

Visual experience shapes the neural networks remapping touch into external space

Abbreviated title: role of vision for tactile localization

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1 **Abstract**

2 Localizing touch relies on the activation of skin-based and externally defined spatial frames of
3 references. Psychophysical studies have demonstrated that early visual deprivation prevents the
4 automatic remapping of touch into external space. We used fMRI to characterize how visual
5 experience impacts on the brain circuits dedicated to the spatial processing of touch. Sighted and
6 congenitally blind humans (male and female) performed a tactile temporal order judgment (TOJ)
7 task, either with the hands uncrossed or crossed over the body midline. Behavioral data confirmed
8 that crossing the hands has a detrimental effect on TOJ judgments in sighted but not in blind.
9 Crucially, the crossed hand posture elicited more activity in a fronto-parietal network in the sighted
10 group only. Psychophysiological interaction analysis revealed that the congenitally blind showed
11 enhanced functional connectivity between parietal and frontal regions in the crossed versus
12 uncrossed hand postures. Our results demonstrate that visual experience scaffolds the neural
13 implementation of touch perception.

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15

16 **Significance statement**

17 Although we seamlessly localize tactile events in our daily life, it is not a trivial operation because
18 the hands move constantly within the peripersonal space. To process touch correctly, the brain has
19 therefore to take the current position of the limbs into account and remap them to their location in
20 the external world. In sighted, parietal and premotor areas support this process. However, while
21 visual experience has been suggested to support the implementation of the automatic external
22 remapping of touch, no studies so far have investigated how early visual deprivation alters the brain
23 network supporting touch localization. Examining this question is therefore crucial to conclusively
24 determine the intrinsic role vision plays in scaffolding the neural implementation of touch
25 perception.

26

27 Introduction

28 Quickly and accurately localizing touch in space is crucial for efficient action planning toward
29 an external stimulus making contact with the body. Although we seamlessly do it in daily life, it is
30 not a trivial operation because the hands move constantly within the peripersonal space as different
31 postures are adopted. Therefore, the brain must transform tactile coordinates from an initial skin-
32 based representation to a representation that is defined by coordinates in external space
33 (Yamamoto and Kitazawa, 2001; Shore et al., 2002; Azañón and Soto-Faraco, 2008; Azañón et al.,
34 2010a, 2015). For example, when sighted individuals have to judge which of their two hands receive
35 a tactile stimulation first (Temporal Order Judgment task – TOJ), they do much more errors when
36 their hands are crossed over the body midline compared to when the hands are uncrossed
37 (Yamamoto and Kitazawa, 2001; Shore et al., 2002; Heed and Azañón, 2014). This crossed-hands
38 deficit has been attributed to the misalignment of anatomical and external frames of reference
39 (Yamamoto and Kitazawa, 2001; Shore et al., 2002). Because the task requirements have nothing
40 spatial (in theory, the task could be solved by using somatotopic coordinates only), this crossing-
41 hand effect compellingly illustrates how the external remapping of touch is automatic in sighted
42 people (Heed and Azañón, 2014). Specific brain networks including parietal and premotor areas
43 have been demonstrated to support this automatic remapping of touch into an external spatial
44 coordinate system (Lloyd et al., 2003; Matsumoto et al., 2004; Azañón et al., 2010a; Takahashi et al.,
45 2013; Wada et al., 2012).

46 Congenitally blind people, in contrast, do not show any crossing-hand deficit when involved
47 in a tactile TOJ task (Röder et al., 2004; Crollen et al., 2017). This suggests that the default
48 remapping of passive touch into external spatial coordinates is acquired during development as a
49 consequence of visual experience. Does the absence of visual experience also alter the neural
50 network typically recruited when people experience a conflict between skin-based and external
51 spatial coordinates of touch? Investigating how congenital blindness reorganizes the brain network
52 supporting touch localization is crucial to conclusively determine the intrinsic role vision plays in

53 scaffolding the neural implementation of the perception of touch location. In order to address this
54 question, we used functional Magnetic Resonance Imaging (fMRI) to characterize the brain activity
55 of congenitally blind individuals and sighted controls performing a tactile TOJ task with either their
56 hands uncrossed or with the hands crossed over the body midline.

