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

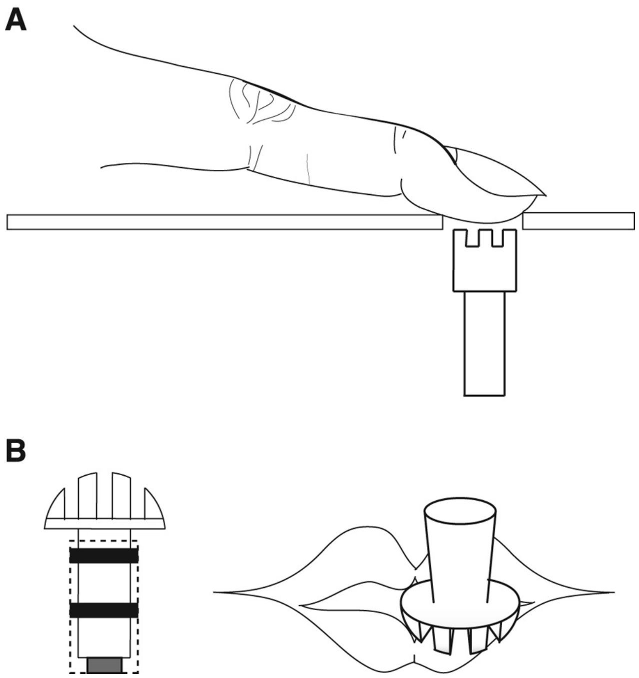

Figure 1. Grating orientation task. ***A***, Finger testing. A computer-controlled rod rotated to press the selected stimulus surface against the fingertip with 50 g of force. The gratings are shown aligned horizontally. ***B***, Lip testing. JVP Domes were held within a plastic tube (dotted rectangle). 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.

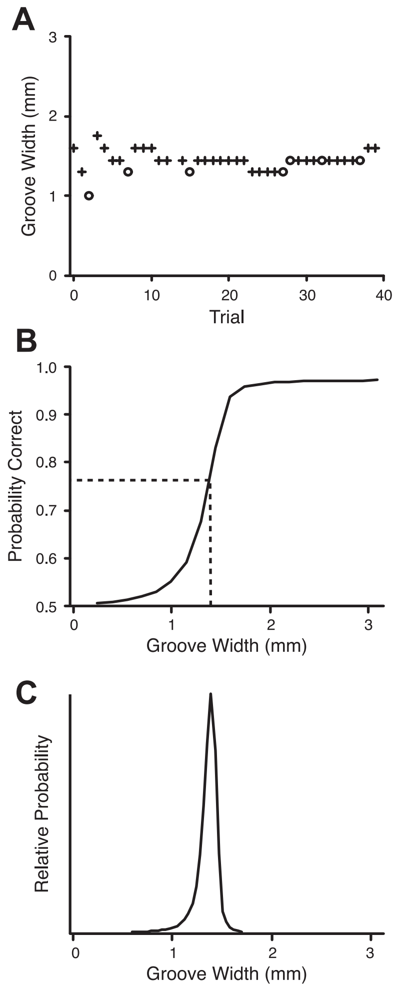

Figure 2. Adaptive psychophysical procedure. ***A***, Correct (+) and incorrect (o) answers of a 30-year-old sighted male tested on the right middle finger. ***B***, Best estimate of the participant's psychometric function. ***C***, Bayesian posterior probability distribution for the participant's 76%-correct 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:

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

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.

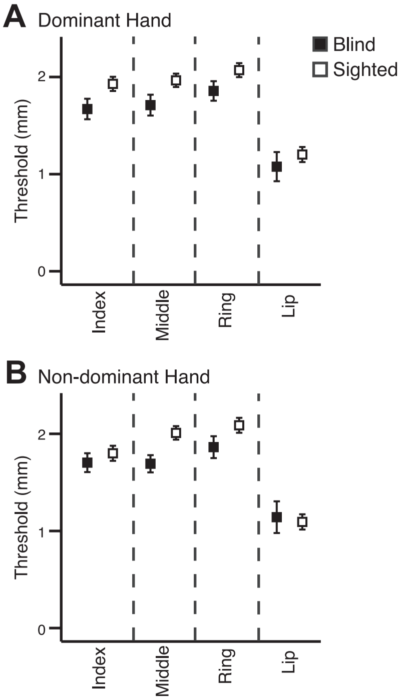

Figure 3. GOT thresholds of blind and sighted participants on fingers and lip. ***A***, Dominant hand and side of lip corresponding to dominant hand. ***B***, Nondominant hand and side of lip corresponding to nondominant hand. Threshold values for all participants were adjusted to those of a sex-neutral 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 × 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

