WHAT DRIVES TACTILE SPATIAL ACUITY ENHANCEMENT IN THE BLIND?

WHAT DRIVES TACTILE SPATIAL ACUITY ENHANCEMENT IN THE BLIND: VISUAL DEPRIVATION OR TACTILE EXPERIENCE?

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Abstract

In recent years, many studies have reported that the tactile spatial acuity of blind participants is enhanced relative to that of sighted participants, but it is unclear what factors drive this enhancement.

In the series of three psychophysics studies (of tactile spatial acuity) presented in this thesis, we attempted to tease apart two hypotheses explaining tactile spatial acuity enhancement in the blind: visual deprivation and tactile experience. To measure tactile spatial acuity in these studies, we used a grating orientation task. In the first study (Chapter 2), we found that blind participants outperformed sighted participants, but only on body parts where tactile experience is presumably greater in blind than in sighted participants (i.e., fingertips, not lips); we found additionally that blind participants' tactile acuity correlated with their Braille reading behaviour (e.g., style, frequency of reading). In the second study (Chapter 3), we found that visual deprivation of sighted participants for periods up to 110 minutes did not enhance their sense of touch. In the third study (Chapter 4), we found that extensive training on a tactile task can substantially improve sighted participants' sense of touch.

The findings from our three studies thus provide consistent support for the hypothesis that tactile experience, but not visual deprivation, drives tactile spatial acuity enhancement in the blind.

Preface

There are a total of five chapters in this thesis. Chapter 1 provides the background and overview for the empirical studies in this thesis, namely Chapters 2 to 4. Chapter 5 discusses the findings and implications of these studies.

Chapters 2 to 4 are empirical studies, two of which have been published in peer-reviewed journals. Chapter 2 is published in the *Journal of Neuroscience*[1] and Chapter 3 is published in the *Public Library of Science ONE (PLoS ONE)*[2]. Chapter 2 is included in this thesis with permission from the *Journal of Neuroscience.* Chapter 3 is an open-access article, included in this thesis under the terms of the Creative Commons Attribution License (CCAL).

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[1] Wong, M., Gnanakumaran, V., & Goldreich, D. (2011). Tactile spatial acuity enhancement in blindness: evidence for experience-dependent mechanisms. *Journal of Neuroscience, 31,* 7028-7037.

[2] Wong, M., Hackeman, E., Hurd, C., & Goldreich, D. (2011). Short-term visual deprivation does not enhance passive tactile spatial acuity. *PLoS ONE*, *6*, e25277.

Declaration of Academic Achievement

Chapter 2.

My graduate advisor, Dr. Daniel Goldreich and an undergraduate thesis student, Vishi Gnanakumaran designed the experiment and collected the initial portion of the data. Upon joining the laboratory, I collected the remainder of the data and was involved in all aspects of preparing the manuscript (e.g., statistical analyses and writing).

Chapter 3.

Experiment 1. This experiment was designed and conducted by Dr. Daniel Goldreich and Erik Hackeman at Duquesne University (Pittsburgh, PA).

Experiments 2 and 3. These experiments were conducted at McMaster University. For these two experiments, I was involved in all aspects of the research: experimental design, programming, data collection, statistical analyses, and writing. An undergraduate volunteer, Caitlin Hurd, assisted in the data collection for Experiments 2 and 3.

Chapter 4.

I was involved in all aspects of the research: experimental design, programming, data collection, statistical analyses, and writing. A graduate student, Ryan Peters, assisted with portions of this work.

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I would also like to thank my lab mates, Jonathan Tong, Luxi Li, Ryan Peters, and particularly, Andy Bhattacharjee for being great friends; I will miss our coffee runs to the hospital cafeteria. Andy, thank you for your words of encouragement, and for listening to me when I needed it most (and for being my desk neighbour all these years!). I would also like to thank my good friends: Mike Chrostowski, Melissa Mt. Pleasant, Bailey Lorv, Maggie Przednowek, and Christian Rutledge. We will have to find some way to continue our gym sessions, video game nights, dinner and movie nights, late-night chats, and "Friends Scene It" nights (Skype? ☺).

Last but not least, I would like to thank my parents for their love, guidance, and support, both emotionally and financially! Thanks to my brother, Nathan, and my cousin, David, for putting up with me for so many years. To anyone else I forgot to mention, thank you!

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GENERAL DISCUSSION

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List of all Abbreviations and Symbols

EEG	Electroencephology
fMRI	Functional magnetic resonance imaging
GOT	Grating orientation task
MEG	Magnetoencephalography
PET	Positron emission tomography
S1	Primary somatosensory cortex
TMS	Transcranial magnetic stimulation

Chapter 1

General introduction

1.1 Studies of tactile spatial perception in the blind: A brief history

Studies investigating whether tactile spatial perception – the ability to discern the spatial details of a stimulus to the skin – is enhanced in blind participants date back to at least the early 20th century. Seashore and Ling (1918), who were among the first investigators to examine this question, reported that the minimum separation required to discern two distinct points (two-point limen test) was no different in blind and sighted participants, irrespective of whether the points were presented to the stationary finger or to the stationary forearm. Several years later, however, Brown and Stratton (1925) reported conflicting results, showing that blind children could discern two points at a smaller separation (i.e., better tactile spatial perception) than could sighted children. It should be noted, however, that Brown and Stratton (1925) used a modified version of the two-point limen test in which participants scanned the point stimuli with their finger.

This controversy remained unsettled into the mid-to-late 20th century. Several studies supported the finding of Seashore and Ling (1918), reporting that tactile spatial perception is no different in blind and sighted participants. Lechelt (1988) reported that blind and sighted participants performed similarly on a line orientation-discrimination task, and Heller (1989) reported that blind and sighted participants did not differ in their ability to discriminate textures, whether by active or passive (finger stationary) touch. Other studies, however, supported the findings of Brown and Stratton (1925), reporting that blind participants were superior to sighted participants on tactile spatial tasks (for review see Jones, 1975). Axelrod (1959) reported some evidence that blind children, at least those who lost sight at an early age, performed better on a two-point discrimination task than did sighted children, and Jones (1972) reported that blind children were better able to localize points indented into the skin than could sighted children.

Towards the end of the 20th century, studies investigating whether the sense of touch is enhanced in the blind were nearly non-existent; investigators were instead interested in the functional organization of the visually deprived brain. Wanet-Defalque et al. (1988) were perhaps the first investigators to examine this; using positron emission tomography (PET), they reported increased metabolic activity in the occipital cortex of blind, relative to sighted, participants during non-visual (tactile and auditory) tasks. The number of studies investigating this phenomenon increased substantially after a study by Sadato et al. (1996) was published; the authors reported results that were similar to those of Wanet-Defalque et al. (1988), that the occipital cortex responded to tactile inputs (as revealed by PET) in blind, but not sighted, participants. These results were later confirmed by many other imaging studies, the majority using functional magnetic resonance imaging (fMRI) (e.g., Burton et al., 2002; Gizewski, Gasser, de Greiff, Boehm, & Forsting, 2003; Ptito, Moesgaard, Gjedde, & Kupers, 2005; Sadato et al., 1998; Sadato, Okada, Honda, & Yonekura, 2002; Sadato, Okada, Kubota, & Yonekura, 2004). Soon after this remarkable phenomenon was reported, interest in the perceptual consequences of blindness surged, presumably motivated by curiosity over whether the occipital cortex could drive perceptual enhancement in the blind.

In contrast to the results of the earlier studies, the results of more recent psychophysics studies – ones published after the study by Sadato et al. (1996) – are in general agreement that tactile spatial acuity is better in blind than in sighted participants (but see Alary et al., 2009; Grant, Thiagarajah, & Sathian, 2000). The tactile superiority of blind participants has been shown on a number of tactile spatial tasks, including: line and point orientation discrimination (Stevens, Foulke, & Patterson, 1996), gap detection (Stevens et al., 1996), Braille-like dot discrimination (Grant et al., 2000), grating detection (Goldreich & Kanics, 2006), and grating orientation discrimination (Goldreich & Kanics, 2003; Norman & Bartholomew, 2011; Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000). The more consistent results reported in recent studies than those reported in the earlier studies perhaps owe to modern psychophysical techniques and tasks. For instance, many of the early studies used now outdated tactile spatial tasks, such as the two-point discrimination task, which has undergone much criticism over the past several decades (Craig & Johnson, 2000; Johnson & Phillips, 1981). More recent studies by contrast have used more rigorous tasks, such as the grating orientation task (GOT), which is considered to be the gold standard test for measuring tactile spatial acuity (Craig & Johnson, 2000) (see section 1.4 for a description of these tasks).

While accumulating evidence suggests tactile spatial acuity is enhanced in the blind, the reason for this enhancement remains unclear. Two hypotheses have been put forth. One hypothesis suggests tactile spatial acuity is enhanced by visual deprivation (visual deprivation hypothesis), and the other suggests tactile spatial acuity is enhanced by increased reliance on the sense of touch (e.g., for Braille reading, navigation) (tactile experience hypothesis). In the following two sections, I will discuss evidence supporting each of these hypotheses in the literature.

1.2 Evidence that visual deprivation drives tactile spatial acuity enhancement

The earliest study that suggested visual deprivation drives tactile spatial acuity enhancement is perhaps the one by Doane, Mahatoo, Heron, and Scott (1959) who showed that two days of multisensory (i.e., vision, audition, and to some extent touch) deprivation improved sighted participants' performance on a two-point discrimination task. Within the next decade, several other investigators reported similar results, showing that multisensory deprivation for at least two days can drive tactile spatial acuity enhancement in sighted participants (Nagatsuka & Maruyama, 1963; Nagatsuka & Suzuki, 1964). Zubek and colleagues later showed that multisensory deprivation was not necessary to drive tactile spatial acuity enhancement; visual deprivation alone could improve participants' performance on a two-point discrimination task (Zubek, Flye, & Aftanas, 1964; Zubek, Flye, & Willows, 1964).

More recently, using modern psychophysics tasks, several studies have confirmed the results of the earlier studies, that visual deprivation improves sighted participants' tactile spatial acuity. Kauffman, Théoret, and Pascual-Leone (2002) and Merabet et al. (2008) showed that five days of visual deprivation improved sighted participants' ability to discriminate Braille characters. More remarkably, Facchini and Aglioti (2003) and Leon-Sarmiento, Hernandez, and Schroeder (2008) showed that a visual deprivation period of 90 minutes or less improved sighted participants' ability to discriminate the orientation of grating stimuli.

1.3 Evidence that tactile experience drives tactile spatial acuity enhancement

There are two lines of evidence suggesting that tactile experience drives tactile spatial acuity enhancement. The first line of evidence comes from studies suggesting that extensive experience with sensorimotor tasks can improve tactile spatial acuity. Van Boven et al. (2000) showed that blind participants performed better on a GOT with their Braille reading fingers than with their non-reading fingers. Moreover, Ragert, Schmidt, Altenmüller, & Dinse (2004) showed that pianists had better two-point discrimination ability than non-musicians on the index fingers; they found additionally that the pianists' performance on this task correlated with their average daily piano-playing duration. Together, these results suggest that extensive tactile experience and/or stimulation of the fingers (e.g., from Braille reading or piano playing) can drive tactile spatial acuity enhancement.

The second line of evidence comes from studies demonstrating that performance on tactile tasks can be improved in the laboratory with training, a phenomenon known as perceptual learning. Perceptual learning has been observed on tactile spatial tasks, including Braille-like dot discrimination (Kauffman et al., 2002; Sathian & Zangaladze, 1998) and to some extent grating orientation discrimination (Sathian & Zangaladze, 1997). Perceptual learning has also been observed on several non-spatial tactile tasks, including frequency discrimination (Harris, Harris, & Diamond, 2001; Imai et al., 2003), pressure detection (Harris et al., 2001), and roughness discrimination (Harris et al., 2001; Sathian & Zangaladze, 1997). Perceptual learning can occur quite rapidly, requiring on average fewer than 300 trials on some tasks (e.g., punctate pressure discrimination, frequency discrimination) (see Harris et al., 2001), and there is some evidence that these training effects, to some degree, are retained for several months (Imai et al., 2003; Sathian & Zangaladze, 1998).

1.4 Measuring tactile spatial acuity: Grating orientation task

The three studies outlined in this thesis were conducted in an attempt to tease apart two competing hypotheses explaining tactile spatial acuity enhancement in the blind: the visual deprivation hypothesis and the tactile experience hypothesis. Because we wished to measure tactile spatial acuity in blind and sighted participants, it was imperative that we use a task that is uncontaminated by non-spatial cues. In this section, I will give a brief history of the development of tactile spatial tasks and explain why the GOT is considered to be the gold-standard test for measuring tactile spatial acuity.

The development of tactile spatial tasks has a long history. Weber was perhaps the first to introduce a task to measure spatial acuity, a task that has been named the two-point limen test. In this task, two points are presented to the skin with progressively closer separations until the participant cannot feel the sensation of two distinct points, a separation that was classically thought to be indicative of one's spatial perceptual resolution (two-point limen) (Weber, 1835).

Since Weber's introduction of the two-point limen test, several variants of this task have been used. Perhaps the most commonly used by tactile researchers is the two-point discrimination task in which a participant is required to discriminate between one and two points (Figure 1.1): one's spatial resolution in this task, similar to the two-point limen test, is considered to be the separation of two points at which a participant can no longer discriminate between one and two points. The two-point discrimination task, however, has undergone much criticism. Johnson and Phillips (1981) found that participants could discriminate one from two points well above chance level even when no physical separation exists between the two points. It is thought that participants are able to discriminate two contacting points from one point based on some non-spatial cue, perhaps, as suggested by Johnson and Phillips (1981), the difference in sensation magnitude elicited by one and two points. That is, given equal indentation depth, the number of action potentials discharged by the primary mechanoreceptive afferents (e.g., slowly adapting type-I afferents) to one point is greater, giving rise to a greater sensation magnitude, than the number of action potentials discharged by the afferents to two closely spaced points (Vega-Bermudez & Johnson, 1999). The two-point discrimination task, therefore, does not appear to provide a pure measure of tactile spatial acuity.

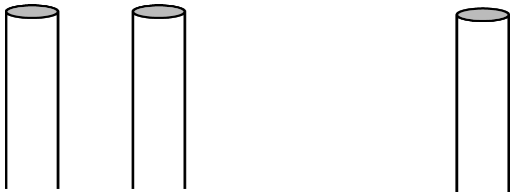

Figure 1. Two-point discrimination task. Two stimulus pieces are illustrated here (not drawn to scale): a stimulus with two points (left), and a stimulus with one point (right).

Because of the problem with the two-point discrimination task, investigators have devised alternative tasks. One such task is the gap detection task in which participants are required to indicate whether the center of a flat surface contains a gap: decreasing the width of the gap increases the difficulty of this task (Figure 1.2). Although some investigators consider this task to provide a measure of spatial acuity (see Craig & Johnson, 2000; Stevens & Choo, 1996), it arguably suffers from the same problem as the two-point discrimination task. Because the surface area contacting the skin differs between the two stimulus surfaces, the number of action potentials elicited by each surface is likely different as well. Thus, participants can presumably perform the gap detection task by basing their decision on the difference in the number of action potentials elicited by the two stimuli, rather than on the spatial arrangement of neural activity.

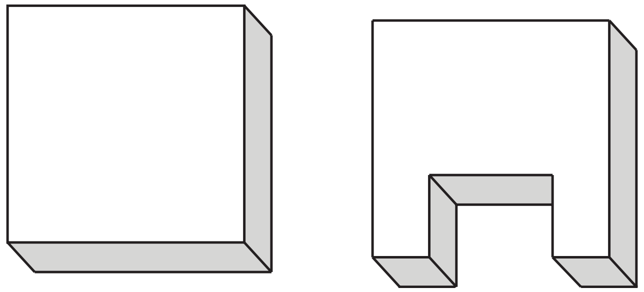

Figure 2. Gap detection task. Two stimulus pieces are illustrated here (not drawn to scale): a stimulus without a gap (left), and a stimulus with a gap (right).

A more rigorous alternative to the two-point discrimination task is the GOT, proposed by Johnson and Phillips (1981). This task requires participants to discriminate between two surfaces with gratings, of equal ridge and groove width, that are aligned in orthogonal orientations: decreasing the groove width increases the difficulty of this task (Figure 1.3). It is assumed that because the number of edges (and the surface area) contacting the skin is equivalent in both orientations, the total number of action potentials elicited by the orientations is similar, eliminating the magnitude cue; participants must therefore discriminate the orientation of the gratings based on the spatial arrangement of the neural activity. For this reason, we have used the GOT to measure tactile spatial acuity in the three studies presented in this thesis.

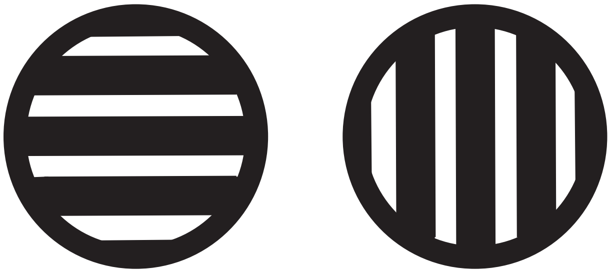

Figure 3. Grating orientation task (GOT). Two grating stimulus surfaces (of equal ridge and groove width) at orthogonal orientations are depicted here (not drawn to scale).

Investigators administering tactile tasks often present stimuli manually, potentially leaving many stimulus-delivery parameters (e.g., contact force, stimulus duration, stability) uncontrolled. Therefore, even though the GOT provides reliable measures of tactile spatial acuity, these measures can be contaminated by unintended non-spatial cues if care is not taken during stimulus delivery. For example, movement of the stimuli upon contact with the test site greatly facilitates grating-orientation perception. Reducing or eliminating such unintended non-spatial cues is nearly impossible when tactile stimuli are delivered manually; we have therefore presented our stimuli (with the exception of the stimuli applied to the lips in chapter 2) using a custom-made fully automated tactile stimulus-delivery device, which we have named the Tactile Automated Passive-finger Stimulator (TAPS) (see Goldreich, Wong, Peters, & Kanics, 2009 for a full description of the device).

1.5 Overview of studies

Although both the visual deprivation hypothesis and the tactile experience hypothesis receive some support from the literature, further investigation is required because very few studies have investigated these hypotheses using a purely tactile spatial task (e.g., GOT), and even fewer studies have presented tactile stimuli mechanically to control for stimulus-delivery parameters.

In the first study (chapter 2), we attempted to tease apart the visual deprivation and the tactile experience hypothesis in a group of blind and sighted participants. Nearly every study that has compared the tactile spatial acuity of blind to sighted participants has done so on the fingertips, and has reported superior spatial acuity of blind to sighted participants (e.g., Goldreich & Kanics, 2003, 2006; Grant et al., 2000; Norman & Bartholomew, 2011; Stevens et al., 1996; Van Boven et al., 2000). Based on these results, however, it is difficult to attribute the superior spatial acuity of blind participants to either visual deprivation or tactile experience because in addition to visual deprivation, blind participants also rely on their fingers to a much greater degree than sighted participants do. Therefore, to investigate the visual deprivation hypothesis in the first study, we tested blind and sighted participants not only on the fingers but also on the lips, where tactile experience is presumably similar in the two participant groups. We found in this study that blind participants performed better than sighted participants with the fingers but not with the lips, suggesting that tactile experience, but not visual deprivation, drives tactile spatial acuity enhancement in the blind. Further supporting the tactile experience hypothesis, we found among the blind Braille readers that GOT performance correlated with Braille reading style, and frequency.

Having found no evidence that visual deprivation drives tactile spatial acuity enhancement in the first study, we investigated the visual deprivation hypothesis further in the second study (Chapter 3) by visually depriving sighted participants. Two recent studies showed that GOT performance improved in sighted participants with visual deprivation periods as short as 45 (Leon-Sarmiento et al., 2008) and 90 minutes (Facchini & Aglioti, 2003); however, these findings contradict those of a number of studies from an earlier literature, which showed that the performance of sighted participants on several other tactile tasks did not improve with visual deprivation periods of up to eight hours (Culver, Cohen, Silverman, & Shmavonian, 1963; Kamchatnov, 1962; Pollard, Uhr, & Jackson, 1963; Reitman & Cleveland, 1964; Cohen, Silverman, & Shmavonian, 1962; for review see Zubek, 1969). In our second study, we attempted to resolve this controversy by testing participants on a GOT in three experiments with progressively longer periods of visual deprivation: under 10 minutes, 70 minutes, and 110 minutes. We found, in agreement with the earlier literature, that sighted participants' tactile spatial acuity did not improve with short-term visual deprivation.

Thus, the results from our first two studies (Chapters 2 and 3) favour the tactile experience hypothesis and provide no support for the visual deprivation hypothesis. To further investigate the tactile experience hypothesis, we conducted a third study to ascertain whether tactile spatial acuity can be improved with training (Chapter 4). Although perceptual learning has been observed on a number of tactile tasks, very few studies have investigated perceptual learning using tactile spatial tasks, particularly the GOT. We found that training participants to discriminate the orientation of gratings for four days led to a substantial improvement in their GOT performance.

Together, the results from our three studies suggest that tactile experience plays a pivotal role in driving tactile spatial acuity enhancement in the blind. While we did not find any evidence that visual deprivation drives tactile spatial acuity enhancement, we cannot rule out a possible facilitatory effect that visual deprivation might have when coupled with tactile experience.