57 **Method**

58 ***Participants***

59 Eleven sighted controls (SC) [four females, age range 22-64 y, (mean \pm SD, 46 \pm 14 y)] and 8
60 congenitally blinds (CB) participants [2 females, age range 24-63 y, (mean \pm SD, 47 \pm 13 y)] took part
61 in the study (see Table 1 for a detailed description of the CB participants). The mean age of the SC
62 and CB groups did not statistically differ ($t(17) = 0.11, p = .92$). At the time of testing, the participants
63 in the blind group were totally blind or had only rudimentary sensitivity for brightness differences
64 and no patterned vision. In all cases, blindness was attributed to peripheral deficits with no
65 additional neurological problems. Procedures were approved by the Research Ethics Boards of the
66 University of Montreal. Experiments were undertaken with the understanding and written consent
67 of each participant. Both groups of participants were blindfolded when performing the task.

68 **Table 1. Characteristics of the blind participants**

69

<i>Participants</i>	<i>Gender</i>	<i>Age</i>	<i>Handedness</i>	<i>Onset</i>	<i>Cause of blindness</i>
CB1	F	61	A	o	Retinopathy of prematurity
CB2	M	63	R	o	Congenital cataracts + optic nerve hypoplasia
CB3	F	32	A	o	Retinopathy of prematurity
CB4	M	56	R	o	Electrical burn of optic nerve bilaterally
CB5	M	24	R	o	Glaucoma and microphthalmia
CB6	M	52	A	o	Thalidomide
CB7	M	45	R	o	Retinopathy of prematurity

CB8

M

45 R

o

Leber's congenital amaurosis

70 Note. M = male; F = female; R = right-handed; A = ambidextrous.

71 ***Task and general experimental design***

72 In this task, two successive tactile stimuli were presented for 50 ms to the left and right
73 middle fingers at 6 different stimulus onset asynchronies (SOAs): -120, -90, -60, 60, 90, 120.
74 Negative values indicated that the first stimulus was presented to the participant's left hand;
75 positive values indicated that the first stimulus was presented to the participant's right hand. Tactile
76 stimuli were delivered using a pneumatic tactile stimulator (Institute for Biomagnetism and
77 Biosignal Analysis, University of Muenster, Germany). A plastic membrane (1 cm in diameter) was
78 attached to the distal phalanges of the left and right middle fingers and was inflated by a pulse of air
79 pressure delivered through a rigid plastic tube. Participants had to press a response button placed
80 below the index finger of the hand that they perceived to have been stimulated first. They had 3550
81 ms to respond otherwise the trial was terminated. Participants were asked to perform the task
82 either with their hands in a parallel posture (i.e., uncrossed posture) or with their arms crossed over
83 the body midline. Stimuli were delivered and responses were recorded using Presentation software
84 (Neurobehavioral Systems Inc.) running on a Dell XPS computer using a Windows 7 operating
85 system.

86 Participants were scanned in 2 fMRI sessions using a block design. One run consisted of 16
87 successive blocks (22 s duration each) separated by rest periods ranging from 11 to 14 s (median 12.5
88 s), during which participants had to perform the TOJ judgments either with the hands uncrossed or
89 with the hands crossed. The starting run (uncrossed or crossed) was counterbalanced across
90 participants. Each block, either uncrossed or crossed, consisted of 6 successive pairs of stimulations
91 (each SOA was randomly presented once in each block).

92 Before the fMRI acquisition, all participants underwent a training session in a mock scanner,
93 with recorded scanner noise played in the bore of the stimulator to familiarize them with the fMRI
94 environment and to ensure that the participants understood the task.

95 Behavioral data analyses

96 The mean percentages of “right hand first” responses were calculated for each participant,
97 SOA and posture. These raw proportions were transformed into their standardized z-score
98 equivalents and then used to calculate the best-fitting linear regression lines of each participant
99 (Shore et al., 2002).

