

## Behavioral manifestations of brain plasticity in blind and low-vision individuals

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Tactile sensitivity enhancement (TSE) observed in blind people is probably a result of intensified tactile training. Although many researchers consider TSE in the blind to be an example of use-dependent plasticity, it is unclear whether the effects of training (Braille reading) are specific, i.e. restricted to the trained function and hand, or if they are more general. To examine this issue further, blind Braille readers, low-vision subjects (Braille readers and non-Braille readers) and sighted controls were tested in two tasks: a texture task resembling the Braille system and a dissimilar groove orientation task. Braille readers, both blind and those with low vision, performed better in both tasks than low-vision non-Braille readers or sighted controls. However, the difference was significant only for the blind (more experienced) Braille readers. In the groove orientation task, the positive influence of training was detectable irrespective of the hand used in the test, but in the coarse texture task this influence was limited to the hand trained in Braille. Thus, it appears that tactile training is of significance in TSE but its effects are, to a large extent, task- and hand-specific.

Key words: tactile acuity, visual deprivation, training, Braille

### INTRODUCTION

Both intramodal and cross-modal brain plasticity effects have been recognized in blind people. Functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) studies have demonstrated cortical reorganization in the somato-sensory and motor cortices in blind individuals, whereby the representation of the fingers involved in Braille reading expands relative to the so-called non-reading fingers (Pascual-Leone and Torres 1993, Hamilton and Pascual-Leone 1998, Sterr et al. 1998, Theoret et al. 2004). Moreover, it has been found that the occipital cortical areas – which in sighted people are implicated in visual perception – are recruited and used in congenitally and early blind individuals during auditory (Kujala et al. 1992, 2005, De Volder et al. 1999, Leclerc et al.

2000, Weeks et al. 2000, Röder et al. 2002) and tactile discrimination tasks (Uhl et al. 1991, 1993, Sadato et al. 1996, 1998, Büchel et al. 1998). Interestingly, activation of these regions was found to be functionally relevant for Braille reading (Cohen et al. 1997, Hamilton and Pascual-Leone 1998, Hamilton et al. 2000, Burton et al. 2002).

Some authors believe that these plastic changes may lead to certain behavioral effects. Although it remains a controversial issue (Grant et al. 2000, Collignon et al. 2006), quite a number of investigations have revealed that blind Braille readers perform better than sighted controls in various tasks involving tactile discrimination, suggesting an enhanced tactile sensitivity in these individuals (Stevens et al. 1996, Van Boven et al. 2000, Goldreich and Kanics 2003). However, the precise mechanisms underlying the behavioral superiority of blind individuals are not fully understood (Hummel et al. 2004). Another unresolved issue relates to which specific tactile functions are improved. Previous studies examining haptic abilities in the blind have yielded mixed

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Received 13 November 2007, accepted 8 January 2008

results. Different and not always precise tests have been used to measure tactile sensitivity. Some were based on a rather subjective assessment of coarseness or separation of raised dots on a scale of 1 to 10 (Merabet et al. 2004), while others used grating orientation tasks in which only two orthogonal directions of grating were applied: along or perpendicular to the long axis of the finger (Craig 1999).

A number of these studies revealed enhanced tactile skills in blind people (Van Boven et al. 2000, Goldreich and Kanics 2003); however, others did not (Grant et al. 2000, Collignon et al. 2006). Furthermore, there have been studies which showed that visual deprivation per se leads to superior tactile acuity (Kaufman et al. 2002, Goldreich and Kanics 2003, Facchini and Aglioti 2003, Sadato 2005), and others claiming that this skill could be developed by training (Büchel et al. 1998, see Zeuner et al. 2002, for enhancement of tactile acuity in dystonic patients). Interestingly, in the majority of studies, the positive significant influence of training was limited to the trained (reading) finger. However, it is not entirely clear whether such an effect is specific, i.e. if it is only the trained function that improves, or whether other tactile functions such as tactile discrimination skills (like estimating orientation or texture) improve as well. It is also uncertain whether enhanced tactile skills in the blind can be ascribed solely to visual deprivation and spontaneous brain plasticity occurring independently of specific haptic training (Braille reading), or if they are specifically influenced by Braille reading practice.