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Chapter 2

2.1 Preface

Many studies have reported better tactile spatial acuity in blind than in sighted participants, but no studies have attempted to directly investigate which hypothesis (visual deprivation or tactile experience) better explains tactile spatial acuity enhancement in the blind, particularly using a tactile spatial task such as the GOT. In Chapter 2, we attempted to tease apart these two hypotheses by testing blind and sighted participants on the GOT on the fingertips and the lips.

We found that spatial acuity was better in blind participants only on body parts where tactile experience is presumably greater in blind than in sighted participants (i.e., fingertips, and not lips). We found additionally that blind Braille readers' spatial acuity correlated with their Braille reading behaviour. This study is the first to provide evidence favouring the tactile experience hypothesis over the visual deprivation hypothesis.

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Behavioral/Systems/Cognitive

Tactile Spatial Acuity Enhancement in Blindness: Evidence for Experience-Dependent Mechanisms

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Tactile spatial acuity is enhanced in blindness, according to several studies, but the cause of this enhancement has been controversial. Two competing hypotheses are the tactile experience hypothesis (reliance on the sense of touch drives tactile-acuity enhancement) and the visual deprivation hypothesis (the absence of vision itself drives tactile-acuity enhancement). Here, we performed experiments to distinguish between these two hypotheses. We used force-controlled grating orientation tasks to compare the passive (finger stationary) tactile spatial acuity of 28 profoundly blind and 55 normally sighted humans on the index, middle, and ring fingers of each hand, and on the lips. The tactile experience hypothesis predicted that blind participants would outperform the sighted on the fingers, and that Braille reading would correlate with tactile acuity. The visual deprivation hypothesis predicted that blind participants would outperform the sighted on fingers and lips. Consistent with the tactile experience hypothesis, the blind significantly outperformed the sighted on all fingers, but not on the lips. Additionally, among blind participants, proficient Braille readers on their preferred reading index finger outperformed nonreaders. Finally, proficient Braille readers performed better with their preferred reading index finger than with the opposite index finger, and their acuity on the preferred reading finger correlated with their weekly reading time. These results clearly implicate reliance on the sense of touch as the trigger for tactile spatial acuity enhancement in the blind, and suggest the action of underlying experience-dependent neural mechanisms such as somatosensory and/or cross-modal cortical plasticity.

Introduction

Previous studies report superior tactile spatial acuity in blind people (Stevens et al., 1996; Van Boven et al., 2000; Goldreich and Kanics, 2003; Legge et al., 2008), but what causes this enhancement? The extraordinary reliance of blind people in general, and Braille readers in particular, on the sense of touch might drive acuity enhancement (tactile experience hypothesis). Alternatively, the absence of vision itself might enhance tactile acuity (visual deprivation hypothesis).

When sighted participants undergo intensive training on a tactile task, their performance on that task improves on the trained finger, and to a lesser degree (if at all) on adjacent and contralateral fingers (Sathian and Zangaladze, 1997; Harris et al., 2001). Thus, a plausible prediction of the tactile experience hypothesis is that the most pronounced acuity enhancement will occur on skin areas receiving the greatest daily stimulation. In contrast, prolonged blindfolding of sighted participants reportedly enhances finger tactile acuity (Kauffman et al., 2002; Facchini and Aglioti, 2003; Merabet et al., 2008) and acuity of other skin areas (Zubek et al., 1964), even without training. Thus, a plausible prediction of the visual deprivation hypothesis is that blind participants will show enhanced acuity throughout the body surface.

In support of the tactile experience hypothesis, Van Boven et al. (2000) found that passive tactile spatial acuity is better on the reading finger than on the nonreading fingers of blind Braille readers. An obvious interpretation of this finding favors the tactile experience hypothesis, but an alternative interpretation is that Braille readers choose to read with the finger that has greatest (pre-existing) acuity. In support of the visual deprivation hypothesis, Goldreich and Kanics (2003) found no significant difference between blind Braille readers and nonreaders in index finger passive tactile spatial acuity; both groups nearly equally outperformed the sighted. One interpretation of this finding is that visual deprivation, not tactile experience, drives acuity enhancement.

Here we tested predictions of the tactile experience and visual deprivation hypotheses by assessing the passive tactile spatial acuity of blind participants with varying levels of Braille expertise and of sighted participants on the index, middle, and ring fingers of each hand and on the lips. Whereas experience with the lips is presumably similar among blind and sighted individuals, experience with the hands differs markedly. We reasoned that, to the extent that tactile experience drives acuity enhancement, blind participants in general

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would outperform the sighted on all fingers, and blind Braille readers would show especially good acuity on their reading fingers. To the extent that loss of vision drives tactile acuity enhancement, blind participants in general would outperform sighted participants on the fingers and lips.

Our results strongly support the tactile experience hypothesis. We discuss our findings with respect to two possible neural mechanisms: experience-driven enlargement of somatosensory cortical representations (Pascual-Leone and Torres, 1993; Sterr et al., 1998, 1999) and recruitment of occipital cortical areas for tactile tasks (Sadato et al., 1996, 1998, 2002, 2004; Cohen et al., 1999; Burton et al., 2002, 2006; Ptito et al., 2005; Stilla et al., 2008).

Materials and Methods

Participants. We tested 55 normally sighted and 28 profoundly blind adults. The sighted group consisted of 29 men and 26 women, ranging in age from 19.8 to 66.1 years (mean, 39 years). Fifty-three were right-hand dominant and two were left-hand dominant, as assessed by a handedness survey (modified from Oldfield, 1971). The blind group consisted of 15 men and 13 women, ranging in age from 19.5 to 65.7 years (mean, 40 years). Twenty-six were right-hand dominant and two were left-hand dominant by handedness survey. Acceptance criteria ensured that blindness was of peripheral origin, that the degree of vision in blind participants did not exceed residual light perception (ability to see vague shapes and shadows, but inability to read print, even with magnification devices), that sighted participants did not have dyslexia (Grant et al., 1999), and that no participants in either group had diabetes (Hyllienmark et al., 1995), nervous system disorders, or index, middle, or ring fingertip injuries or calluses. All participants gave signed consent (consent form read aloud to blind participants) and received monetary compensation or course credit for their participation. All procedures were approved by the McMaster University Research Ethics Board.

We interviewed blind participants about their visual history and Braille expertise level, and proficient Braille readers about their reading history (e.g., age at which they started Braille training), style [which hand(s) and finger(s) they used to read], and habits (average weekly reading time).

The blind participants had no more than residual light perception, but their visual histories were quite varied. At one extreme were participants born with normal vision who then progressed through a stage of low vision (defined here as the ability to read print only by using magnification devices) to reach residual light perception. At the other extreme were participants born with residual light perception or less. Defining childhood as the period between birth and 12 years of age, we classified eight participants as congenitally blind (residual light perception or less at birth), seven as early blind (normal or low vision at birth declining to residual light perception or less by the end of childhood), and 13 as late blind (normal or low vision throughout childhood, declining to residual light perception or less in adulthood). Fourteen participants had residual light perception at the time of testing and 14 had no light perception.

The blind participants exhibited varying degrees of Braille reading expertise. Proficient Braille readers ($n = 19$) were comfortable reading grade 2 (contracted) Braille. This standard Braille form represents common letter combinations (e.g., ch, sh, th) and words (e.g., and, but, can) using single Braille characters. Novice Braille readers ($n = 4$) were comfortable reading grade 1 (un-contracted) but not grade 2 Braille. Grade 1 is a beginner's Braille form that represents each letter of the alphabet with a separate Braille character. Nonreaders ($n = 5$) were blind participants who were either uncomfortable reading grade 1 Braille (e.g., stated that they would require hours or more to read a short grade 1 passage; $n = 3$) or who had never learned to read any form of Braille ($n = 2$). The period of blindness onset associated strongly with Braille expertise; all congenitally blind and early blind participants were proficient Braille readers (Table 1).

Of the 19 proficient Braille readers, 10 read with both hands and nine with a single hand. To determine reading hand and finger preference, we asked all readers to indicate which single finger they would use to read Braille if asked to use just one. All Braille readers identified an index finger as the preferred reading finger. The dominant hand (as determined by handedness survey) was not always the preferred reading hand. Eight proficient readers preferred to read with the index finger of the nondominant hand. The four novice readers read with the index finger of the dominant hand.

Table 1. Blind participants classified by Braille expertise and blindness onset

	Blindness onset			
	Congenitally blind	Early blind	Late blind	Total
Braille expertise				
Proficient Braille reader	8 (2)	7 (1)	4 (3)	19
Novice Braille reader	0	0	4 (4)	4
Nonreader	0	0	5 (4)	5
Total	8	7	13	28 (14)

Number of participants with residual light perception are shown in parentheses.

We timed the proficient Braille readers as they read a short passage (652 characters in grade 2 Braille) silently at their normal reading speed. We observed the reading to verify each participant's reading style. A series of comprehension questions following the reading confirmed that all participants had understood the passage.

Grating orientation task. We used a two-interval forced choice (2-IFC) grating orientation task (GOT) to test the participants' ability to discern the orientations of grooved surfaces (square-wave gratings of equal groove and ridge widths) applied to the distal pads of the stationary index, middle, and ring fingers of each hand, and then to the two sides of the lower lip. The dependent measure (GOT threshold) was the groove width of the grating whose orientation the participant could perceive with 76% probability (corresponding to $d' = 1$ on this 2-IFC task), as determined by a Bayesian adaptive tracking method (see Adaptive psychophysical method, below). We programmed all stimulus control routines in LabVIEW 6.1 for Macintosh (National Instruments).

The GOT provides a well controlled measure of passive tactile spatial acuity, uncontaminated by the nonspatial cues present in measures such as two-point discrimination (Johnson and Phillips, 1981; Craig and Johnson, 2000). Although many tactile activities, including Braille reading, are active tasks, our goal in this study was to test for consequences of tactile experience and/or visual deprivation specifically on passive (finger stationary) tactile spatial acuity, because we wished to isolate the purely sensory ability of the participants from their sensorimotor coordination, which presumably influences active tactile performance.

Finger testing. We used the tactile automated passive-finger stimulator (TAPS), described in detail in Goldreich et al. (2009). Briefly, the participant's arm rested comfortably in prone position on a tabletop. The distal pad of the tested finger lay over a tunnel in the table through which the stimulus surfaces rose to contact the skin. The surfaces, custom-made square-wave gratings (groove widths ranging from 0.25 to 3.10 mm in 0.15 mm increments), moved under computer control to contact the skin with 4 cm/s onset velocity, 50 g of contact force, and ~1 s contact duration (Fig. 1*A*). Plastic barriers placed gently against the sides of the finger prevented lateral movements, while a force sensor (micro switch FS; Honeywell) on the fingernail detected and discarded any trials with upward, downward, forward, or backward movements.

Before testing, the investigator carefully explained the task to the participant and answered any questions the participant had. The investigator then asked the participant to repeat the task instructions back to the investigator. The experiment proceeded only when the investigator was satisfied that the participant fully understood the task. The computer program randomly chose which hand to test first; the index, middle, then ring finger of that hand were tested, followed by the index, middle, then ring finger of the other. A series of practice trials, with auditory feedback identifying correct and incorrect responses, preceded testing on each finger (20 practice trials on the index finger and 10 each on the middle and ring fingers). The subsequent experimental block on each finger consisted of 40 trials without feedback. Participants received a 15 s break

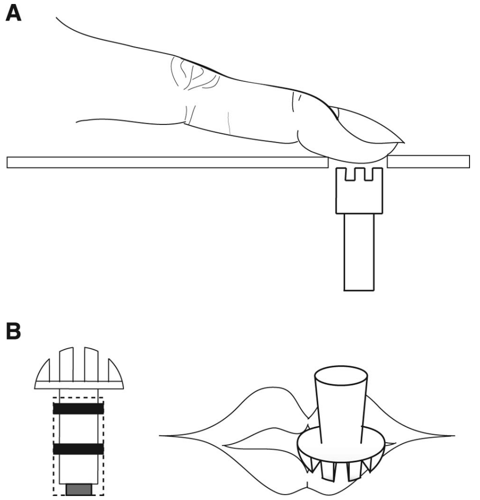

Figure 1. Grating orientation task. ***A***, Finger testing. A computer-controlled rod rotated to press the selected stimulus surface against the fingertip with 50 g of force. The gratings are shown aligned horizontally. ***B***, Lip testing. JVP Domes were held within a plastic tube (dotted rectangle). Two silicone rubber o-rings (thick black lines) surrounding the dome shaft and contacting the inner wall of the tube provided stability with minimal friction, allowing the shaft to slide backwards slightly upon lip contact. A sensor (gray rectangle) at the rear of the tube monitored the force with which the investigator pressed the JVP Dome orthogonally against the lip surface (right). Participants kept their mouths slightly open during stimulus application. The target force was 50 g. The gratings are shown aligned vertically. Images in ***A*** and ***B*** are not drawn to scale.

after every 20 trials, a 1 min break between fingers, and a 5 min break between hands. Each trial consisted of two sequential stimulus presentations (interstimulus interval, 2 s) with gratings of identical groove width but differing 90° in orientation. In one presentation, the grooves were aligned parallel (vertical) to and in the other transverse (horizontal) to the long axis of the finger. Stimulus order was chosen randomly. Participants indicated whether the horizontal orientation occurred in the first or second interval by pressing one of two buttons with the nontested hand. A Bayesian adaptive method (see Lip testing, below) adjusted groove width from trial to trial.

Lip testing. The participant's head was supported comfortably in an optometrist's chin-rest (Richmond Products); a thin sheet of soft foam, with a cut-out to accommodate the bridge of the nose, pressed gently against sighted participants' cheeks below eye level, and extended forward from the face to block the gratings from view. We tested the left and right sides of each participant's lower lip in the same order as the left and right hands, using dome-shaped square-wave gratings (JVP Domes, groove widths 0.35, 0.50, 0.75, 1.00, 1.25, 1.50, 2.00, 2.50, 3.00, and 3.50 mm; Stoelting).

We did not use TAPS to stimulate the lips, because TAPS pushes the stimulus surfaces upward through an opening in a tabletop; hence, the use of TAPS would have required participants to adopt an uncomfortable posture to establish contact between the stimulus surfaces and the lips. Instead, we developed a device to apply grating stimuli to the lips manually but with force control (Fig. 1*B*). We equipped one end of a plastic tube with a force sensor (micro switch FS; Honeywell). The experimenter inserted the shaft of the selected JVP dome into the other end of the tube; holding the tube, the experimenter then pressed the dome orthogonally against the lip vermillion with increasing force. The target force was 50 g, identical to that used during finger testing. The force sensor output was monitored by computer. Auditory tones (audible only to the experimenter through headphones) alerted the experimenter to the applied force. A low-frequency tone sounded at 40 g of contact force to warn the experimenter that the target force was approaching. A high-frequency tone sounded at 48 g to notify the experimenter to withdraw the stimulus. The reaction time of the experimenter was such that maximum applied force was usually close to the target force. Once the target force was reached, the experimenter withdrew the dome from the lips, rotated it 90° within the tube, and reapplied it to the participant's lips. The participant was asked to indicate whether the horizontal orientation occurred in the first or second interval by pressing one of two response buttons. The computer program automatically discarded trials with applied forces exceeding 65 g. An independent samples t test revealed no significant difference between the force applied to the lips of sighted (mean, 53 g; SD, 1 g) and blind (mean, 54 g; SD, 1 g) participants (two-tailed, $t_{(78)} = 1.99$, $p = 0.43$).

For each side of the lip, five practice trials (with feedback for correct and incorrect answers) preceded a block of 30 experimental trials (without feedback). Participants received a 15 s break after every 15 experimental trials and a 3 min break between lip sides. The same computer program (Bayesian adaptive algorithm) used to test the fingers instructed the experimenter which dome to apply in each trial, and in which orientation order [vertical (grooves aligned up-down) then horizontal (grooves aligned left-right) or vice versa].

Adaptive psychophysical method. To estimate each participant's psychometric function, we used the Bayesian adaptive psi (Ψ) algorithm (Kontsevich and Tyler, 1999) (Fig. 2). This method calculates a posterior probability density function (PDF) for each participant's threshold stimulus level, corresponding to 76% correct response probability ($d' = 1$ on the 2-IFC task). We implemented the Ψ algorithm as explained in detail in Goldreich et al. (2009). Briefly, following Kontsevich and Tyler (1999), we modeled d' as a power function of groove width, x, and we modeled the psychometric function (the probability of correct response at x), $\Psi_{a,b,\delta}(x)$, as a mixture of a cumulative normal function and a lapse rate term:

$$d' = \left(\frac{x}{a}\right)^{b}$$

$$\Psi_{a,b,\delta}(x) = \frac{\delta}{2} + (1 - \delta)\frac{1}{\sqrt{2\pi}} \int_{-\infty}^{d'/\sqrt{2}} \exp\left(-\frac{y^{2}}{2}\right) dy.$$

We modified the Ψ algorithm to treat not only a (threshold) and b (slope), but also δ (lapse rate) as unknown parameters. We initialized the algorithm with uniform prior probability density over psychometric function threshold (0.1–3.0 mm), slope (0.5–15.0), and lapse rate (0.01–0.1). After each trial, the algorithm calculates the expected information gain (joint posterior PDF entropy reduction) associated with each groove width in the stimulus set and applies the groove width with the greatest expected information payoff. We marginalized the joint (a, b, δ) posterior PDF over b and δ to generate the posterior PDF for the a parameter. We took the mean of this posterior PDF as the estimate of each participant's tactile acuity (GOT threshold, corresponding to the participant's 76%-correct groove width, where $d' = 1$).

During execution of the experiment, we calculated a likelihood ratio on each trial to determine whether participants were able to perform the task. This likelihood ratio compares the probability of the data under the hypothesis that the participant is guessing (50% correct probability) on every trial, to the probability of the data under the hypothesis that the participant's responses derive from a best-estimate psychometric function [average over the joint posterior PDF of $\Psi_{a,b,\delta}(x)$]. When a subject is not guessing, the likelihood ratio approaches zero rapidly as the experimental block progresses. A likelihood ratio >5 after trial 10 was taken as evidence that the participant was guessing on every trial, and resulted in the termination of the testing block. In such cases, the participant's threshold value for that testing block was set to 3.1 mm, just above the maximum measurable threshold, and equivalent to the largest groove width in the finger testing set.

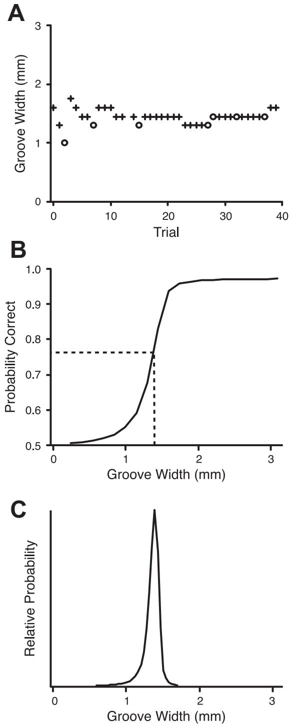

Figure 2. Adaptive psychophysical procedure. ***A***, Correct (+) and incorrect (o) answers of a 30-year-old sighted male tested on the right middle finger. ***B***, Best estimate of the participant's psychometric function. ***C***, Bayesian posterior probability distribution for the participant's 76%-correct GOT threshold (groove width for which $d' = 1$; see dotted lines in ***B***).

The overall block completion rate in the study was 92% (the 83 participants completed a total of 609 of the $83 \times 8 = 664$ testing blocks). A total of 24 blind (86%) and 39 sighted (71%) participants were able to complete all six finger testing blocks; a total of 23 blind (82%) and 54 sighted (98%) participants were able to complete both lip testing blocks. The age of participants was an important factor in their ability to complete the tasks, consistent with Tremblay et al. (2003). The mean age of the 23 participants (seven blind and 16 sighted) who failed to complete at least one of the eight testing block was 51.8 years old (SE, 3.1 years); in contrast, the mean age of the 60 participants who completed all eight testing blocks was 34.8 years old (SE, 2.0 years). The 17.0 year mean difference in ages between these two groups was highly significant ($t_{(81)} = 4.575$, $p < 0.001$).

The Ψ algorithm assumes a stationary psychometric function for each participant, but on occasion a participant may lose concentration at some point in a testing block, resulting in a consistent rightward drift of the estimated psychometric function as the participant begins to respond randomly to previously detectable groove widths. To assess participant concentration, we applied an offline concentration assessment procedure to all completed testing blocks. For each trial, *t*, in the testing block, we derived from the joint posterior PDF a guessing Bayes factor (a generalization of the likelihood ratio described above). This Bayes factor, BF_t, is the ratio of the probability of the participant's data (correct and incorrect responses, *r*) up to and including trial *t*, given random guessing, to the probability of the data given that the participant is using a psychometric function:

$$BF_t = \frac{(0.5)^t}{\iiint\limits_{a,\,b,\,\delta} P(r_1, r_2, \ldots r_t \mid \Psi_{a,b,\delta})\, P(\Psi_{a,b,\delta})\, d_a d_b d_\delta}$$

In the vast majority of completed testing blocks, the Bayes factor fell consistently toward zero as the block progressed, as expected for a participant who is concentrating well on the task. In a small fraction of testing blocks, by contrast, the Bayes factor fell initially only to later rise dramatically, suggesting that the participant had lost concentration. We concluded that a participant had lost concentration during a testing block if the following three criteria were met: (1) at its lowest value during the testing block, the Bayes factor was <0.01, indicating that the participant was initially concentrating well on the task; (2) the mean of the *a* parameter posterior PDF varied by <0.15 mm (equivalent to a single groove width step in the TAPS device) within a window of five consecutive trials that included the trial at which the Bayes factor was lowest, indicating that the algorithm had achieved a stable threshold estimate for the participant; and (3) the Bayes factor on the final trial (i.e., $t = 40$ for finger or 30 for lip) was >100 times the minimum Bayes factor in the testing block, indicating a persistent loss of concentration. In such cases, we took as the participant's threshold the mean of the *a* parameter posterior PDF calculated at the trial where the Bayes factor was minimum. A mere 2% of completed testing blocks were flagged by this procedure as loss-of-concentration blocks (13 of 609 completed blocks).