100 The just noticeable difference (JND; the smallest interval needed to reliably indicate
101 temporal order) was secondly calculated from the mean slope data by subtracting the SOA needed
102 to achieve 75% performance from the one needed to achieve 25% performance and dividing by 2
103 (Shore et al., 2002). This value was calculated for the entire group. It could not be determined
104 independently for all observers because several sighted people obtained a slightly negative slope
105 value for the crossed posture (Shore et al., 2002). This indicated that some participants responded
106 with the opposite hand as the one that has been stimulated first (Yamamoto and Kitazawa, 2001).

107 fMRI data acquisition and analyses

108 **Acquisition.** Functional MRI-series were acquired using a 3-T TRIO TIM system (Siemens, Erlangen,
109 Germany), equipped with a 12-channel head coil. Multislice T₂*-weighted fMRI images were
110 obtained with a gradient echo-planar sequence using axial slice orientation (TR = 2200 ms, TE =
111 30 ms, FA = 90°, 35 transverse slices, 3.2 mm slice thickness, 0.8 mm inter-slice gap, FoV =
112 192×192 mm², matrix size = 64×64×35, voxel size = 3×3×3.2 mm³). Slices were sequentially acquired
113 along the z-axis in feet-to-head direction. The 4 initial scans were discarded to allow for steady state
114 magnetization. Participants’ head was immobilized with the use of foam pads that applied pressure
115 onto headphones. A structural T₁-weighted 3D MP-RAGE sequence (voxel size= 1×1×1.2 mm³; matrix
116 size= 240×256; TR= 2300 ms, TE= 2.91 ms, TI= 900 ms, FoV= 256; 160 slices) was also acquired for all
117 participants.

118 **Analyses.** Functional volumes from the uncrossed and crossed conditions were pre-processed and
119 analyzed separately using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>; Welcome
120 Department of Imaging Neuroscience, London), implemented in MATLAB (MathWorks). Pre-

121 processing included slice timing correction of the functional time series (Sladky et al., 2011),
122 realignment of functional time series, co-registration of functional and anatomical data, a spatial
123 normalization to an echo planar imaging template conforming to the Montreal Neurological
124 institute space, and a spatial smoothing (Gaussian kernel, 8mm full-width at half-maximum,
125 FWHM). Serial autocorrelation, assuming a first-order autoregressive model, was estimated using
126 the pooled active voxels with a restricted maximum likelihood procedure and the estimates were
127 used to whiten the data and design matrices.

128 Following pre-processing steps, the analysis of fMRI data, based on a mixed effects model,
129 was conducted in two serial steps accounting respectively for fixed and random effects. For each
130 subject, changes in brain regional responses were estimated through a general linear model
131 including the responses to the 2 experimental conditions (uncrossed, crossed). These regressors
132 consisted of a boxcar function convolved with the canonical hemodynamic response function.
133 Movement parameters derived from realignment of the functional volumes (translations in x, y and z
134 directions and rotations around x, y and z axes) and a constant vector were also included as
135 covariates of no interest. We used a high-pass filter with a discrete cosine basis function and a cut-
136 off period of 128s to remove artefactual low-frequency trends.

137 Linear contrasts tested the main effect of each condition ([Uncrossed], [Crossed]), the main
138 effects of general involvement in a tactile TOJ task ([Uncrossed+Crossed]), the specific effect of the
139 uncrossed condition ([Uncrossed>Crossed]) and the specific effect of the crossed condition
140 [Crossed>Uncrossed]. These linear contrasts generated statistical parametric maps [SPM(T)]. The
141 resulting contrast images were then further spatially smoothed (Gaussian kernel 8 mm FWHM) and
142 entered in a second-level analysis, corresponding to a random effects model, accounting for inter-
143 subject variance. One-sample t-tests were run on each group separately. Analyses characterized the
144 main effect of each condition ([Uncrossed], [Crossed]), the main effect of general TOJ
145 ([Uncrossed+Crossed]), the specific effects of the uncrossed ([Uncrossed>Crossed]) and the crossed

146 condition [Crossed>Uncrossed]. Two-sample t-tests were then performed to compare these effects
147 between groups ([Blind vs. Sighted]).

