The well-known Pinocchio illusion (Lackner, 1988) is a proprioceptive illusion where vibration applied to the tendons of an arm while grasping the nose, creates an illusory lengthening of the nose. Using a modification of this illusion, de Vignemont, Ehrsson, and Haggard (2005) created an illusory elongation of the finger and found that perceived tactile distances were altered. When the finger felt longer, stimuli were reported as farther apart compared to a control condition. Ehrsson et al. (2005) used fMRI to examine the neural correlates of similarly induced perceptual changes during the "waist-shrinking illusion", and showed that brain changes occur in the cortices lining the left postcentral sulcus and the anterior part of the intraparietal sulcus during such perceptual alterations of the size of the body. It seems that proprioceptively induced illusions may be manipulating a mechanism of body representation in the brain.

While these findings have provided insight into understanding the connection between tactile perception and the sense of our bodies, the results pertain only to one area of tactile perception and do not necessarily apply to more basic tactile sensations such as intensity, acuity and location. Whether altering body representation using non-visually induced changes affects such basic tactile sensations is unknown. Here, we used a modification of the Pinocchio illusion to test whether altering perceived arm and waist size (Figure 5) might affect basic tactile sensations. Experiments 1 and 2 investigated whether illusory elongation or shrinkage of the arm affected tactile acuity and sensitivity. Experiments 3 and 4 tested whether tactile acuity and sensitivity were affected during illusory expansion and shrinkage of the waist. Since tactile judgments are made with respect to the body, a change in tactile ability would be expected if the brain were not able to update and recalibrate body representation during such sudden modifications of perceived body size.

2.1.1. Purpose and Hypotheses

The purpose of these experiments was to directly address whether altering perceived body size by non-visual manipulations could affect basic tactile sensations. Since earlier studies have shown that bodily illusions can impact the tactile perception of external objects, I predict that perceptually changing the size of the body will cause a disruption in body representation, which will in turn affect tactile sensations. The specific hypotheses for Experiments 1-4 are as follows:

1) Lengthening or shortening the perceived size of the arm will cause a reduction of tactile acuity on that arm.

2) Lengthening or shortening the perceived size of the arm will cause a reduction of tactile sensitivity on that arm.

3) Expanding or shrinking the perceived size of the waist will cause a reduction of tactile acuity on the stomach.

4) Expanding or shrinking the perceived size of the waist will cause a reduction of tactile sensitivity on the stomach.

Overall, these findings will further explore the implications that distorting perceived body size has on basic tactile sensations and may provide new insights into the importance that body representation has on sensory processing.

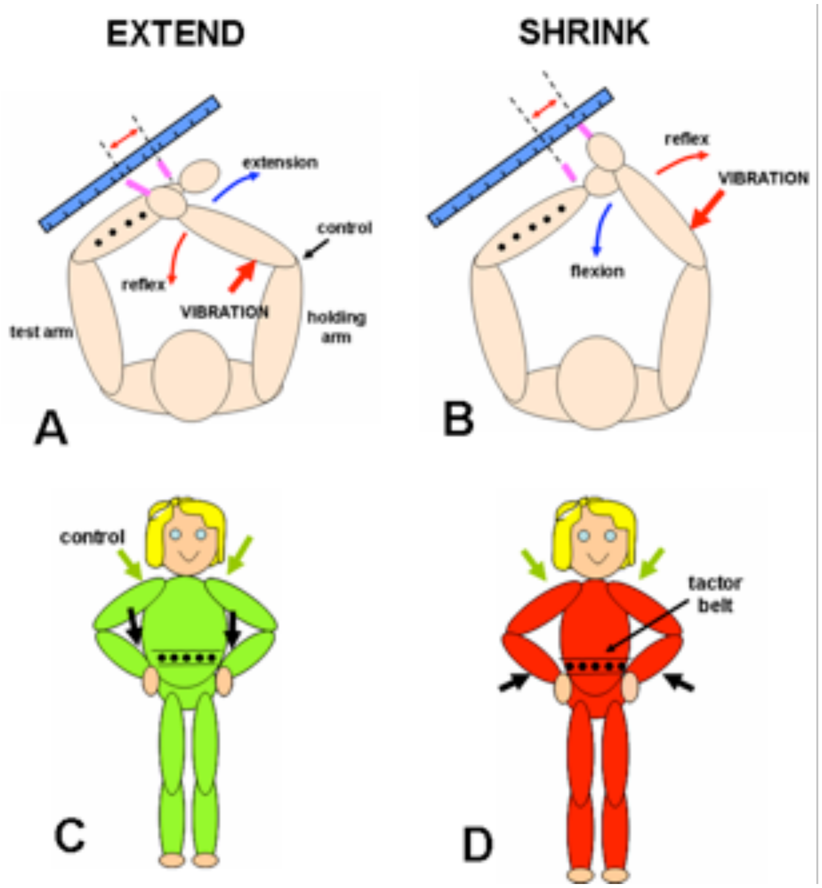


Figure 5. How the arms and waist were perceptually altered. (**A, B**). *How the Pinocchio illusion was implemented on the arm* Stimulating the biceps tendon (**A**) caused the right arm to flex reflexively. When the right arm held the left arm's wrist it caused the left arm to feel extended. The reverse applied after stimulating the triceps tendon (**B**). There were five tactors positioned along the arm, which were used for the acuity experiment. Two of them (mid-arm and closest-to-the-wrist) were also used for the sensitivity experiments. Control vibration was applied to a point on the right forearm near the bony elbow. The ruler used to assess misperception of the position of the right arm is also shown. (**C, D**) *How the Pinocchio illusion was implemented on the waist*. Vibrating the wrist flexor tendons of both arms simultaneously (**C**) made the waist feel it was expanding. Vibrating

the wrist flexor tendons (**D**) had the opposite effect. There were five tactors positioned along a belt, which were used for the acuity experiment. Three of them (1, 3 and 5) were used for the sensitivity experiments. Control vibration was applied to the two shoulders.

2.2. Arm Acuity and Sensitivity: Materials and Methods

2.2.1. Participants

Fifteen participants took part in Experiment 1 (nine females, mean age 29.6 years). Fifteen volunteers participated in Experiment 2 (nine females, mean age 28.8 years). All participants gave written informed consent. All studies were approved by the York University Research Ethics Board and were performed in accordance with the Treaty of Helsinki. Sample size was determined a priori for each experiment, on the basis of statistical power analysis. Prior experiments that used tendon vibration illusions indicated that having a final sample size of ten subjects generally leads to sufficient power but often a larger sample size is required since many participants do not experience the illusion and cannot be included in data analysis. In order to account for potential removal of participants, we determined that the ideal number of participants to run before stopping data collection would be fifteen.

2.2.2 Stimuli

Tactile stimuli (Figure 6) were 50 ms bursts of 250 Hz vibration of variable intensity generated by a 64bit sound card powered by a PC computer played through C2 tactors (Engineering Acoustics, California). Five tactors, with the centres separated by 3 cm, were mounted on a strap that was fastened along the dorsal surface of the left arm. The array was positioned with the central tactor midway between the wrist and the elbow.

Figure 6. Tactors for vibratory stimuli (Model C2, Engineering Acoustics, Florida, USA). In each experiment, five of these tactors were used for the vibrotactile stimuli.

2.2.3 Procedure

Blindfolded participants were seated in a chair and comfortably rested their left forearm, with the tactor array attached, on a cushion that was placed on a table. A strap lightly held the left arm in a relaxed position. The right elbow rested on an armrest arranged as a pivot to allow the right arm to reach the left wrist.

Tendon vibration: Illusory changes in the perceived length of the left arm were induced by vibrating the tendons of the right arm (Hitachi Magic Wand, Japan, shown in Figure 7), while participants held their left wrist with their right hand (Figure 5A & B). Biceps vibration created the perception that the left arm was elongating whereas triceps vibration caused illusory shortening of the left arm. In the control condition, vibration was applied to the forearm near the bony elbow. The frequency of vibration was approximately 83 Hz (device set on “low”) and the skin surface vibrated was about 1 cm^2. The vibrator was held in place by the experimenter and continuous vibration was applied throughout the blocks of trials.

Figure 7. The Hitachi Magic Wand (HV-250R) was used for tendon vibration.

Effectiveness of the illusion: In order to assess the effectiveness of the illusion, blindfolded participants were asked to reach for their left wrist with their right hand at the beginning of each block. A ruler was placed parallel to the left arm and measurements were recorded using the position of the right index finger. Four measurements were taken when no vibration was present to ensure that subjects were providing reliable and accurate judgments. Errors in reaching with the right arm indicated that tendon vibration was effective in eliciting illusory extension or flexion of that arm. As an additional test, after the end of each experimental block, participants were asked to report if their left arm felt longer, shorter, or of regular length. Only subjects who reliably experienced the illusion based on both these two measures were included in the analysis (Experiment 1: n = 13/15; Experiment 2: n = 15/15).

2.2.4. Experimental Design

For each of the two experiments, three conditions were tested - perceptually elongating and shortening the arm, as well as a control condition where arm length was not perceptually altered. The three conditions were run in interleaved blocks of 20 trials presented in a random order. Continuous vibration was applied throughout each block at the tendon or control site with each block taking between 90-110 seconds.

Experiment 1 - Tactile acuity: In order to measure tactile acuity on the arm we used the method of constant stimuli with a two-alternative forced choice (2AFC) design. Each trial consisted of two intervals - one interval containing a single touch and one interval containing two simultaneous touches. The intervals were delineated by three auditory beeps (250 Hz, 0.1 ms). Tactors in the two-tactor interval were spatially separated by one to four tactor separations (3, 6, 9, or 12 cms). For separations of 3, 6, or 9 cm, the pair of tactors to stimulate was chosen at random. Intensity was always suprathreshold but was manipulated to assure that vibration intensity would not be a reliable indicator for which interval contained two touches. For intervals containing two stimulations, the intensity was 5%, 7.5%, or 10% of maximum intensity for both tactors in the pair. For intervals containing one touch, the intensity was independently chosen from 10%, 15%, or 20% of maximum.

Participants identified which interval contained the two simultaneous touches and reported their response using foot pedals (Yahama FC5 foot pedals), where the left foot was lifted to report the first interval, and the right was lifted for the second interval. Each of the four tactor separations was presented 20 times for each of the three conditions for a total of 240 trials. The experiment was divided into 12 blocks, four for each of the three conditions.

Experiment 2 - Tactile sensitivity: Tactile detection thresholds were measured under the three conditions for two tactors on the array (middle of the left arm and close to the left wrist). A QUEST adaptive staircase procedure (Watson & Pelli, 1983) was used with a 2AFC design to obtain a detection threshold estimate at each touch location. Each trial consisted of two intervals – one interval containing a touch and one interval containing nothing - delineated by auditory beeps as for the acuity experiment. Participants identified whether the first or second interval contained the touch and responded using the foot pedals, left for the first interval, right for the second. Their response determined the intensity of the next stimulus according to the QUEST. There were three blocks per condition (for a total of 9 blocks) with 20 trials per block (total of 20 x 9 trials) corresponding to 30 trials for each tactor/condition.