The present study included four groups of subjects who differed in their degree of visual deprivation and in Braille reading training: blind Braille readers, low-vision Braille readers, low-vision non-Braille readers and sighted controls. Testing both low-vision Braille readers and non-Braille readers allowed us to make inferences about the possible effects of tactile training (Braille reading). Participation of low-vision subjects in addition to blind and sighted people made it possible to examine whether the degree of visual deprivation influences the enhancement of tactile sensitivity. All Braille readers examined read Braille in the following way: right index finger leads left index finger along the lines of text and the left index finger “reads” the characters. This technique gives rise to another difference: general training resulting from visual deprivation involves both hands, where-

as Braille reading is based predominantly on tactile information coming from the left hand. Thus, we wanted to test whether the effects of training (Braille reading) are specific, i.e. restricted to the trained function and hand, or if they are more general.

Two tasks were designed to measure tactile sensitivity: a coarse texture task resembling the Braille system, and a groove orientation task that is dissimilar to the Braille alphabet. In both tasks, a simple criterion for assessing stimuli discrimination was used: the subjects were asked to assess whether two stimuli were the same or different depending on texture coarseness or groove orientation. We predicted that in the coarse texture task, similar to the Braille system, tactile sensitivity would be enhanced in the Braille reading groups, especially when using the trained left hand. In the groove orientation task, which is more connected to shape discrimination and is dissimilar to Braille reading, tactile sensitivity ought to be heightened in both hands for all visually deprived groups, since they depend more on tactile modality in everyday activities, and this effect should be most pronounced in the blind group.

## METHODS

### Subjects

Fifty-four subjects were studied: 14 blind subjects, all of whom were Braille readers (group 1); 14 Braille-reading low-vision subjects (group 2); 12 non-Braille reading low-vision subjects (group 3); and 14 sighted control subjects (group 4). All participants gave their informed consent prior to the testing. The blind group consisted of eight men and six women, with a mean age of 29 (age range 18 to 53) in whom the onset of blindness had occurred before the age of 4. None of the blind subjects had any residual light perception (for further details see Table I). The subjects began reading Braille at a mean age of 7 (range 6 to 9 years). Braille reading averaged 1.5 hours per day (range 30 minutes to 4 hours). The group of Braille-reading low-vision subjects consisted of seven men and seven women, with a mean age of 35 (age range 18 to 53). The subjects began reading Braille at a mean age of 12 (range 7 to 19 years). Braille reading averaged 0.7 hours per day (range 0 to 3 hours). The group of non-Braille reading low-vision subjects consisted of five men and seven women with

Table I

Blind Braille reading subjects participating in the study				
Patient	Age	Sex	Handness	Visual impairment
1	38	M	R	retinopathy of prematurity
2	30	M	R	retinal blastoma
3	40	M	R	retinal blastoma
4	53	M	R	mechanical injury of eyeballs
5	18	M	R	retinal blastoma
6	19	M	R	optic nerve damage
7	18	M	R	retinopathy of prematurity
8	27	M	R	genetic defect
9	23	F	R	retinal blastoma
10	50	F	R	optic nerve damage due to incubation
11	32	F	R	congenital glaucoma
12	20	F	R	corneal atrophy, eyeballs hypoplasia
13	19	F	R	lenticular adhesions
14	21	F	R	genetic defect

a mean age of 29 (age range 18 to 52). The low-vision subjects from groups 2 and 3 had visual acuity between 20/70 and 20/400 with the best possible correction, and/or a visual field of 20 degrees or less (for further details see Tables II and III). Low-vision subjects retained only partial sight, or sight that was not

fully correctable with surgery, pharmaceuticals, contact lenses or glasses. This resulted in a loss of sharpness or acuity, and sometimes also loss of field of vision, light sensitivity, distorted vision or loss of contrast. Low-vision subjects developed amblyopia during the early years of life. None of the visually impaired subjects had any neurological problems. The sighted control group consisted of seven men and seven women with a mean age of 30 (age range 23 to 60). None of this group was familiar with Braille. All had (corrected or uncorrected) 20/20 vision and a normal neurological and medical condition on examination. All of the 54 participants were right-hand dominant as assessed by the Edinburgh Handedness Inventory (Oldfield 1971), and all had completed secondary education (IQ of the subjects was not tested).