148 **Statistical inferences.** Statistical inferences were performed at a threshold of $p < 0.05$ after
149 correction for multiple comparisons (Family Wise Error method) over either the entire brain volume,
150 or over small spherical volumes (15 mm radius) located in structures of interest. Coordinates of
151 interest for small volume corrections (SVCs) were selected from the literature examining brain
152 activations related to the external representation of space in sighted participants.

153 Standard stereotactic coordinates (x,y,z) used for SVC (in MNI space).

154 Frontal locations : Left precentral gyrus (preCG): -46, -10, 40 (Matsumoto et al., 2004) ; -46, 8, 46; 24,
155 4, 58 (Lloyd et al., 2003); -40, 4, 40 (Takahashi et al., 2013). Dorsolateral prefrontal cortex: -52, 14, 26
156 (Takahashi et al., 2013). Parietal locations: left precuneus (superior parietal lobule): -8, -56, 58 ; -14, -
157 66, 52 (Matsumoto et al., 2004), -32, -54, 62 (Takahashi et al., 2013); right precuneus: 24, -44, 72 (
158 Lloyd et al., 2003) ; right posterior parietal cortex (PPC): 26, -54, 42; 24, -54, 58 (Lloyd et al., 2003);
159 26, -58, 43 (Azañón et al., 2010) ; 24, -51, 42 (Zaehle et al., 2007); left PPC: -46, -64, 38 (Lloyd et al.,
160 2003); left medial intraparietal area (MIP): -46, -52, 50 (Lloyd et al., 2003). Superior parietal gyrus: -
161 26, -72, 32 (Takahashi et al., 2013). Temporal locations: right middle temporal gyrus : 46, -40, 2
162 (Takahashi et al., 2013).

163 **Psychophysiological interaction.** Psychophysiological interaction (PPI) analyses were computed to
164 identify any brain regions showing a significant change in the functional connectivity with seed
165 regions (the left precuneus and the left MIP) that showed a significant activation in the ([CB>SC] x
166 [crossed > uncrossed]) contrast. In each individual, time-series of activity (first eigenvariate) were
167 extracted from a 10mm sphere centered on the local maxima detected within 10 mm of the
168 identified peaks in the second level analysis (SC>CB)x(Crossed>Uncrossed). New linear models were
169 generated at the individual level, using three regressors. One regressor represented the condition
170 (Crossed > Uncrossed). The second regressor was the activity extracted in the reference area. The
171 third regressor represented the interaction of interest between the first (psychological) and the

172 second (physiological) regressors. To build this regressor, the underlying neuronal activity was first
173 estimated by a parametric empirical Bayes formulation, combined with the psychological factor and
174 subsequently convolved with the hemodynamic response function (Gitelman et al., 2003). The
175 design matrix also included movement parameters. A significant PPI indicated a change in the
176 regression coefficients between any reported brain area and the reference region, related to the
177 experimental condition (Crossed > Uncrossed). Next, individual summary statistic images obtained
178 at the first level (fixed-effects) analysis were spatially smoothed (6-mm FWHM Gaussian kernel) and
179 entered in a second-level (random-effects) analysis using a one-sample t-test contrasting CB>SC
180 and SC>CB. Statistical inferences were conducted as for the main-effect analysis described above.