2.2.5. Data analysis

The number of correct responses was expressed as a fraction of the total number of trials and plotted as a function of stimulus separation (Experiment 1, acuity) or intensity (Experiment 2, sensitivity). Data were fitted with a cumulative Gaussian psychometric function (Eq. 1) using the curve fitting toolbox in MATLAB (version 2012a).

$$y = 0.50+0.50/(1+\exp(-(x-x_o)/b)) \qquad \text{(eq 1)}$$

where x_o is the 75% threshold, b is the standard deviation and x is the stimulus separation or intensity for Experiments 1 and 2 respectively.

For Experiment 2, “standard thresholds” were measured in the presence of control vibration applied to the non-tendon site. Detection thresholds were converted to decibels relative to this standard threshold using:

dB = 10 x log 10 (threshold/standard threshold)……………………………………..(eq 2)

The statistical analysis comprised of repeated measures analysis of variances (ANOVAs). For all tests, alpha was set at $p < 0.05$. All multiple comparisons were made using Bonferroni correction.

2.3. Results

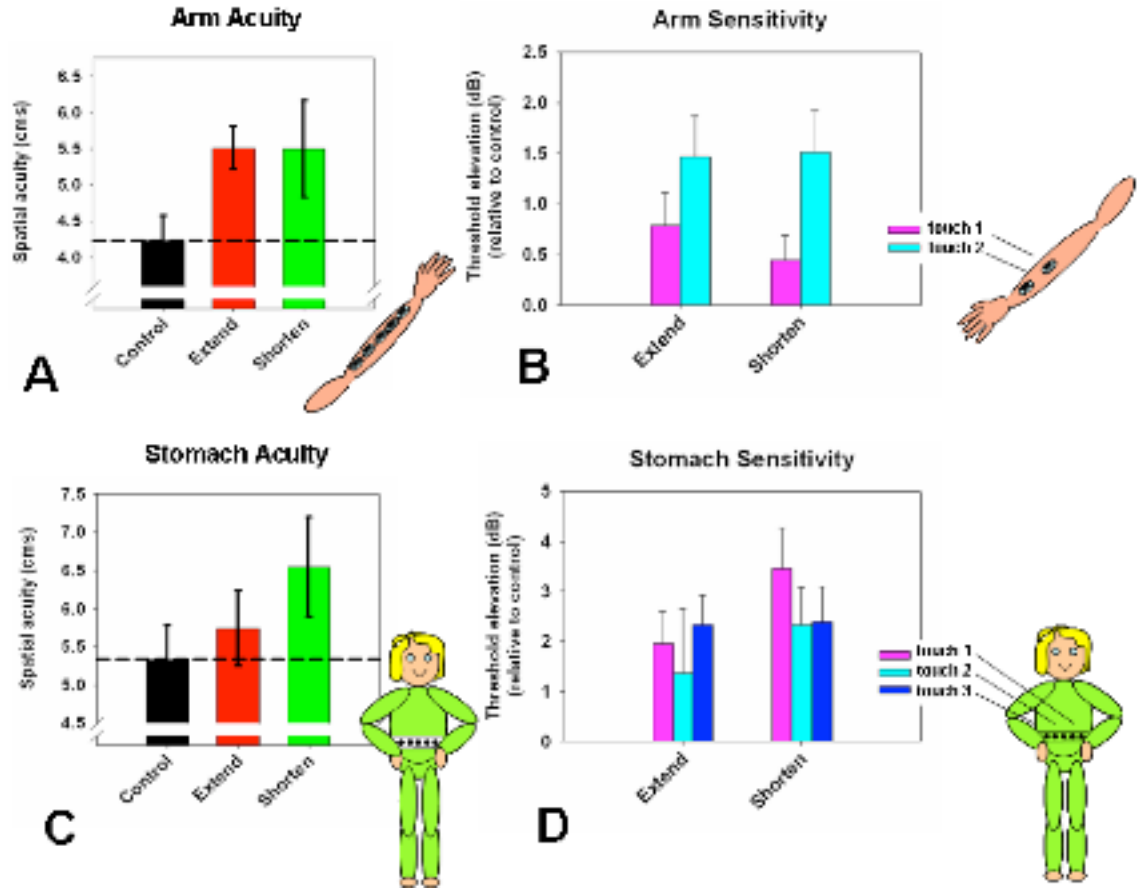


Figure 8. The effect of expanding or shrinking a body part on tactile sensations. Tactile spatial acuity (**A, C**) and sensitivity (**B, D**) of the arm (**A,B**) and stomach (**C, D**) for each of the three conditions. Spatial acuity thresholds are plotted in cm for the control, extend and shorten conditions. The dashed horizontal lines represent the acuity on the arm (**A**) and stomach (**C**) under control conditions. The elevation in detection thresholds are given in decibels relative to detection thresholds measured under control conditions (**elbow, B or shoulders, D**). Detection thresholds are shown for two points on the forearm and three on the waist as indicated in the inserts. Error bars represent standard errors.

2.3.1. Tactile Acuity on a Perceptually Distorted Arm

Figure 8A shows the mean tactile acuity thresholds for the three conditions: elongation, shortening, and control. A repeated measures ANOVA with a Greenhouse-Geisser correction determined that mean acuity thresholds differed significantly between conditions, $F(1.17, 14.06) = 5.85$, $p = .026$, $\eta_p^2 = .33$. Planned comparisons were conducted to determine if altering the perceived size of the arm impacted tactile acuity. Significant differences in acuity thresholds between the control condition and both of the tendon vibration conditions were revealed (elongation: $t(12) = -6.33$, $p < .001$; shorten: $t(12) = -2.8$, $p = .016$). Participants had higher thresholds (the stimuli had to be further apart to be distinguished) both while the arm was perceptually elongated (MD = 1.27 cm, SE = .20) and shortened (MD = 1.27 cm, SE = .45).

2.3.2. Tactile Sensitivity on a Perceptually Distorted Arm

The elevation in detection thresholds for the elongation and shorten conditions relative to the control condition are shown in Figure 8B. A 2 (touch location) x 3 (control, elongation, shorten conditions) repeated measures ANOVA was conducted to examine whether tactile sensitivity was affected when arm length was perceptually altered. The control condition was 0dB by definition. There was a significant main effect of touch location, $F(1, 14) = 5.39$, $p = .036$, $\eta_p^2 = .28$, as well as of condition, $F(2, 28) = 8.52$, $p = .001$, $\eta_p^2 = .38$. A significant interaction between touch location and condition was also found, $F(2, 28) = 2.19$, $p = .049$, $\eta_p^2 = .19$, revealing that the effect of condition on tactile sensitivity depended on location. This interaction was investigated further by evaluating the simple effects of condition separately for each touch location. Simple-effects analyses showed that only detection thresholds for the touch located closest to the wrist were increased when the arm was perceptually extended (MD = 1.46, SE = .408, p = .009) or shortened (MD = 1.51, SE = .406, p = .007). All comparisons between conditions were not significant for the mid-arm touch location.

2.4. Waist Acuity and Sensitivity: Materials and Methods

2.4.1. Participants

Sixteen participants took part in Experiment 3 (twelve females, mean age 22.5 years). Fifteen volunteers participated in Experiment 4 (ten females, mean age 24.4 years). All participants gave written informed consent. All studies were approved by the York University Research Ethics Board and were performed in accordance with the Treaty of Helsinki. The same rules that were used in Experiments 1 and 2 apply for determining sample size and stopping data collection.

2.4.2. Stimuli

Tactile: Tactile stimuli were the same as for Experiments 1 and 2. Five tactors, separated by 3 cm, were mounted on a belt that was worn around the waist with the central tactor positioned 3 cm below the navel.

2.4.3. Procedure

Blindfolded participants stood with their arms akimbo with the palms of their hands in contact with their waist and with the tactor belt fastened around their waist (Figure 5C & D).

Tendon vibration: A variation of the Pinocchio illusion was used to create illusory changes in waist size. Vibration was applied to the tendons of either both wrist extensors (producing an illusory shrinking of the waist) or both flexor muscles (producing an illusory expansion of the waist). In the control condition, vibration was applied to both shoulders. The vibrators and vibration properties were the same as in Experiments 1 and 2. The vibrators were held in place with two adjustable stands.

Effectiveness of the illusion: At the end of each block, participants (still blindfolded) were asked to indicate their perceived waist size by holding out their hands, palms facing inwards. The distance between the two hands was measured using a tape measure. Four measurements of perceived waist size were taken when no vibration was present. Discrepancies between these estimates indicated that tendon vibration effectively experienced changes in their perceived waist size. Participants were also asked at the end of each block if their waist had felt like it had expanded, shrunk, or was unaffected. Only subjects who reliably experienced the illusions based on these two measures were included in the analysis (Experiment 3: n = 14; Experiment 4: n = 13).

2.4.4. Experimental Design

Participants were tested under three conditions – when the waist was perceptually expanded, shrunk, and during control vibration. The three conditions were run in interleaved blocks presented in random order. Continuous vibration was applied throughout each block, with each block lasting between 90-110 seconds.

Experiment 3 - Tactile acuity: The experimental design was identical to Experiment 1 except for location of the touch stimuli and response method. Since participants were required to stand throughout the experiment, the experimenter recorded their verbal responses as to whether the two touches were in the first or second periods.

Experiment 4 – Tactile sensitivity: Tactile detection thresholds were measured at three locations (6 cm to the left of the midline, on the midline, and 6 cm to the right). The experimental design was the same as for Experiment 2 except for location of the touch stimuli and that responses were given verbally as for Experiment 3. There were three blocks per condition with a total of 24 trials per block (24 trials for each tactor).

2.4.5. Data analysis

As for Experiments 1 and 2 except one-tailed *p*-values were used for the planned comparisons.

2.5. Results

2.5.1. Tactile Acuity on a Perceptually Distorted Waist

Two-point discrimination thresholds are plotted for each condition in Figure 8C. To determine if altering the perceived size of the waist impacted tactile acuity, a repeated measures ANOVA was performed. The results show that there was a significant effect of condition, $F(1.27, 16.53) = 6.58$, $p = .015$, $\eta_p^2 = .34$, (Greenhouse-Geisser correction applied). Planned comparisons showed that thresholds were significantly increased when waist size was altered compared to the control condition. Thresholds increased from 5.34 cm ± .45 both when the waist was perceptually expanded (increased to 5.74 cm ± .49, $t(13) = -2.17$, $p = .0245$) and when the waist was shrunk (increased to 6.55 cm ± .65, $t(13) = -3.39$, $p = .0025$).

