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ORIGINAL ARTICLE

Visual loss alters multisensory face maps in humans

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Abstract

Topographically organised responses to visual and tactile stimulation are aligned in the ventral intraparietal cortex. The critical biological importance of this region, which is thought to mediate visually guided defensive movements of the head and upper body, suggests that these maps might be hardwired from birth. Here, we investigated whether visual experience is necessary for the creation and positioning of these maps by assessing the representation of tactile stimulation in congenitally and totally blind participants, who had no visual experience, and late and totally blind participants. We used a single-subject approach to the analysis to focus on the potential individual differences in the functional neuroanatomy that might arise from different causes, durations and sensory experiences of visual impairment among participants. The overall results did not show any significant difference between congenitally and late blind participants; however, single-subject trends suggested that visual experience is not necessary to develop topographically organised maps in the intraparietal cortex, whilst losing vision disrupted topographic maps' integrity and organisation. These results discussed in terms of brain plasticity and sensitive periods.

Keywords Brain plasticity · Intraparietal cortex · Blindness · Touch · fMRI

Introduction

Humans, such as other primates, are predominantly visual animals. The adaptive importance of vision is reflected in the extensive neural representation of visual information, with over half of the primate brain responsive to visual stimulation (Felleman and Van Essen 1991; Sereno and Allman 1991). In turn, experience with the visual world has been found to affect a number of non-visual cognitive modules, such as spatial memory and representation (Pasqualotto et al. 2013b; Guerreiro et al. 2015), semantic processing and memory (Bedny et al. 2011; Pasqualotto et al. 2013a), multisensory integration (Cecchetti et al. 2015; Hötting and Röder 2004), number representation (Castronovo and Seron 2007; Pasqualotto et al. 2014) and even olfactory perception (Araneda et al. 2016). The crucial role of visual experience has been revealed by studies that tested people blind from birth, or congenitally blind, in comparison with those who have acquired blindness (or late blind). It has been documented that congenital blindness also has a profound effect on the physical structure of the brain (Jiang et al. 2009; Pan et al. 2007; Qin et al. 2013), potentially giving rise to greater individual differences in functional neuroanatomy as a function of visual experience.

The aim of this study is to investigate the role of visual experience on the multisensory topographical maps representing stimuli delivered near/to the face, which were recently discovered in human superior parietal cortex (Sereno et al. 2001; Sereno and Huang 2006; Huang et al. 2012, 2017). By adapting methods originally used to localise and characterise these areas in non-human primates (Cooke and Graziano 2003; Graziano and Gandhi 2000), they showed that these aligned maps used head-centred coordinates. This suggests that this neocortical area provides a crucial system for mapping objects moving near/to the face. Being able to align visual information with tactile information in such a way as to cancel the effects of eye position is crucial for

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protecting the face from collision, on the one hand, or for efficiently bringing food to the mouth, on the other. Given the fact that somatosensory coordinates dominate over retinocentric (visual) coordinates in the anterior portion of the intraparietal cortex (in contrast to more posteriorly located intraparietal areas where retinocentric coding is dominant, Sereno and Huang 2006), the authors surmised that areas such as VIP (ventral intraparietal, see Colby et al. 1993) might best be thought of as a somatosensory area with additional visual inputs. This suggests that the formation of tactile maps in parietal cortex might proceed even in the absence of visual experience.

Here, we assessed whether spatially organised somatosensory maps of the face in human intraparietal cortex can develop independently of external visual stimulation, or whether they require visual experience. Although there is still some disagreement on the exact homology of VIP between human and non-human primates, there are several studies showing functional equivalence in several cortical areas across humans and primates, included the posterior parietal cortex (Bremmer et al. 2001; Culham and Kanwisher 2001; Sereno and Tootell 2005). Moreover, although different research groups tend to use different names to indicate VIP (e.g. DIPSA and aIPS), there is abundant literature supporting the claim that human and primate VIP are functionally overlapping (Culham et al. 1998; Orban et al. 2003; Astafiev et al. 2003). Yet, in our study, we will refer to the putative human VIP (hVIP) identified, among the others, by Sereno and Huang (2006).