Data analysis. We performed *t* tests and analyses of covariance (ANCOVA) using SPSS Statistics v19 (IBM) for Macintosh, with an α-level of 0.05. The ANCOVA models, with age as a covariate, were type III sum-of-squares testing for main effects of all factors, and for within-subject factor by between-subject factor interactions. The mean of the *a* parameter posterior PDF (participant's 76%-correct GOT threshold) was the dependent measure used in all statistical analyses, with the exception of the analyses on the combined data from the present study and a previous GOT study from our lab (Goldreich and Kanics, 2003).

Goldreich and Kanics (2003) used TAPS with a two-down one-up adaptive staircase protocol to measure 70.71% GOT thresholds from 43 blind and 47 sighted participants on a single index finger: the preferred index reading finger of Braille readers and the index finger of the dominant hand in blind nonreaders and sighted participants. They tested each participant on five blocks at 50 g of contact force, and 5 blocks at 10 g of contact force. The experiments reported in Goldreich and Kanics (2003) took place in Duquesne University (Pittsburgh, PA), and the current study took place in McMaster University (Hamilton, ON, Canada). The two studies provide independent participant samples: none of the participants in the present study had previously participated in Goldreich and Kanics (2003). For the combined-data analyses (see Combined data support effects of Braille expertise and weekly reading time on tactile acuity, below), we used the mean 50 g threshold for each participant tested in Goldreich and Kanics (2003), the same contact force used in the present study. For each participant in the present study, we identified the index finger corresponding to that tested in Goldreich and Kanics (2003): for Braille readers, the preferred reading finger; for blind nonreaders and sighted participants, the index finger of the dominant hand. We used the participant's best-estimate psychometric function on that finger to derive the 70.71% GOT threshold. To compare the thresholds of blind Braille readers, blind nonreaders, and sighted participants, we matched the categorization method used in Goldreich and Kanics (2003) by collapsing the proficient and novice Braille reader groups in the present study together into a single Braille reader group. To assess the effect of weekly Braille reading time, we included the reading time data from all readers with recorded reading times; this included all Braille readers tested in Goldreich and Kanics (2003) and all proficient readers tested in the present study.

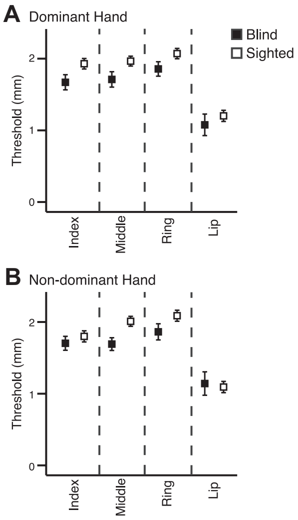

Figure 3. GOT thresholds of blind and sighted participants on fingers and lip. ***A***, Dominant hand and side of lip corresponding to dominant hand. ***B***, Nondominant hand and side of lip corresponding to nondominant hand. Threshold values for all participants were adjusted to those of a sex-neutral 39-year-old (the mean age of the participant sample). Means ± 1 SE.

Table 2. Effect sizes for age, sex, and vision by test site

	Test site							
	Dominant				Nondominant			
	Index	Middle	Ring	Lip	Index	Middle	Ring	Lip
Age	0.025	0.017	0.018	0.019	0.020	0.022	0.022	0.024
Sex	0.413	0.226	0.413	(0.243)	0.213	0.221	0.315	(0.231)
Vision	0.259	0.256	0.214	(0.125)	0.096	0.318	0.225	(−0.048)

Effect sizes for age (millimeter threshold increase per year), sex (male − female threshold difference, in millimeters; positive values indicate that women outperformed men), and vision (sighted − blind threshold difference, in millimeters; positive values indicate that blind outperformed sighted) by test site. Averages of the entries for the six fingers: age effect, 0.02 mm per year; sex effect, 0.3 mm; vision effect, 0.2 mm. Parentheses denote parameter estimates associated with nonsignificant main effects.

Results

Blind participants outperformed sighted peers on the fingertips but not on the lips

To compare the tactile acuity of blind and sighted participants on the fingers, we performed a 2 × 2 × 3 × 2 (vision × hand × finger × sex) age-controlled ANCOVA on the grating orientation thresholds of all study participants. This analysis revealed significant main effects of vision ($F_{(1,79)} = 5.527$, $p = 0.021$), finger ($F_{(2,158)} = 3.080$, $p = 0.049$), age ($F_{(1,79)} = 54.654$, $p < 0.001$), and sex ($F_{(1,79)} = 10.285$, $p = 0.002$) (Fig. 3, Table 2). Blind participants outperformed their sighted peers by an average of 0.2 mm; acuity worsened with age by 0.02 mm per year; and women outperformed men by 0.3 mm. Each of these effects was equivalent across the fingers (no significant finger × vision, finger × age, or finger × sex interactions). In addition, polynomial contrasts indicated a significant increase in threshold from index to middle to ring finger (linear contrast, $F_{(1,79)} = 4.488$, $p = 0.037$; quadratic contrast, not significant). Thresholds did not vary significantly by hand (dominant vs nondominant).

In contrast to the marked acuity differences between blind and sighted participants on the fingers, the two groups performed equivalently with the lips (Fig. 3). A 2 × 2 × 2 (vision × lip side × sex) age-controlled ANCOVA revealed a significant main effect of age ($F_{(1,79)} = 26.187$, $p < 0.001$) but no significant effects of vision ($F_{(1,79)} = 0.068$, $p = 0.795$), sex, or lip side. Although not significant, women tended to outperform men on the lips ($F_{(1,79)} = 2.793$, $p = 0.099$) (Table 2). Since the procedures we used to test the fingers (automated stimulus delivery using custom-made gratings) differed from those we used to test the lips (manual stimulus delivery using JVP Domes), we did not perform statistical analyses to compare finger performance to lip performance. We note, however, that lip thresholds were clearly lower than finger thresholds.

Proficient Braille readers on the reading hand outperformed blind nonreaders

Since the blind participants significantly outperformed their sighted peers on the fingers but not on the lips, we next attempted to discern the cause of the superior finger performance by investigating determinants of tactile acuity within the blind group. For this purpose, we classified the blind participants according to three factors: Braille reading expertise, blindness onset period, and current light perception. The Braille expertise factor comprised three levels: proficient, novice, and nonreaders. The blindness onset factor comprised three levels: congenital, early, and late blind. The light perception factor comprised two levels: residual light perception and no light perception.

To examine the effects of these three factors on finger tactile acuity, for each blind participant we performed a 2 × 3 × 3 × 3 × 2 × 2 (hand × finger × Braille expertise × blindness onset × light perception × sex) age-controlled ANCOVA. The hand factor comprised two levels: preferred reading hand (or dominant hand for nonreaders) and opposite hand. This analysis revealed a marginally significant main effect of Braille expertise ($F_{(2,20)} = 3.317$, $p = 0.057$), but no effects of blindness onset or of light perception (Fig. 4). Parameter estimates revealed that the acuity of proficient readers on the index and middle fingers of the preferred reading hand was significantly better than that of nonreaders on the corresponding fingers of the dominant hand (index finger: nonreader − proficient reader threshold difference, 1.12 mm, $p = 0.009$; middle finger: nonreader − proficient reader threshold difference, 0.96 mm, $p = 0.036$) (Fig. 4*A*). No other significant differences were observed between proficient, novice, and nonreaders.

As with the fingers, we tested for effects of Braille expertise, blindness onset, and light perception on lip thresholds. We performed a 2 × 3 × 3 × 2 × 2 (lip side × Braille expertise × blindness onset × light perception × sex) age-controlled ANCOVA. This analysis revealed no main effects of Braille expertise, blindness onset, or light perception (Fig. 4).

Among proficient Braille readers, the reading finger outperformed the opposite index finger, and reading finger acuity correlated with weekly reading time

The previous analysis suggested an association between Braille reading and heightened tactile acuity on the index finger. To further investigate effects of Braille reading on tactile acuity, we analyzed for effects of Braille reading frequency (reading hours per week) and Braille reading style (one index finger or both index fingers) among the proficient Braille readers.

We reasoned that if Braille reading enhances tactile acuity, participants who read with a single index finger would have lower

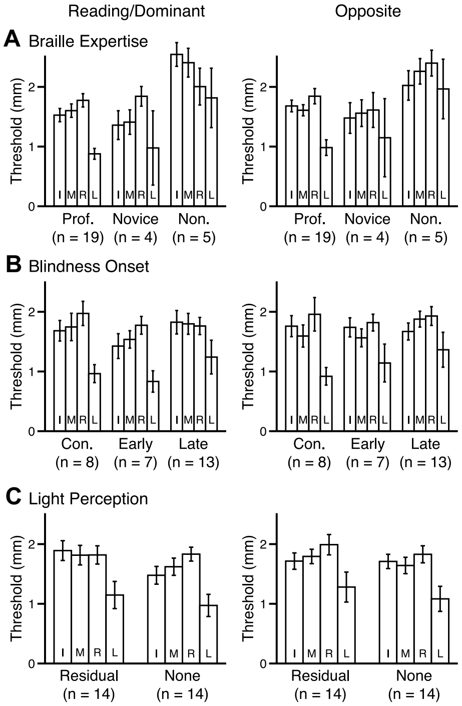

Figure 4. Effects among blind participants of blindness characteristics. ***A***, Braille expertise [proficient (Prof.), novice, nonreader (Non.)]. ***B***, blindness onset [congenital (Con.), early, late]. ***C***, Light perception (residual, none). Left, Preferred reading or dominant hand; right, opposite hand. Threshold values for all participants were adjusted to those of a sex-neutral 39-year-old. Numbers of participants in each subgroup are indicated in parentheses. Bars show mean threshold ± 1 SE, on index (I), middle (M), and ring (R) fingers, and lip (L).

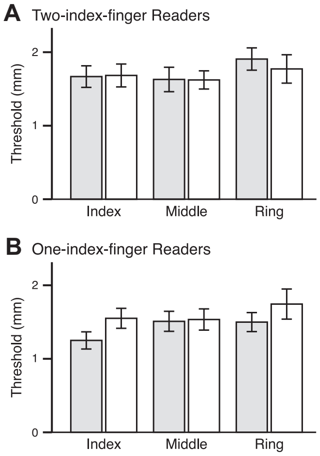

Figure 5. GOT thresholds of proficient Braille readers on all six fingers. ***A***, Two-index-finger readers ($n = 10$). ***B***, One-index-finger readers ($n = 9$). Gray bars, Mean threshold of each finger on the preferred reading hand; white bars, mean threshold of each finger on the opposite hand. Means ± 1 SE.

thresholds on that finger than on the opposite, nonreading index finger. In contrast, those who read with both index fingers might have equal acuity on the two fingers. Consistent with these predictions, paired-samples *t* tests revealed that the reading index finger of one-index finger readers had significantly lower mean threshold than the opposite index finger (one-tailed, $t_{(8)} = 1.894$, $p = 0.047$), whereas the preferred reading index finger and opposite index finger of two-index readers did not differ significantly in threshold (one-tailed, $t_{(9)} = 0.125$, $p = 0.45$), nor did thresholds differ significantly between homologous middle or ring fingers among either one-index or two-index readers (one-tailed paired-sample *t* tests, *p* values Bonferroni corrected for multiple comparison, $p > 0.05$) (Fig. 5).

We further reasoned that if Braille reading enhances tactile acuity, participants who read more frequently would show lower thresholds on the preferred reading finger. For each finger of the proficient readers, we performed an ANCOVA with independent variables weekly Braille reading time, Braille reading speed, sex, and age. Consistent with the prediction, on the preferred reading index finger, we found a significant effect of weekly Braille reading time ($F_{(1,14)} = 6.186$, $p = 0.026$). This effect was exclusive to the preferred reading index finger; no significant main effect of weekly reading time or reading speed was found on any of the other five fingers (Fig. 6*A*). Further, the trend for thresholds to decrease with weekly reading time extended to both index fingers among participants who read with both hands (Fig. 6*B*), but was evident only on the single reading index finger among those who read with just one hand (Fig. 6*C*).

Combined data support effects of Braille expertise and weekly reading time on tactile acuity

Finally, we asked whether the effects of Braille experience on tactile spatial acuity would hold true when the present data were combined with data from a previous GOT study from our laboratory that tested 34 blind Braille readers, nine blind nonreaders, and 47 sighted participants on a single index finger only (Goldreich and Kanics, 2003): for Braille readers, the preferred reading finger; for blind nonreaders and sighted participants, the index finger of the dominant hand. This combined analysis included 173 participants: 57 Braille readers, 14 blind nonreaders, and 102 sighted participants.

We first compared the index finger thresholds [as defined in Goldreich and Kanics 2003] (see Materials and Methods, above) of blind Braille readers, blind nonreaders, and sighted participants, with a 3 (participant group: blind Braille reader, blind nonreader, sighted) × 2 (sex) × 2 (study) age-controlled ANCOVA. This analysis revealed significant main effects of participant group ($F_{(2,167)} = 9.390$, $p < 0.001$), sex ($F_{(1,167)} = 10.585$, $p = 0.001$), and age ($F_{(1,167)} = 56.639$, $p < 0.001$). The analysis showed no significant effect of study ($F_{(1,167)} = 0.078$, $p = 0.78$), indicating that, in general, thresholds did not differ significantly between Goldreich and Kanics (2003) and the current study.

Post hoc pairwise comparisons with Bonferroni correction indicated a significant difference between the thresholds of Braille readers and sighted participants ($p < 0.001$); thresholds tended to increase from Braille readers to blind nonreaders to sighted participants (Fig. 7*A*). Parameter estimates revealed that Braille readers outperformed their sighted peers by 0.38 mm (95% confidence interval, 0.21–0.55 mm), nonreaders (nonsignificantly)

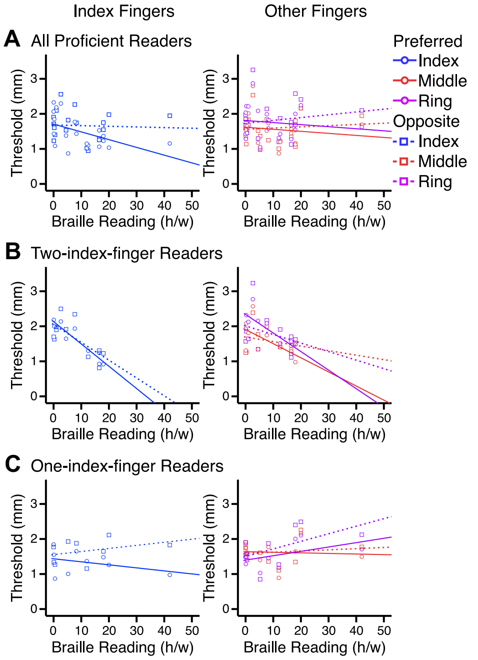

Figure 6. GOT thresholds of proficient Braille readers versus Braille reading hours per week (h/w). ***A***, All proficient readers ($n = 19$). ***B***, Those who read with both index fingers ($n = 10$). ***C***, Those who read with a single index finger ($n = 9$). Circles, Fingers on preferred reading hand; squares, fingers on opposite hand; left, index fingers; right, middle and ring fingers. Regression lines are shown for each finger (solid, preferred reading hand; dotted, opposite hand). Threshold values were adjusted to those of a sex-neutral 39-year-old.

outperformed their sighted peers by 0.14 mm (95% confidence interval, −0.16–0.45 mm), women outperformed men by 0.27 mm, and acuity worsened with age by 0.021 mm per year. The effect of age tended to be more pronounced in sighted than in blind participants. Among sighted participants, thresholds increased with age ($p < 0.001$) by 0.026 mm per year (95% confidence interval, 0.019–0.032 mm/year); among blind participants, thresholds increased with age ($p < 0.001$) by 0.016 mm/year (95% confidence interval, 0.007–0.025 mm/year).

Last, focusing on the Braille readers, we assessed the effect of weekly Braille reading time on the acuity of the preferred reading finger. An ANCOVA with independent variables sex, age, weekly reading time, and study revealed significant main effects of weekly reading time ($F_{(1,48)} = 5.300$, $p = 0.026$) and of study ($F_{(1,48)} = 4.126$, $p = 0.048$). Like the data from the present study, the data from Goldreich and Kanics (2003) showed a trend for acuity to improve with increasing reading time. The proficient Braille readers tested in the current study, however, tended to outperform the Braille readers tested in Goldreich and Kanics (2003) and to show steeper improvement in acuity with weekly reading. Collectively, the data from the two studies reveal significant acuity improvement with weekly reading time: GOT thresholds decreased by 0.011 mm per hour weekly reading (95% confidence interval, 0.001–0.021 mm per hour) (Fig. 7*B*).

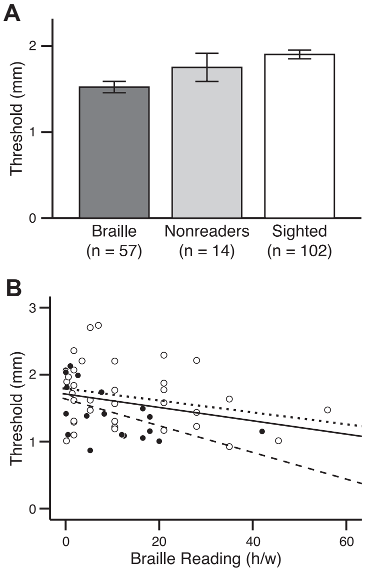

Figure 7. Index finger GOT thresholds of participants from the current study and from Goldreich and Kanics (2003). ***A***, Blind Braille readers, blind nonreaders, and sighted participants' thresholds combined across the two studies. Thresholds for Braille readers are from the preferred reading index finger; for blind nonreaders and sighted participants, from the index finger of the dominant hand. ***B***, Braille readers' GOT thresholds versus Braille reading hours per week (h/w). Filled circles and dashed regression line, Current study participants; open circles and dotted regression line, participants from Goldreich and Kanics (2003); solid line, regression on data from all participants, combined across studies. Threshold values are 70.71%-correct thresholds, adjusted to those of a sex-neutral 39-year-old.

Thus, the combined data from the present study and Goldreich and Kanics (2003) confirm that both Braille expertise (Fig. 7*A*) and Braille use (Fig. 7*B*) correlate with index finger tactile spatial acuity.

Discussion

We found that blind participants better resolve spatial details with the stationary fingertips than do sighted participants, but that the two groups perceive equivalently with the lips. Furthermore, we found evidence linking Braille reading with enhanced fingertip acuity. These results suggest that tactile experience drives tactile acuity enhancement in blindness.

Effects of test site, sex, and age

Here we compare our findings to those of previous grating orientation task studies. The GOT is a rigorous test of passive tactile spatial acuity, as it requires participants to attend to the spatial pattern of the afferent population discharge, unlike other tests, such as two-point discrimination or smooth-groove discrimination, that involve neural response magnitude as well as spatial cues (Johnson and Phillips, 1981; Craig and Johnson, 2000; Gibson and Craig, 2002, 2006; Goldreich and Kanics, 2006).

As previously reported (Van Boven and Johnson, 1994; Sathian and Zangaladze, 1996), we found that acuity on the lips exceeds that on the fingertips. We found further that acuity worsens from index to middle to ring fingertips, consistent with previous reports showing significant effects or trends in this direction (Sathian and Zangaladze, 1996; Vega-Bermudez and Johnson, 2001; Grant et al., 2006; Duncan and Boynton, 2007).

We found that women outperformed men on the fingertips, as reported previously (Goldreich and Kanics, 2003; Peters et al., 2009). Passive spatial acuity worsens with increasing fingertip surface area, perhaps reflecting lower Merkel mechanoreceptor density in larger fingers; thus, on average women have better acuity than men because women have smaller fingers (Peters et al., 2009). Consistent with Chen et al. (1995) and Wohlert (1996), we found that women also tended to outperform men on the lips; the basis for a sex difference in lip acuity is unclear.

We found that thresholds on index, middle, and ring fingertips increased with age at a rate similar to that reported in previous index fingertip studies (Goldreich and Kanics, 2003; Manning and Tremblay, 2006; for non-grating-orientation studies, see Stevens et al., 1996; Goldreich and Kanics, 2006). Thresholds also increased with age on the lips, as reported previously (Wohlert, 1996; for non-grating-orientation studies, see Stevens et al., 1996; Caisey et al., 2008). Age-associated receptor loss may underlie these effects (Bruce, 1980). Interestingly, whereas passive spatial acuity worsens with age in blind and sighted participants, active acuity worsened with age in sighted individuals (Legge et al., 2008; Master et al., 2010) but not in blind Braille readers (Legge et al., 2008), perhaps reflecting superior sensorimotor coordination in Braille readers, or superior ability to interpret temporally modulated stimuli (Bhattacharjee et al., 2010).

