Visual loss alters multisensory face maps in humans

Achille Pasqualotto [1 2 3 *], Michele Furlan[4], Michael J. Proulx [1 2], and Martin I. Sereno [5]

Citation at time of acceptance, and published version:

Pasqualotto, A., Furlan, M. U. A., Proulx, M. J., & Sereno, M. I. (in press). Visual loss alters multisensory face maps in humans. *Brain Structure & Function.*

https://link.springer.com/article/10.1007%2Fs00429-018-1713-2

[1] School of Biological and Chemical Sciences, Queen Mary University of London, UK

[2] Department of Psychology, University of Bath, UK

[3] Faculty of Arts and Social Sciences, Sabanci University, Turkey

[4] SISSA (Scuola Internazionale Superiore di Studi Avanzati), Italy

[5] San Diego State University, USA

*Correspondence: Achille Pasqualotto, FASS, Sabanci University, Tuzla 34956, Istanbul, Turkey, Email: achille@sabanciuniv.edu

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. 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, like 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 and Huang 2006; Huang et al. 2012; Huang et al. 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 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, aIPS, etc.), 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 and collaborators 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 and collaborators (e.g. Huang and Sereno 2007; Huang et al. 2012). Additionally, 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 twelve 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 Figure 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 counter-clockwise series), each lasting 520 seconds. Each series included 8 full circles, each of them lasting 64 seconds, for a total of 512 seconds of stimulation. Within each runs, eight seconds 'blank 'preceded the stimulation.

Data acquisition. Standard echoplanar images were collected on a 1.5-Tesla Siemens Avanto, with a 32-channel coil (20 coils remaining after removing the top). Functional data were acquired using a T_2*-weighted gradient-recalled echo-planar imaging (EPI) sequence (260 volumes per scan, 3.2 mm^3 voxel size, flip angle 90° , TE=39 ms, TR=2000 ms, 64x64 matrix, bandwidth 1474 Hz/pixel). Structural data were acquired using a T_1-weighted 3D anatomical

scan (MPRAGE, 1x1x1 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 (BrainInnovation, 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 seconds) and the duration of the TR (i.e., 2 seconds), 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 Figure 1) was used to illustrate the phase of the 8 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, in order 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 in order to remove spurious activations.

[Table 1 about here]

[Figure 1 about here]

Results

Late blind participants. In order 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 Figure 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 Figure 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 Figure 3 the late blind side). On the other hand, late blind participants presented robust phase activation of the primary motor/somatosensory cortices (late blind No 1, 2, 3, and 5), occipital cortex (late blind No 1, 4, and 5 [right hemisphere]), prefrontal cortex (late blind No 2 [right hemisphere] and 4 [left hemisphere]), and MST (late blind No 3) (see Figure 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 Figure 2b and Table 3.

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 Figure 3, congenitally blind side). Additionally, congenitally blind participants presented robust phase activation of the primary motor/somatosensory cortices (congenitally blind No 1 [right hemisphere], 2, 3, 4 [right hemisphere], and 5), occipital cortex (congenitally blind No 1 [left hemisphere], 2, 3 [left hemisphere], and 4 [left hemisphere]), prefrontal cortex (congenitally blind No 1 and 2), and medial superior temporal area, and MST (congenitally blind No 1 and 5 [right hemisphere]) (see Figure 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 [$F(1,8) = 162.08$, $q(FDR) < 0.05$, $p < 0.000001$].

[Figure 2 about here]

[Table 2 about here]

[Table 3 about here]

[Figure 3 about here]

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 and colleagues (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). Additionally, recent studies have suggested that MST is also multisensory (Beer et al., 2013; 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 and colleagues 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 Figure 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 Figure 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 and colleagues 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 and colleagues 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.

References

Ackroyd C, Humphrey NK, Warrington EK (1974) Lasting effects of early blindness: A case study. Q J Exp Psychol 26:114-124

Araneda R, Renier LA, Rombaux P, Cuevas I, De Volder AG (2016). Cortical plasticity and olfactory function in early blindness. Front Sys Neurosci 10:75

Astafiev SV, Shulman GL, Stanley CM, Snyder AZ, Van Essen DC, Corbetta M (2003) Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. J Neurosci 23:4689-4699

Bedny M, Pascual-Leone A, Dodell-Feder D, Fedorenko E, Saxe R (2011) Language processing in the occipital cortex of congenitally blind adults. Proc Nat Acad Sci USA 108:4429-4434

Beer AL, Plank T, Greenlee MW (2011) Diffusion tensor imaging shows white matter tracts between human auditory and visual cortex. Exp Brain Res 213:200-308