We used a similar procedure to that used by Sereno and Huang (2006), but here we tested congenitally blind participants (i.e. without visual experience), and late blind participants. In their articles, Sereno et al. reported that when sighted individuals perceived tactile stimuli delivered to the face they exhibited the activation of the primary and secondary somatosensory cortices (S1 and S2, respectively), but also temporo-parietal areas such as the posterior superior temporal sulcus (pSTS), the medio-temporal cortex (MT/MST), and the lateral and ventral intraparietal cortices (LIP and VIP, respectively). Finally, they reported activation of frontal areas such as the dorsolateral prefrontal cortex (DLPFC) and the frontal eye fields (FEF) (Huang and Sereno 2018; Huang et al. 2017 Experiment 1, 2018).

Given the evidence that visual impairment can lead to plastic changes in the functioning of brain areas, and also structural changes in the grey and white matter of the brain (Noppeney et al. 2005), we used a single-subject analysis to portray the maps present in individual participants. We also compared groups for a standard statistical analysis. As with clinical neuroimaging studies, the individual differences can influence the averaging of such data, making the single-subject approach useful in this regard (Fadiga 2007). If visual experience is not necessary to develop spatial maps of the stimuli occurring near/on the face, then congenitally and late blind participants would both have spatial maps in (for example in hVIP). How can topographical maps in the intraparietal cortex develop in total absence of vision (i.e. in congenitally blind individuals)? Aside receiving visual (Uesaki et al. 2018) and somatosensory inputs (Sereno and Huang 2006), the intraparietal cortex is known to receive auditory input as well (Beer et al. 2011). Therefore, auditory input might be able to 'substitute' for the missing visual input, and thus allow for the development of 'normal' topographical maps. Indeed, we found a trend suggesting that congenitally blind participants possessed topographical maps better developed than late blind participants, thus suggesting that visual experience is not mandatory for their development.

Method

Participants

We tested ten right-handed blind participants: five congenitally blind (four males) and five late blind participants (four males) (see Table 1). The average age for the congenitally blind group was 50.4 (SD 16.5) and 51.8 (SD 10.5) for the late blind group. On average, late blind participants lost vision at 18.6 years of age. They were screened for MRI contraindications according to standard procedures, and written consent was obtained. The procedure was approved by the ethics committee at Birkbeck University of London. We did not include any sighted group because the very same apparatus ('dodecapus') and empirical question had already been extensively investigated in sighted participants by Sereno et al. (e.g. Huang and Sereno 2007; Huang et al. 2012). In addition, the aim of the present work is to investigate the effect of visual experience, thus we tested congenitally and late participants only as this between group comparison provides the necessary contrast to assess the impact of developmental visual experience.

Apparatus and procedure

Participants were placed into the scanner with 12 MR-compatible plastic air tube nozzles (Huang and Sereno 2007) arranged in a circle around the outer edge of the face as numbers are arranged on the clock-face (see Fig. 1). Participants were told to attend the 'air-puffs' emitted by the air tubes, which were delivered from computer-controlled valves to produce light tactile stimulation by adjusting the driving pressure from a compressed cylinder of medical-grade air. Air-puffs were perceived as light, slightly cool touches on a localised region of the face. Face stimulation consisted of four series of air-puffs (two clockwise and two

Table 1 Details of the participants (PP)