### Materials and procedure

The study consisted of two tasks in which subjects assessed texture coarseness and groove orientation. The subjects were seated in a quiet room, given their instructions, blindfolded if sighted or low-vision, and then tested. The testing session lasted approximately one hour. Subjects were requested to complete the tasks using their index finger. The hand with which the subjects performed the separate trials within the tasks as well as the order of the tasks were alternated and balanced across all subjects.

Table II

Low vision Braille reading subjects participating in the study				
Patient	Age	Sex	Handness	Visual impairment
1	18	M	R	retinopathy – light perception, ability to discriminate shapes
2	53	M	R	congenital glaucoma in both eyes
3	47	M	R	light perception, ability to discriminate shapes and colours
4	56	M	R	1 eye only light perception, myopia (−2.0) in the other
5	19	M	R	retinopathy – light perception, ability to discriminate shapes
6	28	M	R	congenital cataract, nystagmus
7	47	M	R	light perception, ability to discriminate shapes
8	36	F	R	light perception, ability to discriminate shapes
9	22	F	R	blindness of one eye, hyperopia (+6.0) in the other
10	20	F	R	blindness of one eye, optic atrophy
11	23	F	R	blindness of one eye, optic atrophy
12	53	F	R	myopia (−4.0; −4.5), daltonism, astigmatism
13	27	F	R	congenital optic nerve damage after toxoplasmosis
14	46	F	R	myopia (−30.0) in both eyes, retinal degeneration

Table III

Low vision non-Braille reading subjects participating in the study				
Patient	Age	Sex	Handness	Visual impairment
1	27	M	R	blindness of one eye, hyperopia (+6.5), cataract in both eyes
2	52	M	R	myopia (−16.0) in both eyes
3	44	M	R	blindness of one eye, 75% loss of sight in the other
4	18	M	R	congenital glaucoma in both eyes
5	22	M	R	congenital optic nerve damage
6	47	F	R	myopia (−11.0; −13.0), astigmatism
7	36	F	R	96% loss of sight in 1 eye and 76% in the other after toxoplasmosis
8	20	F	R	myopia (−17.0; −18.0)
9	19	F	R	retinal anaemia, blurred picture
10	20	F	R	blindness of one eye, congenital retinal defect in the other eye
11	19	F	R	macular atrophy, myopia (−9.0; −11.0), optic atrophy, astigmatism
12	28	F	R	detached retina

### Coarse texture task

In the first task, a set of 12 wooden cylindrical rods of diameter 15 mm with sandpaper glued to their upper curved surface was used in order to assess tactile sensitivity. The sandpapers differed in texture. Rods were arranged in pairs in such a way that each of the three rods with sandpaper coarseness 320, 400, and 500 was matched up with one rod with the same sandpaper coarseness (i.e. 320 and 320; 400 and 400; 500 and 500) and with one rod with a different sandpaper coarseness (i.e. 320 and 360; 400 and 600; 500 and 800). In this way six pairs were obtained. Each pair was attached to a small pad to prevent movement of the rods. These configurations were chosen on the basis of the results of a pilot study conducted as preparation for this project. The “coarse texture task” required subjects to estimate, using their index finger, whether or not the upper surfaces of two cylindrical rods in a pair had the same texture. There were five trials for each of the six pairs. Participants were instructed to study one rod for 2 seconds and then move to the other and study it for 2 seconds. This sequence was repeated until they made a decision: “the same” or “different”. Pairs for each trial were selected randomly. Each subject was presented with an equal number of comparisons varying in the level of difficulty. Both errors and correct answers were counted.