Bremmer F, Schlack A, Jon Shah N, Zafiris O, Kubischik M, Hoffmann K-P, et al. (2001) Polymodal motion processing in posterior parietal and premotor cortex: A human fMRI study strongly implies equivalencies between humans and monkeys. Neuron 29:287-296

Burkhalter A, Bernardo KL (1989) Organization of corticocortical connections in human visual cortex. Proc Natl Acad Sci USA 86:1071-1075

Carlson S, Hyvärinen L, Raninen A (1986) Persistent behavioural blindness after early visual deprivation and active visual rehabilitation: A case report. Brit J Ophthal 70:607-611

Castronovo J, Seron X (2007) Semantic numerical representation in blind subjects: The role of vision in the spatial format of the mental number line. Q J Exp Psychol 60:101-119

Cecchetti L, Ricciardi E, Handjaras G, Kupers R, Ptito M, Pietrini P (2015) Congenital blindness affects diencephalic but not mesencephalic structures in the human brain. Brain Struc Funct 1-16

Colby CL, Duhamel JR, Goldberg ME (1993) Ventral intraparietal area of the macaque: Anatomic location and visual response properties. J Neurophysiol 69:902-902

Coluccia E, Mammarella I, Cornoldi, C (2009) Centred egocentric, decentred egocentric, and allocentric spatial representations in the peripersonal space of congenital total blindness. Perception 38:679-693

Cooke DF, Graziano MS (2003) Defensive movements evoked by air puff in monkeys. J Neurophysiol 90:3317-3329

Culham JC, Kanwisher NG (2001) Neuroimaging of cognitive functions in human parietal cortex. Curr Opin Neurobiol 11:157-163

Culham JC, Brandt SA, Cavanagh P, Kanwisher NG, Dale AM, Tootell RB (1998) Cortical fMRI activation produced by attentive tracking of moving targets. J Neurophysiol 80:2657-2670

Fadiga L (2007) Functional magnetic resonance imaging: Measuring versus estimating. Neuroimage 37:1042-1044

Felleman DJ & Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1-47

Fine I, Wade AR, Brewer AA, May MG, Goodman DF, Boynton GM, et al. (2003) Long-term deprivation affects visual perception and cortex. Nat Neurosci 6:915-916

Finocchietti, S., Cappagli, G., & Gori, M. (2017). Auditory spatial recalibration in congenital blind individuals. Front Neurosci 11:76

Gori M, Sandini G, Martinoli C, Burr DC (2010) Poor haptic orientation discrimination in nonsighted children may reflect disruption of cross-sensory calibration. Curr Biol 20:223-225

Gori M, Sandini G, Martinoli C, Burr DC (2014) Impairment of auditory spatial localization in congenitally blind human subjects. Brain 137:288-293

Graziano MS, Gandhi S (2000) Location of the polysensory zone in the precentral gyrus of anesthetized monkeys. Exp Brain Res 135:259-266

Greenlee MW, Frank SM, Kaliuzhna M, Blanke O, Bremmer F, Churan J, et al. (2016) Multisensory integration in self motion perception. Multisens Res 29:525-556

Guerreiro MJ, Putzar L, Röder B (2015) The effect of early visual deprivation on the neural bases of multisensory processing. Brain 138:1499-1504

Hensch TK (2005) Critical period plasticity in local cortical circuits. Nat Rev Neurosci 6:877-888

Hötting K, Röder B (2004) Hearing cheats touch, but less in congenitally blind than in sighted individuals. Psychol Sci 15:60-64

Huang RS, Sereno MI (2007) Dodecapus: An MR-compatible system for somatosensory stimulation. Neuroimage 34:1060-1073

Huang RS, Sereno MI (2018) Multisensory and sensorimotor maps. Handbook Clin Neurol 151:141-161

Huang RS, Chen CF, Sereno MI (2017) Mapping the complex topological organization of the human parietal face area. Neuroimage 163:459-470

Huang RS, Chen CF, Sereno MI (2018) Spatiotemporal integration of looming visual and tactile stimuli near the face. Hum Brain Map 39:2156-2176

Huang RS, Chen CF, Tran AT, Holstein KL, Sereno MI (2012) Mapping multisensory parietal face and body areas in humans. Proc Nat Acad Sci USA 109:18114-18119

Kakei S, Hoffman DS, Strick PL (1999) Muscle and movement representations in the primary motor cortex. Science 285:2136-2139

Kosslyn SM, Pascual-Leone A, Felician O, Camposano S, Keenan JP, Ganis G, et al. (1999) The role of area 17 in visual imagery: Convergent evidence from PET and rTMS. Science 284:167-170

Kourtzi Z, Kanwisher N (2000) Activation in human MT/MST by static images with implied motion. J Cogn Neurosci 12:48-55

Jiang J, Zhu W, Shi F, Liu Y, Li J, Qin W, et al. (2009) Thick visual cortex in the early blind. J Neurosci 29:2205-2211