Evidence that tactile experience drives acuity enhancement

As predicted by the tactile experience hypothesis, we found that blind participants outperformed sighted participants on the fingertips, which blind individuals rely upon to an extraordinary degree in daily life. In contrast, and also as predicted by the tactile experience hypothesis, blind and sighted participants performed equivalently on the lips (Fig. 3). These results are in agreement with previous studies comparing blind and sighted participants on the fingers (Stevens et al., 1996; Van Boven et al., 2000; Goldreich and Kanics, 2003, 2006; but see Grant et al., 2000; Alary et al., 2009) and lips (Stevens et al., 1996).

In further support of the tactile experience hypothesis, we found that on their preferred reading index finger, Braille readers outperformed blind nonreaders (Fig. 4); that among those who read Braille proficiently with a single index finger, that finger outperformed the homologous finger on the opposite hand (Van Boven et al., 2000); and that among those who read with both index fingers, those two fingers had equivalent acuity (Fig. 5).

Finally, among proficient readers, we found a significant correlation between weekly reading time and tactile acuity on the preferred reading index finger. This trend extended to both index fingers among participants who read with both hands, but was seen only on the single reading index finger among those who read with just one hand (Fig. 6).

These results provide clear and consistent support for the hypothesis that tactile experience drives acuity enhancement.

We note that Braille reading style varies widely among proficient readers; nonindex fingers commonly assist index fingers in reading or tracking the line. In addition, index finger acuity enhancement may transfer partially to adjacent fingers (Sathian and Zangaladze, 1997; Harris et al., 2001). These considerations may explain the acuity difference observed between blind nonreaders and Braille readers on the middle finger of the reading hand (Fig. 4*A*) and the apparent influence of weekly reading on the acuity of some nonindex fingers (Fig. 6*B*, right).

The results of the current study are generally in agreement with those of a previous GOT study from our laboratory. Testing participants on a single index finger, Goldreich and Kanics (2003) reported effects of blindness, sex, and age very similar to those reported here and, like the current study, found no effects of blindness onset period or light perception level. Unlike the current study, however, Goldreich and Kanics (2003) did not find performance differences between Braille readers and blind nonreaders. This difference between the studies is due, we suspect, to random sampling variability: the Braille readers in Goldreich and Kanics (2003) performed somewhat worse, and the nonreaders better, than those here. Nevertheless, the combined data reveal that Braille readers (who experience more frequent tactile stimulation than blind nonreaders) tend to outperform blind nonreaders, and that blind nonreaders (who rely more on touch than do sighted participants) tend to outperform sighted participants (Fig. 7*A*). Further, among Braille readers, the combined data reveal significant improvement in tactile acuity with weekly reading time (Fig. 7*B*). These observations are consistent with the tactile experience hypothesis.

In conclusion, although we cannot rule out a concomitant permissive or facilitatory influence of visual deprivation, the most parsimonious explanation for our data is that tactile experience drives tactile spatial acuity enhancement in blindness. An interesting question for future research is whether, to produce lasting acuity enhancement, tactile experience must be accompanied by focused attention such as occurs during Braille reading and other purposeful tasks. In this regard, it is noteworthy that prolonged, unattended vibratory stimulation reversibly improves fingertip spatial acuity (Godde et al., 2000; Hodzic et al., 2004).

Possible neural mechanisms

Two neural mechanisms that might mediate tactile acuity enhancement in blindness are intra-modal somatosensory plasticity and cross-modal plasticity. Intra-modal somatosensory plasticity occurs when intensive reliance on particular fingers (e.g., for Braille reading) enlarges the parietal somatosensory cortical representations of those fingers (Pascual-Leone and Torres, 1993; Sterr et al., 1998, 1999). Several lines of evidence link larger somatosensory cortical representations to better tactile spatial acuity. Three hours of low-frequency vibration applied to the index finger both enhanced spatial acuity and enlarged the finger's cortical representation (Hodzic et al., 2004). Although receptor density—at least for the relatively easily visualized Meissner corpuscles—is apparently conserved across digits (Dillon et al., 2001), the digits with a larger cortical representation also have better acuity (Duncan and Boynton, 2007). Thus, intra-modal somatosensory plasticity may underlie the associations between Braille reading and tactile acuity observed in the present study.

Cross-modal plasticity occurs when occipital cortical areas, deprived of their normally dominant visual input, acquire tactile responsiveness. This happens in blindfolded sighted participants (Merabet et al., 2007, 2008) and blind participants (Sadato et al., 1996, 1998, 2002, 2004; Cohen et al., 1999; Burton et al., 2002, 2006; Ptito et al., 2005; Stilla et al., 2008). Several lines of evidence suggest a functional role for cross-modal plasticity: a congenitally blind Braille reader developed alexia for Braille after suffering a bilateral occipital stroke (Hamilton et al., 2000), occipital transcranial magnetic stimulation (TMS) impairs blind participants' tactile performance (Cohen et al., 1997, 1999; Kupers et al., 2007), and occipital TMS elicits sensations on the fingers in some participants (Ptito et al., 2008).

Cross-modal plasticity appears to occur most extensively when visual deprivation is coupled with intensive tactile experience. Cross-modal plasticity was more pronounced in the hemisphere contralateral to the Braille reading hand in early blind participants (Burton et al., 2002). Moreover, Braille reading habits predicted the number of occipital cortical sites in blind participants that elicited sensations in the fingers when stimulated with TMS (Ptito et al., 2008). Training of blind participants on a task involving the tongue was necessary both to induce cross-modal plasticity (Ptito et al., 2005) and for occipital TMS to elicit tactile sensations on the tongue (Kupers et al., 2006). Thus, cross-modal plasticity, like intra-modal somatosensory plasticity, may contribute to experience-dependent tactile perceptual enhancement in blindness.

Interestingly, these two forms of neural reorganization may play a role beyond tactile acuity enhancement. Blind participants show superior auditory perception (Lessard et al., 1998; Röder et al., 1999) and both intra-modal and cross-modal cortical plasticity for auditory tasks (Kujala et al., 1995, 2005; Weeks et al., 2000; Elbert et al., 2002; Gougoux et al., 2005; Collignon et al., 2007). Future neurophysiological, psychophysical, and computational modeling research will elucidate how these forms of plasticity may improve acuity in the intact senses.

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Chapter 3

3.1 Preface

In Chapter 2, we found that spatial acuity on the lips is equivalent between blind and sighted participants, suggesting that visual deprivation does not drive tactile spatial acuity enhancement. This finding, however, contradicts the findings of two recent studies, which demonstrated that short-term visual deprivation (of 90 minutes or less) improved sighted participants' tactile spatial acuity (Facchini & Aglioti, 2003; Leon-Sarmiento et al., 2008).

In Chapter 3, we investigated the effects of short-term visual deprivation further by visually depriving sighted participants (in three experiments) for: under 10 minutes, 70 minutes, and 110 minutes. Unlike Facchini and Aglioti (2003) and Leon-Sarmiento et al. (2008), who presented the GOT manually, we presented the GOT in our study mechanically using TAPS. With controlled tactile testing (and a larger sample size than in the other two studies), we found in Chapter 3 that short-term visual deprivation does not enhance tactile spatial acuity. Chapter 3 thus provides an important negative result in the literature that questions the ability of short-term visual deprivation to enhance tactile spatial acuity.

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Short-Term Visual Deprivation Does Not Enhance Passive Tactile Spatial Acuity

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Abstract

An important unresolved question in sensory neuroscience is whether, and if so with what time course, tactile perception is enhanced by visual deprivation. In three experiments involving 158 normally sighted human participants, we assessed whether tactile spatial acuity improves with short-term visual deprivation over periods ranging from under 10 to over 110 minutes. We used an automated, precisely controlled two-interval forced-choice grating orientation task to assess each participant's ability to discern the orientation of square-wave gratings pressed against the stationary index finger pad of the dominant hand. A two-down one-up staircase (Experiment 1) or a Bayesian adaptive procedure (Experiments 2 and 3) was used to determine the groove width of the grating whose orientation each participant could reliably discriminate. The experiments consistently showed that tactile grating orientation discrimination does not improve with short-term visual deprivation. In fact, we found that tactile performance degraded slightly but significantly upon a brief period of visual deprivation (Experiment 1) and did not improve over periods of up to 110 minutes of deprivation (Experiments 2 and 3). The results additionally showed that grating orientation discrimination tends to improve upon repeated testing, and confirmed that women significantly outperform men on the grating orientation task. We conclude that, contrary to two recent reports but consistent with an earlier literature, passive tactile spatial acuity is not enhanced by short-term visual deprivation. Our findings have important theoretical and practical implications. On the theoretical side, the findings set limits on the time course over which neural mechanisms such as crossmodal plasticity may operate to drive sensory changes; on the practical side, the findings suggest that researchers who compare tactile acuity of blind and sighted participants should not blindfold the sighted participants.

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Introduction

Does visual deprivation cause tactile acuity enhancement? This question, important to neuroscientific understanding of tactile perception and of the interaction between the senses, has been investigated for decades.

Early studies reported that tactile perception improved upon prolonged simultaneous deprivation of multiple sensory modalities. Doane and colleagues [1] observed that participants deprived for two days of patterned vision, audition and touch improved in their ability to discriminate one from two points indented into the skin, a finding later confirmed by Nagatsuka and colleagues [2,3]. Zubek [4] demonstrated that participants deprived for seven days of patterned vision and audition improved in their performance on a tactile fusion task. Participants were presented with successive air jets at progressively increasing frequencies until the stimuli become perceptually fused; fusion at higher frequencies was indicative of better performance.

These findings were soon followed by reports that prolonged visual deprivation alone sufficed to improve tactile perception. Zubek et al. [5,6] demonstrated that seven days of visual deprivation produced tactile acuity enhancement, as assessed by two-point and tactile fusion tasks; the investigators observed facilitatory effects of visual deprivation when participants were completely light deprived, and also (but to a lesser degree) when participants were deprived of patterned vision.

For a period of several decades following these intriguing early studies, interest in the field seems to have faded. With the advent of functional imaging, interest resurged as many studies revealed that tactile stimuli activate occipital cortical areas in blind participants (crossmodal plasticity) [7–14]. Concurrently, perceptual studies revealed heightened tactile acuity in blind compared to sighted participants [15–23]. Together, these findings led researchers to hypothesize that visual-deprivation-induced crossmodal plasticity might enable supernormal tactile perception.

It was soon discovered that the occipital cortex of visually deprived sighted participants becomes hyperexcitable [24,25] and, as observed in blind participants, responsive to tactile inputs [26,27]. Reexamining the effects of prolonged visual deprivation on the tactile acuity of sighted participants, Kauffman et al. [28] reported that participants' ability to discriminate Braille characters pressed against the passive fingertip improved after five days of visual deprivation, a finding in general agreement with the early literature [1–6]. Merabet et al. [27] further showed that transcranial magnetic stimulation applied to the occipital cortex disrupted the ability to distinguish Braille characters among participants who had been blindfolded (and trained on Braille) for five days, but did not affect Braille character discrimination among a control group that had been trained without blindfolding. This result suggested a functional role for the tactile responsiveness acquired by occipital cortex during long-term blindfolding. Neither Kauffman et al. [28] nor Merabet et al. [27] assessed tactile acuity following short-term visual deprivation.

Because tactile responsiveness of occipital cortex occurred within 90 minutes of blindfolding according to one study [26] (but required 5 days of blindfolding according to another [27]), an important unresolved question is whether short-term visual deprivation also results in tactile acuity improvement. The literature on this topic has been controversial. The early literature provided no indication that participants' performance on tactile tasks improved as a consequence of multisensory deprivation spanning two [29,30], four [31], or eight hours [32], or with eight hours of visual deprivation [33] (see Table 1). However, in some of these early studies the participants were not fully light deprived, but were instead deprived only of patterned vision [31,32]; furthermore, these early studies used now-outdated assessments, such as two-point discrimination, that have come under serious criticism as invalid measures of tactile spatial acuity [34].

In contrast to the early literature, two modern studies reported significant effects of short-term visual deprivation on tactile acuity. Comparing a ''non-deprived'' control group to a visually deprived experimental group, Facchini and Aglioti [35] observed significant tactile acuity improvement upon 90 minutes of visual deprivation. Testing a group of participants first in the light and then upon 45-minutes of visual deprivation, Leon-Sarmiento et al. [36] observed that participants' tactile acuity was significantly better in the second test. Both studies employed the grating orientation task (GOT), a modern gold standard test of passive tactile spatial acuity that is not beset by the limitations of the two-point test [34,37,38].

Nevertheless, particular technical aspects of these modern studies may have led the investigators to mistaken conclusions. For instance, Facchini and Aglioti [35] blindfolded all participants for testing; therefore, the performance of their ''non-deprived'' participants is not necessarily representative of tactile acuity under normal visual conditions. Leon-Sarmiento et al. [36] did not use a counterbalanced design, nor did they perform a post-deprivation test upon the restoration of normal vision, or include a non-deprived control group. In the absence of any of these proper controls it is not possible to know whether their data reflect an effect of visual deprivation or simply a practice effect. Finally, both studies used difficult-to-control manual stimulus delivery, in which the investigator presses the tactile gratings by hand onto the participant's fingertip; unintended manual stimulus variability has the potential to mask differences between conditions or to produce apparent differences where none exist.

Here, we report the results of a study designed to resolve the controversy surrounding the effects of short-term visual deprivation on passive tactile spatial acuity. Ours is the first study of short-term visual deprivation to use a precision-controlled automated tactile grating orientation task [39], and the first to examine the effects of different short-term periods of visual deprivation. In a series of three experiments, we assessed the effects on GOT performance of visual deprivation periods ranging from under 10 to over 110 minutes. The experiments consistently showed that GOT performance does not improve with short-term visual deprivation. We conclude, in agreement with the earlier literature [29–33], that passive tactile spatial acuity is resistant to short-term visual deprivation.

Results

In three experiments involving 158 participants, we assessed whether tactile spatial acuity improves with short-term visual deprivation. We tested 48 participants in Experiment 1, 44 participants in Experiment 2, and 66 participants in Experiment 3. We used the GOT, a rigorous test of tactile spatial acuity [34,37,38], to assess each participant's ability to discern the orientation of grating stimuli applied to the stationary distal index finger pad of the dominant hand (Figure 1). In all three experiments, we used the Tactile Automated Passive-Finger Stimulator (TAPS), a precision-controlled fully automated tactile stimulus device [39].

Experiment 1

To investigate whether tactile spatial acuity improves upon brief periods (e.g., under 10 min) of visual deprivation, we used a 2x2 counterbalanced repeated-measures design, testing 48 sighted participants under all four combinations of ambient lighting (light or pitch-dark) and eyelid state (eyes opened or eyes closed) (Figure 2). After the completion of the four conditions (iteration 1), each participant was tested again on the same four conditions in the same order (iteration 2). Two participants could not complete the majority of the test blocks and were excluded from data analysis.

To examine the effects of ambient lighting and eyelid state, we performed a 2 (ambient lighting) x 2 (eyelid state) x 2 (iteration) x 2 (sex) ANOVA. This analysis revealed significant main effects of ambient lighting ($p = 0.010$) and of sex ($p = 0.029$). Participants' tactile acuity worsened significantly with visual deprivation, and women significantly outperformed men. On average, thresholds in the dark were 0.09 mm higher than in the light (95% confidence interval, 0.02 – 0.15 mm) (Figure 3A), and men's thresholds were 0.25 mm higher than women's (95% confidence interval, 0.03–0.48 mm).

Although the effect of eyelid state was not significant ($p = 0.077$), participants tended to perform better with eyes opened than closed. The effect of iteration was not significant ($p = 0.396$), but participants tended to perform better in iteration 2 than iteration 1, suggestive of a practice effect (Figure 3B).

We next examined whether the elevation of tactile threshold in the dark depended upon the dark/light testing order. For each participant we computed a difference score: threshold of first iteration 1 test in the dark – threshold of first iteration 1 test in the light. For instance, for a participant tested in the order LC, DC, DO, LO (see Figure 3 legend for definitions), the difference score was DC threshold minus LC threshold. We compared the differences scores of participants tested initially in the light to those of participants tested initially in the dark. An independent-samples t test revealed no significant difference between groups ($p = 0.251$), but the mean difference score was considerably larger for participants initially tested in the dark (0.16 mm ±0.11 mm; mean ± SE) than for those initially tested in the light (-0.03 mm ±0.13 mm). We observed the same (non-significant, $p = 0.129$) trend in the data from iteration 2: the mean difference score (threshold of first iteration 2 test in the dark – threshold of first iteration 2 test in the light) was considerably larger for participants initially tested in the dark (0.20 mm ±0.10) than for those initially tested in the light (-0.02 mm ±0.09). A parsimonious explanation for this order effect is that it is due to the superposition of two underlying effects: while visual deprivation worsens acuity (elevates threshold), practice tends to improve acuity (lower threshold). Thus, for participants tested in the dark then light, the two effects acted in the same direction, producing a large threshold difference;

Table 1. Summary of visual/multisensory deprivation studies since 1959.

	Deprivation condition				
Study	**Vision**	**Audition**	**Touch**	**Deprivation Period**	**Task**
Doane et al. (1959) [1]	Translucent goggles	Mechanical noise	Cotton gloves; forearm-length cardboard cuffs	2–3 days	2-point discrimination -index finger -forearm -upper arm* -forehead*
Cohen et al. (1962) [29]	Pitch-dark room	Sound-attenuated room	Not deprived	2 hours	2-point discrimination -palm -back of hand Letter tracing -forehead -back of hand
Kamchatnov (1962) [33]	Dark room	Not deprived	Not deprived	8 hours	2-point discrimination -index finger -thumb -upper arm
Pollard et al. (1963) [32]	Translucent dome or translucent goggles	White noise	Cotton mittens; feet separated & bound	8 hours	2-point discrimination -test site not specified
Nagatsuka & Maruyama (1963) [2]	Translucent goggles	Semi-soundproof Room	Cardboard cuffs	2 days	2-point discrimination -back of hand*
Culver et al. (1964) [30]	Pitch-dark room	Sound-attenuated room	Not deprived	2 hours	Tactile localization -palm
Nagatsuka & Suzuki (1964) [3]	Translucent goggles	Semi-soundproof room	Cardboard cuffs	2 days	2-point discrimination -back of hand*
Reitman & Cleveland (1964) [31]	Translucent goggles	White noise	Cotton gloves; arm-length cardboard cuffs	4 hours	Punctate pressure detection -index finger -wrist 2-point discrimination -forearm
Zubek (1964) [4]	Translucent goggles	White noise	Heavy leather gloves	7 days	Tactile fusion -index finger* -forearm*
Zubek et al. (1964a) [6]	Black mask	Not deprived	Not deprived	7 days	2-point discrimination -palm* Tactile fusion -index finger* -forearm*
Zubek et al. (1964b) [5]	Translucent goggles	Not deprived	Not deprived	7 days	2-point discrimination -palm Tactile fusion -index finger* -forearm*
Kauffman et al. (2002) [28]	Blindfold	Not deprived	Not deprived	5 days	Braille dot discrimination -index finger*
Facchini & Aglioti (2003) [35]	Opaque goggles	Not deprived	Not deprived	90 minutes	Grating orientation -index finger*
Merabet et al. (2008) [27]	Blindfold	Not deprived	Not deprived	5 days	Punctate pressure detection

Table 1. Cont.

	Deprivation condition				
Study	Vision	Audition	Touch	Deprivation Period	Task
					-index finger
					Braille dot discrimination
					-index finger*
					Grating orientation
					-index finger
Leon-Sarmiento et al. (2008) [36]	Opaque goggles	Not deprived	Not deprived	45 minutes	Grating orientation
					-index finger*

*Statistically significant improvement. For a review of the early studies, see Zubek et al. [52].
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for participants tested in the light then dark, the two effects acted in opposite directions, nullifying the threshold difference.

Experiment 2

Having observed no improvement in tactile spatial acuity with brief visual deprivation (Experiment 1), we wondered whether a longer period of visual deprivation would improve participants' tactile spatial acuity and, if so, whether the improvement would occur abruptly or gradually. Accordingly, in Experiment 2 we lengthened the visual deprivation period to 70 minutes.

Participants were assigned to one of four groups. In the non-deprived group, participants were tested in the light 10 times. In the three visually deprived groups, participants were tested in the light twice before and three times after a period of 90 minutes in the pitch-dark. The sequence of events in the dark differed by group (Figure 4). We conducted the experiment until each group contained 10 participants who had successfully completed testing. This required the testing of 44 participants in total, because four participants could not perform the task beyond chance level and were therefore excluded from data analysis.

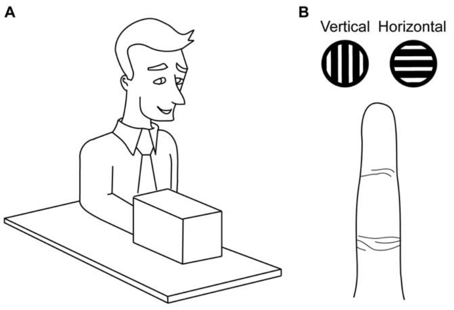

Figure 1. Grating orientation task (GOT). A. Participants were seated upright with their tested hand resting in prone position on a tabletop. In Experiments 2 and 3, a box occluded the participant's tested hand from view. B. In each trial, a grating stimulus contacted the tested finger pad twice, once with the gratings aligned vertically, and once with the gratings aligned horizontally. The images in A and B are not drawn to scale.
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To analyze the data from each group, we performed a one-way repeated-measures ANOVA across testing blocks. We observed no significant change in GOT performance within any group (Figure 5): non-deprived (10 blocks, $p = 0.711$), repeatedly tested (10 blocks, $p = 0.941$), passively stimulated (6 blocks, $p = 0.677$), unstimulated (6 blocks, $p = 0.361$). These results indicate both that the participants' performance in the dark was equivalent to their performance in the light, and that performance did not improve significantly with practice. As in Experiment 1, the data suggested a non-significant practice trend (e.g., compare the first and final test block thresholds in Fig. 5B, C, D).