### Groove orientation task

The second task used a set of wooden cylindrical rods of diameter 15 mm with a 1 mm wide groove cut into the curved upper surface of each at the center. Groove depth was sufficient to prevent the skin from contacting the bottom of the groove. Rods were arranged in pairs in such a way that one of them with the groove cut at an angle of 22.5° was matched with either a rod with a groove cut at the same angle (22.5°) or with a rod with the groove at a different angle (10.5°, 14.5°, 18.5°, 26.5°, 30.5°, 34.5°). In this way seven pairs were obtained. As in the first task, each pair was attached to a small pad with a distance of 15 mm between the two rods. The difference between the angles of two paired rods ranged from 4 to 12 degrees. These configurations were chosen on the basis of the results of a pilot study. The “groove orientation task” consisted of the subject assessing whether or not the grooves present in the upper surfaces of two paired cylindrical rods were at the same angle. There were six trials for each of the seven pairs: 3 trials in which a rod with the groove cut at an angle of 22.5° was placed on the right side, and 3 trials in which this rod was placed on the left side. Participants were instructed to study one rod for 2 seconds and then study the other for 2 seconds. This sequence was repeated until they made a decision: “the same” or “different”. Pairs for each trial were selected randomly. Each subject was presented with an equal number of comparisons varying in difficulty level. Errors and correct answers were counted.

## RESULTS

To test our hypotheses we performed two-way ANOVA for each task with repeated measurement of “group” and “hand”. The dependent variable was the percentage of correct answers. *Post-hoc* comparisons were made using pairwise *t*-tests with the Bonferroni correction.

### Coarse texture task

Two-factorial analysis of variance with repeated measures revealed a significant effect of “group” ( $F_{3,11}=5.02$ ,  $P=0.02$ ). The notion that tactile sensitivity would be enhanced in Braille reading groups especially when using the left hand was confirmed by the results of pairwise comparisons (Fig. 1), which showed some differences between the groups only when using the left hand. Low vision non-Braille readers differed significantly from both blind and low-vision Braille readers ( $P=0.01$  and  $P=0.006$ , respectively). Braille readers performed significantly better. Blind Braille readers also had higher accuracy than sighted controls at a trend level of significance ( $P=0.072$ ). The factor “hand” and the interaction of “group”  $\times$  “hand” were not significant since differences between the groups also had the same pattern for the right hand, although they were not significant.

In addition, correlation coefficients were calculated between the average performance of the task and the following variables: the average amount of time spent on daily Braille reading ( $r=0.077$ ); the age at which subjects began reading Braille ( $r=-0.098$ ); and the age of subjects ( $r=0.135$ ). None of these correlations was statistically significant.

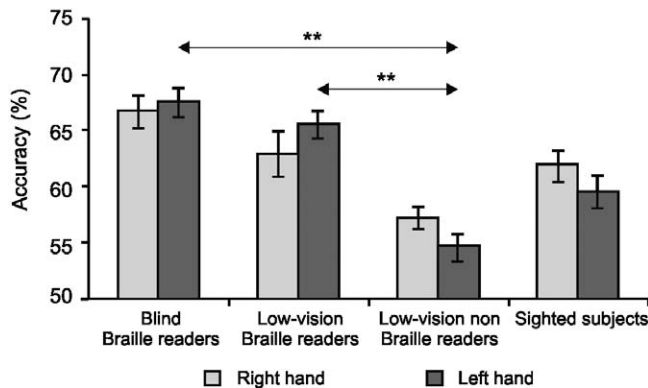


Fig. 1. Performance in the coarse texture (Braille related) task. Bars represent SEM. \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ .

### Groove orientation task

Two-factorial analysis of variance with repeated measures revealed a significant effect of “group” ( $F_{3,11}=3.890$ ,  $P=0.05$ ). Pairwise comparisons revealed that in the case of trials using the right hand (Fig. 2), low-vision non-Braille readers performed significantly worse than every other group: blind Braille readers ( $P=0.005$ ), low vision Braille readers ( $P=0.01$ ) and sighted controls ( $P=0.015$ ). Similar analysis for the left hand revealed that blind Braille readers performed better than both low-vision non-Braille readers ( $P=0.024$ ) and sighted controls ( $P=0.001$ ). Blind Braille readers also showed slightly higher accuracy than low-vision Braille readers, but this effect was only marginally significant ( $P=0.085$ ).

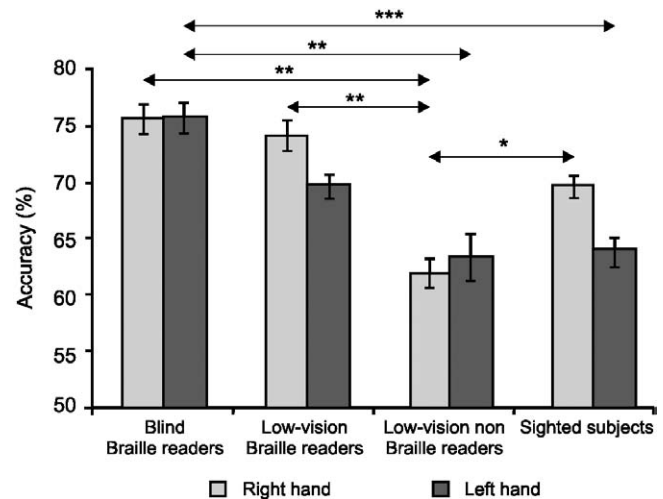


Fig. 2. Performance in the groove orientation (no-Braille related) task. Bars represent SEM. \* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ .

## DISCUSSION

In this study, we aimed to disentangle the influence of haptic training like Braille reading from cortical reorganization occurring in visually-deprived people due to spontaneous brain plasticity. If the enhanced tactile sensitivity of the blind does indeed result from training, it is important to know whether its effect is specific to the trained hand and task. The coarse texture task used here resembles the system of raised dots that constitutes the Braille alphabet (Millar 1985), whereas the groove orientation task is more a test of spatial orientation and shape discrimination skills. It



might therefore be anticipated that specific training by Braille reading should induce more apparent tactile sensitivity enhancement (TSE) that facilitates the coarse texture task rather than the groove orientation task. In addition, since the subjects were taught to use their left hand for Braille character identification, the effect of training should mainly benefit left hand performance.

As anticipated, the Braille reading groups (blind and low-vision) showed the greatest accuracy of all the studied groups in the coarse texture task. Also as predicted, these differences were significant only when using the left hand (trained in Braille reading). Thus, our results indicate that in the case of a task that is similar to Braille reading (coarse texture task) enhanced performance is limited to the trained hand (finger). Notably, blind Braille readers not only performed better than sighted controls, they also outperformed low-vision non-Braille readers. This result suggests that enhancement of tactile sensitivity also depends on the degree of visual deprivation and would explain why a previous study (Goldreich and Kanics 2003) found no significant effect of the degree of childhood vision or residual light perception level on tactile acuity. Nevertheless, we cannot exclude the possibility that the two groups (blind and low-vision Braille readers) differed not only in their visual abilities but also in their Braille reading training. The low-vision Braille readers learned to read Braille at school where it was compulsory, but did not treat it as a necessity. Most members of this group reported that they now seldom read Braille despite previous acquisition of this ability. Some said that they did not wish to be tagged as “blind” or “impaired” and tried to rely on their residual vision in everyday life. Consequently, it may be concluded that low-vision Braille readers did not have as much tactile training as blind Braille readers, which might explain why their performance was not significantly better than that of sighted controls.