PP	Sex	Age	Hand	Education	Onset	Aetiology	Braille	Visual imagery	Residual vision
CB1	M	59	Rx	Uni	Birth	RoP	Y	N	N
CB2	F	31	Rx	Sec	Birth	Genetic retinal dysplasia	Y	N	N
CB3	M	34	Rx	Uni	Birth	Eyes did not develop	N	N	N
CB4	M	65	Rx	Sec	Birth	RoP	Y	N	N
CB5	M	63	Rx	Uni	Birth	RoP	Y	N	N
LB1	F	47	Rx	Uni	11	Optic nerve degeneration	Y	Y	N
LB2	M	41	Rx	Uni	20	Ret pigm	Y	Y	L/D
LB3	M	45	Rx	Uni	21	Ret pigm	N	Y	L/D
LB4	M	64	Rx	Sec	11	Accident	Y	Y	N
LB5	M	62	Rx	Sec	30	Ret pigm	Y	Y	N

Uni university level, *Sec* secondary school level, *Y* yes, *N* no, *L/D* light/darkness sensitivity

Aetiology abbreviations: *RoP* retinopathy of prematurity, *Ret* pigm retinitis pigmentosa

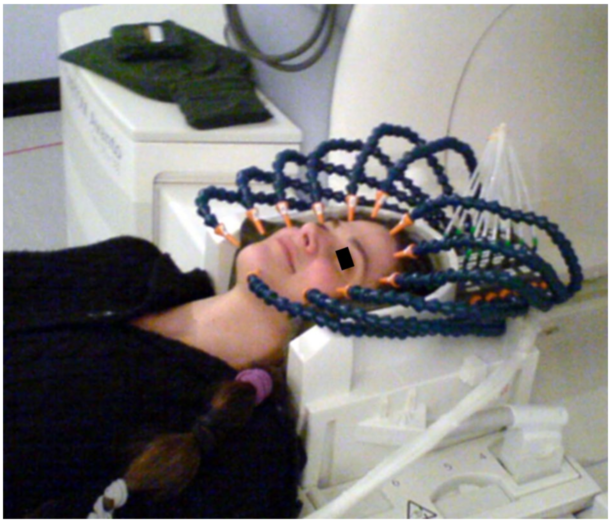
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Fig. 1 The experimental apparatus

counter-clockwise series), each lasting 520 s. Each series included eight full circles, each of them lasting 64 s, for a total of 512 s of stimulation. Within each runs, 8 s ‘blank’ preceded the stimulation.

Data acquisition

Standard echoplanar images were collected on a 1.5-T Siemens Avanto, with a 32-channel coil (20 coils remaining after removing the top). Functional data were acquired using a T2*-weighted gradient-recalled echoplanar imaging (EPI) sequence (260 volumes per scan, 3.2 mm^3 voxel size, flip angle 90°, TE = 39 ms, TR = 2000 ms, 64 × 64 matrix, bandwidth 1474 Hz/pixel). Structural data were acquired using a T1-weighted 3D anatomical scan (MPRAGE, $1 \times 1 \times 1\ \text{mm}^3$, flip angle 7°, TE = 3.57 ms, TR = 8.4 ms, TI = 1000 ms, bandwidth 190 Hz/pixel).

Data analysis

Data were analysed using Brain Voyager QX 2.3 (Brain-Innovation, The Netherlands). The first four volumes were discarded to allow image intensity to stabilise. Three-dimensional motion correction and slice time correction were performed. The data were temporally high pass filtered at 3 cycle/run (~ 0.01 Hz). The pre-processed EPI scans were then co-registered with the anatomy. Finally, both functional and anatomical data were normalised and aligned into Talairach space. The temporal phase of the response to the rotating sequence of air-puffs at each voxel was obtained by fitting a model to the time series. Phase was taken as an indicator of air-puff position in terms of polar angle. Given the timing of the stimulation (i.e. 64 s) and the duration of the TR (i.e. 2 s), a full cycle lasted 32 TRs and all of them were used as lags in the phase-encoding mapping. A colour scale (red to blue to green, see Fig. 1) was used to illustrate the phase of the eight cycles per scan response, which corresponds to a particular position around the face. For each participant, data from different runs were averaged and projected on an inflated representation of the grey matter. Then, all the data were averaged separately for each group, to investigate what regions were consistently activated by the stimulation. A spatial threshold of 50 mm^2 and a statistical threshold ($R^2 = 0.22$) were applied to the inflated brain to remove spurious activations.