To examine the effect of sex, we averaged the threshold of each participant across all test blocks and performed an independent-samples t test to compare the mean thresholds for women and men. This analysis revealed that women significantly outperformed men ($p = 0.015$). On average, men's thresholds were 0.35 mm higher than women's (95% confidence interval, 0.07 – 0.63 mm).

Experiment 3

Having observed no improvement in tactile spatial acuity in Experiments 1 and 2, we wondered whether a somewhat longer period of deprivation might result in acuity enhancement. In

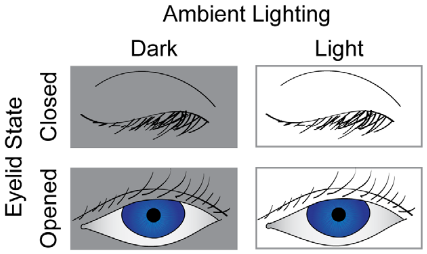

Figure 2. Experiment 1 conditions. In a two-by-two repeated measures design, every participant was tested under four conditions: two conditions of ambient lighting (dark and light) by two conditions of eyelid state (eyes opened and eyes closed). Each participant completed the four conditions twice. The experiment duration was approximately 80 minutes.
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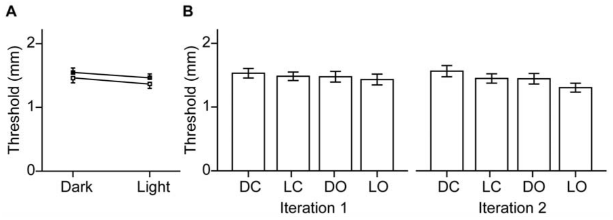

Figure 3. Experiment 1 data. A, Participants' mean 70.71% thresholds are shown for the two conditions of ambient lighting (pitch-darkness, left; indoor fluorescent lighting, right) and eyelid state (eyes closed, filled squares; eyes opened, open squares). The solid lines connecting the symbols illustrate the effect of ambient lighting. Errors bars represent 1 SEM; the error bars on upper and lower symbols are displaced in opposite directions for visual clarity. B, Participants' mean 70.71% thresholds are plotted for each condition in the first and second iterations separately (darkness with eyes closed, DC; light with eyes closed, LC; darkness with eyes opened, DO; light with eyes opened, LO). Data in (A) and (B) are from 46 participants.
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addition, we wondered whether participants might have lost alertness during the visual deprivation period in Experiment 2, perhaps resulting in a worsening of performance that masked a true benefit of visual deprivation. Accordingly, we further lengthened the visual deprivation period to 110 minutes, and to safeguard participant alertness we recruited participants in sets of three and encouraged conversation during the visual deprivation period. In keeping with Facchini and Aglioti [35], we decided to use just two groups of participants – a visually deprived group and a non-deprived group – and to test each participant just three times.

We tested 66 participants. Five participants could not perform the task beyond chance level, and were therefore excluded from data analysis. Each set of three participants was assigned to one of two groups: a non-deprived group (n = 29) and a visually deprived group (n = 32). Participants in both groups were tested three times: before a 110-minute conversation period, immediately following the conversation period, and 120 minutes following the second test. Whereas participants in the non-deprived group were always in the light, those in the visually deprived group were in the pitch-dark during the conversation period and the second test (Figure 6).

To examine whether 110 minutes of visual deprivation improves GOT performance, we performed a 3 (test block) x 2 (group: visually deprived, non-deprived) x 2 (sex) ANOVA. This analysis revealed a significant main effect of sex (p = 0.008), indicating that women outperformed men. There was no significant main effect of test block or of group, nor was there a significant test block x group interaction. Thus, visual deprivation did not affect tactile spatial acuity.

One-way repeated-measures ANOVAs performed separately for each group confirmed that across the three test blocks there was no significant change in the performance of participants in the visually deprived group (p = 0.435) (Figure 7A) or the non-deprived group (p = 0.115) (Figure 7B). As in Experiments 1 and 2, however, we observed a non-significant trend for improvement with repeated testing. In both groups, first test thresholds were greater than second and third test thresholds; from test 1 to test 2, thresholds decreased on average by 0.15 mm in the non-deprived group (Figure 7A) and by 0.09 mm in the visually deprived group (Figure 7B).

To quantify the difference between thresholds of men and women, we averaged each participant's thresholds across the three tests (without regard to group). On average, men's thresholds were 0.28 mm higher than women's (95% confidence interval, 0.08 – 0.48 mm).

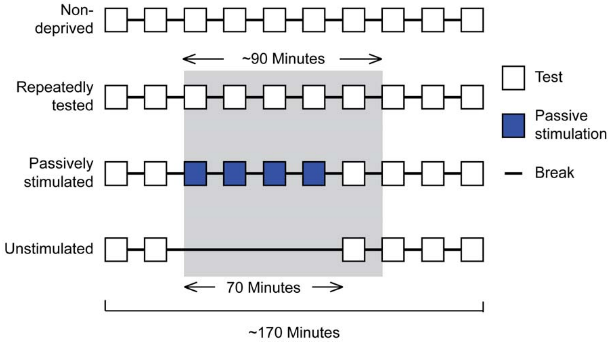

Figure 4. Experiment 2 conditions. One group of non-deprived and three groups of visually deprived participants were tested on the GOT (white squares). In the passively stimulated group, participants received grating stimuli that they were not required to discriminate (blue squares). Blocks were separated by 8-minute rest periods (short horizontal lines). The shaded rectangle indicates the period of visual deprivation. The experiment duration was approximately 170 minutes.
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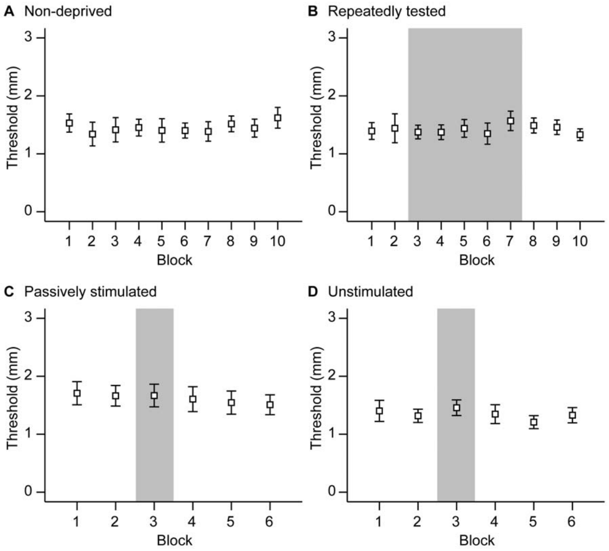

Figure 5. Experiment 2 data. GOT performance (mean 76% threshold) of the four groups (n = 10 participants per group): A, non-deprived. B, repeatedly tested. C, passively stimulated. D, unstimulated. The shaded rectangles in B–D delineate the visual deprivation period. Errors bars represent ±1 SEM.
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Discussion

Contrary to previous reports [35,36], we have shown that short-term visual deprivation does not improve tactile spatial acuity as measured with the GOT. Across three experiments, participants' ability to discern grating orientation either worsened slightly or remained stable following visual deprivation.

Short-term visual deprivation does not enhance tactile spatial acuity

The experiments reported here provide clear and consistent evidence that short-term visual deprivation does not enhance passive tactile spatial acuity.

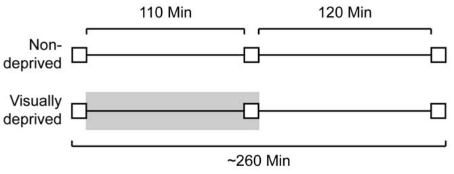

Figure 6. Experiment 3 conditions. A non-deprived group and a visually deprived group of participants were tested three times on the GOT (white squares). A 110-minute conversation period separated the first and second tests, and a 120-minute break separated the second and third tests. The shaded rectangle indicates the period of visual deprivation. The experiment duration was approximately 260 minutes.
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Using a counterbalanced repeated-measures design, we found in Experiment 1 that tactile spatial acuity actually worsened to a small but significant degree upon short-term visual deprivation. Participants performed significantly worse in the dark than in the light, and tended (although not significantly) to perform worse with their eyes closed than opened. Of the four conditions under which they were tested, participants performed best on average in the condition with the greatest visual stimulation (eyes opened in the light). These results may be attributable to a loss of alertness experienced during visual deprivation, or to some other cause.

Tracking tactile spatial acuity over 70 minutes of visual deprivation, we found in Experiment 2 that this period of deprivation did not result in tactile perceptual improvement. This was true irrespective of whether during visual deprivation the participant received no tactile stimulation, unattended tactile stimulation, or repeated GOT testing. Similarly, in Experiment 3, participants performed equivalently before and after 110 minutes of visual deprivation. Thus, our results consistently show that tactile spatial acuity does not improve during short-term visual deprivation.

In contrast to Experiment 1, in Experiments 2 and 3 we did not observe a significant worsening of GOT performance upon visual deprivation. We propose that this apparent discrepancy is explained by two factors: 1) The fact that all visually-deprived participants in Experiments 2 and 3 were first tested in the light, whereas half the participants in Experiment 1 were first tested in the dark, and 2) The fact that all three experiments revealed a trend (although non-significant) for thresholds to decrease slightly with repeated testing, consistent with previous reports (for non-significant GOT practice effects, see [17,40]; for significant practice effect, see [41]).

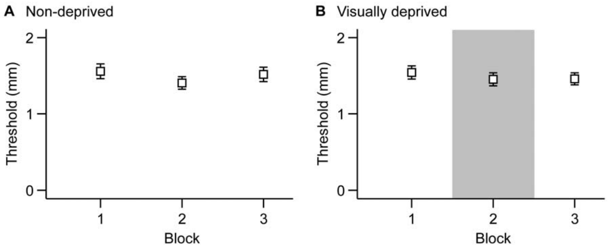

Figure 7. Experiment 3 data. GOT performance (mean 76% threshold) of the two groups: A, non-deprived (n = 29 participants). B, visually deprived (n = 32 participants). The shaded rectangle in B delineates the visual deprivation period. Error bars represent ±1 SEM.
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Because of the practice effect trend, participants tested first in the light and then in the dark will tend to show nearly equivalent performance on the two tests: the worsening of acuity due to visual deprivation is counteracted to some degree by the practice effect. This phenomenon seems evident in much of the data from Experiments 2 and 3. For instance, Figures 5C and D (and, to a lesser extent, Fig. 5A) suggest a tendency for thresholds to lower with repeated testing in the light. That practice effect trend, however, appears to be largely arrested (Fig. 5C) or counteracted (Fig. 5D) upon visual deprivation, resuming only upon the return of the participant to the light (Fig. 5B, C, D). Similarly, Figures 7A and B both show a trend for thresholds to lower between blocks 1 and 2, but this trend is slightly smaller in Figure 7B than in Figure 7A, presumably because the effect of visual deprivation partially counteracted the practice-associated threshold reduction.

Consistent with this interpretation, we noticed in Experiment 1 that the mean threshold difference score (first test in the dark – first test in the light) was large and positive only among participants who were initially tested in the dark (0.16 mm). The corresponding difference score for participants who were initially tested in the light (−0.03 mm) indicates that those participants did not on average worsen when subsequently tested in the dark. This trend repeated in iteration 2 (0.20 mm vs. −0.02 mm). A parsimonious explanation for this order effect is that it is due to a trend for practice to improve acuity (lower thresholds) from one testing block to the next, together with a trend for visual deprivation to worsen acuity (raise thresholds).

This explanation reconciles the apparent discrepancy between Experiment 1, which revealed a slight but significant worsening of acuity under conditions of visual deprivation, and Experiments 2 and 3, which did not. Experiment 1 used a counterbalanced design so that the average difference observed between conditions was robust against practice effects, whereas Experiments 2 and 3 always tested participants in the light prior to testing them in the dark.

Most importantly, we note that Experiments 1, 2 and 3 all clearly support the conclusion that short-term visual deprivation does not *improve* tactile spatial acuity. If our explanation above is correct, all three experiments indeed lend support to the conclusion that tactile spatial acuity tends to *worsen* under short-term visual deprivation.

Comparison to previous visual deprivation GOT studies

Our results stand in stark contrast to those of Facchini and Aglioti [35], who reported that participants' tactile spatial acuity significantly improved after 90 minutes of visual deprivation, and Leon-Sarmiento et al. [36], who reported improvement after just 45 minutes of visual deprivation (each study reported approximately 0.2 mm average reduction in GOT threshold following light deprivation). Although our results disagree with those of Facchini and Aglioti [35] and Leon-Sarmiento et al. [36], they are in general agreement with the results of earlier studies [29–33] that reported no effects on tactile acuity of short-term visual or multisensory deprivation. The results from the present study, however, are most directly comparable to those of Facchini and Aglioti [35] and Leon-Sarmiento et al. [36], because unlike the earlier studies, Facchini and Aglioti [35], Leon-Sarmiento et al. [36] and the current study used the GOT to test passive tactile spatial acuity.

How might the results of Facchini and Aglioti [35] and Leon-Sarmiento et al. [36] be understood in light of the results of the present study? It is possible but unlikely that the discrepancy between these studies and ours owes to random statistical fluctuation. Facchini and Aglioti [35] tested 28 participants divided equally into visually deprived and non-deprived groups. Leon-Sarmiento et al. [36] tested 13 neurologically normal participants (for comparison with hyperhidrosis patients). Each of our experiments had sample sizes greater than those of [35,36]. Given the respectable sample sizes of the three studies, we would expect random statistical fluctuation to produce only minor variation in average threshold values.

If the discrepancy between studies did not arise from statistical fluctuation, another possibility is that it arose from unintended variability in stimulus-delivery parameters. The GOT provides a rigorous measure of tactile spatial acuity by assessing participants' ability to discern the orientation of grating stimuli pressed orthogonally against a body part [34,37,38]. However, even small non-orthogonal movement upon contact with the test site greatly facilitates perception of grating orientation. Following common practice, Facchini and Anglioti [35] and Leon-Sarmiento et al. [36] used manual stimulus delivery, the investigator pressing the gratings by hand against the participant's skin. In such cases, avoiding unintended movement and controlling a host of other stimulus-delivery parameters (e.g., contact force, onset velocity, stimulus duration) is very difficult even with great care and concentration on the part of the experimenter. It is for these reasons that we prefer to use a precision-controlled automated testing device to conduct the GOT [39].

Two additional methodological considerations may explain the discrepancy between these studies and ours. First, Leon-Sarmiento et al. [36] tested all subjects initially in the light, and next at the end of a 45-minute period of visual deprivation. Unfortunately, the investigators did not use a counterbalanced design (in which half the participants would have been tested in the opposite order), nor did they include a third test after restoration of the light, or test a non-deprived control group. In the absence of any of these controls it is not possible to know whether the results obtained were due to an effect of visual deprivation, or simply to a practice effect.

Second, Facchini and Aglioti [35] used opaque goggles to blindfold the participants in both groups for testing purposes. Thus, one of their groups (the ''visually deprived'' group) was continuously blindfolded (during test 1, a 90-minute inter-test interval, and test 2), whereas the other (the ''non-deprived'' group) was in fact also blindfolded, but only during testing. Perhaps these intermittently blindfolded participants performed poorly on each test, as their attention to the task was distracted by the recent addition of the goggles, whereas the continuously blindfolded participants likewise performed poorly on the first test but then habituated to the goggles over time, returning towards normal performance for the second test. (When later tested blindfolded for a third time, following a prolonged period of light exposure, the performance of both groups would once again worsen towards a similar level, as observed). Unfortunately, Facchini and Aglioti [35] did not test participants un-blindfolded and in the light, either before or after the blindfold tests. In the absence of this crucial comparison condition, it is not possible to know whether the apparent improvement of their continuously blindfolded group was in fact simply a return towards normal performance.

Practical implications for sensory testing studies

In light of the results of Experiment 1, we caution against the blindfolding of sighted participants in tactile psychophysics studies, as this procedure may inadvertently worsen participants' tactile acuity. For instance, although it is becoming increasingly clear that the tactile acuity of blind participants is better than that of sighted participants [15–23], blindfolding sighted participants during testing may exaggerate the extent to which blind participants are better. This may explain the larger mean GOT difference between blind and sighted participants (0.42 mm) reported by Van Boven et al. [22] – who blindfolded their sighted participants – than by Goldreich and Kanics [17] (0.33 mm) and Wong et al. [23] (0.2 mm), who tested their sighted participants un-blindfolded and in the light.

Another practical consequence of this study is that investigators of tactile spatial acuity should be aware of the tendency for women to outperform men, and design and analyze their studies accordingly. In all three experiments reported here, we found that women significantly outperformed men on the GOT. This result is consistent with previous reports [17,22,23,42]. A study from our laboratory [42] revealed that the better acuity of women owes to their smaller fingers, and provided some evidence in support of the hypothesis that Merkel mechanoreceptors are more densely packed within smaller fingers. Thus, we recommend that investigators performing between-groups studies (e.g., comparisons between blind and sighted participants) take care to maintain participant sex ratios equal across groups, and / or to incorporate participant sex – if not finger size - as a factor in their statistical analyses.

Effects of prolonged visual deprivation and crossmodal plasticity

In contrast to short-term visual deprivation, several studies have reported that prolonged visual deprivation does drive tactile acuity enhancement [5,6,27,28]. Surprisingly, however, Merabet et al. [27] found that five days of visual deprivation coupled with Braille training were insufficient to improve participants' performance on the GOT beyond the levels of improvement observed in a non-visually-deprived Braille-trained control group (a significant effect of visual deprivation was found only on a Braille character recognition task, not on the GOT). Thus, it is possible that the GOT taps into a feature of tactile processing that is particularly resistant to improvement with visual deprivation. Alternatively, it is possible that the multi-day tactile training regimen undertaken by the participants in Merabet et al. [27] resulted in ceiling GOT performance, precluding additional effects of visual deprivation. These possibilities should be investigated in future studies.

What neural mechanism might underlie visual deprivation-induced tactile acuity enhancement?

In the absence of vision, the visual cortex becomes responsive to tactile inputs (crossmodal plasticity) [26,27]. Tactile activation of primary visual cortex appears to be weak, if present at all, within two hours of visual deprivation [26,43], and emerges more robustly after five days of deprivation [27]. Correspondingly, the results of the present study and others indicate that tactile acuity is unaffected by short-term (minutes to hours) visual deprivation [29–33], but improves upon long-term (days) visual deprivation [5,6,27,28]. These observations raise the hypothesis that crossmodal plasticity underlies the tactile acuity enhancement observed upon prolonged visual deprivation. In support of this hypothesis, transcranial magnetic stimulation (TMS) applied to the occipital cortex of sighted participants who were visually deprived for five days disrupted their ability to perform a Braille character discrimination task on which they had been previously trained [27].

Crossmodal plasticity coupled with extensive daily reliance on the sense of touch may also underlie tactile acuity enhancement in blindness [15–23].

Conclusion

In three experiments, we show consistently that short-term visual deprivation for periods up to 110 minutes does not enhance passive tactile spatial acuity. We note that in contrast to short-term visual deprivation, prolonged visual deprivation does reportedly drive tactile acuity enhancement. Investigations that couple perceptual testing with neural imaging will help to elucidate the mechanism by which prolonged visual deprivation enhances tactile acuity.

Materials and Methods

We conducted three experiments involving 158 participants. None of the participants tested in one experiment were tested in any other. None of the participants had previous experience with the grating orientation task. Experiment 1 was conducted at Duquesne University (Pittsburgh, PA, USA) and Experiments 2 and 3 at McMaster University (Hamilton, ON, Canada).

Ethics Statement

Experiment 1 was approved by the Duquesne University Institutional Review Board; Experiments 2 and 3 were approved by the McMaster University Research Ethics Board. All participants provided written consent and received monetary compensation and/or course credit for their participation.

Experiment 1

Participants. Forty-eight normally sighted participants (24 men, 24 women, ages 18.4–22.8 years, median age 20.9 years) took part in Experiment 1. Inclusion criteria ensured that participants did not have (by self report) dyslexia, diabetes, nervous system disorders, or injuries or calluses on the index finger of the dominant hand (the finger was inspected in the laboratory to verify its condition). Dyslexia was an exclusion criterion because it has been shown to adversely affect tactile spatial perception [44]. Diabetes was an exclusion criterion because it can affect peripheral nerve conduction, even when neuropathy is not evident [45]. Hand dominance was assessed by a handedness questionnaire (modified from [46]). A subset of the data collected from these participants (performance in the light-eyes open condition) has been reported previously [42].