As far as hand specificity is concerned, many previous studies support the view that the effect of tactile training like Braille reading is relatively position-specific and not readily transferable to other sites or fingers (Semenza et al. 1996, Van Boven et al. 2000). The study of Van Boven and coauthors (2000) which showed heightened abilities in tactile spatial acuity in a grating orientation task in the blind compared to sighted controls, revealed that the subjects’ performance tended to be best using the finger dominantly

used for Braille character identification. Another study proved that blind subjects, who preferred using their right hand to read Braille, were better at detecting small differences in Braille notation, such as accents over Braille characters, with their right hand compared to their left (Semenza et al. 1996). Additional support comes from magnetic resonance studies which revealed enlargement of the representation of the finger used for Braille reading in the somatosensory cortex of blind individuals in comparison to sighted controls (Pascual-Leone and Torres 1993). In agreement with this finding, Sterr and coworkers (1998) who examined Braille readers using magnetic source imaging, discovered alterations in cortical topography and the enlargement of representation restricted to the fingers used for reading in comparison to sighted controls. Our study has shown that specific effects linked to usage and training of the hand used in Braille reading are transferable to TSE in tasks similar to the trained function.

With regard to the between-group comparisons in the groove orientation task, the pattern of results appears to be more complicated. We hypothesised that performance in this task should be related to general training resulting from visual deprivation and therefore the visually-deprived groups should demonstrate the highest accuracy irrespective of the hand used. There are good grounds to assume that the groove orientation task assesses functions which are employed in shape discrimination. In sighted subjects, discrimination of grating orientation and object recognition were found to be associated with activity in the same areas of the visual cortex (Zangaladze et al. 1999, Amedi et al. 2001, Pascual-Leone and Hamilton 2001, Pascual-Leone et al. 2005). In everyday life, blind people tend to use two hands for shape discrimination, which might explain their increased performance with both hands in the groove orientation task. In contrast, the sighted subjects, who were all right-handed, preferentially use their right hand in everyday manual activities thus providing this hand with greater tactile stimulation. In agreement with these differences in tactile experience between blind and sighted subjects, the blind differed significantly from the controls only in their left hand performance. Interestingly, they performed better than the low-vision non-Braille readers with both their left and right hands. This might suggest that the latter group could be considered as generally less active, which would be in line with the fact that they did not

take up Braille. They performed the worst of all the groups including the sighted controls. Similar and equally unexpected results were obtained by Lessard and colleagues (1998) when comparing sound source localization by early blind, low-vision and sighted subjects. Low-vision individuals were less accurate than all other subjects.

If indeed Braille training positively influences accuracy, one might expect a correlation between Braille reading experience and tactile sensitivity in the coarse texture task. However, there was no correlation between the performance in this task and the average daily amount of time spent on Braille reading or the age at which subjects began reading Braille. Possible reasons for such a result are the small number of subjects and the imprecise method of estimating Braille reading training, based on declarations of the participants. Similarly, Goldreich and Kanics (2006) also failed to find such a correlation.

It is interesting to consider whether the observed differences in tactile sensitivity between the studied groups are in agreement with present knowledge of the mechanisms of plastic reorganization in the visual cortex. Several researchers have hypothesized that compensation in blind subjects depends on the recruitment of the deafferented sensory areas which become unmasked from visual input (Jacobs and Donoghue 1991, Burton 2003). Hence, it could be argued that these areas would not show a similar amount of plasticity if they were still stimulated, albeit at a reduced rate, by their normal afferents, as is the case in low-vision individuals (Lessard et al. 1998). In line with this hypothesis, Lambertz and coworkers (2005) found that cortical reorganization of the auditory cortex comprising the primary auditory fields is only present in subjects with total hearing loss, whereas residual hearing ability seems to inhibit cross-modal plasticity related to sign language. However, our results revealed a great discrepancy between low-vision and blind subjects in tactile sensitivity. A neuroimaging study might clarify whether there are differences in plastic changes in the visual cortex in low-vision and blind subjects and the extent to which the cross-modal reorganization due to training is specific for the trained function.