2.5.2. Tactile Sensitivity on a Perceptually Distorted Waist

The elevation in tactile thresholds while the waist was perceptually made to feel expanded or shrunk are plotted in decibels relative to the control condition in Figure 8D.

A 3 (touch locations – left, right, and centre) x 3 (control, expand, shrink conditions) repeated measures ANOVA was conducted to examine whether altering the perceived size of the waist affected tactile sensitivity. A significant main effect was found for condition, $F(2, 24) = 10.56$, $p = .001$, $\eta_p^2 = .47$, indicating that distorting the perceived width of the waist using tendon vibration did affect sensitivity. There was no difference between touch locations, $F(2, 24) = .37$, $p = .696$, $\eta_p^2 = .03$ and no interaction between condition and touch location, $F(4, 48) = .92$, $p = .458$, $\eta_p^2 = .07$, that is, all locations were affected equally. Pairwise comparisons between conditions revealed that thresholds were significantly increased both in the shrink condition (MD = 2.47 dB, SE = .60, p = .002) and the expand condition (MD = 1.45 dB, SE = .583, p = .042) relative to the control condition.

2.6. Discussion

The aim of our experiments was to investigate the role that body representation plays in tactile sensation. We used bodily illusions to perceptually alter body size and tested the impact that changes in perceived size had on tactile acuity and sensitivity. We found that illusory changes in body size caused degradation of tactile acuity and sensitivity for both the arm and the waist, demonstrating for the first time that even basic tactile sensations are influenced by perceived body size. Interestingly, we found a reduction of tactile performance for both illusory enlargement and shrinkage. These results provide evidence of how essential body representation is for tactile perception by showing how distorting body size, even for just 90 seconds, can influence the ability to perceive basic touches.

We postulate that manipulations of perceived body size initiate a disruption in the body representation. It is a consequence of the initiation of such a change that we postulate may underlie our results. Putting the representation of the body into a state of flux would upset tactile perception that requires an accurate body representation to which touch sensations can be related. Altering body representation would lead to less reliability in this mapping process and thus add noise to all aspects of tactile perception. The reduction in acuity and sensitivity that we observe would then correspond to this noisy, temporarily unreliable body representation in the early stages of changing itself. Plasticity of body representation has been shown to occur in cases of amputation (Ramachandran & Hirstein, 1998) and brain-damaged patients (Sposito, Bolognini, Vallar, Posteraro, & Maravita, 2010) but these changes can often take months or years following injury to fully consolidate (Ramachandran & Hirstein, 1998).

2.6.1. Asymmetry

Changes in tactile perception of objects pressed against the skin have been reported only for increases in perceived body size, with no corresponding effects reported in response to perceptual shrinking. The explanation usually suggested (e.g., de Vignemont et al., 2005) for this asymmetry is that our bodies are more capable of enlarging, for example during normal growth, than shrinking and that therefore only perceptually enlarging body parts can influence body representation. However, we found changes in tactile sensations following both perceptual expanding and shrinking. This supports our general disruption model that we postulate to occur whenever body representation is altered in either direction. Improvements in tactile perception are found when additional information is provided, such as vision (Bruno & Bertamini, 2010; Marino et al., 2010; Moseley et al., 2008; Taylor-Clarke et al., 2004), multisensory information (Pavani & Zampini, 2007), or training (Moseley & Wiech, 2009; Wong, Peters, & Goldreich, 2013), so it makes sense that decreased tactile performance would occur when information is removed or interfered with. Support for this line of thought comes from the case of pain. Distorted body representations and correspondingly decreased tactile acuity has been observed in individuals who suffer from pain disorders such as complex regional pain syndrome (Moseley, 2005), phantom limb pain (Flor, Nikolajsen, & Staehelin Jensen, 2006), and chronic back pain (Moseley, 2008).

2.6.2. Possible Limitations

Self report

One of the main limitations of these experiments is that a self-report method was used to ensure and measure the extent that the participants experienced the waist size-changing illusion. An objective method would allow for a more accurate and precise measure of illusory distortions in perceived body size. This, along with a bigger sample size, would allow for additional analyses to be conducted that could explore whether the extent of the illusion affects the amount of degradation in tactile thresholds.

Low number of trials

The low number of trials tested and the QUEST method are also major possible limitations that may impact final threshold values that were obtained for each participant. The QUEST is a staircase method that hones in on its estimate of thresholds. If a participant makes an error in entering their response, the QUEST can take some time to recover. A larger number of trials would make this technique less sensitive to response errors and could provide more reliable threshold estimates. However, more trials takes longer and the choice of trial number is always a balance between collecting useable data and stretching participants’ tolerance levels.

Unmotivated subjects

Using York University's Undergraduate Research Participant Pool (URPP) involves some rather unmotivated participants compared to selecting subjects from a more motivated group, such as graduate students. This is another potential limitation that may have caused less consistent and reliable data. Messier data could have resulted because participants may have lacked interest or understanding about how to properly complete the experiments.

2.6.3. Future Directions

Other methods of distorting the body

These studies suggest a variety of different directions for future research. Testing tactile acuity and sensitivity thresholds when perceived body size is altered using visual manipulations, as opposed to the proprioceptive method used in this thesis, would add to the understanding of how body representation influences basic tactile sensations.

Generality of the effect

In addition, studies could be conducted to test whether tactile sensations are altered at sites on the body that are not directly being distorted by tendon vibration.

Testing vestibular involvement

Recent research (Lopez, Schreyer, Preuss, & Mast, 2012; Pfeiffer, Serino, & Blanke, 2014) has shown that the vestibular system may help create the perception of the self. To further extend knowledge in this area, the same experiments presented in this chapter could be repeated but with GVS stimulation added to create another type of disruption to body representation.

Clinical directions

Potential future directions could also involve research that explores the clinical and practical implications for those with body perception distortions.

2.6.4. Rationale for Masking Experiments

During the course of these experiments, a difference in tactile sensitivity between the two touch locations was observed (see Figure 5B). Since this difference occurred even during the control condition, it seemed that the presence of vibration on a particular part of the contralateral arm was a possible explanation: the control condition itself might be having an effect on our measures. Though it seemed highly unlikely that the experimental findings could simply be a result of such remote vibration, it was important to rule the possibility out. Therefore, I designed the following set of experiments to explore contralateral masking on the forearm.

CHAPTER 3:

Contralateral Masking Between Forearms

The body of this text has been published in *Experimental Brain Research.* I have added sections 3.1.1., 3.4.5., and 3.4.6. for this thesis. The published paper is included as Appendix A.

3.1. 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 side 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 (Y Iwamura, Tanaka, Iriki, Taoka, & Toda, 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 & 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 (Braun et al., 2005; Sherrick, 1964; Tamè, Farnè, & Pavani, 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.

3.1.1. Purpose and Hypotheses

These experiments set out to investigate contralateral tactile masking on the forearm. The purpose of Experiment 1 was to ensure that the experimental results from Chapter 2 were not affected by the presence of vibration. This was done, with the hands touching, by testing whether tactile sensitivity thresholds on one forearm were affected by the presence of a vibrating stimulus on the corresponding spot of the opposite arm. Having found contralateral masking effects in Experiment 1, Experiment 2 was conducted to determine if contralateral masking also occurs when the hands are not touching and to measure the spatial tuning of this effect.

The general prediction of these experiments is that contralateral masking on the forearm will impact tactile sensitivity. The specific hypotheses tested in these experiments are listed below:

1) Tactile sensitivity thresholds on one forearm will be increased when a masking stimulus is applied to the corresponding point on the opposite forearm.

2) Contralateral masking will occur independent of whether the hands are in contact but that this effect will be stronger when the hands are touching.

3) Measuring tactile sensitivity thresholds on one forearm during five different masking positions along the opposite forearm will demonstrate that contralateral masking is spatially tuned. The greatest effect will occur when the masking stimulus is in the spot corresponding to the test stimulus.

In sum, these experiments will explore the phenomenon of tactile masking by investigating contralateral tactile masking on the forearm.

3.2. Methods

3.2.1. 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.

3.2.2. 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 half way between the inner angle of the elbow and the wrist crease (Figure 9). 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 4cm. 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 (Figure 9A), 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 (Figure 9B), a control position (on the front of the shoulder), half way up the upper arm (half way between the outer angle of the elbow and the top of the shoulder), on the outside part of the elbow, half way along the forearm at the (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.

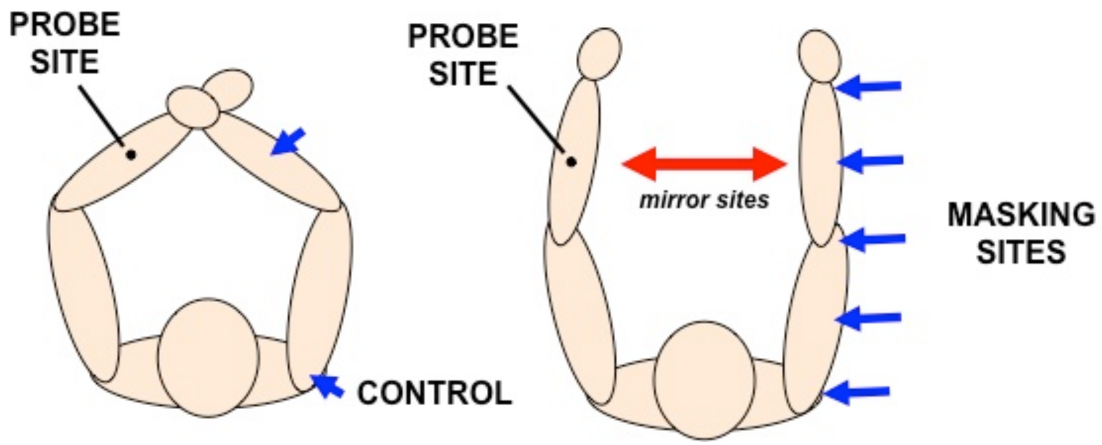


Figure 9. Showing the sites of masking (arrows) and test stimuli (dots) for two arm positions. (**A**) For Experiment 1, the right hand was resting lightly on the left wrist. Only two masking sites were used. (**B**) For Experiment 2, the arms were held parallel to each other. For this experiment there were five equally spaced masking sites. The test site was the same in both experiments.

3.2.3. 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 1s periods marked by three beeps (5kHz, 3kHz and 5kHz; duration 100ms) and identified in which period the touch was present. Stimulus intensity was controlled by a QUEST psychometric procedure (Watson and Pelli 1983) running in MATLAB (version 2011b) on a PC. Each block of 20 trials and was repeated twice for each masking condition, for a total of 40 trials for each condition. Each block took about 40s. 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 (Figure 9A). 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 4 blocks, with masking sites alternating between blocks. Participants reported 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 (Figure 9B) 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 were chosen for each subject using a Latin square and repeated twice in the same order.