Psychophysical Procedures. We assessed each participant's ability to discern the orientation of grating stimuli applied to the distal index finger pad of the dominant hand. The stimuli were a set of custom-made square-wave gratings, with groove widths ranging from 0.25 mm to 3.1 mm (in increments of 0.15 mm). We used the Tactile Automated Passive-finger Stimulator (TAPS) to mechanically deliver the grating stimuli; see [39] for a complete description of this computer-controlled device. Briefly, the participant's dominant arm rested on a tabletop in prone position, with the distal index finger pad placed over a small circular opening in the table; the gratings were mechanically driven to rise through this opening to contact the finger pad for approximately 1 s (50 g contact force, 4 cm/s onset velocity). Plastic barriers surrounded the finger to ensure that it remained centered on the opening, and a force sensor on the cuticle detected even minor finger movements; the computer system automatically discarded any trials in which finger movements occurred.

In each two-interval forced-choice (2-IFC) trial, the participant's tested finger pad was contacted twice by the grating stimuli, once with the gratings aligned parallel to the long axis of the finger (vertical), and once with the gratings aligned transverse to the long axis of the finger (horizontal); the presentation order was chosen randomly (i.e., horizontal before vertical, or vertical before horizontal). An interstimulus interval of 2s separated the presentation of the two orientations. The participant indicated, by pressing one of two buttons with the non-tested hand, whether the horizontally aligned gratings contacted the tested finger in the first or second interval (Figure 1). Participants were given auditory feedback for correct and incorrect responses after each trial.

We used a two-down one-up adaptive staircase procedure [47] to estimate the groove width that corresponds to 70.71% correct performance (70.71% threshold) – the dependent measure for this experiment. Each staircase began at a groove width of 1.45 mm; thereafter, the groove width was made incrementally thinner (more difficult to perceive) for every two consecutive correct responses, and incrementally wider (easier to perceive) for each incorrect response. To quickly bracket each participant's 70.71% correct threshold, we used an increment size of 0.3 mm until three reversal points occurred (trials at which the staircase changes direction). To obtain a more precise estimate of each participant's 70.71% threshold, we then reduced the increment size to 0.15 mm and ran the staircase until 11 further reversal points were encountered. We averaged the groove widths of these final 11 reversal points to obtain an estimate of the participant's 70.71% threshold. If the participant responded correctly twice at the thinnest groove width (0.25 mm) or incorrectly once at the widest groove width (3.1 mm), that groove width was used as the participant's last reversal point; we then averaged the groove widths beginning with the fourth reversal point and ending with this last reversal point to obtain an estimate of the participant's 70.71% threshold.

Experimental Design & Conditions. We tested every participant twice under all four combinations of ambient lighting (light or pitch-dark) and eyelid state (eyes opened or eyes closed). The order of conditions was counterbalanced across participants, such that each of the 24 men was tested on one of the 24 (i.e., 4 factorial) possible combinations of these four conditions, and similarly for each of the 24 women. After completing the four conditions, the participant was tested again on the same conditions and in the same testing order.

Participants took on average 8 minutes to complete a testing block. The mean elapsed time between the end of one block and the start of the next was 2 minutes for blocks within the same iteration. The mean elapsed time between iterations (end of block 4 of iteration 1 to start of block 1 of iteration 2) was 3 minutes. The experiment duration averaged approximately 80 minutes.

During the light conditions, the participants were tested under fluorescent overhead room lighting typical of a well-lit indoor environment. During the dark conditions, the participants were tested in the pitch-dark. Room darkness was such that no visual input was perceptible, even of large nearby objects (e.g., it was not possible to see one's own hand placed in front of the face). The light intensity was less than 0.01 lux, the lower detection limit of our light meter (Mannix DLM2000). To achieve visual deprivation, we chose here (and in Experiments 2 and 3) to use a pitch-dark room rather than blindfolding the participants. A simple cloth blindfold does not screen out all light, and also rubs and tickles against the eyes and face, causing a tactile distraction. Opaque goggles (such as painted swim goggles) can screen out all light, but require tight fits to the eye sockets, and are consequently both distracting and uncomfortable. We wished to test participants without light, and without inducing discomfort or distraction.

An experimenter remained in the testing room at all times to ensure the participants' compliance with the eyelid state (eyes opened or closed) instructions appropriate to the condition. During the light conditions, the experimenter simply viewed the participant's eyes with unaided vision. During the dark conditions, the experimenter periodically verified that the participant's eyes were opened or closed as per condition with the aid of an infrared night vision monocular (Bushnell). Because the infrared beam cast by the night vision device bled somewhat into the visible red, we secured an opaque occluder with a pinhole cutout over the beam source to reduce the size of the beam to the bare minimum needed to obtain a view of the participant.

Experiment 2

Participants. Forty-four normally sighted right hand-dominant students from McMaster University (14 men, 30 women, ages 20.1–25.75 years, median age 21.1 years) participated in Experiment 2. Hand dominance was confirmed by questionnaire (modified from [46]). Inclusion criteria ensured that participants did not have (by self report) dyslexia, diabetes, nervous system disorders, or injuries or calluses on the index finger of the right hand.

Psychophysical Procedures. The TAPS device used in Experiment 1 was again used in Experiment 2 to administer the GOT. Here we programmed TAPS to follow a more sophisticated psychophysical adaptive procedure than that used in Experiment 1, a modified version of the Bayesian adaptive ψ-method [39,48], to estimate each participant's 76% correct threshold – the dependent measure used in this experiment. We implemented a "Bayesian guessing factor" (described in detail in [23,39]) to assess whether each participant was capable of performing the GOT. Those deemed to be guessing by the Bayesian guessing factor were excluded from data analysis.

Before finger testing commenced, participants were familiarized with the GOT by completing 20 practice trials with auditory feedback. Participants then completed a series of test blocks consisting of 40 trials each (without auditory feedback). Participants were not blindfolded, nor were they instructed to close their eyes during the test blocks. Previous studies have shown that tactile acuity improves when the participant views the tested hand [49–51]; therefore, we covered the participant's tested hand from view with a box (Figure 1) in order to avoid the possible confound that participants might perform better in the light – not because of differences between the light and dark conditions per se – but simply because they could view the back of their hand.

As in Experiment 1, participants were tested in the light (fluorescent overhead room lighting) and the pitch-dark (<0.01 lux). Unlike in Experiment 1, the investigator did not remain in the testing room with the participants. Therefore, participants in the dark were required to put on light-occluding goggles for a brief period (approximately 2–3 minutes) as the experimenter entered the room to initialize the equipment before each stimulation block. Except for these very brief periods, the participants were not blindfolded.

Experimental Design & Conditions. Participants were assigned to one of four groups in pseudorandom order. Participants in the non-deprived group completed 10 test blocks in the light and were never visually deprived. Participants in the other three (visually deprived) groups completed two test blocks before (in the light) – to obtain baseline tactile acuity – and three test blocks after (in the light) experiencing a period of visual deprivation. The sequence of events during the visual deprivation period (in the pitch-dark) differed by visual deprivation group (Figure 4).

To investigate whether short-term visual deprivation alone improves tactile spatial acuity, as reported [35,36], we administered one test block after a 70-minute visual deprivation period to participants in the unstimulated group; these participants listened to music of their choice during the visual deprivation period.

To investigate whether and how tactile acuity changes over time with visual deprivation, we administered five test blocks during the visual deprivation period to participants in the repeatedly tested group.

To investigate whether unattended grating stimulation in the dark would improve tactile acuity, we administered four passive stimulation blocks followed by one test block during the visual deprivation period to participants in the passively stimulated group. These participants were instructed to ignore the grating stimuli contacting the finger during a passive stimulation block; during the passive stimulation, they listened to music of their choice. As in the test blocks, in each trial of a passive stimulation block the participant's tested finger was contacted with a grating twice, once oriented vertically and once horizontally (order chosen randomly). However, unlike during testing, the participant did not make any response (the computer program produced a sham response 700 ms after the end of stimulation, and the next trial therefore automatically commenced). The sequence of grating groove widths contacting the participant's finger in a passive stimulation block was the same sequence the participant experienced during the first or second test block, chosen randomly (if the participant had made a finger-movement error during the first or second test block, resulting in a discarded trial, the largest groove width in the stimulus set, 3.1mm, was given in its place during passive stimulation).

Participants took on average 7 minutes to complete a test or passive stimulation block; including set-up time by the experimenter, each block lasted approximately 9 minutes. Successive blocks were separated by 8-minute break periods during which participants were free to listen to music of their choice. For participants in the repeatedly tested and passively stimulated groups, the average elapsed time between the start of the initial block in the dark and the start of the final block in the dark was 68 minutes; participants in the unstimulated group sat in the dark for exactly 70 minutes before being tested. Participants in all three visually deprived groups remained in pitch-darkness during the break following the final testing block in the dark; these participants sat in a pitch-dark room for approximately 90 minutes (Figure 4).

Experiment 3

Participants. Sixty-six normally sighted right hand-dominant students from McMaster University (35 men, 31 women, ages 18.1–25.7 years, median age 19.5 years) participated in Experiment 3. The same qualification criteria and handedness questionnaire used in Experiment 2 were used here.

Psychophysical Procedures. The psychophysical procedures were identical to those used in Experiment 2.

Experimental Design & Conditions. To ensure participant alertness, we recruited participants in sets of three and encouraged conversation during the visual deprivation period. Each set of three was assigned to one of two groups in alternating order: non-deprived and visually deprived.

Every participant was tested three times. The first test block served as a measure of the participant's baseline tactile acuity. This was followed by a 110-minute conversation period during which participants talked with one another or with an experimenter. The conversation period was followed by a second test block, after which the participant left the laboratory to take a 120-minute break. Following the break, the participant returned to the laboratory to complete a final test block. Participants took on average 8 minutes to complete a test block.

Non-deprived participants were always in the light. Visually deprived participants were in the pitch-dark during the conversation period and while completing the second test block. The visually deprived participants were in the pitch-dark for an average duration of 120 minutes.

The test blocks were administered in a testing room, and the conversation period took place in a separate conversation room. Participants in each set of three were tested sequentially (Figure S1). It was therefore inevitable that, as participants rotated into the different phases of the experiment, the first and third participant would at different times be alone in the conversation room. To maintain participant alertness during these periods, the participant in the conversation room conversed by remote two-way audio either with the experimenter or with a fellow participant who was waiting outside the laboratory.

Data Analysis

We performed analyses of variance (ANOVA) with SPSS v19 (IBM Corp., Somers, NY) for Macintosh, with an alpha-level of 0.05. The dependent measure used in the statistical analysis of Experiment 1 was the participant's 70.71% correct threshold, obtained using a two-down one-up staircase procedure [47]. The dependent measure used in the statistical analyses of Experiments 2 and 3 was the mean of the posterior PDF of the participant's 76% correct threshold, obtained using a modified version of the ψ-method [39,48].

Supporting Information

Figure S1 Sequence of events in Experiment 3. (A–C) The participants were tested sequentially in the testing room, and then seated sequentially in the conversation room. (D) Each participant

spent a total of 110-minutes in the conversation room. (E–G) The participants were then tested sequentially a second time. (H) All three participants left the laboratory for a 120-minute break and returned sequentially to be tested a final time (not shown). The image is not drawn to spatial or temporal scale.
(TIF)

Author Contributions

Conceived and designed the experiments: DG EH. Performed the experiments: MW EH CH DG. Analyzed the data: MW EH DG. Wrote the paper: MW DG.

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3.8 Supplementary figure

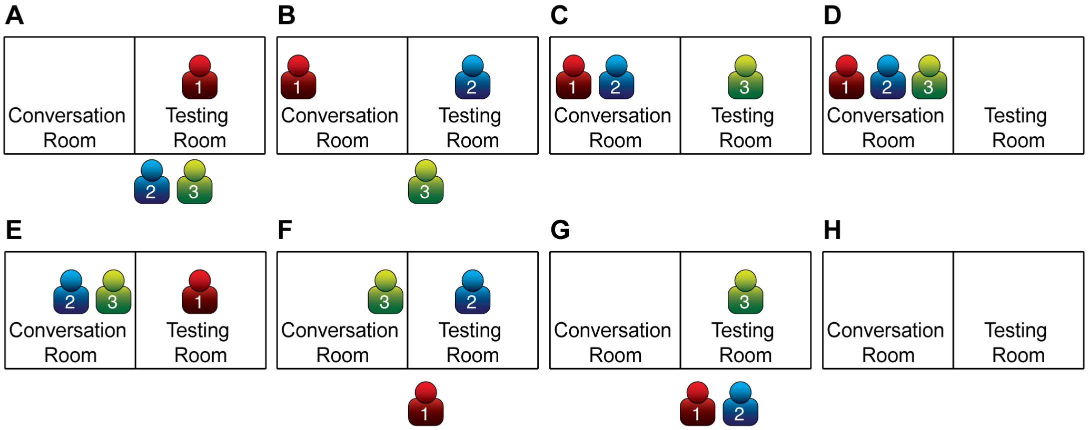

Figure S1. Sequence of events in Experiment 3. See pages 42-43 for figure caption.

Chapter 4

4.1 Preface

The results from the previous two chapters provide no support for the visual deprivation hypothesis and suggest instead that tactile experience drives tactile spatial acuity enhancement in blind participants. In Chapter 4, we further investigated the tactile experience hypothesis by investigating whether participants' tactile spatial acuity can be improved with training, a question that has received very little attention in the literature.

Here we showed that participants trained to discriminate the orientation of grating stimuli for four days improved their performance on the GOT. The results of this study therefore provide further support for the tactile experience hypothesis, showing directly that tactile spatial acuity can be improved with experience. In this study, we showed additionally for the first time that finger size, which might reflect receptor density, sets the limit to tactile spatial acuity.

4.2 Abstract

Perceptual performance improves with training – a phenomenon known as perceptual learning. Studies have suggested that reliance on the sense of touch improves tactile perception. For example, blind participants, particularly Braille readers, outperform sighted participants on tactile spatial tasks (Goldreich & Kanics, 2003; Wong et al., 2011). However, it is unclear whether sighted participants, with training, can improve their tactile spatial acuity, and, if so, what sets the limit to this improvement. We investigated these questions by training sighted participants to discriminate the orientation of square-wave gratings applied to the stationary index or ring finger. Using an automated stimulus apparatus (Goldreich et al., 2009), we trained participants over 4 days (up to ten 50-trial blocks/day, each block at a single groove width) on a two-interval forced-choice task, providing distinct auditory feedback tones for correct and incorrect responses. We shifted participants to a thinner groove width when they achieved ≥ 90%-correct block performance. We found that participants' spatial acuity improved markedly on the trained finger, to a degree that was determined by the participants' pre-training performance. We found additionally that performance correlated with finger size after but not before training, suggesting that tactile spatial acuity is limited by finger size, which we have reason to believe reflects receptor density.

4.3 Introduction

In touch, as in vision, perception is able to resolve fine spatial details. These perceptual systems do not operate at a fixed level of resolution, however. Rather, humans differ from one another in their spatial acuity, and individuals are able to improve, to varying degrees, with practice (perceptual learning) (for reviews see Fahle, 2005; Sathian, 1998; Seitz & Dinse, 2007).

There is some evidence that training on spatial perceptual tasks drives spatial acuity towards an unsurpassable limit. In particular, perceptual learning reportedly occurs to a greater extent in participants with poorer pre-training performance (Fahle & Henke-Fahle, 1996). Participants with good pre-training performance improve less with training, suggesting that their pre-training performance was already near its limit.

These observations raise the question: What sets the limit to spatial perceptual acuity? Because sensory stimuli are first encoded by activity in the peripheral receptor population, spatial acuity is presumably constrained by receptor density (e.g., photoreceptor density for visual tasks, mechanoreceptor density for tactile tasks). Here we test the hypothesis that, with training, humans are able to improve their tactile spatial acuity, to a limit permitted by their fingertip receptor density. If the limit to spatial acuity is determined by receptor density, then spatial acuity, once driven to this limit, should be better in participants with more densely distributed receptors. Here we use a grating orientation task (GOT) (Craig, 1999; Johnson & Phillips, 1981) to test this prediction.

Several lines of evidence suggest that mechanoreceptor density is reflected in finger size. Histological studies have observed that the density of Meissner's corpuscles (primary mechanoreceptors for low-frequency vibrations; see Johnson, 2001) is greater in smaller fingers (e.g., Dillon, Haynes, & Henneberg, 2001). Additionally, sweat pores, beneath which Merkel cells (primary mechanoreceptors for spatial information; see Johnson, 2001) cluster (Yamada, 1996), are more densely distributed in smaller fingers (Peters et al., 2009); therefore, the density of Merkel cells, like Meissner's corpuscles, might also be greater in smaller fingers. If receptor density, as reflected in finger size, determines the limit of tactile spatial acuity, the correlation between spatial acuity and finger size should be better after training than before: participants with smaller fingers should, particularly after training, have better spatial acuity than participants with larger fingers.

We trained participants for four days (on either the index or ring fingertip) on an automated, precision-controlled GOT (Goldreich, Wong, Peters, & Kanics, 2009), progressively decreasing the grating groove width in order to drive participants' performance efficiently towards its limit. We found that participants' performance on the GOT improved on the trained finger. Furthermore, the improvement occurred to a greater extent in participants with poorer pre-training performance. In addition, and in accordance with our hypothesis, spatial acuity correlated better with finger size after than before the training session.

4.4 Methods

Participants

We tested ten participants (4 men, 6 women), ranging in age from 18.1 to 30.9 (median age: 20.8). All participants indicated that they were free of diabetes, dyslexia, nervous system disorders, and injuries and calluses on the index and ring finger of the dominant hand; 8 participants were right-hand dominant, and 2 were left-hand dominant. Handedness was assessed by a questionnaire (modified from Oldfield, 1971).

Grating orientation task

We used the Tactile Automated Passive-Finger Stimulator (TAPS), a custom-made mechanical stimulus-delivery device (Goldreich et al., 2009), to deliver grating stimuli. The grating stimuli were custom-made square-wave gratings with groove widths that ranged from 0.25 mm to 3.1 mm, in increments of 0.15 mm. Because a complete description of the device has been published previously (see Goldreich et al., 2009), only a brief description will be given here. The participant rested the dominant hand in prone position with the distal finger pad (index or ring) placed over a tunnel in the table. The grating stimuli were mechanically driven through the tunnel to contact the stationary finger pad for ~1 s (50 g contact force, 4 cm/s onset velocity). A force sensor resting on the fingernail detected and discarded any trials in which a finger movement was made. In each trial, the participant was presented twice with a grating stimulus (2 s interstimulus interval), once with the gratings aligned parallel (vertical), and once with the gratings aligned transverse (horizontal) to the proximal-distal axis of the finger (order chosen randomly) (Figure 1A). The participant was required to indicate the interval that contained the horizontally aligned grating by pressing one of two buttons with the non-tested hand.

Assessing tactile spatial acuity

To assess each participant's tactile spatial acuity before (day 1) and after (day 5) the training session, we used a GOT. Groove width was adaptively adjusted from trial-to-trial using a modified version of the Bayesian ψ-method (Goldreich et al., 2009; Kontsevich & Tyler, 1999), to determine the groove width whose orientation the participant could correctly discriminate with 76% probability (threshold) (Figure 1B). Testing on each finger began with a series of 20 practice trials with auditory feedback. This was followed by a series of 80 experimental trials without feedback. Participants received a 1-min break halfway through the testing on a particular finger (i.e., at experimental trial 40), and a 1-min break between the testing of the two fingers. We initially assigned participants to be tested first on either the index or the ring finger, in alternating order upon their entry into the study. We found, however, that most participants who were tested first on the ring finger were unable to meet our qualification criterion (see below); only one out of five people first tested on the ring finger qualified (the rest were let go). Because the initial two participants who were tested first on the index finger qualified, we modified our protocol to test every subsequent participant first on the index finger. Thus, of the 10 participants who completed the study, just one (P2) was tested first on the ring finger; the other nine were tested first on the index finger.

Qualification criterion

Due to the duration of our training protocol, we required a high degree of concentration from our participants. We initially accepted participants whose 90% confidence interval width of their threshold parameter estimate (as measured by the modified version of the ψ method) did not exceed five groove widths. This criterion, however, was too stringent: only two out of eight participants were able to qualify, even after we switched the order of finger testing (described above). We therefore relaxed the criterion to accept participants whose 80% confidence interval width of their threshold parameter estimate did not exceed five groove widths.

Training Protocol

Participants who met the qualification criterion were then trained for four days to discriminate the orientation of grating stimuli. We assigned participants in alternating order to be trained on either the index or the ring finger. Immediately following the first testing session, the participants completed eight training blocks (of 50 trials each) (day 1). The participants then returned to the laboratory over the next three consecutive days (days 2-4) for further training (ten blocks per day). Thus, over the four days of training, each participant completed a total of 1900 training trials (38 blocks x 50 trials per block). The training session began with the groove width nearest the participant's 76%-correct threshold (mode of the threshold probability distribution function, PDF). Within a training block, the groove width was held constant. From one training block to the next, the groove width was adjusted based on the participant's performance on the preceding block: the groove width was decreased by 0.15 mm if the percent correct performance was 90% or greater; the groove width was left unchanged if the percent correct performance was between 60-90%; and the groove width was increased by 0.15 mm if the percent correct performance was 60% or lower (Figure 1C). Throughout training, we provided participants with auditory feedback for correct and incorrect responses after every trial. Participants received 1-min breaks between training blocks.

Measuring fingertip surface area

Upon completion of the second testing session (day 5), we scanned the distal portion of the participant's trained (and then untrained) finger with a flatbed scanner (Epson Perfection 1260). Scanning resolution was set to 400 d.p.i. The participants placed their hand on a glass-scanning surface in prone position and an opaque shield was lowered over the hand. The surface area of the distal portion of the finger was digitally measured using ImageJ (National Institute of health). This procedure is identical to that used in Peters, Hackeman, & Goldreich (2009), where sample measurement images can be found.