## CONCLUSIONS

To our knowledge, the present study is the first on TSE in visually-impaired people that takes into con-

sideration the role of multiple factors including the degree of visual deprivation, the influence of tactile training (Braille reading) and specificity of its effects relating to the studied tactual task and the trained hand. Although our results leave a number of questions unanswered, they provide further evidence for the notion that training is of fundamental importance in TSE and that its effects are, to some extent, task- and hand-specific.

## REFERENCES

- Amedi A, Malach R, Hendler T, Peled S, Zohary E (2001) Visuo-haptic object-related activation in the ventral visual pathway. *Nat Neurosci* 3: 324–330.
- Büchel C, Price C, Frackowiak RSJ, Friston K (1998) Different activation patterns in the visual cortex of late and congenitally blind subjects. *Brain* 121: 409–419.
- Burton H, Snyder AZ, Conturo TE, Akbudak E, Ollinger JM, Raichle ME (2002) Adaptive changes in early and late blind: an fMRI study of Braille reading. *J Neurophysiol* 87: 589–607.
- Burton H (2003) Visual cortex activity in early and late blind people. *J Neurosci* 23: 4005–4011.
- Cohen LG, Celnik P, Pascual-Leone A, Corwell B, Falz L, Dambrosia J, Honda M, Sadato N, Gerloff C, Catala MD, Hallett M (1997) Functional relevance of cross-modal plasticity in blind humans. *Nature* 389: 180–183.
- Collignon O, Renier L, Bruyer R, Tranduy D, Veraart C (2006) Improved selective and divided spatial attention in early blind subjects. *Brain Res* 1075: 175–182.
- Craig JC (1999) Grating orientation task as a measure of tactile spatial acuity. *Somatos Mot Res* 16: 197–206.
- De Volder AG, Catalan-Ahumada M, Robert A, Bol A, Labar D, Coppens A, Michel C, Veraart C (1999) Changes in occipital cortex activity in early blind humans using a sensory substitution device. *Brain Res* 826: 128–134.
- Facchini S, Aglioti SM (2003) Short term light deprivation increases tactile spatial acuity in humans. *Neurology* 60: 1998–1999.
- Goldreich D, Kanics IM (2003) Tactile acuity is enhanced in blindness. *J Neurosci* 23: 3439–3452.
- Goldreich D, Kanics IM (2006) Performance of blind and sighted humans on a tactile grating detection task. *Percept Psychophys* 68: 1363–1371.
- Grant AC, Thiagarajah MC, Sathian K (2000) Tactile perception in blind Braille readers: a psychophysical study of acuity and hyperacuity using gratings and dot patterns. *Percept Psychophys* 62: 301–312.