Results

Late blind participants

To inspect how sensory information delivered on the face is mapped on the cortex, and how these maps are affected by visual experience, we used the phase-encoding maps. For the late blind group, the areas of interest exhibiting the strongest activation for tactile stimuli delivered to the face (air-puffs) are shown in Fig. 2a. Tactile stimuli delivered to the face are here associated with a robust inter-hemispheric asymmetry, with the activations in the left hemisphere being wider and shifted with respect to the activations in the right hemisphere. On the left hemisphere this activation is mapped around the inferior portion of the precentral sulcus, in particular on a posterior portion of cortex commonly associated with the primary motor cortex (M1) controlling the face (Penfield and Boldrey 1937), and with an anterior portion commonly associated with the premotor cortex (pMC, Rizzolatti et al. 2002). On the right hemisphere, the activation is near the inferior part of the Intraparietal Sulcus, a region associated with the secondary visual cortex (V2; Burkhalter and Bernardo 1989). The coordinates and the volumes of these clusters are reported in Fig. 2a and Table 2.

Thus, considering the entire group of late blind individuals, it seems that there is no evidence of topographic maps of the face in intraparietal cortex, and in particular in hVIP. Is it the same when we look at single brains? Indeed, topographic maps are sparsely present in the intraparietal cortex of late blind participants. In fact, only late blind no. 3 (right hemisphere) and late blind no. 5 (left hemisphere) presented topographic maps in correspondence of hVIP (see Fig. 3 the late blind side). On the other hand, late blind participants presented robust phase activation of the primary motor/somatosensory cortices (late blind nos. 1, 2, 3 and 5), occipital cortex [late blind nos. 1, 4 and 5 (right hemisphere)], prefrontal cortex [late blind nos. 2 (right hemisphere) and

Table 2 Volumes and coordinates of the clusters resulting from the phase-encoding mapping of air-puffs in the late blind participants (Talairach and Tournoux 1988)

Hemisphere	*x*	*y*	*z*	mm^3
Right V2	14	− 78	27	464
Left M1	− 49	− 15	34	2094
Left pMC	− 56	0	30	945