181 **Results**

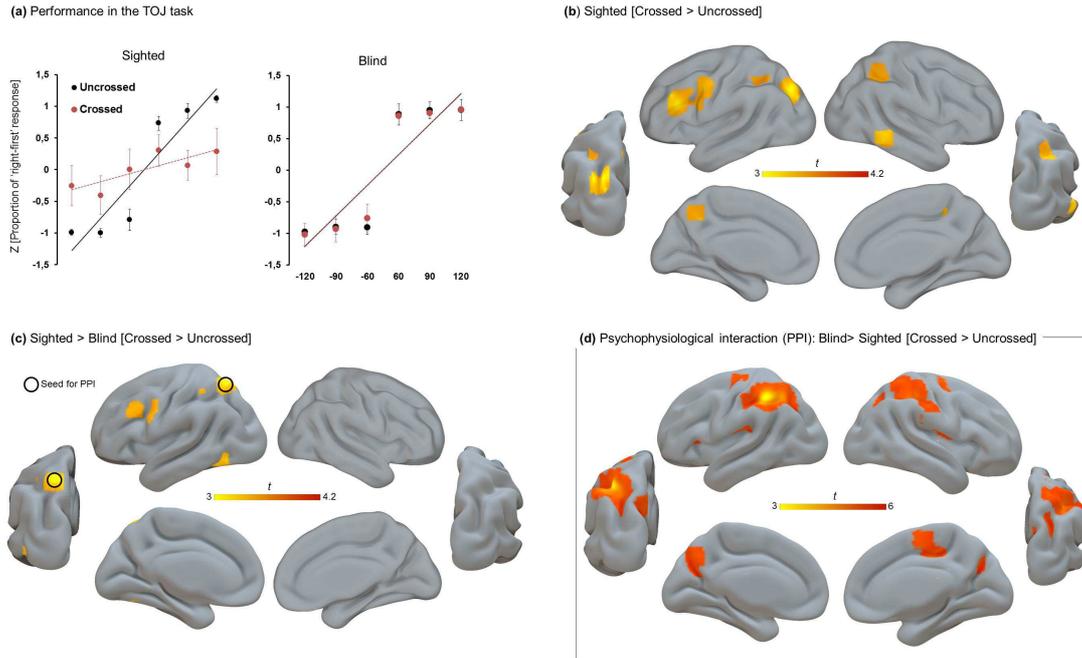
182 ***Behavioral data***

183 The slopes of each individual line (calculated from the z-scores of the mean percentages of
184 “right hand first” responses) were submitted to an ANOVA with posture (uncrossed vs. crossed) as
185 the within-subject factor and group (SC, CB) as the between-subject variable. Results showed: (1) a
186 significant effect of posture [$F(1, 17) = 6.52, p = .02, \eta^2 = .28$], the regression line for the uncrossed
187 posture being steeper ($M = .95 \pm .01$) than the regression line for the crossed posture ($M = .58 \pm .14$);
188 (2) a significant effect of group [$F(1, 17) = 8.27, p = .01, \eta^2 = .33$], the CB ($M = .97 \pm .11$) performing
189 better (steeper regression) than the SC ($M = .57 \pm .09$); and (3) a significant posture x group
190 interaction [$F(1, 17) = 6.75, p = .02, \eta^2 = .28$]. To further examine this interaction, paired samples t-
191 tests compared hand positions in each group separately. In SC, participants’ performance was better
192 in the uncrossed posture ($M = .94 \pm .02$) than in the crossed posture ($M = .20 \pm .24$), [$t(10) = -3.04, p =$
193 $.01$]. In deep contrast, the CB group did not show any effect of posture [$t(7) = 1.05, p = .33$], the slope
194 of the regression lines being similar in the uncrossed ($M = .96 \pm .004$) and crossed postures ($M = .97 \pm$
195 $.004$). In SC, the Just Noticeable Difference (JND) was equal to 27 ms in the uncrossed position and
196 125 ms in the crossed posture. In the CB group, the JND was equal to 26 ms in both postures.

197 ***fMRI data***

198 We first tested whether our paradigm allowed us to observe the activation of the external
199 remapping network in SC. Results revealed that the crossed condition, compared to the uncrossed
200 posture, elicited brain responses in a large fronto-parietal network including the left superior
201 parietal gyrus, the right posterior parietal cortex (PPC), the left precuneus, the left precentral gyrus,
202 the left dorso-lateral prefrontal cortex, and the right middle temporal gyrus (see Fig. 1B and Table
203 2). The same contrast [crossed > uncrossed] performed in the CB group did not reveal any significant
204 result. When the [crossed > uncrossed] contrast was directly compared between groups [SC vs CB],
205 SC showed significantly more activity than the CB in the left precuneus, the left MIP, the left dorso-
206 lateral prefrontal cortex and the right middle temporal gyrus (see Figure 1c and Table 2). CB did not
207 show more activity than sighted for this contrast in any region.