3.2.4. 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.

$$\text{Percent correct} = 0.50+0.50/(1+\exp(-(x-xo)/b)) \ldots\ldots\ldots\ldots \text{(eq 1)}$$

where x0 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.

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

3.3. Results

3.3.1. Experiment 1: Hands Touching

A paired sample 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* = .007 (.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 Figure 10.

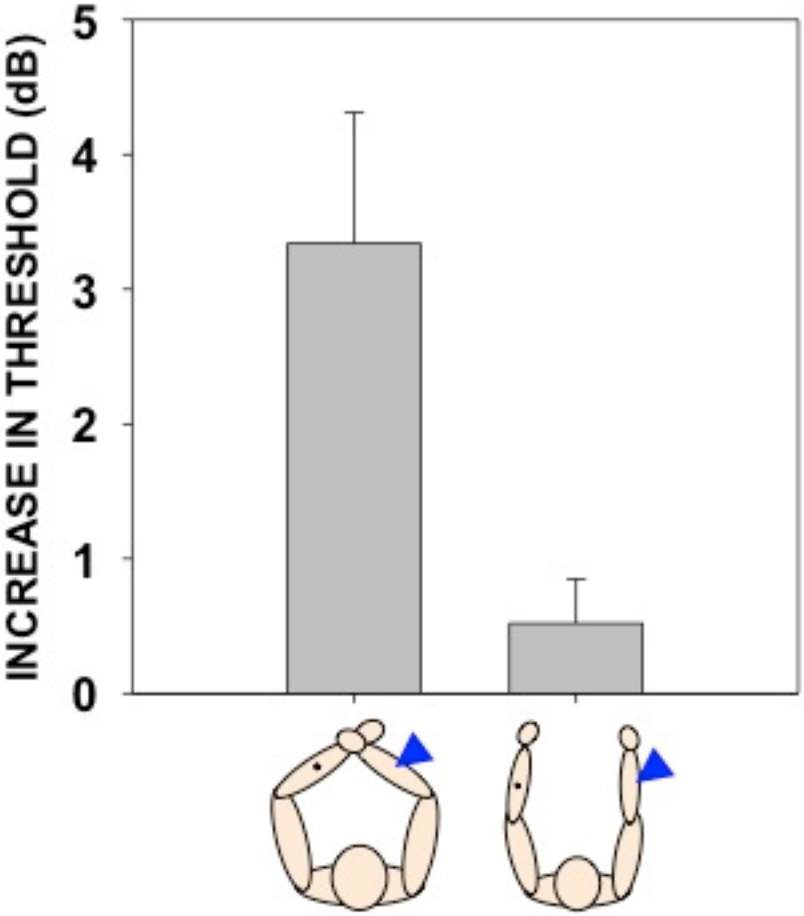


Figure 10. The effect of arm position on the increase in tactile threshold at a site on the left forearm (dot) caused by the application of a masking stimulus (triangles) at the corresponding point on the opposite arm. The left bar is with the right hand resting lightly on the left wrist (Experiment 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.

3.3.2. Experiment 2: Hands Separate

A paired sample 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 Figure 11 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%.

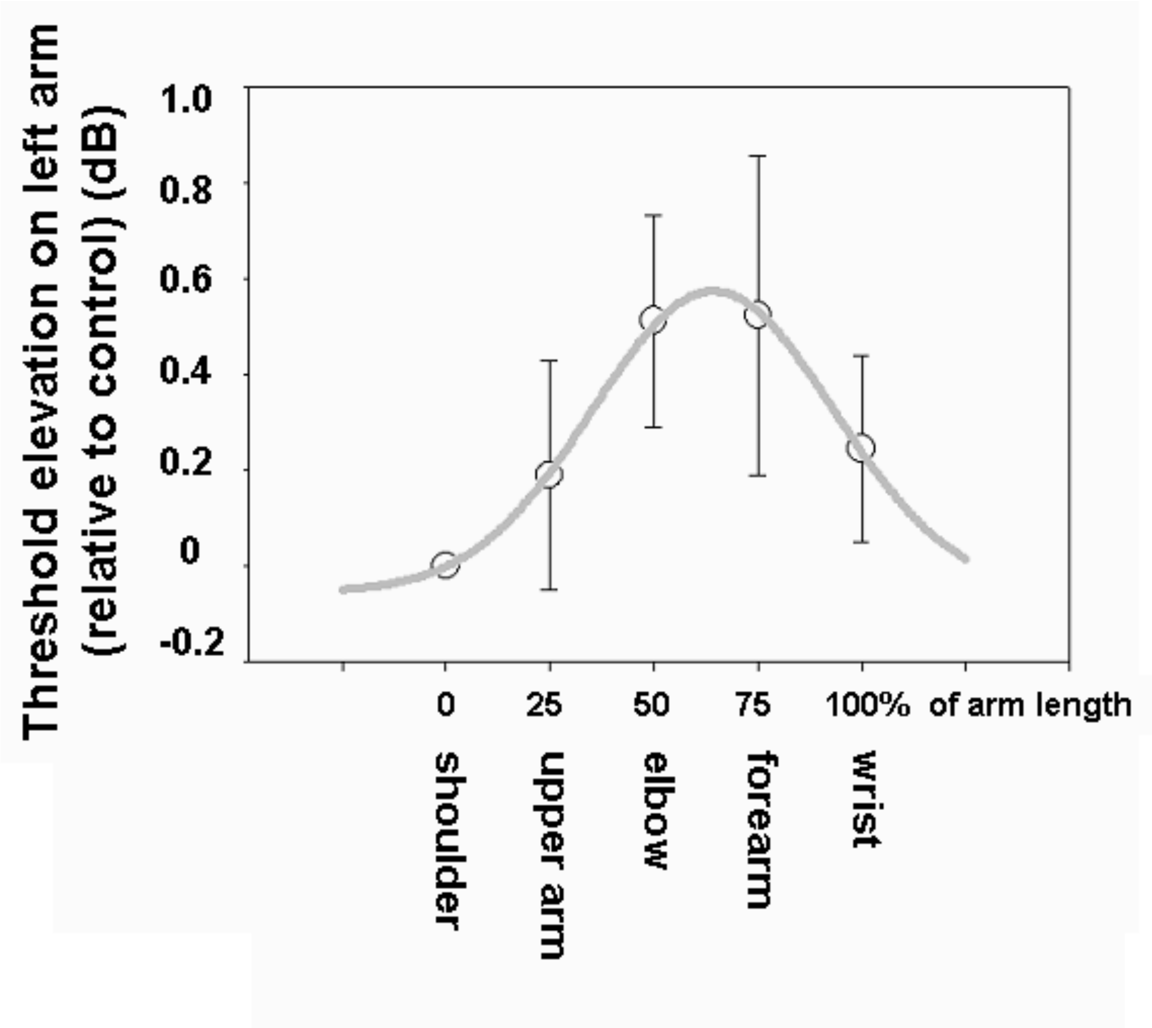


Figure 11. Thresholds on the left forearm as a function of masking stimulus location on the right arm. All thresholds are expressed in decibels relative to the control thresholds obtained when the vibrotactile stimulus was applied to the right shoulder. The control is plotted as zero on the graph. The peak and width of the best-fit Gaussian curve (solid line) are 64% and ± 29% of arm length respectively. Error bars are standard errors.

3.3.3 Experiment 1 vs. Experiment 2: Effect of arm location

To determine if arm position had an effect on the extent of masking, an independent sample t-test (corrected using Levene's Test for Equality of Variances) was conducted on the threshold elevations in Experiment 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, $t(9.872) = 4.335$, $p = .002$, with a mean difference of 2.81 dB ± 1.02. This is shown in Figure 7.

3.4. 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 to if they were parallel (3.3 dB compared to 0.52 dB).

3.4.1. Comparison with Previous Reports

Ipsilateral tactile masking has been extensively investigated since von Békésy using electrical stimulation (Schmid, 1961; Uttal, 1960), pressure (Abramsky, Carmon, & Bentontt, 1971), and vibrotactile stimulation (Gilson, 1969; Sherrick, 1964). Contralateral tactile masking, in contrast, has been regarded mostly as a curiosity and there has been little investigation since the 60's when it was established that the effect shared temporal tuning properties with its ipsilateral cousin (Abramsky et al., 1971; Bird, 1964; Halliday & Mingay, 1961). When a stimulus is present on corresponding points on both sides of the body, sensitivity (Gilson, 1969; Snyder, 1977) and discrimination performance (Harris, Harris, & Diamond, 2001) are reduced and the ability to locate near-threshold stimuli applied to fingers of the other hand is also degraded (Braun et al., 2005; Schweizer, Maier, Braun, & Birbaumer, 2000). 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 (Braun et al., 2005; Harris & Diamond, 2000).

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?

3.4.2. 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 (Y Iwamura, Iriki, & Tanaka, 1994; Yoshiaki Iwamura, Tanaka, Sakamoto, & Hikosaka, 1993; M Taoka, Toda, & Iwamura, 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 (M 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, Gould, Cusick, Pons, & Kaas, 1983; Miki Taoka, Toda, Iriki, Tanaka, & Iwamura, 2000) suggests that this might be a general principle reflecting the somatosensory organization of all regions of the body (Alliusi et al. 1965).

3.4.3. 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.

3.4.4. 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.

3.4.5. Possible Limitations

More precise masking stimulus

The main limitation of these studies surrounds trying to obtain a precise measurement of the spatial tuning curve. The masking stimulus vibrator is quite large and covers a diameter of approximately 4 cm, which could account for less precision than is required for reliable measurements of the five positions along the arm. A vibrator with a smaller diameter would be better suited in attaining more accurate measurements for a more in depth look into the spatial tuning curve.

Trial numbers and participants

Some limitations from the studies discussed in Chapter 2 are also possible in these experiments. The low number of trials tested and the QUEST method may impact final threshold values that were obtained for each participant. A larger amount of trials would be less sensitive to response errors and could provide more reliable threshold estimates. Using URPP participants compared to selecting subjects from a more exclusive group, such as graduate students, is another potential limitation that may have caused less consistent and reliable data. Messier data could have resulted because participants may have lacked interest or understanding about how to properly complete the experiments.

3.4.6. Future Directions

Optimal masking stimulus properties

The findings from these experiments suggest a variety of directions for future research. Although the results demonstrate contralateral masking effects, they have only been tested using one type of vibration. Replicating these studies using different vibration frequencies and varying surface area of the masking stimulus could further our understanding of how extensive contralateral masking is.

Generalizability

Additionally, it may be of interest to explore whether contralateral masking effects can be found for other areas of the body, such as the legs, or to test if it occurs through the arm. Such experiments could reveal unexpected connections between other body parts or within a limb that could shed light on how the three-dimensional body is represented within the brain.