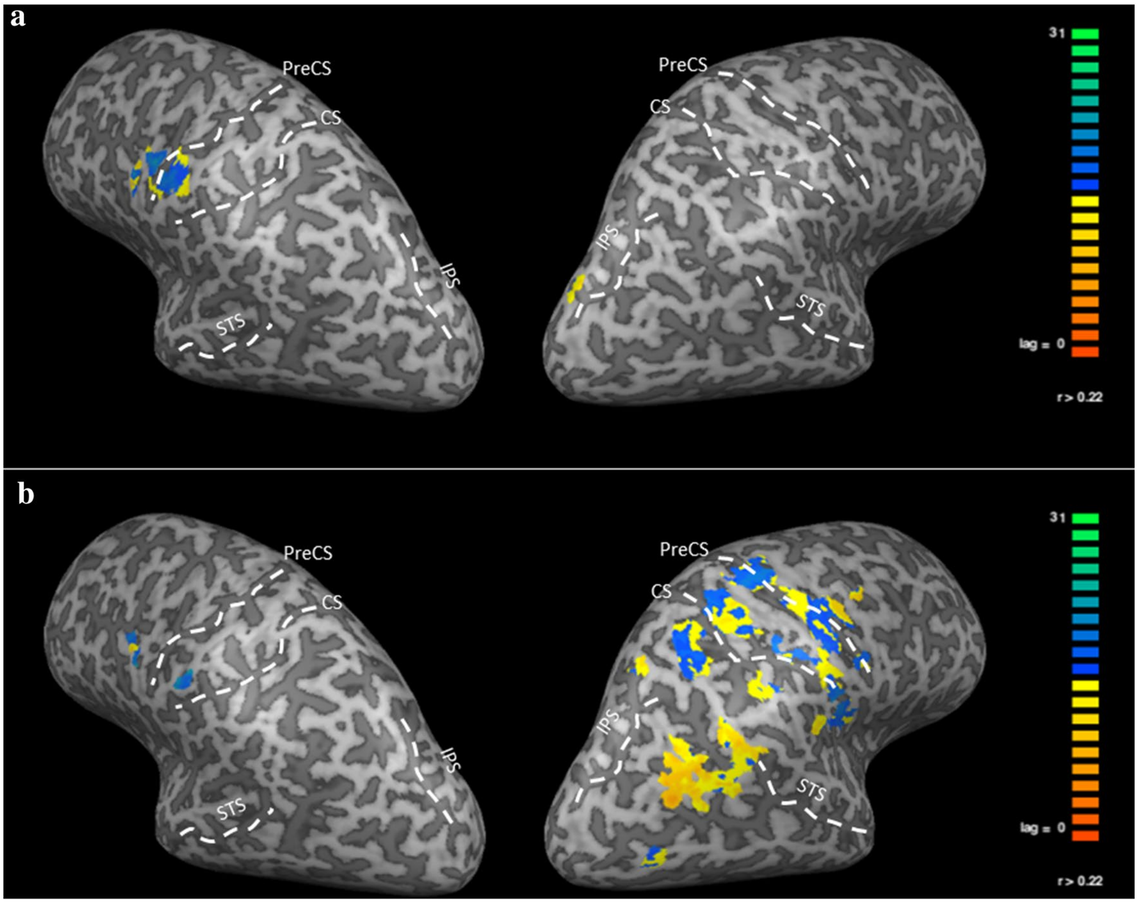

Fig. 2 **a** Group averaged polar angle maps. The maps obtained with the sensory stimulation were averaged across the late blind participants using the normalised space (Talairach). Gross anatomy landmarks refer to the precentral sulcus (PreCS), the central culcus (CS), the superior temporal sulcus (STS) and the interparietal sulcus (IPS). **b** Group averaged polar angle maps for the congenitally blind participants with references to the principal sulci (as per late blind participants)