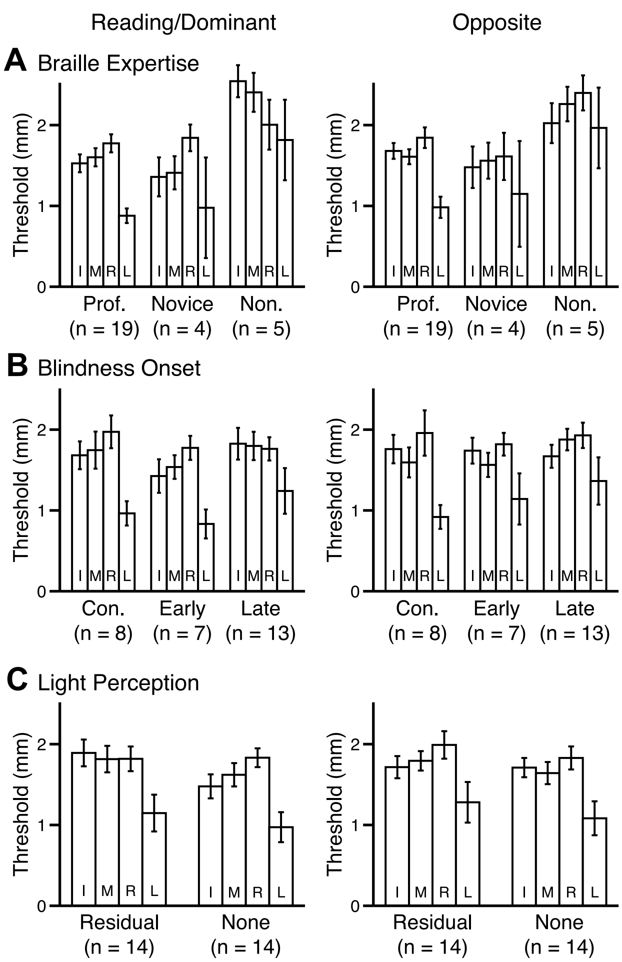

Figure 4. Effects among blind participants of blindness characteristics. ***A***, Braille expertise [proficient (Prof.), novice, nonreader (Non.)]. ***B***, blindness onset [congenital (Con.), early, late]. ***C***, Light perception (residual, none). Left, Preferred reading or dominant hand; right, opposite 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).

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

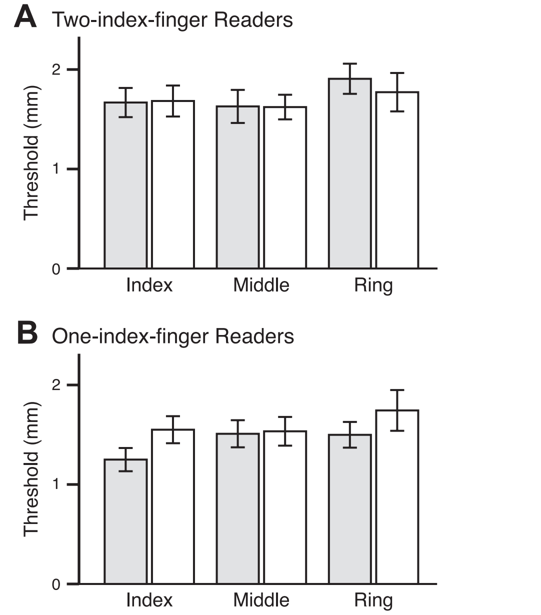

Figure 5. GOT thresholds of proficient Braille readers on all six fingers. ***A***, Two-index-finger readers ($n = 10$). ***B***, One-index-finger readers ($n = 9$). Gray bars, Mean threshold of each finger on the preferred reading hand; white bars, mean threshold of each finger on the opposite hand.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