The effect of posture

In the current experiments, the effect of arm location was briefly examined by comparing the strength of the effect when the hands were touching or separate. Though a difference was found, it cannot be concluded whether it is caused from actual skin contact or arm position. To answer this question, I have recently conducted an experiment testing contralateral masking during a variety of different arm positions of both the test and masking arms.

CHAPTER 4:

Vibrotactile Masking through the Body

The body of this text has been published in *Experimental Brain Research.* I have added sections 4.1.1., 4.4.3., and 4.4.4. for this thesis. The published paper is included as Appendix B.

4.1. Introduction

Somatosensory information about the body surface is split into two in the brain with each hemisphere receiving information from only one half of the body (Penfield & Boldrey, 1937). The two representations are connected through callosal pathways, so that even by area 5 many of the cells receive inputs from both sides (Manzoni, Barbaresi, Bellardinelli, & Caminiti, 1980; Manzoni, Barbaresi, Conti, & Fabri, 1989). Even by this stage of processing the body-in-the-brain is treated as an integrated whole. However, this arrangement does not help us understand how the “flat map” in the cortex is turned into a useable representation of a three-dimensional body. Research investigating the representation of touch has tended to focus on the fingers and hands, with relatively few studies examining the whole body (but see Cholewiak et al. 2004; van Erp 2008). Here we look for interactions between the front and back of the body to look for evidence of how the three-dimensional shape of the body is represented.

An important way to study the tactile sense is through the use of masking in which the sensitivity at one location is affected by vibration applied at a remote site. Traditionally, long-range tactile masking effects have been studied using the fingers, hands and arms, where masking has been found to occur between mirror-symmetric points across the body (Braun et al., 2005; D’Amour & Harris, 2014; Sherrick, 1964). Long-range reciprocally inhibitory pathways have been demonstrated between cortical tactile maps of the two halves of the body (Reed et al., 2011) which may be the neurophysiological explanation of these long-range interactive effects. However, the mobile limbs may be a special case and concentrating on these body parts ignores the body as a whole. Few studies have explored tactile masking using more extensive areas of the body (e.g., Alliusi et al. 1965; Geldard and Sherrick 1965; Craig 1966).

One reason that the limbs might be a special case, apart from their obvious motility, is that they fall within the visual field. Recent evidence (Harrar & Harris, 2010; Pritchett & Harris, 2011; Tipper et al., 2001) has suggested, counter-intuitively, that tactile location may be coded at least partially in visual coordinates. However, we can never completely see our entire body and many regions, for example the back, can never be seen. How then might the back be represented? Are we to postulate different coding systems for different parts of the body? Or might unseen parts of the body be somehow "linked" to corresponding visible areas?

To investigate the brain's representation of invisible body parts, we explored whether long-range interactions could be found between the visible front and the invisible back of the body. Having found evidence of through the body masking, we then measured the spatial tuning of the effect.

4.1.1. Purpose and Hypotheses

This chapter seeks to explore the brain's representation of invisible body parts by investigating whether long-range interactions, comparable to those found in Chapter 3, can be found between the visible front and the invisible back of the body. First, through the body masking will be investigated by testing whether tactile sensitivity on the front of the stomach is affected by a masking stimulus on the corresponding point of the back. Second, I measured spatial tuning curves for around the side of the trunk and up the back. Having demonstrated contralateral masking between forearms, I predict that through the body masking will impact tactile sensitivity. Specifically, I hypothesize that:

1) Tactile sensitivity thresholds on the front of the stomach will be increased when a masking stimulus is applied to a nearby point on the front.

2) Tactile sensitivity thresholds on the front of the stomach will be increased when a masking stimulus is applied to the corresponding point on the back.

3) Measuring tactile sensitivity thresholds on the front during three different masking positions around the side of the trunk will show that masking is spatially tuned. The greatest effect will occur at the front masking position closest to the test site.

4) Measuring tactile sensitivity thresholds on the front using four different masking positions up the back will demonstrate through the body masking. I expect that this effect is not spatially tuned and that increases in thresholds will only occur for the back masking position that corresponds to the test site spot on the front.

Taken together, these experiments will explore how the body is represented in the brain by investigating the connection between the front and the back of the trunk. This research aims to challenge our understanding of how the three-dimensional body is represented in the brain.

4.2. Methods

4.2.1. Participants

Ten participants took part in Experiment 1 (nine females, mean age 21.1 years, SD = 2.1 years) and 14 individuals participated in Experiment 2 (eight females, mean age 19.9 years, SD = 2.8 years). They were recruited from the York University 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.

4.2.2. Stimuli

Detection stimulus: Tactile stimuli were 100 ms bursts of 250 Hz vibration of variable intensity controlled by a 64 bit sound card powered by a PC computer played through C2 tactors (Audio Research, California). Two tactors were mounted on a belt worn around the waist. The tactors were positioned 12 cm on each side of the midline and 3 cm below the navel.

Masking stimulus: The masking stimulus was provided by a Magic Wand vibrator (Hitachi, Japan) 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”. In Experiment 1, the masking stimulus was applied to one of four sites on the body: on the front (on the left side of the stomach about 3 cm above the left tactor), on the back (directly behind the left tactor), and at control sites on both shoulders. These sites are shown in Figure 12A-C. For

Experiment 2, the masking stimulus was applied at one of seven sites equally spaced around the left side of the trunk and up the back on the left side as shown in the insets to Figures 12E and F. These masking sites were (1) on the front (on the left side of the stomach 2 cm to the left of the left tactor), (2) on the side (on the left side of the trunk), (3) half way between the side and the back position, (4) on the back (directly behind the left tactor), (5) mid back (half way up the back on the left side), (6) top back (near the top of the back on the left side), and (7) control (on the back of the left shoulder). The masking vibrator was held in place by an adjustable stand and was left on throughout the duration of each experimental block (less than 2 mins).

4.2.3. Procedure

Blindfolded participants stood for the duration of each block. The experimenter arranged the adjustable stand to apply the masking stimulus to the pre-chosen body site and left it running in place while a block of trials was run. Using a two-alternative forced choice (2AFC) paradigm, participants were presented with two 1s periods marked by three beeps (5kHz, 3kHz and 5kHz; duration 100ms) and identified in which period the touch was present. Stimulus intensity was controlled by a QUEST psychometric procedure (Watson & Pelli, 1983) running in MATLAB (version 2011b) on a PC. Participants verbally reported the period in which the stimulus was thought to occur.

4.2.4. Experimental Design

For Experiment 1, tactile detection thresholds for the two tactors on each side of the stomach were measured in the presence of the masking vibration at one of the four sites shown in Figure 12A-C. Each combination had 30 trials per tactor. Trials were divided into three blocks per condition with 20 trials per block (of a total of 12 blocks). Each block took less than 2 min.

For Experiment 2, tactile detection thresholds on the left side of the stomach were measured in the presence of masking vibration at one of the seven sites shown in Figures 12E and F. Each condition had 40 trials. Trials were divided into two blocks per condition with 20 trials per block (for a total of 14 blocks). Each block took less than 2 min.

The sets of blocks for each experiment were run in a counterbalanced order, chosen for each subject using a Latin square, repeated as required.

4.2.5. 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 log (intensity) used for each trial and fitted with a cumulative Gaussian (eq. 1) using the curve fitting toolbox in MATLAB.

$$y = 0.50+0.50/(1+\exp(-(x-x_o)/b)) \quad \text{(eq. 1)}$$

where x_o is the 75% threshold value, x is the log (intensity) tested and b is the standard deviation.

Detection thresholds were converted to decibels relative to the threshold measured when the control vibration was applied to the control sites using:

dB = 10 x log 10 (threshold/control threshold)…………………………………..(eq. 2)

Results for Experiment 1 were not affected by which control was used and so only data relative to the right shoulder control are reported for that experiment. Statistical analyses were conducted using these threshold elevations in dB.

4.3. Results

4.3.1. Experiment 1

All thresholds were expressed as elevations in decibels relative to the thresholds measured in the control condition and are shown in Figure 12D. Paired sample *t*-tests were conducted to determine if tactile detection thresholds were significantly increased when the masking stimulus was applied to the front and to the back compared to the control (right shoulder). All *p*-values are reported as one-tailed values. Thresholds for the left tactor were significantly increased by a masking stimulus on the front 3 cm from the left testing site, $t(9) = 2.489$, $p = .0175$ by 1.71 dB ± .69, and most importantly for this study, were also increased when the masking stimulus was on the corresponding point on the left side of the back, $t(9) = 3.748$, $p = .0025$ by .83 dB ± .22. Significant differences were found between the left and right tactor locations when the masking stimulus was on the left side of the front, $t(9) = 2.183$, $p = .0285$ (with a 1.69 dB ± .78 increase of the left relative to the right) and when the masking stimulus was on the left side of the back, $t(9) = 3.063$, $p = .0065$ (with a 1.12 dB ± .37 increase of the left relative to the right). Thus, we report an effect of masking through the body in which detection thresholds on the ipsilateral side of the stomach were elevated when a masking stimulus was applied to the back. Experiment 2 investigated the spatial tuning of this effect.

4.3.2. Experiment 2

Threshold elevations for the tactor on the left side of the stomach were expressed as dB elevations relative when thresholds were measured in the presence of masking vibration applied to the control site on the back of the left shoulder. A repeated measures ANOVA was conducted on conditions in which the masking stimulus was applied to the three sites spaced around the waist (sites 1, 2 and 3, see Figure 12E) and a significant effect of condition, $F(2, 26) = 14.70$, $p < .001$, $\eta_p^2 = .531$ was found. Bonferroni corrected post-hoc tests revealed that the threshold for the front condition (site 1) was significantly increased relative to both the side (site 2, 2.269 dB ± .670, $p = .015$) and back half (site 3, 2.997 dB ± .631, $p = .001$) conditions. An exponential was fitted through these three threshold increases (see Figure 12E) and showed a fall off with a space constant of 1.21 tactor spacings.

A repeated measures ANOVA was also conducted on the four back conditions (sites 4-7; back, mid back, top back, and control, see Figure 12F). The control condition was of course, by definition 0. A significant effect of condition was found, $F(3, 39) = 4.696$, $p = .007$, $\eta_p^2 = .265$. Post-hoc tests showed that the back condition was significantly increased from the control condition (site 4, 1.245 dB ± .398, $p = .048$). An exponential was fitted through these four threshold increases (see Figure 12F) and showed a fall off with a space constant of 0.63 tactor spacings.