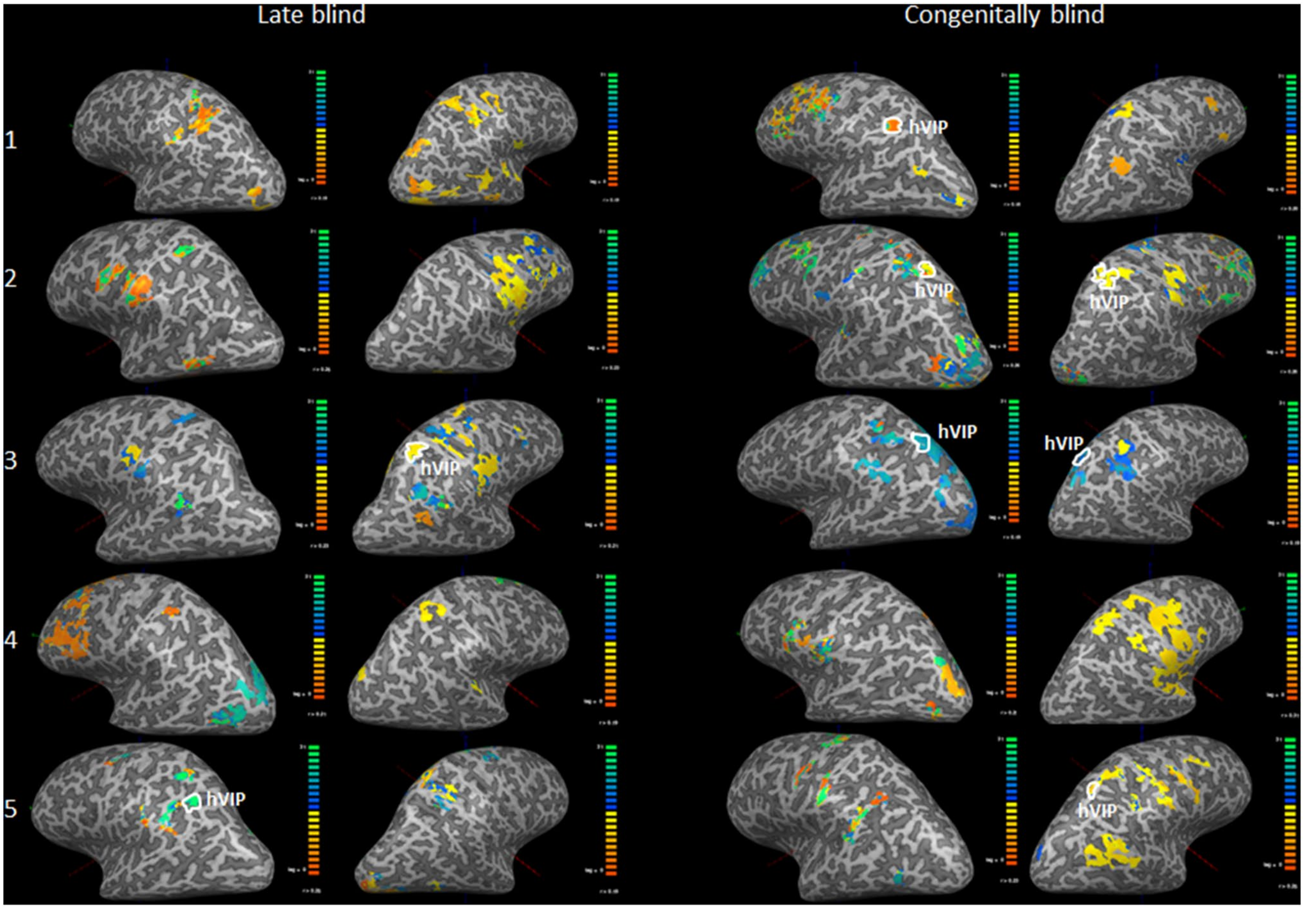

Fig. 3 Brain hemispheres of each late and congenitally blind participant; hVIP area is indicated

4 (left hemisphere)] and MST (late blind no. 3) (see Fig. 3 late blind side).

Congenitally blind participants

Overall, congenitally blind participants presented different activations with respect to late blind participants. However, also in this case the activation was asymmetrical, with the right hemisphere showing a wider set of areas on which the stimulus was mapped. On the left hemisphere, similarly to late blind participants, the brain regions sensitive to the stimulation were located around the inferior portion of the precentral sulcus, more specifically on a posterior portion of cortex commonly identified as the primary motor cortex (M1) controlling the face (Penfield and Boldrey 1937), and an anterior portion commonly associated with the premotor cortex (pMC, Rizzolatti et al. 2002). On the right hemisphere, stimuli were mapped along the precentral sulcus both anteriorly (premotor cortex, pMC; Rizzolatti et al. 2002) and posteriorly (primary motor cortex, M1; Kakei et al. 1999), along the central sulcus both anteriorly (primary motor cortex, M1) and posteriorly (primary somatosensory cortex, S1; McCarthy et al. 1993), and the medial superior temporal area (MST, the large area near the superior temporal sulcus, STS; Takemura et al. 2002), see Fig. 2b and Table 3.