208 Psychophysiological interaction (PPI) analyses were computed to identify between-group
209 differences in the functional connectivity maps of the regions involved in the automatic external
210 remapping of touch identified in the sighted group. For these analyses, the left precuneus (-20, -66,
211 60 mm) was selected as seed region since it displayed the strongest between-group differences for
212 the contrast [SC > CB] x [Crossed > Uncrossed] and also because this region was already reported in
213 the literature as the neural basis of the external remapping of touch (Lloyd et al., 2003; Matsumoto
214 et al., 2004; Azañón et al., 2010a; Takahashi et al., 2013; Wada et al., 2012). Interestingly, the results
215 revealed that the seed regions showed stronger connectivity with and extended parietal network in
216 CB compared to SC for the crossed over uncrossed posture (see Figure 1D).



217
 218 **Figure 1.** (A) Standardized z-score equivalents of the mean proportions of right-hand responses and
 219 best-fitting linear regression lines for the uncrossed (black lines) and crossed (red lines) postures for
 220 sighted and congenitally blind; (B) Results of the whole brain analyses probing brain activity
 221 obtained from the contrast testing which regions are specifically dedicated to the external
 222 remapping process in sighted ([Sighted] x [Crossed > Crossed]). There were no activations observed
 223 for this contrast in the blind group. (C) Regions selectively more active in the sighted group over the
 224 blind group in the crossed over the uncrossed posture ([Sighted > Blind] x [Crossed > Crossed]). (D)
 225 Functional connectivity changes. An increase of functional connectivity was observed between the
 226 left precuneus (seed encircled) and a bilateral fronto-parietal network when congenitally blind
 227 performed the TOJ task in the crossed over uncrossed posture. Whole brain maps are displayed at
 228 $p < .001$ uncorrected ($k > 15$) for visualization purpose only (see methods for the assessment of
 229 statistical significance).

230 **Table 2. Functional results summarizing the main effect of groups for the different contrasts of**
 231 **interests**

Area	Cluster Size	x	y	z	Z	p
(A) [SC] x [Crossed > Uncrossed]						
L superior parietal gyrus	89	-28	-80	36	3.68	0.004*
R PPC	204	22	-46	46	3.64	0.004*
L precuneus	99	-14	-56	50	3.16	0.017*
L PreCG	142	-40	-2	40	3.41	0.008*
L dorso-lateral prefrontal cortex	91	-60	10	30	3.36	0.01*
R middle temporal gyrus	42	40	-46	-2	3.50	0.006*
(B) [CB] x [Crossed > Uncrossed]						
No Significant Responses						

(C) [SC > CB] x [Crossed > Uncrossed]

with inclusive mask (0.001) of [SC] x [Crossed > Uncrossed]

L Precuneus	81	-20	-66	60	3.31	0.01*
L MIP	20	-46	-46	58	3.21	0.01*
L dorso-lateral prefrontal cortex	79	-52	8	38	3.15	0.01*
L precentral gyrus	15	-48	18	36	3.11	0.02*
R MTG	25	40	-44	-4	3.20	0.01*

(D) [CB > SC] x [Crossed > Uncrossed]

No Significant Responses

(E) PPI -20 -66 60 [CB > SC] x [Crossed > Uncrossed]

with inclusive mask (0.001) of [CB] x [Crossed > Uncrossed]

L MIP	1381	-40	-46	52	4.69	0.03 [#]
R PPC	1348	28	-42	48	4.22	0.001*
R IPS	127	20	-64	36	3.45	0.01*

232

233 Table 1. Brain activations significant ($p_{corr} < .05$ FWE) after correction over over the whole brain
 234 volume ([#]) or over small spherical volumes of interest (*). Cluster size represents the number of
 235 voxels in specific clusters when displayed at $p(\text{uncorr}) < .001$. SC: sighted controls, CB: congenitally
 236 blind, L: left, R: Right, MIP: medial intraparietal area, MTG: middle temporal gyrus, PPC: posterior
 237 parietal cortex; IPS: intraparietal sulcus.