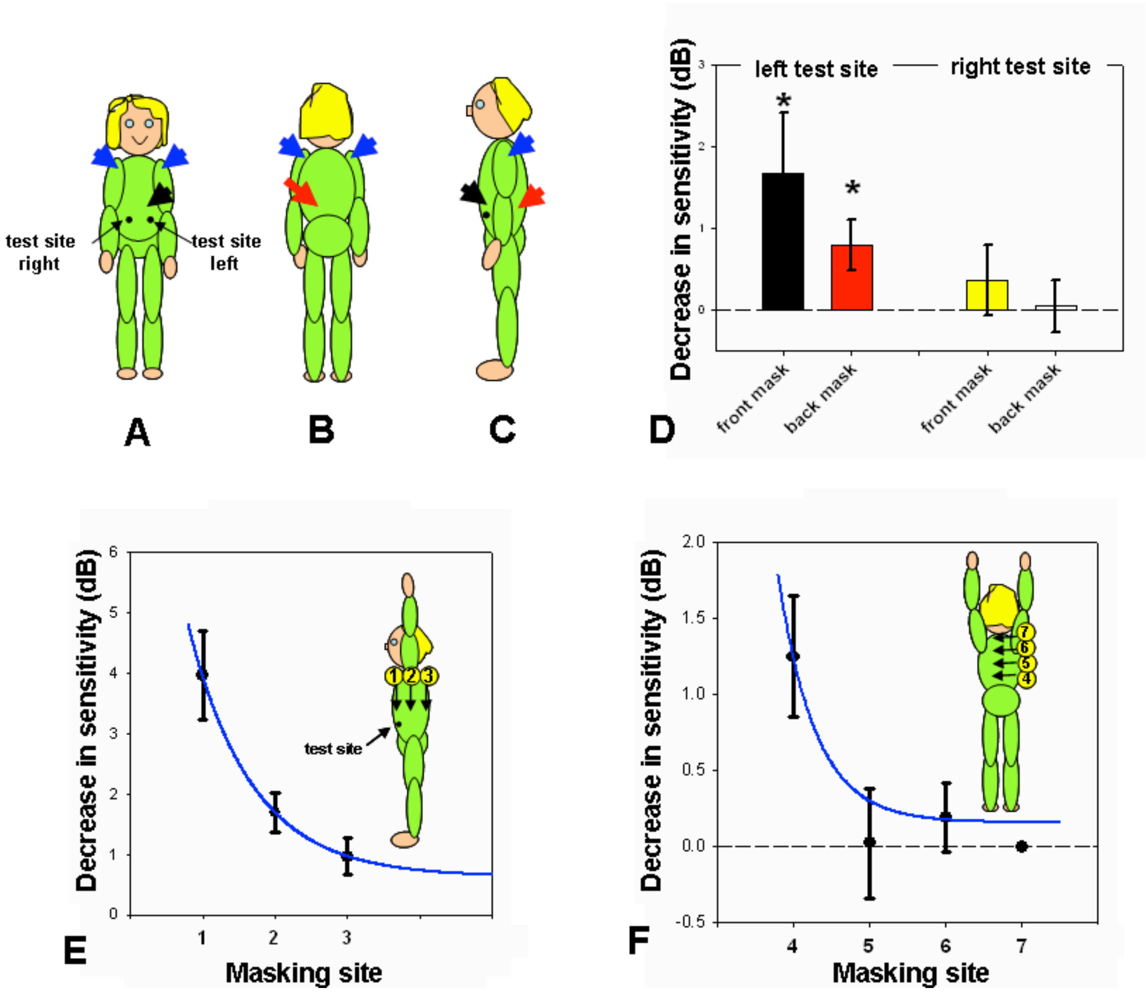


Figure 12. Procedure and results for through the body masking. Experiment 1 (**A-C**): The sites where masking vibration was applied: *black arrow* near the left test site on the front, *red arrow* on the corresponding point of the back. *Blue arrows* indicate the sites of vibration used as a control condition. Masking stimuli caused a significant increase in thresholds relative to control (*asterisks* correspond to $p < .05$) when applied either near

the test site on the front (*black bar* in **D**) or at the corresponding point on the back (*red bar* in **D**). No effect was found at the test site on the side of the body contralateral to the masking sites (*yellow bars* in **D**). *Error bars* are SEs. Experiment 2 (**E-F**): The masking effects when the masking stimulus was applied to sites on the front (**E**) or sites on the back (**F**) (masking sites shown numbered in the *insets*). Standard error bars are shown (location 7 was the control relative to which other data were expressed and therefore has a standard error of 0). Exponentials are plotted through the data points.

4.4. Discussion

For the first time, we have demonstrated tactile masking through the body in which vibration on the back elevates tactile thresholds at the corresponding point on the front. We further demonstrated that through-the-body masking, like contralateral masking, is spatially tuned. By varying the location of the masking stimulus with respect to the corresponding point on the back (Figure 12F) we showed a spatial constant of 0.63 tactor spacings which is around 2 cm (more precise estimates cannot be given because tactor spacings varied from person to person and our masking stimulus was quite large relative to these distances). Our study reveals a special relationship between the front and the back of the torso that may provide insight into how the body might be represented in the brain.

4.4.1. No Contralateral Masking on the Trunk

Interestingly, thresholds were only increased when the masking stimulus was applied to the same side of the body as the test stimulus (Figure 12D). This is in contrast to the cross-body masking effects that have been shown between the hands and arms (Bird, 1964; Braun et al., 2005; D'Amour & Harris, 2014; Halliday & Mingay, 1961; Sherrick, 1964; Tamè et al., 2011). This could be due to the different nature of the trunk in comparison with the fingers, hands, and arms and may be connected to the motility of the limbs.

4.4.2. The Representation of the Body in the Brain

Localizing stimuli in space requires a three-dimensional representation of the body. How might this be achieved? For tactile stimuli felt on the hand and limbs, it requires knowledge of limb location in space and, although proprioceptors in the joints and muscles contribute to this assessment, limb location in space is most reliably provided by the visual system (Fuentes & Bastian, 2010; Graziano, 1999). Visual coding also seems to be important for locating touch applied to the front of the torso (Pritchett, Carnevale, & Harris, 2012) but how might the location in space of points on the back be known? We postulate that the back may be "pinned" to the front with some kind of special connection that is revealed by the present through-the-body masking. Under this "flat body hypothesis" the location of points on the back would be coded at some level in terms of the location of the corresponding point on the front. This model has been suggested to explain the observation that the perceived location of touch on the back is shifted in the same direction as touch on the front during eccentric gaze (either both towards the left or both towards the right side of the body) (Pritchett, Carnevale, & Harris, under review). Similarly, when asked to identify tactile patterns on the back of the torso or on the back of the head, participants make errors consistent with the patterns being perceived as if pressed through the body, or viewed from behind (Natsoulas & Dumanoski, 1964).

4.4.3. Possible Limitations

The possible limitations for these experiments are the same as the limitations discussed for the experiments in Chapter 3 especially the low trial numbers and motivation of the participants (see section 3.4.5). Trying to obtain precise measurements of the spatial tuning curve at the masking sites around the side of the stomach was difficult because of the large contact zone that the masking stimulus vibrator had. The spacing between each masking site was fairly close, roughly three to four inches apart, depending on trunk diameter size of each individual participant. Using a vibrator with a smaller diameter would be ideal for attaining more accurate measurements to further explore the spatial tuning curve.

4.4.4. Future Directions

As for the contralateral masking demonstrated in Chapter 3, these studies could be extended using different vibration frequencies and varying the surface area of the masking stimulus to explore how a phenomenon through the body masking is. The whole body representation could be explored by additional studies that systemically varied positions of the test site on the front or back. An obvious modification is to confirm that the masking is two ways. It seems likely that masking between one arm and the other is reciprocal but it is not so obvious that because vibration on the back masks a stimulus on the front that vibration on the front would mask a stimulus on the relatively insensitive back.

CHAPTER 5:

General Discussion

This thesis has investigated the connections between body representation and tactile thresholds by exploring if distorting the representation of the body impacted tactile detection and acuity thresholds and if tactile stimulation to one part of the body alters thresholds at other sites. Overall, I have demonstrated the critical role that body representation can play in how we perceive tactile stimuli and have shown how altering body representation has consequences even for the most basic tactile sensations.

5.1. Summary of Major Findings

Chapter 2 investigated whether distorting body representation, using tendon vibration illusions, affects tactile thresholds. I found that both tactile acuity and sensitivity thresholds increased when perceived arm and waist size was perceptually distorted in either direction. These results demonstrate that changes in the perceived size of the body send the brain's body representation into turmoil. This turmoil is revealed by degradation in tactile acuity and sensitivity. Rather than observing effects of stretching and shrinking in opposite directions (as might be expected if neural representations were getting stretched or compacted) distortions in either direction has degrading effects and elevated both detection and acuity thresholds. If we look back at the summary figure from Longo et al. (2010) given in the introduction and reproduced here as Figure 13, we can see that the arrow connecting "body model" and "touch metrics" is not a simple process but one that represents a transformation of the body from the arbitrary proportions of the somatosensory cortex into a representation of the body as it is perceived to be. In other words the body representation is plastic and alterations are consequential.

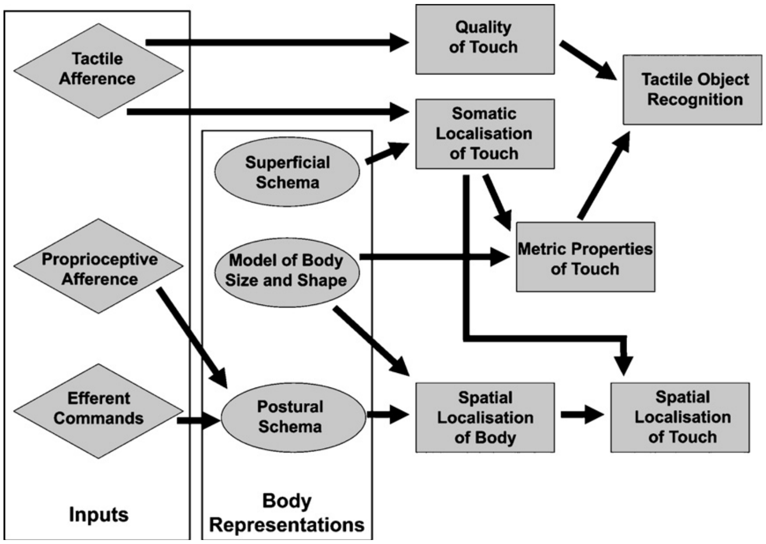


Figure 13. A model of somato-perceptual information processing which highlights the role of body representations in the construction of somatic percepts. Inputs are depicted as diamond shapes, body representations as ovals, and perceptual processes as rectangles. My thesis concentrates on the effects of the model of body size and shape on the "metric properties of touch". Taken from *Longo, Azañón, & Haggard (2010*)

Plasticity in the internal representation of the body is a vital part of coping with changing body size during development, pregnancy or actual (or as I have demonstrated, perceived) changes in body size. Failures to respond adaptively to such changes may underlie phantom limb pain and body-image-related disorders. Some of the ways this could be further explored were described in section 2.6.3.