Table 3 Volume and coordinates of the clusters resulting from the phase-encoding mapping of air-puffs in the congenitally blind participants

Hemisphere	*x*	*y*	*z*	mm^3
Right pMC	42	– 16	42	4317
Right pMC	51	– 7	29	289
Right pMc	45	– 23	23	1922
Right M1	46	– 56	23	5820
Right M1	40	– 38	41	818
Right M1	42	– 72	4	509
Right S1	37	– 1	43	285
Right S1	26	– 45	50	2144
Right MST	25	– 37	51	2662
Right MST	23	– 24	54	1192
Left M1	17	– 60	52	483
Left pMC	– 50	– 1	33	806

Again, considering an entire group, in this case congenitally blind individuals, it seems that that there is poor evidence of topographic maps of the face in the intraparietal cortex, especially hVIP. However, looking at single participants, we discovered that several of them possessed topographic maps in the intraparietal cortex; in particular, congenitally blind no. 1 (left hemisphere), congenitally blind no. 2 (bilaterally), congenitally blind no. 3 (bilaterally) and congenitally blind no. 5 (right hemisphere) (see Fig. 3, congenitally blind side). In addition, congenitally blind participants presented robust phase activation of the primary motor/somatosensory cortices [congenitally blind nos. 1 (right hemisphere), 2, 3, 4 (right hemisphere) and 5], occipital cortex [congenitally blind nos. 1 (left hemisphere), 2, 3 (left hemisphere) and 4 (left hemisphere)], prefrontal cortex (congenitally blind nos. 1 and 2), and medial superior temporal area, and MST [congenitally blind nos. 1 and 5 (right hemisphere)] (see Fig. 3, late blind side).

An ANOVA comparing voxel-by-voxel activation across the two groups of participants (late vs. congenitally blind), corrected by multiple comparisons, and using False Discovery Rate reported non-significant results [$F(1,8) = 162.08$, $q(\mathrm{FDR}) < 0.05$, $p < 0.000001$].

Discussion

The fundamental difference across the two groups of blind participants is the availability or the lack of visual experience. Our results suggested that visual experience is not required for the formation of topographic maps in intraparietal cortex (e.g. in hVIP). In fact, using a single-subject approach, we could discover that people without visual experience (congenitally blind) exhibited topographic maps in hVIP. On the other hand, late blind individuals exhibited sparse evidence of the existence of topographic maps in the intraparietal cortex. Although we could not scan the brain of the late blind participants when they were still sighted, as suggested by the studies on sighted participants by Sereno et al. (Huang and Sereno 2018; Huang et al. 2017 Experiment 1, 2018), it is highly probable that our late blind participants did possess intraparietal topographic maps, which were later disrupted by the loss of vision. Taken together, these results suggest that topographic maps can be established without any visual input, while topographic maps established when visual input is available are lost when visual input is no longer available.

Another interesting result is that we found phase activity in MST, which plays a role in movement pursuit (both real and apparent) and optic flow perception (Kourtzi and Kanwisher 2000; Uesaki and Ashida 2015). In addition, recent studies have suggested that MST is also multisensory (Beer et al. 2011; Greenlee et al. 2016). In our experiment, participants were required to attend to 12 air-puffs delivered to the face by following a serial order, thus producing an 'apparent movement' of the tactile stimulation around the face. In fact, air-puff number 1 ceased its air flow when air-puff number 2 began its air flow, air-puff number 2 ceased its air flow when air-puff number 3 began its air flow and so on, thus simulating the movement of the tactile stimulus from location to location (for the equivalent visual illusion see Sherrick and Rogers 1966). Therefore, the fact that we found a trend showing that MST is more active in congenitally blind (both as a group and as single participants) than late blind participants, suggests that this brain area can develop without visual experience, but it is impaired by the loss of vision. As a matter of fact, studies by Sereno et al. testing sighted participants showed the involvement of MT/MST (Huang and Sereno 2018; Huang et al. 2017 Experiment 1, 2018).