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)

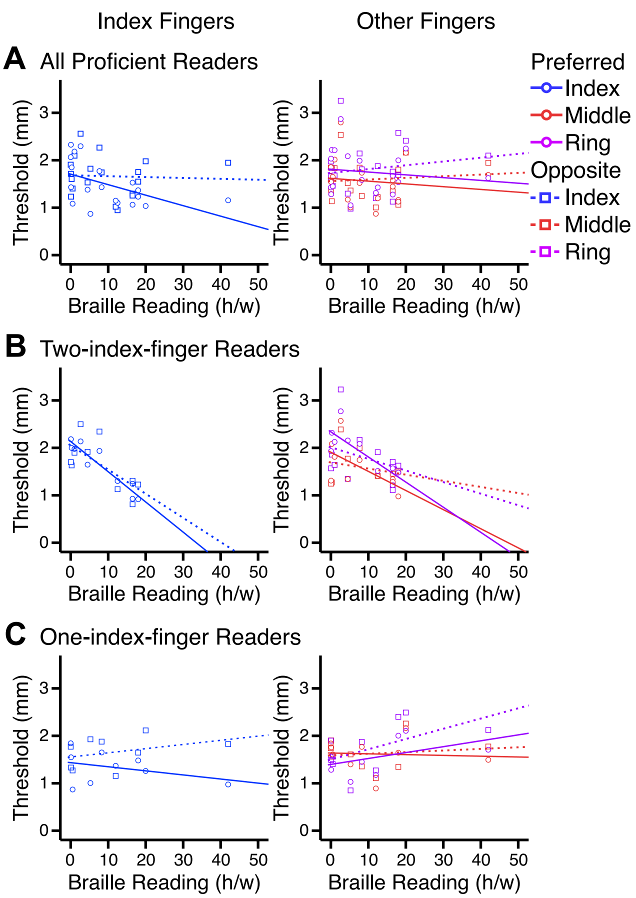

Figure 6. GOT thresholds of proficient Braille readers versus Braille reading hours per week (h/w). ***A***, All proficient readers ($n = 19$). ***B***, Those who read with both index fingers ($n = 10$). ***C***, Those who read with a single index finger ($n = 9$). Circles, Fingers on preferred reading 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.

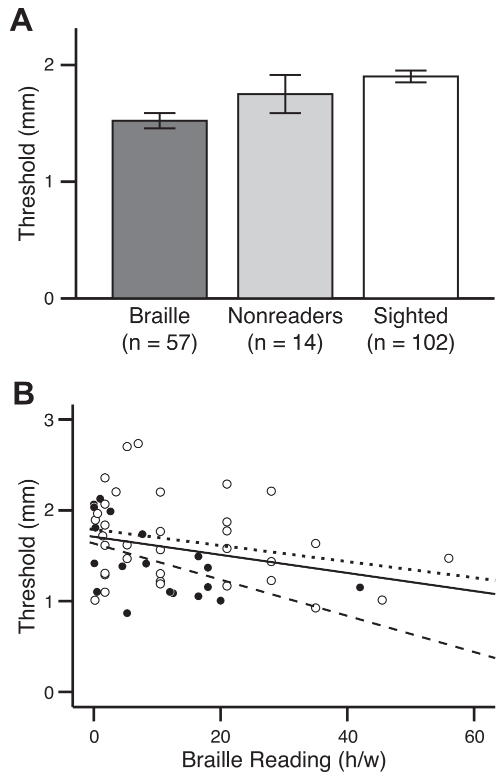

Figure 7. Index finger GOT thresholds of participants from the current study and from Goldreich and Kanics (2003). ***A***, Blind Braille readers, blind nonreaders, and sighted participants' thresholds combined across the two studies. Thresholds for Braille readers are from the preferred reading index 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.

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*).

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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