Chapter 3 explored the effects of contralateral tactile masking on tactile sensitivity thresholds. The results showed that thresholds on one forearm increase in the presence of a masking stimulus applied to the corresponding point on the opposite forearm. I found that this effect was also spatially tuned. These findings reveal long-range interactions that can be helpful in understanding the overall arrangement of sensory systems.

Chapter 4 sought to expand on Chapter 3 by testing the effects of through the body masking on tactile sensitivity thresholds and investigating whether long-range interactions can be found between the visible front and the invisible back of the body. I found that thresholds on the stomach increase when a masking stimulus is applied to a nearby point on the front and when a masking stimulus is applied to the corresponding point on the back. This simple technique demonstrates results that modify and challenge our understanding of how the three-dimensional body is represented in the brain.

The specific implications of masking across and through the body were discussed in the discussion sections of chapters 3 and 4 respectively. I envisage a representation of the body that is not just another homunculus, corrected from the distorted representations of the somatosensory cortex illustrated in Figure 2 to be made to look more human. Instead we have a complex arrangement in which different parts may be connected together: another grotesque distortion perhaps, but one that allows us to function as a whole three dimensional body. Many more experiments will be needed of the type I have pioneered here before we fully understand how the body's representation is established in the brain and how it compensates for the fact that only some body part are visible, the massive variation in sensitivities and its dependence on and variation with our ever-changing posture.

5.2. Conclusions

Two overall conclusions can be drawn from the results of the experiments in this thesis. First, it can be concluded that tactile thresholds depend on a stable body representation. Second, tactile thresholds depend on what is happening elsewhere in the body representation. Taken together these findings emphasize that the body representation is critical for understanding tactile perception. Any model of the body representation has to be able to account for the findings I present here. The strange connections I have revealed across and through the body suggest that the arrangement may not be intuitive – like a little homunculus in the brain – but a rather non-linear arrangement in which areas that are separated in space may not be so separate in the brain.

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Appendix A

Contralateral masking between forearms

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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

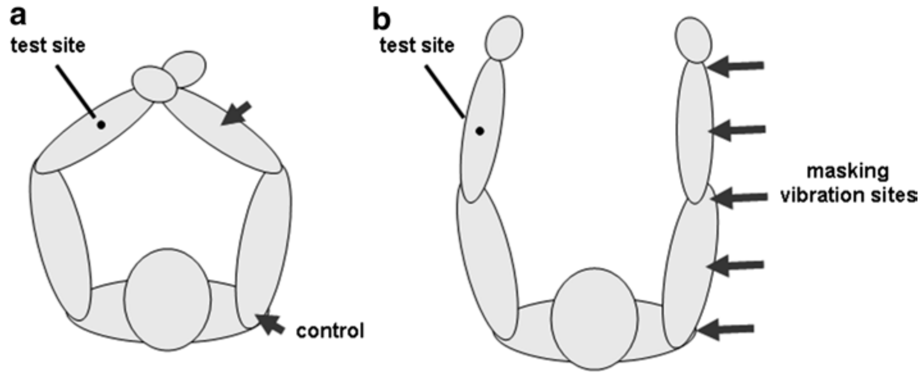

Fig. 1 Showing the sites of masking (*arrows*) and test stimuli (*dots*) for two arm positions. **a** For Experiment 1, the right hand was resting lightly on the left wrist. Only two masking sites were used. **b** For Experiment 2, the arms were held parallel to each other. For this experiment, there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

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

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.

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

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.

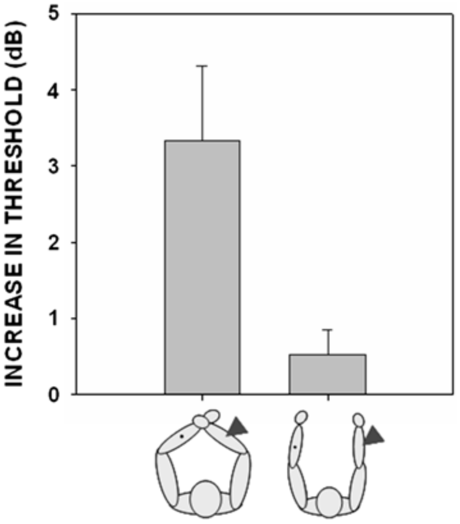

Fig. 2 The effect of arm position on the increase in tactile threshold at a site on the left forearm (*dot*) caused by the application of a masking stimulus (*triangles*) at the corresponding point on the opposite arm. The *left bar* is with the right hand resting lightly on the left wrist (Experiment 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

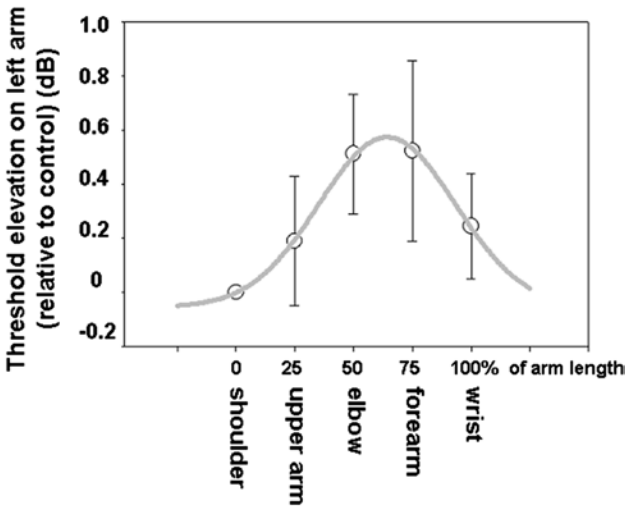

Fig. 3 Thresholds on the left forearm as a function of masking stimulus location on the right arm. All thresholds are expressed in decibels relative to the control thresholds obtained when the vibrotactile stimulus was applied to the right shoulder. The control is plotted as zero on the graph. The peak 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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Appendix B

Vibrotactile masking through the body

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Exp Brain Res
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RESEARCH ARTICLE

Vibrotactile masking through the body

Sarah D'Amour · Laurence R. Harris

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Abstract Touches on one hand or forearm can affect tactile sensitivity at contralateral locations on the opposite side of the body. These interactions suggest an intimate connection between the two sides of the body. Here, we explore the effect of masking not across the body but through the body by measuring the effect of a masking stimulus on the back on the tactile sensitivity of the corresponding point on the front. Tactile sensitivity was measured on each side of the stomach, while vibrotactile masking stimulation was applied to one side of the front and to points on the back including the point directly behind the test point on the front. Results were compared to sensitivity, while vibrotactile stimulation was applied to a control site on the shoulder. A reduction in sensitivity of about .8 dB was found that required the masking stimulus to be within about 2 cm of the corresponding point on the back.

Keywords Long-range tactile masking · Somatosensory sensitivity · Tactile detection thresholds · Body representation · Flat body hypothesis

Introduction

Somatosensory information about the body surface is split into two in the brain with each hemisphere receiving information from only one-half of the body (Penfield and Boldrey 1937). The two representations are connected through callosal pathways, so that even by area 5 many of the cells receive inputs from both sides (Manzoni et al. 1980, 1989). Even by this stage of processing the body-in-the-brain is treated as an integrated whole. However, this arrangement does not help us understand how the "flat map" in the cortex is turned into a useable representation of a three-dimensional body. Research investigating the representation of touch has tended to focus on the fingers and hands, with relatively few studies examining the whole body (but see Cholewiak et al. 2004; van Erp 2008). Here, we look for interactions between the front and back of the body to look for evidence of how the three-dimensional shape of the body is represented.

An important way to study the tactile sense is through the use of masking in which the sensitivity at one location is affected by vibration applied at a remote site. Traditionally, long-range tactile masking effects have been studied using the fingers, hands and arms, where masking has been found to occur between mirror-symmetric points across the body (Sherrick 1964; Braun et al. 2005; D'Amour and Harris 2014). Long-range reciprocally inhibitory pathways have been demonstrated between cortical tactile maps of the two halves of the body (Reed et al. 2011) which may be the neurophysiological explanation of these long-range interactive effects. However, the mobile limbs may be a special case and concentrating on these body parts ignores the body as a whole. Few studies have explored tactile masking using more extensive areas of the body (e.g., Alliusi et al. 1965; Geldard and Sherrick 1965; Craig 1966).

One reason that the limbs might be a special case, apart from their obvious motility, is that they fall within the visual field. Recent evidence (Tipper et al. 2001; Harrar and Harris 2010; Pritchett and Harris 2011) has suggested, counterintuitively, that tactile location may be coded at least partially in visual coordinates. However, we can never completely see our entire body and many regions, for example the back can never be seen. How then might the

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back be represented? Are we to postulate different coding systems for different parts of the body? Or might unseen parts of the body be somehow linked to corresponding visible areas?

To investigate the brain's representation of invisible body parts, we explored whether long-range interactions could be found between the visible front and the invisible back of the body. Having found evidence of through-the-body masking, we then measured the spatial tuning of the effect.

Methods

Participants

Ten participants took part in Experiment 1 (nine females, mean age 21.1 years, SD = 2.1 years) and 14 individuals participated in Experiment 2 (eight females, mean age 19.9 years, SD = 2.8 years). They were recruited from the York University 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

Tactile stimuli were 100 ms bursts of 250 Hz vibration of variable intensity controlled by a 64-bit sound card powered by a PC computer played through C2 tactors (Audio Research, California). Two tactors were mounted on a belt worn around the waist. The tactors were positioned 12 cm on each side of the midline and 3 cm below the navel.

Masking stimulus

The masking stimulus was provided by a Magic Wand vibrator (Hitachi, Japan) 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." In Experiment 1, the masking stimulus was applied to one of the four sites on the body: on the front (on the left side of the stomach about 3 cm above the left tactor), on the back (directly behind the left tactor) and at control sites on both shoulders. These sites are shown in Fig. 1a–c. For Experiment 2, the masking stimulus was applied at one of seven sites equally spaced around the left side of the trunk and up the back on the left side as shown in the insets of Fig. 1e, f. These masking sites were (1) on the front (on the left side of the stomach 2 cm to the left of the left tactor), (2) on the side (on the left side of the trunk), (3) half way between the side and the back position, (4) on the back (directly behind the left tactor), (5) mid back (half way up the back on the left side), (6) top back (near the top of the back on the left side) and (7) control (on the back of the left shoulder). The masking vibrator was held in place by an adjustable stand and was left on throughout the duration of each experimental block (<2 min).

Procedure

Blindfolded participants stood for the duration of each block. The experimenter arranged the adjustable stand to apply the masking stimulus to the pre-chosen body site and left it running in place while a block of trials was run. Using a two alternative forced choice (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 and Pelli 1983) running in MATLAB (version 2011b) on a PC. Participants verbally reported the period in which the stimulus was thought to occur.