238 **Discussion**

239 We assessed the role visual experience plays in shaping the neural correlates of tactile
 240 localization. For this purpose, SC and CB participants were scanned while performing TOJ
 241 judgments with the hands uncrossed or crossed over the body midline. At a behavioral level, we
 242 observed that crossing the hands massively disrupted TOJ performance in SC but not in CB (see
 243 Figure 1A), replicating previous demonstration by Röder et al. (2004). While exploring the
 244 neurophysiological underpinning of this effect, we observed that the crossed condition, when
 245 compared to the uncrossed posture, elicited significantly more activity in the parietal and premotor
 246 areas in sighted, but not in blind participants. Our findings thus compellingly demonstrated that
 247 visual experience plays a crucial role in the development and/or engagement of a parieto-frontal
 248 network involved in this coordinate transformation process.

249 In sighted individuals, vision is a dominant sense for processing space due to the typically
 250 higher reliability, when compared to other senses, of the signal it provides for such a process. For
 251 instance, auditory or tactile information are typically remapped toward visual positions if inputs are
 252 spatially misaligned (Alais and Burr, 2004; Charbonneau et al., 2013); owls reared with prisms

253 deviating their vision show permanent biases in auditory localization (Knudsen and Knudsen, 1989);
254 and short-term adaptation to spatially conflicting visual and auditory stimuli biases auditory
255 localization toward the visual source (Recanzone, 1998; Zwiers et al., 2003). Vision can even over-
256 ride the proprioceptive sensation of a limb in space by displacing the position of a hidden arm
257 toward a rubber one (Botvinick and Cohen, 1998). Actually, when we hear or feel something
258 approaching or touching the body, we typically orient our vision toward this event and then use our
259 motor system to guide appropriate action plans based on a precise location of the target in the
260 external world (Goodale, 2011). As a result of their lack of visual experience, congenitally blind
261 people have to rely exclusively on spatial information delivered by the remaining intact senses, such
262 as hearing and touch. Thus, it seems likely that spatial perception in congenitally blind and in
263 sighted people develops along different trajectories, and operates in a qualitatively different way in
264 adulthood. Several studies have indeed pointed toward a reduced sense of external space in early
265 blind individuals (Andersen et al., 1984; Bigelow, 1987; Dunlea, 1989; Millar, 1994; Ruggiero et al.,
266 2012).

267 It has been shown that parietal and dorsal premotor regions play a crucial role in co-
268 registering spatial information collected from various senses and frames of reference into a common
269 coordinate system for the guidance of both eye and limb movements onto the external world
270 (Graziano et al., 1994, 1997; Duhamel et al., 1998; Colby and Goldberg, 1999; Lloyd et al., 2003;
271 Mulette-Gillman et al., 2005; Makin et al., 2007). For instance, it was shown that the position of the
272 arm is represented in the premotor (Graziano, 1999) and parietal (Graziano, 200) cortex of the
273 monkey by means of a convergence of visual and proprioceptive cues onto the same neurons. More
274 particularly, these regions are thought to be part of a network responsible for the remapping of skin-
275 based touch representations located in somatosensory regions into external spatial coordinates
276 (Lloyd et al., 2003; Matsumoto et al., 2004; Bolognini and Maravita, 2007; Zhaele et al., 2007;
277 Azañón et al., 2010a; Longo et al., 2010; Takahashi et al., 2013; Wada et al., 2012). Accordingly,
278 transiently disrupting the activity of the right posterior parietal cortex with Transcranial Magnetic

279 Stimulation (TMS) selectively impairs the tactile remapping process but does not disrupt
280 proprioceptive and somatosensory localization processes, highlighting the causal role of this region
281 in remapping touch into external space (Azañón et al., 2010a).

282 When the hands are crossed, the conflict between external and anatomical representations
283 of the hands increases the computational demands of the external remapping process which is
284 typically observed in the “default” uncrossed posture (Melzack and Bromage, 1973; Bromage, 1974).
285 Crossing the hands therefore triggers enhanced activity in the dorsal parieto-frontal network (see
286 Figure 1B). In early blind people, the absence of a mandatory external remapping process prevents
287 the increased recruitment of this neural network while crossing the hands. Therefore, by using
288 blindness as a model system, we demonstrated that developmental vision plays a causal role in
289 developing the computational architecture of parietal and dorsal premotor regions for transforming
290 tactile coordinates from an initial skin-based representation to a representation that is defined by
291 coordinates in external space.