These phenomena can be explained by taking into consideration the existence of 'sensitive periods' during the early phase of human development when brain plasticity is at its peak. During sensitive periods the brain can better adapt to environmental conditions (Hensch 2005; Sadato et al. 2002). The role of sensitive periods is highlighted by studies on congenitally blind people who regained vision after the end of the sensitive period. Although these studies are rather rare, the consensus is that the brain is only partially able to utilise the new visual input (Ackroyd et al. 1974; Carlson et al. 1986; Fine et al. 2003). In our case, people born blind spent their sensitive period without any visual input, and the brain adapted to this condition; this is shown by the existence of topographic maps in congenitally blind participants. On the other hand, people born sighted spent their sensitive period with visual input, and the brain adapted to this condition; yet, after the end of the sensitive period these people lost vision and their brain was not fully able to adapt to this new condition; this is shown by the lack of well-established topographic maps in late blind participants. Our conclusion is supported by a recent study reporting that late blind participants exhibited white matter atrophy on a larger scale than congenitally blind participants (Wang et al. 2013).

Although late blind individuals possessed sparsely organised topographic maps in the intraparietal cortex, it is extremely unlikely that they had trouble perceiving the air-puffs, or had problems localising them (all participants reported that the air-puffs were salient stimuli occurring around their faces). In fact, late blind individuals can perform the vast majority of tasks at the same level as sighted individuals (e.g. Papadopoulos et al. 2011; Pasqualotto and Newell 2007). Therefore, it is likely that to track tactile stimuli delivered to the face late blind participants were using mechanisms that did not involve intraparietal topographic maps. In fact, looking at the topographic maps displayed in Fig. 2a (group maps), we can notice that the late blind participants exhibit topographic maps in correspondence of the primary motor cortex (M1), in particular at the level of the area representing the face (Kakei et al. 1999), and the premotor cortex (Rizzolatti et al. 2002). The single-subject view offers further indications of how late blind participants monitored tactile stimuli. In particular the occipital activation exhibited by some late blind participants suggests that they might use visual imagery (Kosslyn et al. 1999), while prefrontal activation suggests that they might use conscious strategies (see Fig. 3 late blind side). This suggests that, instead of intraparietal topographical maps, different brain networks were used by late blind participants to monitor tactile stimuli delivered on the face, and they were thus unable to show the same compensatory plasticity as the congenitally blind. In particular, the involvement of motor areas (e.g. M1), and the strong hemispheric lateralisation in both late and congenitally blind participants is likely to support compensatory plasticity; in fact, Sereno et al. did not find the activation of motor areas and strong lateralisation in sighted participants performing tactile perception tasks (Huang and Sereno 2018; Huang et al. 2017 Experiment 1, 2018).

Several studies reported that congenitally blind show specific deficits for spatial tasks requiring allocentric spatial representation (i.e. representing the position of an object in terms of its spatial relations with other objects) (Gori et al. 2010, 2014; Finocchietti et al. 2017; Iachini et al. 2014; Postma et al. 2008; Röder et al. 2004; Vercillo et al. 2016; see; Pasqualotto and Proulx 2012 for a review). For example, Röder et al. reported that congenitally blind individuals lack or have a less functional allocentric spatial representation, which does not interfere with the egocentric spatial representation. Therefore, the existence of topographical maps in congenitally blind participants might seem inconsistent with the abovementioned results. Nevertheless, in our experiment participants had to passively perceive tactile stimuli in relation with their own face, which requires the use of egocentric spatial representation (i.e. representing the position of an object in terms of its spatial relations with the position of the observing/perceiving individual), which is entirely within the abilities of congenitally blind individuals (Coluccia et al. 2009; Iachini et al. 2014; Loomis at al. 1993).

Finally, an important limitation of our study is the small number of participants that, nevertheless, allowed us to draw some cautious conclusions, which are consistent with the available literature and represent a seminal work for future studies. Yet, using a single-subject design can be a strength too, because it eliminates the danger of averaging across important individual differences and obtain a misleading map (Fadiga 2007; Smith and Little 2018). In fact, our participants were highly variable in their brain activations and neuroanatomy, and in many cases we could only explain the results by looking at the single-subject views (e.g. topographical maps in congenitally blind's hVIP). Our study suggests that changes in sensory experience have strong effects across many levels of the cortical hierarchy.

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