Experimental design

For Experiment 1, tactile detection thresholds for the two tactors on each side of the stomach were measured in the presence of the masking vibration at one of the four sites shown in Fig. 1a–c. Each combination had 30 trials per tactor. Trials were divided into three blocks per condition with 20 trials per block (of a total of 12 blocks). Each block took less than 2 min.

For Experiment 2, tactile detection thresholds on the left side of the stomach were measured in the presence of masking vibration at one of the seven sites shown in Fig. 1e, f. Each condition had 40 trials. Trials were divided into two blocks per condition with 20 trials per block (for a total of 14 blocks). Each block took less than 2 min.

The sets of blocks for each experiment were run in a counterbalanced order, chosen for each subject using a Latin square, repeated as required.

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 log (intensity) used for each trial and fitted with a

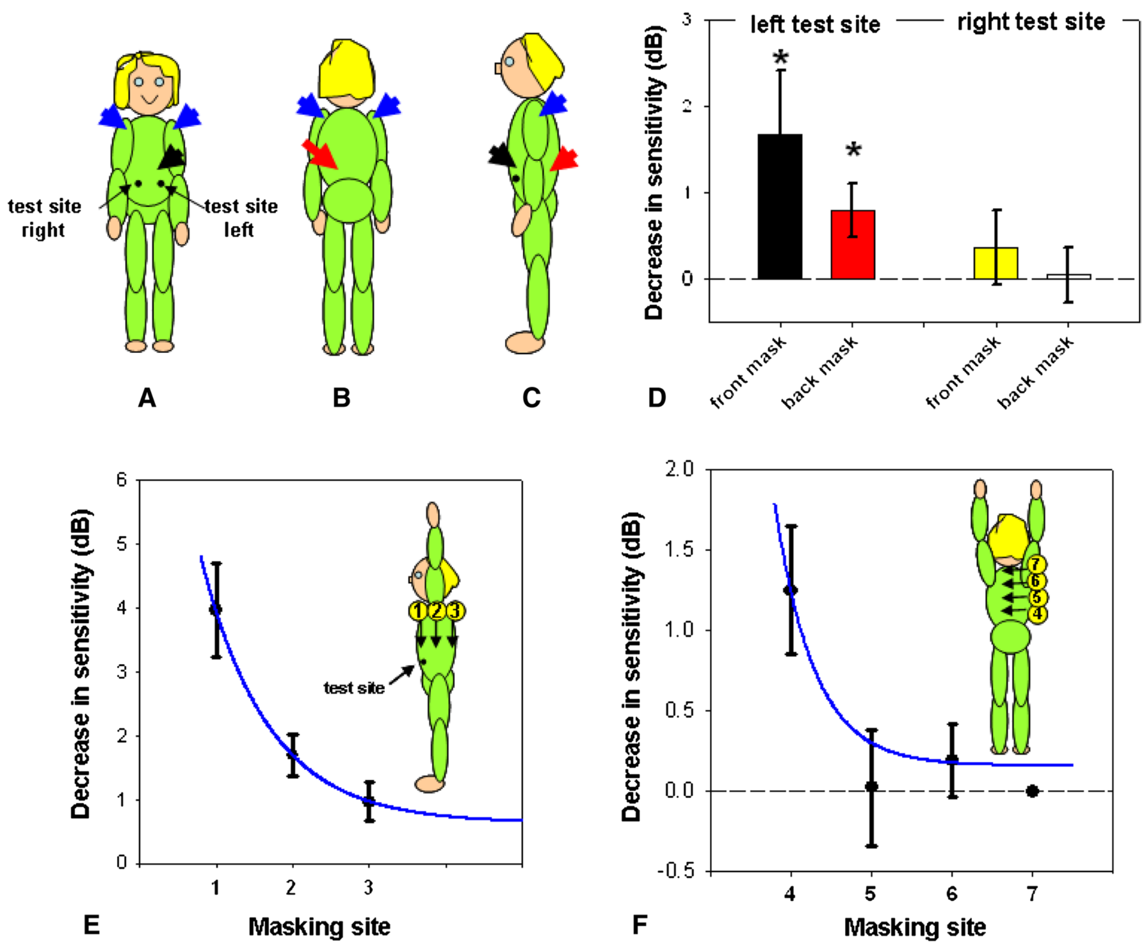

Fig. 1 Experiment 1: **a–c** The sites where masking vibration was applied: *black arrow* near the left test site on the front, *red arrow* on the corresponding point of the back. *Blue arrows* indicate the sites of vibration used as a control condition. Masking stimuli caused a significant increase in thresholds relative to control (*asterisks* correspond to $p < .05$) when applied either near the test site on the front (*black bar* in **d**) or at the corresponding point on the back (*red bar* in **d**). No effect was found at the test site on the side of the body contralateral to the masking sites (*yellow bars* in **d**). *Error bars* are SEs. Experiment 2: The masking effects when the masking stimulus was applied to sites on the front (**e**) or sites on the back (**f**) (masking sites shown numbered in the *insets*). Standard error bars are shown (location 7 was the control relative to which other data were expressed and therefore has a standard error of 0). Exponentials are plotted through the data points (color figure online)

cumulative Gaussian (Eq. 1) using the curve fitting toolbox in MATLAB.

$$y = 0.50 + 0.50/(1 + \exp(-(x - x_o)/b)) \qquad (1)$$

where x_o is the 75 % threshold value, x is the log (intensity) tested and b is the standard deviation.

Detection thresholds were converted to decibels relative to the threshold measured when the control vibration was applied to the control sites using:

$$\mathrm{dB} = 10 \times \log 10\,(\mathrm{threshold}/\mathrm{control\ threshold}) \qquad (2)$$

Results for Experiment 1 were not affected by which control was used and so only data relative to the right shoulder control are reported for that experiment. Statistical analyses were conducted using these threshold increases in dB.

Results

Experiment 1

All thresholds were expressed as increases in decibels relative to the thresholds measured in the control condition and are shown in Fig. 1d. Paired sample t tests were conducted to determine whether tactile detection thresholds were significantly increased when the masking stimulus was applied to the front and to the back compared to the control (right shoulder). All p values are reported as one-tailed values. Thresholds for the left tactor were significantly increased by a masking stimulus on the front 3 cm from the left testing site, $t(9) = 2.489$, $p = .0175$ by 1.71 ± .69 dB, and most importantly for this study, were also increased when the masking stimulus was on the corresponding point on the left side of the back, $t(9) = 3.748$, $p = .0025$ by .83 ± .22 dB. Significant differences were found between the left and right tactor locations when the masking stimulus was on the left side of the front, $t(9) = 2.183$, $p = .0285$ (with a 1.69 ± .78 dB increase in the left relative to the right) and when the masking stimulus was on the left side of the back, $t(9) = 3.063$, $p = .0065$ (with a 1.12 ± .37 dB increase in the left relative to the right). Thus, we report an effect of masking through the body in which detection thresholds on the ipsilateral side of the stomach were increased when a masking stimulus was applied to the back. Experiment 2 investigated the spatial tuning of this effect.

Experiment 2

Threshold increases for the tactor on the left side of the stomach were expressed as dB increases relative when thresholds were measured in the presence of masking vibration applied to the control site on the back of the left shoulder. A repeated measures ANOVA was conducted on conditions in which the masking stimulus was applied to the three sites spaced around the waist (sites 1, 2 and 3, see Fig. 1e) and a significant effect of condition, $F(2, 26) = 14.70$, $p < .001$, $\eta_\rho^2 = .531$ was found. Bonferroni corrected post hoc tests revealed that the threshold for the front condition (site 1) was significantly increased relative to both the side (site 2, 2.269 ± .670 dB, $p = .015$) and back half (site 3, 2.997 ± .631 dB, $p = .001$) conditions. An exponential was fitted through these three threshold increases (see Fig. 1e) and showed a fall off with a space constant of 1.21 tactor spacings.

A repeated measures ANOVA was also conducted on the four back conditions (sites 4–7; back, mid back, top back and control, see Fig. 1f). The control condition was of course, by definition, 0. A significant effect of condition was found, $F(3, 39) = 4.696$, $p = .007$, $\eta_\rho^2 = .265$. Post hoc tests showed that the back condition was significantly increased from the control condition (site 4, 1.245 ± .398 dB, $p = .048$). An exponential was fitted through these four threshold increases (see Fig. 1f) and showed a fall off with a space constant of .63 tactor spacings.

Discussion

For the first time, we have demonstrated tactile masking through the body in which vibration on the back increases tactile thresholds at the corresponding point on the front. We further demonstrated that through-the-body masking, like contralateral masking (D'Amour and Harris 2014), is spatially tuned. By varying the location of the masking stimulus with respect to the corresponding point on the back (Fig. 1f), we showed a spatial constant of .63 tactor spacings which is around 2 cm (more precise estimates cannot be given because tactor spacings varied from person to person and our masking stimulus was quite large relative to these distances). Our study reveals a special relationship between the front and the back of the torso that may provide insight into how the body might be represented in the brain.

No contralateral masking on the trunk

Interestingly, thresholds were only increased when the masking stimulus was applied to the same side of the body as the test stimulus (Fig. 1d). This is in contrast to the cross-body masking effects that have been shown between the hands and arms (Halliday and Mingay 1961; Sherrick 1964; Bird 1964; Braun et al. 2005; Tamè et al. 2011; D'Amour and Harris 2014). This could be due to the different nature of the trunk in comparison with the fingers, hands, and arms and may be connected to the motility of the limbs.

The representation of the body in the brain

Localizing stimuli in space requires a three-dimensional representation of the body. How might this be achieved? For tactile stimuli felt on the hand and limbs, it requires knowledge of limb location in space and, although proprioceptors in the joints and muscles contribute to this assessment, limb location in space is most reliably provided by the visual system (Graziano 1999; Fuentes and Bastian 2010). Visual coding also seems to be important for locating touch applied to the front of the torso (Pritchett et al. 2012) but how might the location in space of points on the back be known? We postulate that the back may be "pinned" to the front with some kind of special connection that is revealed by the present through-the-body masking. Under this "flat body hypothesis," the location of points on the back would be coded at some level in terms of the location of the corresponding point on the front. Support for this idea comes from the observation that when asked to identify tactile patterns on the back of the torso or on the back of the head, participants make errors consistent with the patterns being perceived as if pressed through the body, or viewed from behind (Allen and Rudy 1970; Duke 1966; Natsoulas and Dumanoski 1964; Parsons and Shimojo 1987). Such a coding mechanism might be economical as a coding system for representing a complex three-dimensional structure in two-dimensional cortical maps. Any potential front–back confusion may be acceptable for a part of the body where tactile pattern recognition is not of primary importance.

The present study using a simple technique provides an unexpected result that modifies and challenges our understanding of how the three-dimensional body is represented in the brain.

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