Data Analysis

Analysis of variance (ANOVA), analysis of covariance (ANCOVA), and linear regressions were performed with SPSS v20 (IBM Corp., Somers, NY) for Macintosh with an alpha-level of 0.05. The ANOVA and ANCOVA models were all full-factorial type III sums-of-squares. Unless otherwise stated, the dependent measure used in the analyses was the mean of the posterior probability distribution function (PDF) of the participant's 76% correct threshold, as determined by our modified version of the ψ-method (Goldreich et al., 2009; Kontsevich & Tyler, 1999).

Because the ψ procedure returns a posterior PDF over threshold, we have not only a single best-estimate (posterior mean) for each participant's threshold, but also a full probability distribution reflecting the precision (confidence) of the measurement. We therefore were able to calculate the probability that an individual participant's performance on a particular finger had improved, by comparing the participant's post-training (day 5) and pre-training (day 1) posterior PDFs. The probability of improvement is the probability that the post-training threshold (x_{post}) was less than the pre-training threshold (x_{pre}). We call this the *S* index:

$$S = p(x_{post} < x_{pre}) = \int_{x_{post}=0}^{\infty} p(x_{post}) \left(\int_{x_{pre}=x_{post}}^{\infty} p(x_{pre})\, dx_{pre} \right) dx_{post}$$

In essence, the *S* index is a measure of similarity between the two posterior PDFs reflecting confidence in the statement: "the participant has improved" (as opposed to "the participant has worsened"). The index can take any value between 0 and 1. S=0 if the post-training threshold PDF is shifted completely (non-overlapping) to the right of the pre-training threshold PDF, indicative of a certain worsening in performance; S=0.5 if the two PDFs are identical, indicative of no obvious change in performance; and S=1 if the post-training threshold PDF is shifted completely (non-overlapping) to the left of the pre-training threshold PDF, indicative of a certain improvement in performance.

4.5 Results

To examine whether training improves GOT performance, we conducted a 2 (finger: trained and untrained) x 2 (session: pre and post training) repeated measures ANOVA. This ANOVA revealed a significant main effect of session ($p = 0.030$). There was no significant main effect of finger ($p = 0.280$), and no significant finger x session interaction ($p = 0.611$). The trained finger improved by an average of 0.50 mm (SE 0.19), and the untrained finger improved by an average of 0.37 mm (SE 0.22) (Figure 2). The average improvement in performance was dramatic: as a proportion of pre-training mean performance, post-training mean performance was 0.70 on the trained finger and 0.79 on the untrained finger.

We next calculated a similarity index (S), between the pre- and post-training threshold PDFs, for the trained and untrained finger of each participant to measure individual degrees of improvement (see methods). With a 0.9 criterion applied to these values, seven participants improved on the trained finger and five participants improved on the untrained finger. There were some instances (two on the trained finger; three on the untrained finger) where S fell below 0.5, suggesting that the participant's performance worsened upon training (Table 1). We note additionally that the rate at which participants improved with training was quite variable; for instance, the number of blocks required for participants to improve beyond their pre-training threshold groove width ranged from 2 to 30 (Figure 3).

Having found a significant improvement in GOT performance on the trained finger, we next investigated whether pre-training performance determines the degree of learning; that is, participants with exceptionally good pre-training performance might improve very little with training because their tactile spatial acuity is already near its limit. Consistent with this prediction, a linear regression revealed that the degree to which a participant improved on the GOT (pre-training – post-training threshold) was predicted by the participant's pre-training performance ($p = 0.020$) (Figure 4A).

If receptor density, as reflected in finger size, determines the limit of spatial acuity, finger size will necessarily affect the degree of improvement, i.e., participants with larger fingers, but with the same pre-training performance, should improve less than participants with smaller fingers. We therefore repeated the previous analysis with fingertip-size-adjusted pre-training threshold as the independent variable. We adjusted all participants' threshold to have an equivalent finger size, using the mean effect size of 0.25 mm/cm^2 obtained from 100 participants in Peters et al. (2009). This analysis revealed that finger-size-adjusted pre-training thresholds predicted GOT improvement ($p = 0.002$) with an even stronger significance than was predicted by the non-adjusted pre-training thresholds (Figure 4B).

Two linear regressions with pre- and with post-training thresholds as the dependent variable and finger size as the independent variable revealed that participants' thresholds were predicted by finger size after ($p = 0.023$) but not before ($p = 0.945$) training (Figure 5); this result further supports the conclusion that training drove participants' spatial acuity to a limit that is determined by their finger size.

Having found a significant finger size effect (post-training), we next compared the finger size effect obtained in the present study to the finger size effect obtained in Peters et al. (2009), which had a much larger sample size (N = 100). Because participants in Peters et al. (2009) were tested on multiple blocks, we pooled each participant's performance across testing blocks to obtain a single estimate of their mean threshold PDF. We then used these values and the post-training thresholds from the present study as the dependent variable in an ANCOVA, with study (present study, Peters et al., 2009) as a factor and finger size as a covariate. This analysis revealed a significant main effect of finger size ($p = 0.001$), with no significant main effect of study ($p = 0.364$), and no significant study x finger size interaction (*$p = 0.619$*). Thus, in the present study, by intensively training just 10 participants we were able to reveal the same finger size effect on tactile spatial acuity as was revealed only with a much larger sample of untrained participants in Peters et al. (2009). Although not significant, there was a trend for participants in the present study (post-training) to perform better than participants in Peters et al. (2009) (Figure 6).

4.6 Discussion

We found that participants trained to discriminate the orientation of grating stimuli improved their GOT performance on the trained finger. The degree of improvement was predicted by the finger's pre-training performance, with worse pre-training performance associated with more training-induced improvement. Furthermore, when adjusted for fingertip surface area, pre-training performance even better predicted GOT improvement, and performance after training correlated well with fingertip surface area.

Performance improves with training

While performance on many tactile tasks improves with training (Harris, Harris, & Diamond, 2001; Imai et al., 2003; Kauffman, Théoret, & Pascual-Leone, 2002; Sathian & Zangaladze, 1997, 1998; Weiss et al., 2007), several studies have reported that performance on the GOT improves very little, if at all, with repeated testing (Goldreich & Kanics, 2003; Van Boven & Johnson, 1994; Wong, Hackeman, Hurd, & Goldreich, 2011; but see Sathian & Zangaladze, 1998). We found, contrary to many of these GOT studies, that participants' performance on the GOT can be markedly improved by training, perhaps because participants in our study received many more grating orientation-discrimination trials than did participants in the other studies (particularly at subthreshold groove widths, e.g., below 75% correct performance). Alternatively, in those studies that adaptively adjusted groove width from trial-to-trial (Goldreich & Kanics, 2003; Wong, Hackeman, et al., 2011), the absence (or reduction) of perceptual learning might be a result of intermixing gratings of different groove widths within a testing block; intermixing stimulus values has been reported to reduce or abolish perceptual learning on a visual contrast-discrimination task (see Yu, Klein, & Levi, 2004).

Transfer of perceptual learning

Perceptual learning has been found to transfer from the trained finger to adjacent untrained fingers (Harris et al., 2001; Imai et al., 2003; Sathian & Zangaladze, 1997, 1998), but it is unclear whether perceptual learning transfers to the fingers beyond the adjacent ones (e.g., from a trained index finger to the untrained ring finger of the same hand). Although Harris et al. (2001) reported no such transfer effect, their data suggest a non-significant trend for the untrained finger situated two fingers away from the trained finger to perform better after than before the training session. Interestingly, Imai et al. (2003), who used a more intensive training protocol (14,080 trials over 22 days) than the one used by Harris et al. (2001) (< 300 trials in one day), found that perceptual learning (on a frequency-discrimination task) extended from the trained finger to all other untrained fingers of both hands (the thumbs were not tested). In agreement with Imai et al. (2003), the results of the present study indicate that with an intensive training protocol

(1,900 trials over four days), perceptual learning transferred from the trained finger to a non-adjacent untrained finger.

Degree of perceptual learning is determined by pre-training performance

Our results suggest that the degree of perceptual learning is determined by the participant's pre-training performance, a finding in general agreement with a study in the visual literature (Fahle & Henke-Fahle, 1996). Using a tactile task, Sathian & Zangaladze (1997) obtained similar results, although this was not reported in their paper; we performed a linear regression on the data reported in their table 1 and found that the degree to which participants improved on a Braille dot-discrimination task was determined by their initial performance on that task ($p = 0.009$).

Although the factor(s) that determines pre-training acuity is unclear, there is some evidence that tactile experience might play a role. Pianists and blind participants outperform non-musicians and sighted participants on tactile tasks (Goldreich & Kanics, 2003, 2006; Ragert, Schmidt, Altenmüller, & Dinse, 2004; Stevens, Foulke, & Patterson, 1996; Van Boven, Hamilton, Kauffman, Keenan, & Pascual-Leone, 2000; Wong, Gnanakumaran, & Goldreich, 2011), suggesting that perhaps extensive experience with sensorimotor tasks and/or increased tactile reliance for everyday activities can drive tactile acuity enhancement. Consistent with this notion, our laboratory reported that blind participants outperformed their sighted peers on a GOT only on body parts where tactile experience is presumably greater in blind than in sighted participants; furthermore, the tactile spatial acuity of blind Braille readers on their reading fingers correlated with their weekly reading experience (Wong, Gnanakumaran, et al., 2011). Thus, in the current study, those participants whose initial performance was exceptionally good possibly learned very little because their tactile acuity had already been driven towards its limit by daily tactile reliance.

Tactile spatial acuity is limited by finger size

We found a better correlation between pre-training performance and GOT improvement when pre-training thresholds were adjusted for finger size than when they were not adjusted. That is, given the same pre-training performance, participants with larger fingers learned less than participants with smaller fingers. Our interpretation for this finding is that a large-fingered participant who has the same pre-training threshold as a smaller-finger participant is in fact performing relatively better (closer to the participant's lowest achievable threshold). Thus, tactile spatial acuity is limited by finger size. Further, we found that after training, when the participants' performance was presumably driven towards its limit, participants' GOT thresholds correlated much better with finger size than before training; participants with larger fingers had higher GOT thresholds than participants with smaller fingers, perhaps because the receptors are more sparsely distributed in larger fingers (Dillon et al., 2001; Peters et al., 2009; Yamada et al., 1996).

Previously, we found that without training GOT thresholds increased significantly with finger size (Peters et al., 2009). In that study, there was substantial variability in thresholds even among participants with similar finger sizes (perhaps due to inter-subject differences in lifetime tactile experience); for this reason, a large number of participants (N = 100) was required to convincingly reveal the finger size effect. In the present study, however, we showed that with training the finger size effect becomes apparent with few participants (N = 10), presumably because training drove participants' performance towards its limit, thereby reducing the variability in thresholds. We found additionally that while the finger size effect was similar between the two studies, the participants in the present study tended (non-significantly) to have better performance, post-training, than did the participants in Peters et al. (2009).

Possible neural mechanism mediating tactile perceptual learning

Although the neural basis of perceptual learning is largely speculative, there is some evidence that tactile perceptual learning is mediated by expansions of the somatosensory cortical representations in parietal cortex. Several studies have observed that, in humans and animals, extensive tactile experience is accompanied by an expansion of the somatosensory cortical areas representing the trained body part (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Jenkins, Merzenich, Ochs, Allard, & Guíc-Robles, 1990; Pascual-Leone & Torres, 1993; Recanzone, Merzenich, Jenkins, Grajski, & Dinse, 1992; Sterr et al., 1998; Xerri, Coq, Merzenich, & Jenkins, 1996; Xerri, Merzenich, Jenkins, & Santucci, 1999). More convincingly, some studies have observed a correlation between tactile performance improvement and somatosensory cortical representational expansion in the same participants (Hodzic, Veit, Karim, Erb, & Godde, 2004; Recanzone et al., 1992).

Conclusion

We show here that training improves GOT performance on the trained finger, to a degree that was determined by the trained finger's pre-training performance. We found additionally that tactile spatial acuity correlated better with finger size after than before the training session. Together, these results suggest that tactile experience accounts in part for the variability in pre-training tactile spatial acuity, and that the limit of tactile spatial acuity is predicted by finger size, which possibly reflects receptor density.

4.7 Figures and table

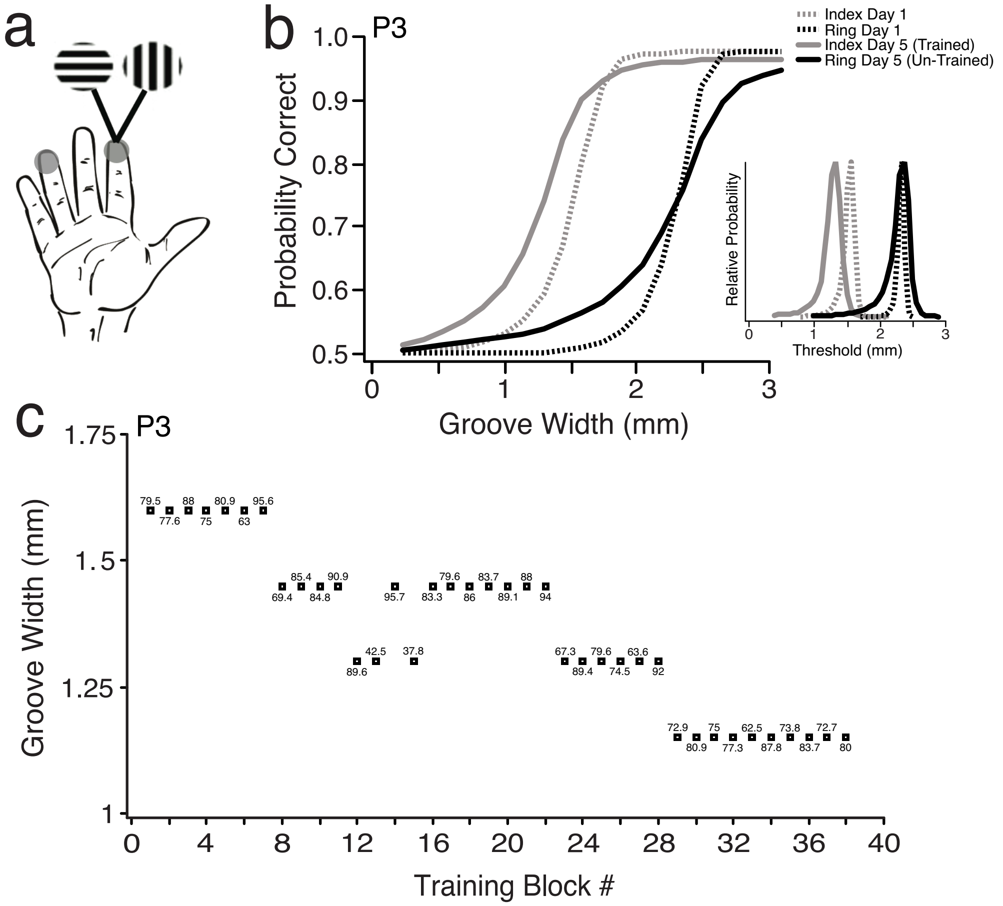

Figure 1. Grating orientation task and sample training data. **a.** Two-interval forced-choice GOT. Participants discriminated the orientation (horizontal, displayed on the left; vertical, displayed on the right) of grating stimuli with the stationary index or ring fingertip. **b.** Best-estimate of the psychometric function of a sample participant (P3) on days 1 (dashed) and 5 (solid) for the index (grey) and ring fingers (black); training took place on the index finger. The psychometric function for the index finger shifted leftward from day 1 to day 5, indicating that learning occurred on the trained finger; in this participant, the

psychometric function for the ring finger did not shift, indicating that learning did not transfer to the untrained finger. Inset: Corresponding posterior PDFs for the 76%-correct threshold. **c.** Groove widths tested for P3 across 38 training blocks (50 trials per block). Percent correct on each training block is given above or below each corresponding data point (black square).

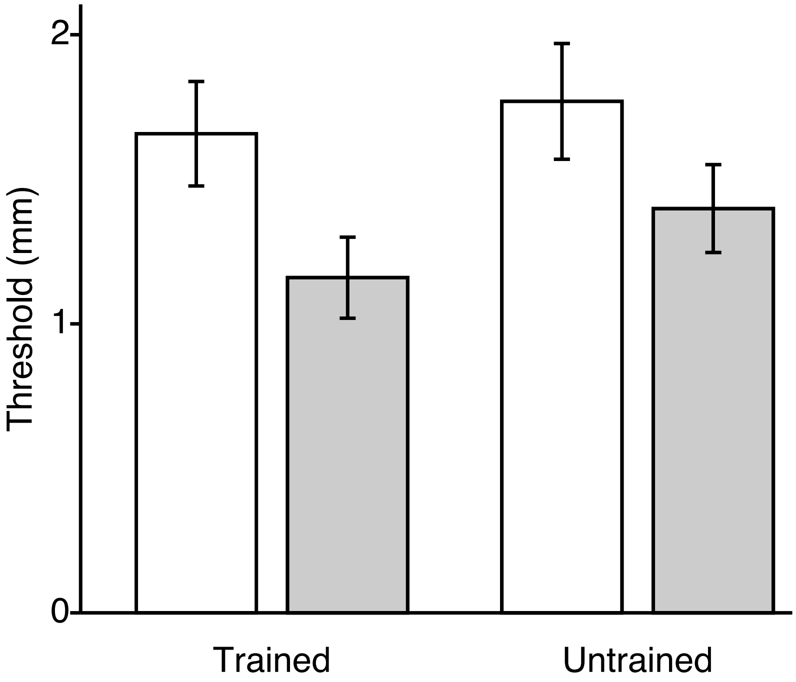

Figure 2. Pre- and post-training thresholds on the trained and untrained finger. White bars, Mean pre-training threshold. Grey bars, Mean post-training threshold. Error bars: ± 1 SE.

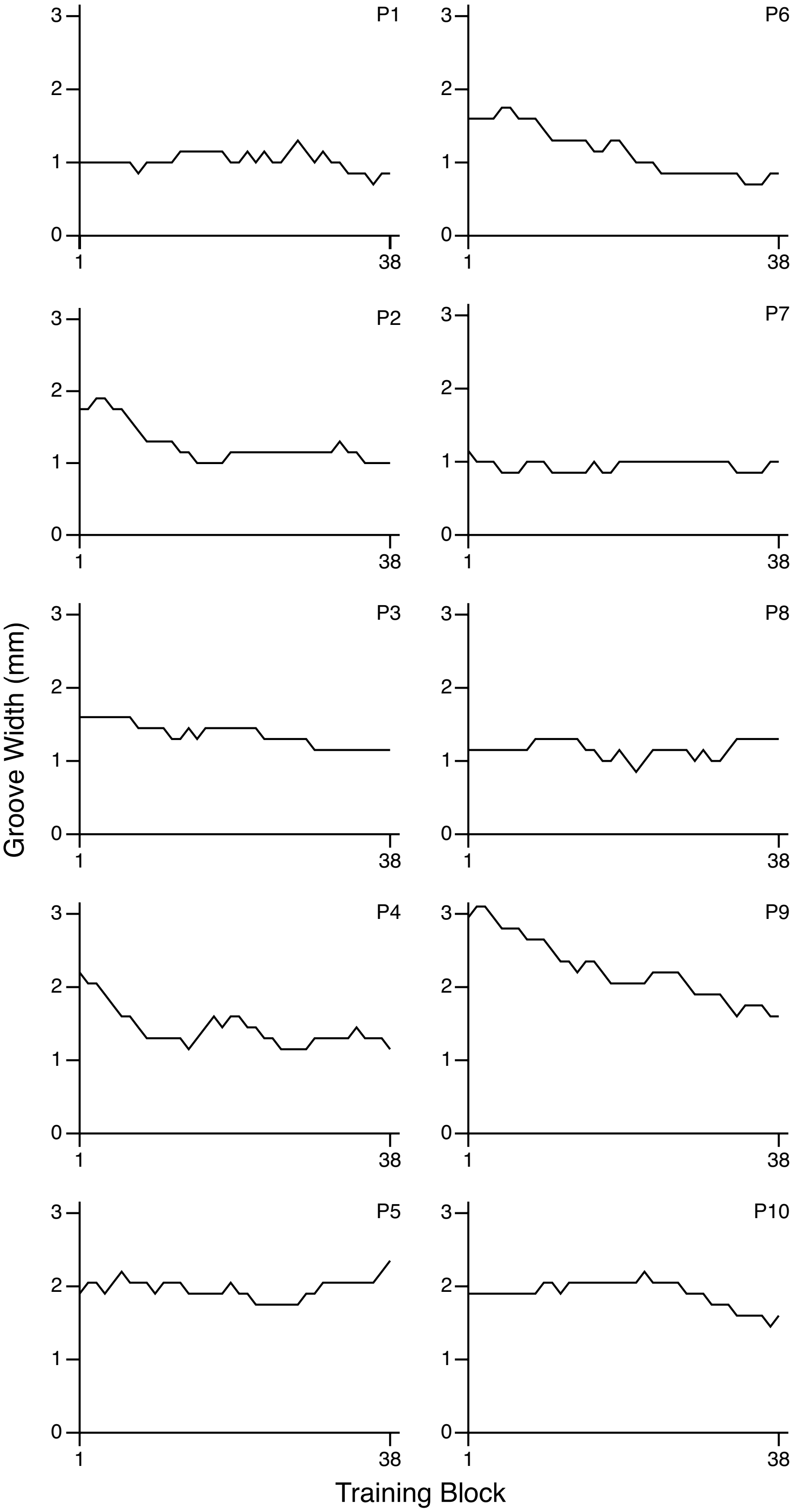

Figure 3. Learning curves (groove width vs. training block) for each participant (P).