- Hamilton R, Pascual-Leone A (1998) Cortical plasticity associated with Braille learning. *Trends Cogn Sci* 2: 168–174.
- Hamilton R, Keenan JP, Catala M, Pascual-Leone A (2000) Alexia for Braille following bilateral occipital stroke in an early blind woman. *Neuroreport* 11: 237–240.
- Hummel F, Gerloff C, Cohen LG (2004) Cross-modal plasticity and deafferentation. *Cogn Processing* 5: 152–158.
- Jacobs KM, Donoghue JP (1991) Reshaping the cortical motor map by unmasking latent intracortical connections. *Science* 251: 944–947.
- Kaufman T, Théoret H, Pascual-Leone A (2002) Braille character discrimination in blindfolded human subjects. *Neuroreport* 13: 571–574.
- Kujala T, Alho K, Paavilainen P, Summala H, Näätänen R (1992) Neural plasticity in processing of sound localization by the early blind: an event-related potential study. *Electroencephalogr Clin Neurophysiol* 84: 469–472.
- Kujala T, Palva MJ, Salonen O, Alku P, Huotilainen M, Jarvinen A, Näätänen R (2005) The role of blind humans' visual cortex in auditory change detection. *Neurosci Lett* 379: 127–131.
- Lambertz N, Gizewski ER, de Greiff A, Forsting M (2005) Cross-modal plasticity in deaf subjects dependent on the extent of hearing loss. *Cogn Brain Res* 25: 884–890.
- Leclerc C, Saint-Amour D, Lavoie ME, Lassonde M, Lepore F (2000) Brain functional reorganization in early blind humans revealed by auditory event-related potentials. *Neuroreport* 11: 545–550.
- Lessard N, Pare M, Lepore F, Lassonde M (1998) Early-blind human subjects localize sound sources better than sighted subjects. *Nature* 395: 278–280.
- Merabet L, Thut G, Murray B, Andrews J, Hsiao S, Pascual-Leone A (2004) Feeling by sight or seeing by touch? *Neuron* 42: 173–179.
- Millar S (1985) The perception of complex patterns by touch. *Perception* 14: 293–303.
- Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia* 9: 91–113.
- Pascual-Leone A, Torres F (1993) Plasticity of the sensorimotor cortex representation of the reading finger in Braille readers. *Brain* 116: 39–52.
- Pascual-Leone A, Hamilton RH (2001) The metamodal organization of the brain. *Prog Brain Res* 134: 427–445.
- Pascual-Leone A, Amedi A, Fregni F, Merabet LB (2005) The plastic human brain cortex. *Annu Rev Neurosci* 28: 337–401.
- Röder B, Stock O, Bien S, Neville H, Rösler F (2002) Speech processing activates visual cortex in congenitally blind humans. *Eur J Neurosci* 16: 930–936.
- Sadato N, Pascual-Leone A, Grafman J, Ibanez V, Deiber MP, Dold G, Hallett M (1996) Activation of the primary visual cortex by Braille reading in blind subjects. *Nature* 380: 526–528.
- Sadato N, Pascual-Leone A, Grafman J, Deiber MP, Ibanez V, Hallett M (1998) Neural networks for Braille reading by the blind. *Brain* 121: 1213–1229.
- Sadato N (2005) How the blind “see” Braille: lessons from functional magnetic resonance. *Neuroscientist* 11: 577–582.
- Semenza C, Zoppello M, Gidiuli O, Borgo F (1996) Dichaptic scanning of Braille letters by skilled blind readers: lateralization effects. *Percept Mot Skills* 82: 1071–1074.
- Sterr A, Müller MM, Elbert T, Rockstroh B, Pantev C, Taub E (1998) Perceptual correlates of changes in cortical representation of fingers in blind multifinger Braille readers. *J Neurosci* 18: 4417–4423.
- Stevens JC, Foulke E, Patterson MQ (1996) Tactile acuity, aging, and Braille reading in long-term blindness. *J Exp Psychology: Applied* 2: 91–106.
- Theoret H, Merabet L, Pascual-Leone A (2004) Behavioral and neuroplastic changes in the blind: evidence for functionally relevant cross-modal interactions. *J Physiol Paris* 98: 221–233.
- Uhl F, Franzen P, Lindinger G, Lang W, Deecke L (1991) On the functionality of the visually deprived occipital cortex in early blind persons. *Neurosci Lett* 124: 256–259.
- Uhl F, Franzen P, Podreka I, Steiner M, Deecke W (1993) Increased regional cerebral blood flow in inferior occipital cortex and cerebellum of early blind humans. *Neurosci Lett* 150: 162–164.
- Van Boven RW, Hamilton RH, Kauffman T, Keenan JP, Pascual-Leone A (2000) Tactile spatial resolution in blind Braille readers. *Neurology* 54: 2230–2236.
- Weeks R, Horwitz B, Aziz-Sultan A, Tian B, Wessinger M, Cohen LG, Hallett M, Rauschecker JP (2000) A positron emission tomographic study of auditory localization in the congenitally blind. *J Neurosci* 20: 2664–2672.
- Zangaladze A, Epstein CM, Grafton ST, Sathian K (1999) Involvement of visual cortex in tactile discrimination of orientation. *Nature* 401: 587–590.
- Zeuner KE, Bara-Jimenez W, Noguchi PS, Goldstein SR, Dambrosia JM, Hallett M (2002) Sensory training for patients with focal hand dystonia. *Ann Neurol* 51: 593–598.