292 Interestingly, it has recently been suggested that the integration of spatial information from
293 different reference frames actually depends on the relative weight attributed to the internal and
294 external coordinates (Azañón et al., 2010a; Badde et al., 2015; Badde and Heed, 2016). While
295 integration seems mandatory in SC (Yamamoto and Kitazawa, 2001; Shore et al., 2002, Azañón et
296 al., 2010b) the relative weight attributed to each coordinate system seems to be more dependent on
297 tasks demands and instructions in CB (Heed and Röder, 2014; Heed et al., 2015; Crollen et al., 2017).
298 Further studies should examine whether the external remapping network could therefore be active
299 in CB while performing a task emphasizing external instructions. It is indeed possible that the
300 external coordinate system is less automatically activated in CB than in SC but this does not mean
301 that this system is not readily accessible when the task requires it (as, for example, when people
302 perform an action directed toward the external world: Fiehler et al., 2009; Lingnau et al., 2014).

303 A recent study in the sighted demonstrated that the crossed-arms posture elicited stronger
304 functional connectivity between the left IPS on the one hand and the right frontal gyrus and the left

305 PPC on the other hand (Ora et al., 2016). By performing task-dependent functional connectivity
306 analyses (Psychophysiological interactions), we demonstrate that blind individuals rely on enhanced
307 integration between dorsal regions (Heine et al., 2015) while experiencing a conflict between body-
308 centered and world-centered coordinates (see Figure 1D). This raises the intriguing possibility that
309 changes in the connectivity pattern of the parietal cortex gates the activation, or not, of the external
310 remapping process in congenitally blind people depending on task demands. Enhanced parieto-
311 frontal connectivity in the crossed posture in the blind may therefore prevent the automatic
312 remapping process from occurring in a task that does not necessitate such a computation (the TOJ
313 task can be resolved by using pure skin-based coordinates). This could potentially explain the
314 enhanced performance of the blind population in the crossed condition of the TOJ task (see Figure
315 1A).

316 In conclusion, we demonstrate that early visual deprivation alters the development of the
317 brain network involved in the automatic multisensory integration of touch and proprioception into a
318 common, external, spatial frame of reference. Moreover, the enhanced connectivity between dorsal
319 regions in CB may provide a mechanistic framework to understand how blind people differently
320 weight specific spatial coordinate systems depending on the task at play (Badde et al., 2015; Badde
321 and Heed, 2016). These results have far-reaching implications for our understanding of how visual
322 experience calibrates the development of brain networks dedicated to the spatial processing of
323 touch.

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325 **Author contributions:** VC and OC designed research; VC, LL, and AB performed research; VC, OC,
326 and MR analyzed data; VC and OC wrote the paper; FL provided laboratory resources for the
327 optimal recruitment and testing of participants.

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435 **Figure legend**

436 **Figure 1.** (A) Standardized z-score equivalents of the mean proportions of right-hand
437 responses and best-fitting linear regression lines for the uncrossed (black lines) and crossed (red
438 lines) postures for sighted and congenitally blind; (B) Results of the whole brain analyses probing
439 brain activity obtained from the contrast testing which regions are specifically dedicated to the
440 external remapping process in sighted ([Sighted] x [Crossed > Crossed]). There were no activations
441 observed for this contrast in the blind group. (C) Regions selectively more active in the sighted group
442 over the blind group in the crossed over the uncrossed posture ([Sighted > Blind] x [Crossed >
443 Crossed]). (D) Functional connectivity changes. An increase of functional connectivity was observed
444 between the left precuneus (seed encircled) and a bilateral fronto-parietal network when
445 congenitally blind performed the TOJ task in the crossed over uncrossed posture. Whole brain maps
446 are displayed at $p < .001$ uncorrected ($k > 15$) for visualization purpose only (see methods for the
447 assessment of statistical significance).

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