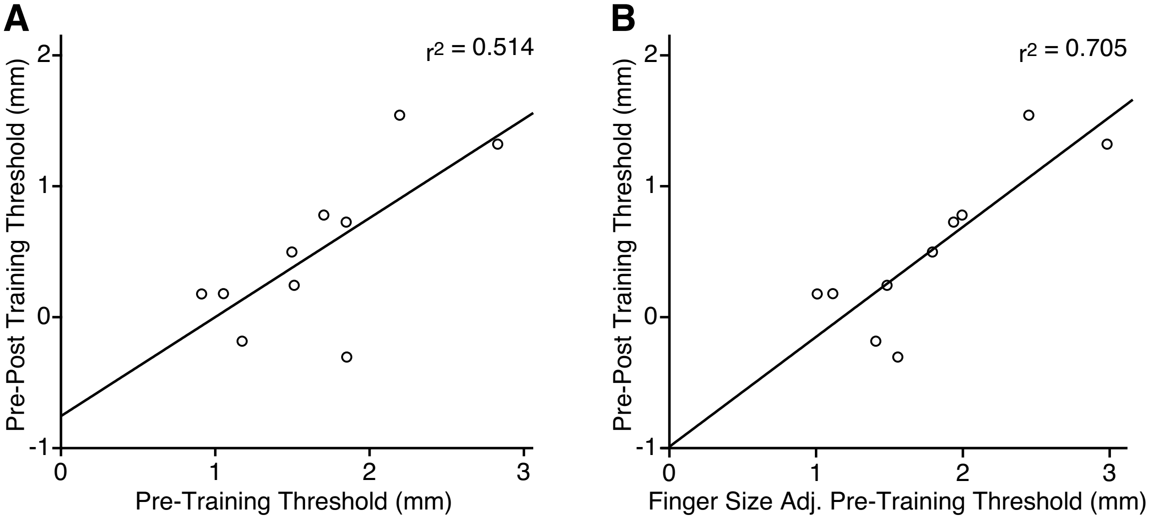

Figure 4. Threshold improvement (pre – post training) versus pre-training threshold on the trained finger. A, non-adjusted pre-training thresholds. B, pre-training thresholds adjusted to a fingertip surface area of 4.39 cm^2. Regression lines are shown.

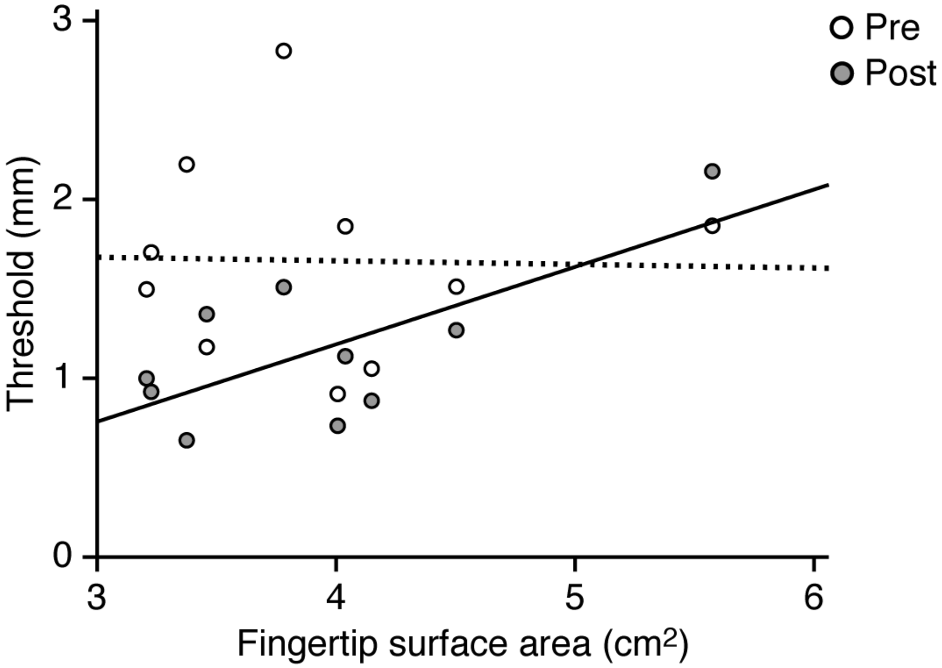

Figure 5. Scatterplot of threshold versus fingertip surface area. Pre-training, Open circles and dotted regression line (r^2=0.001). Post-training, Shaded circles and solid regression line (r^2=0.494).

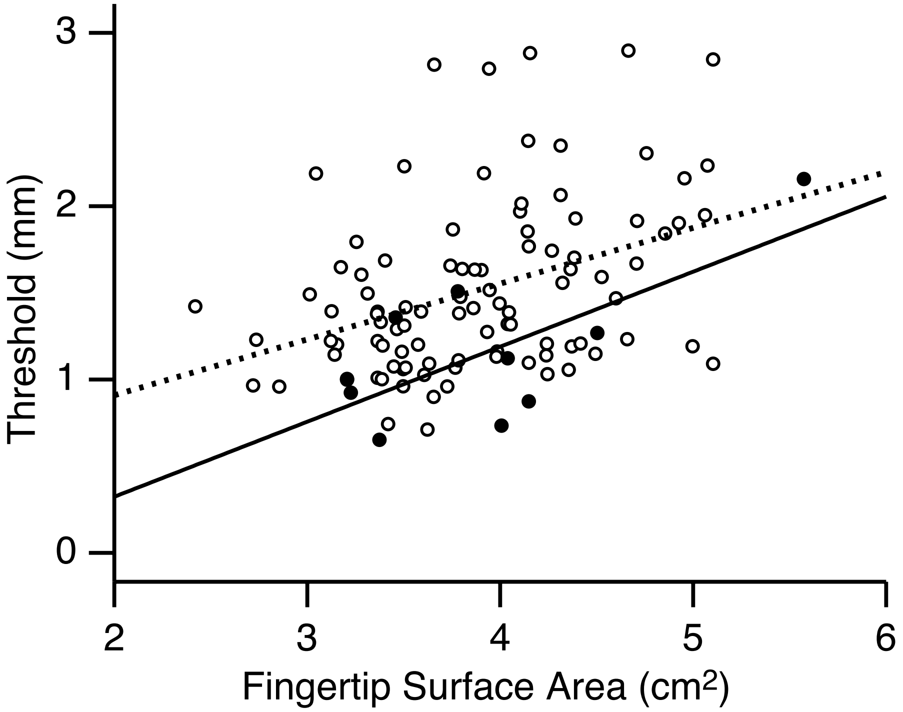

Figure 6. Combined scatterplot of threshold versus fingertip surface area. Present study, filled circles and solid regression line (r^2=0.494). Peters et al. (2009), Open circles and dotted regression line (r^2=0.149).

	Finger	
Participant	Trained	Untrained
1	0.81	0.24
2	0.99	1.0
3	0.90	0.47
4	1.0	0.60
5	0.97	0.99
6	0.96	0.99
7	0.91	0.0
8	0.40	0.96
9	1.0	0.99
10	0.21	0.69

Table 1. Similarity index (S) values on the trained and the untrained finger.

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Chapter 5

General discussion

5.1 Summary of studies

Although it is becoming increasingly clear that tactile spatial acuity is enhanced in the blind, it has been unclear whether this enhancement is better explained as the result of visual deprivation or of increased tactile experience. In the three studies presented in this thesis, we sought to tease apart these two hypotheses. The results strongly support the tactile experience hypothesis, and provide no support for the visual deprivation hypothesis.

In the first study (Chapter 2), we compared the GOT performance of blind and sighted participants on the fingers and lips. We found, in agreement with the literature, that tactile spatial acuity on the fingers is better in blind than in sighted participants (Stevens et al., 1996; Grant et al., 2000; Van Boven et al., 2000; Goldreich & Kanics, 2003, 2006; Norman & Bartholomew, 2011). We found additionally that blind and sighted participants have equivalent acuity on the lips, a finding also reported by Stevens et al. (1996). The better acuity of blind than sighted participants on the fingers, but not lips (where tactile experience is presumably similar in the two participant groups), suggests tactile experience, rather than visual deprivation, drives tactile spatial acuity enhancement in the blind. In further support of the tactile experience hypothesis, we found that blind Braille readers' GOT performance correlated with their Braille reading style (e.g., one and two-index-finger readers) and frequency (i.e., weekly reading duration).

In two follow-up studies, we further investigated the effects of visual deprivation and tactile experience by visually depriving sighted participants in one study (Chapter 3) and training sighted participants on a tactile task in the other study (Chapter 4). In Chapter 3, we found in three experiments that sighted participants' GOT performance did not improve with visual deprivation periods spanning from under 10 minutes to over 110 minutes. We found in Experiment 1 that participants' performance was worse when tested in pitch darkness than when tested in the light. In two follow-up experiments in which we extended the visual deprivation periods to 70 (Experiment 2) and 110 minutes (Experiment 3), we again observed no improvement in participants' performance with visual deprivation: the participants' performance remained relatively stable across the testing sessions, irrespective of whether the participants experienced visual deprivation.

Having observed no effect of visual deprivation in the previous two studies (Chapters 2 and 3), we next investigated the effects of tactile experience further. In Chapter 4, we found that training sighted participants to discriminate the orientation of gratings for four days led to a substantial improvement in their GOT performance. The results of Chapter 4 thus provide direct evidence that tactile experience can drive tactile spatial acuity enhancement.

5.2 Possible neural mechanisms mediating tactile spatial acuity enhancement

5.2.1 Somatosensory cortical plasticity

Our results suggest that tactile experience drives tactile spatial acuity enhancement in the blind, but what neural mechanisms might mediate this enhancement? One possibility is the expansion of the primary somatosensory cortical representation (of the trained body part) in parietal cortex that has been shown to accompany tactile experience (somatosensory cortical plasticity). In a seminal paper, Jenkins, Merzenich, Ochs, Allard, & Guíc-Robles (1990) trained monkeys to place their fingers atop a rotating drum that consisted of alternating grooves and ridges to obtain a food reward: the monkeys were free to repeat this task for as many trials as they wished for 10 days. After these 10 days, the areas representing the stimulated fingers in primary somatosensory cortical area 3b were found to increase in size, relative to the pre-stimulation area 3b representations, with the greatest increase observed in the most-stimulated finger. Similar findings have been reported in follow-up studies: Recanzone, Merzenich, Jenkins, Grajski, and Dinse (1992) reported that monkeys who were trained on a frequency-discrimination task showed enlargements of the area 3b representation for the skin site that was stimulated in that task; and Xerri and colleagues reported that, in monkeys, there were expansions of the area 3b representations of the fingers that were used extensively to pick up food pellets from a narrow dish (Xerri, Coq, Merzenich, & Jenkins, 1996; Xerri, Merzenich, Jenkins, & Santucci, 1999).

At least three studies, perhaps motivated by the non-human primate studies by Merzenich and colleagues (Jenkins et al., 1990; Recanzone et al., 1992; Xerri et al., 1996, 1999), have observed similar results in humans. Using a combination of electroencephalography (EEG) and transcranial magnetic stimulation (TMS), Pascual-Leone & Torres (1993) reported that the representation of the Braille reading index finger in primary somatosensory cortex (S1) of blind participants was larger than the homologous non-reading finger on the opposite hand. Two other studies, using magnetoencephalography (MEG), have reported similar results. Sterr et al. (1998), in addition to reporting enlargements of the Braille reading finger representations in S1 among blind Braille readers, reported that blind Braille readers who read Braille with more fingers also have a greater area of S1 representing the fingers of the Braille reading hand. Elbert, Pantev, Wienbruch, Rockstroh, and Taub (1995) reported further, in general agreement with the blind studies, that in musicians the representations of the fingers that are used frequently during string instrument playing are enlarged relative to the representations of the fingers of non-musicians.

An obvious question then is: does an enlarged cortical representation give rise to enhanced perceptual abilities for that body part? Evidence from several studies suggests this may be the case. Recanzone et al. (1992) who trained monkeys on a frequency-discrimination task found that monkeys that improved the most on this task also had the greatest area 3b representation for the trained skin site. Similar results have been reported in human studies. Duncan & Boynton (2007) found that the performance of participants on a Braille-like dot discrimination task worsened progressively from the index finger to the little finger. Correspondingly, the S1 representational sizes, as measured with fMRI, decreased in size from the index finger to the little finger. Although it could be argued that these findings simply reflect a difference in receptor density at the fingers, it must be noted that receptor density, at least of the Meissner's corpuscles, has been shown to be similar across the fingers (Dillon, Haynes, & Henneberg, 2001). Additionally, Hodzic, Veit, Karim, Erb, and Godde (2004) reported that participants whose index finger was stimulated by a probe for several hours displayed both an increase in the S1 representational size (as revealed by fMRI) and an improvement in GOT performance on the stimulated finger.

5.2.2 Cross-modal cortical plasticity

In addition to somatosensory cortical plasticity, another fascinating change has been observed in the brain of blind participants: the occipital cortex, which normally processes visual inputs in the sighted, becomes responsive to nonvisual (e.g., tactile) inputs in the blind (cross-modal plasticity). Cross-modal plasticity has been speculated to drive tactile spatial acuity enhancement in blind participants. Wanet-Defalque et al. (1988) were perhaps the first to observe cross-modal plasticity in humans; using PET, they showed that the occipital cortex of blind participants exhibited greater metabolic activity during non-visual tasks than the occipital cortex of sighted participants. Many other studies have since shown similar results, reporting that areas that are normally visual in sighted participants are responsive to non-visual inputs in blind participants (e.g., Burton et al., 2002; Gizewski et al., 2003; Ptito et al., 2005; Sadato et al., 1996, 1998, 2002, 2004). More recently, this phenomenon has been observed in sighted participants who underwent short-term visual deprivation (Merabet et al., 2007, 2008). Although investigated to a lesser extent than in humans, cross-modal plasticity has also been observed in several animal species (blinded by enucleation, often at birth), including: monkeys (Hyvärinen, Carlson, & Hyvärinen, 1981), hamsters (Izraeli et al., 2002), short-tailed opossums (Kahn & Krubitzer, 2002), and rats (Piché et al., 2007). In these studies, neurons located in areas that are normally visual (e.g., primary visual cortex) in sighted animals were reported to respond to non-visual inputs in blind animals.

Some studies have provided evidence that cross-modal plasticity is functional; that is, the occipital cortex of blind participants might be involved in non-visual processing. These studies have shown that disruption of the occipital cortex impairs normal tactile processing in blind individuals. In a case study, a blind woman was reported to have lost her ability to read Braille after suffering a bilateral stroke to the occipital cortex (Hamilton et al., 2000). Moreover, several studies have shown that TMS applied to the occipital cortex of blind, but not sighted, participants impairs their ability to identify embossed Roman characters and to read Braille (Cohen et al., 1997, 1999; Kupers et al., 2007). More recently, Merabet et al. (2008) showed that TMS applied to the visual cortex of sighted participants who were visually deprived for five days (and whose occipital cortex was observed to respond to tactile stimuli) impaired their performance on a Braille character discrimination task. These studies therefore suggest a functional role for the occipital cortex of blind participants in tactile processing.

At first glance, the possibility that cross-modal plasticity mediates tactile spatial acuity enhancement in the blind seems contradictory given the results of our studies, which suggest tactile experience rather than visual deprivation drives tactile spatial acuity enhancement in the blind; this is especially the case when considering the emergence of cross-modal plasticity, according to many studies, requires visual deprivation. Interestingly, however, some recent evidence suggests cross-modal plasticity requires and is possibly influenced by tactile experience. Ptito and colleagues showed that stimulating the tongue did not elicit occipital cortical activation (Ptito et al., 2005), nor did TMS applied to the occipital cortex induce sensations in the tongue (Kupers et al., 2006), in blind participants until after they were trained to use a vision (to tongue) substitution device. Cross-modal plasticity seems not only to require tactile experience, but also to be influenced by it. Burton et al. (2002) observed using fMRI that cross-modal plasticity among a group of early blind Braille readers was greater in the hemisphere contralateral than ipsilateral to the Braille reading hand. Additionally, Ptito et al. (2008) showed that the number of occipital cortical sites that when stimulated with TMS elicited sensations in the fingers correlated with blind participants' Braille reading skill and frequency. More remarkably, Saito, Okada, Honda, Yonekura, and Sadato (2006) showed that visual deprivation might not be required to induce cross-modal plasticity if the participant has extensive tactile experience. In a fMRI study, they showed that V1 was activated among a group of sighted expert, but not naïve, Mah-Jong[3] players (who could normally identify

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[3] A game with a set of tiles that are engraved with symbols and Chinese characters.

Mah-Jong tiles by touch) when they tactilely discriminated either Mah-Jong tiles or Braille characters.

5.3 Future directions

5.3.1 Unresolved question

Although our studies suggest tactile experience, but not visual deprivation, drives tactile spatial acuity enhancement in the blind, our conclusion stands in contrast to some results in the literature. For instance, Kauffman et al. (2002) reported that five days of blindfolding led to a significant improvement in sighted participants' ability to discriminate Braille characters with the index finger, a finding that appears to support the visual deprivation hypothesis. However, an alternative explanation for this finding is that the improvement in index finger performance was simply a result of an increased reliance on the fingers during the five-day visual deprivation period; that is, when visually deprived, participants have no choice but to rely on the other non-deprived sensory modalities for everyday activities. In fact, the authors of that study reported that the blindfolded participants used "their sense of touch extensively during activities of daily living, such as washing themselves, eating, operating their radio, telling time, etc." (Kauffman et al., 2002, p. 572). This alternative explanation of Kauffman et al.'s (2002) data explains a puzzling result from their study quite well; that is, among a group of visually deprived participants (who did not undergo tactile training) only the right (but not left) index finger improved with visual deprivation, perhaps because these participants were all strongly right-handed and relied on this hand to a greater degree than the left hand during the visual deprivation period.

That being said, the findings from an earlier literature suggest that visual deprivation of sighted participants for ≥ 2 days can drive tactile acuity enhancement, even on body parts where it seems unlikely that reliance would increase with visual deprivation (e.g., forehead, upper arm) (see Doane et al., 1959). It must be noted, however, that the early studies used outdated psychophysics tasks, such as the two-point discrimination task, which as described in chapter 1 (section 1.4) is not without problems, particularly as a measure of tactile spatial acuity. The problems with the tasks used in these early studies perhaps explain the variability in reported improvements with visual (and/or multisensory) deprivation; for example, while Doane and colleagues (1959) found that 2-3 days of visual deprivation improved sighted participants' performance on a two-point discrimination task on the forehead and upper arm, they did not find that the same participants improved (on the same task) on the index finger or forearm.

The effect of long-term visual deprivation (i.e., days) on tactile spatial acuity therefore requires further investigation. To address the aforementioned concerns, it would be necessary to use a modern psychophysics test of tactile spatial acuity (e.g., GOT), testing visually deprived sighted participants before and after several days of visual deprivation on a body part such as the lips or forearm, where reliance would not be expected to increase with visual deprivation. Such studies would reveal whether visual deprivation alone without tactile experience improves tactile spatial acuity.

5.3.2 Tactile experience and cross-modal plasticity

If tactile experience is required to drive cross-modal plasticity, why has this gone largely unnoticed in the literature? One possibility is that the majority of studies investigating cross-modal plasticity in blind participants have done so on the fingertips, where tactile reliance is already quite high. Because very few studies have shown that cross-modal plasticity requires tactile experience (e.g., Ptito et al., 2005), this question requires further investigation. More studies are needed to test, as done by Ptito et al. (2005), whether stimulating a body part that normally receives little tactile experience (e.g., tongue, lips) in blind participants elicits occipital cortical activation (without training).

Assuming tactile experience is required to drive cross-modal plasticity, it would be interesting to investigate how much tactile experience is necessary for cross-modal plasticity to emerge. Saito et al. (2006) observed cross-modal plasticity in non-visually deprived sighted Mah-Jong experts who had many years of experience identifying Mah-Jong tiles by touch. This finding raises the question: are many years of tactile experience required to drive cross-modal plasticity? Interestingly, two studies have observed cross-modal plasticity in visually deprived participants after only a few days of training. Ptito et al. (2005) observed cross-modal plasticity in blind participants who were trained for seven days to use a tactile device on the tongue, and Merabet et al. (2008) observed cross-modal plasticity in a group of sighted participants who were visually deprived and who received intensive tactile training for five days. However, it is unclear whether the few days of tactile training received by those participants would have been sufficient to drive cross-modal plasticity if they had not also been visually deprived; that is, visual deprivation might have facilitated the rate at which cross-modal plasticity was acquired. To address this question, it would be necessary to train non-visually deprived participants intensively for a few days (as in Chapter 4) and subsequently observe whether their occipital cortex responds to tactile inputs.

5.4 Conclusion

The results from the three studies presented in this thesis suggest that the tactile spatial acuity enhancement of blind participants is driven by their increased reliance on the sense of touch. Two likely candidates mediating this enhancement are somatosensory and cross-modal cortical plasticity. Future studies are required to elucidate what role, if any, visual deprivation, alone and when coupled with tactile experience, has on tactile spatial acuity.

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