Iachini T, Ruggiero G, Ruotolo F (2014) Does blindness affect egocentric and allocentric frames of reference in small and large scale spaces? Behav Brain Res 273:73-81

Loomis JM, Klatzky RL, Golledge RG, Cicinelli JG, Pellegrino JW, Fry PA (1993) Nonvisual navigation by blind and sighted: assessment of path integration ability. J Exp Psychol Gen 122:73-91

McCarthy G, Allison T, Spencer DD (1993) Localization of the face area of human sensorimotor cortex by intracranial recording of somatosensory evoked potentials. J Neurosurg 79:874-884

Noppeney U, Friston KJ, Ashburner J, Frackowiak R, Price CJ (2005) Early visual deprivation induces structural plasticity in gray and white matter. Curr Biol 15:488-490

Orban GA, Fize D, Peuskens H, Denys K, Nelissen K, Sunaert S, et al. (2003) Similarities and differences in motion processing between the human and macaque brain: Evidence from fMRI. Neuropsychologia 41:1757-1768

Pan WJ, Wu G, Li CX, Lin F, Sun J, Lei H (2007) Progressive atrophy in the optic pathway and visual cortex of early blind Chinese adults: A voxel-based morphometry magnetic resonance imaging study. Neuroimage 37:212-220

Papadopoulos K, Koustriava E, Kartasidou L (2011) The impact of residual vision in spatial skills of individuals with visual impairments. J Special Educ 45:118-127

Pasqualotto A, Newell FN (2007) The role of visual experience on the representation and updating of novel haptic scenes. Brain Cogn 65:184-194

Pasqualotto A, Proulx MJ (2012) The role of visual experience for the neural basis of spatial cognition. Neurosci Biobehav Rev 36:1179-1187

Pasqualotto A, Lam JSY, Proulx MJ (2013a) Congenital blindness improves semantic and episodic memory. Behav Brain Res 244:162-165

Pasqualotto A, Taya S, Proulx MJ (2014) Sensory deprivation: Visual experience alters the mental number line. Behav Brain Res 261:110-113

Pasqualotto A, Spiller MJ, Jansari AS, Proulx MJ (2013b) Visual experience facilitates allocentric spatial representation. Behav Brain Res 236:175-179

Penfield W, Boldrey E (1937) Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. Brain 60:389-443

Postma A, Zuidhoek S, Noordzij ML, Kappers AML (2008) Keep an eye on your hands: On the role of visual mechanisms in processing of haptic space. Cogn Proc 9:63-68

Qin W, Liu Y, Jiang T, Yu C (2013) The development of visual areas depends differently on visual experience. Plos One 8: e53784

Rizzolatti G, Fogassi L, Gallese V (2002) Motor and cognitive functions of the ventral premotor cortex. Curr Opin Neurobiol 12:149-154

Röder B, Rösler F, Spence C (2004) Early vision impairs tactile perception in the blind. Curr Biol 14:121-124.

Sadato N, Okada T, Honda M, Yonekura Y (2002) Critical period for cross-modal plasticity in blind humans: A functional MRI study. Neuroimage 16:389-400

Sherrick CE, Rogers R (1966) Apparent haptic movement. Perc Psychophys 1:75-180

Sereno MI, Allman JM (1991) Cortical visual areas in mammals. In: Leventhal AG (ed) The Neural Basis of Visual Function. Macmillan, London, pp 160-172

Sereno MI, Tootell RB (2005) From monkeys to humans: What do we now know about brain homologies? Curr Opin Neurobiol 15:135-144

Sereno MI, Huang RS (2006) A human parietal face area contains aligned head-centered visual and tactile maps. Nat Neurosci 9:1337-1343

Sereno MI, Pitzalis S, Martinez AM (2001) Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. Science 294:1350-1354

Smith PL, Little Dr (2018) Small is beautiful: In defense of the small-N design. Psychon Bull Rev Doi.org/10.3758/s13423-018-1451-8

Talairach J, Tournoux P. (1988). Co-Planar Stereotaxic Atlas of the Human Brain. Thieme, Stuttgart.

Takemura A, Kawano K, Quaia C, Miles FA (2002) Population coding in cortical area MST. Ann NY Acad Sci 956:284-296

Uesaki M, Ashida H (2015) Optic-flow selective cortical sensory regions associated with self-reported states of vection. Front Psychol 6: 775

Uesaki M, Takemura H, Ashida H (2018) Computational neuroanatomy of human stratum proprium of interparietal sulcus. Brain Struc Funct 223:489-507

Vercillo T, Burr D, Gori M (2016) Early visual deprivation severely compromises the auditory sense of space in congenitally blind children. Develop Psychol 52:847-853

Wang D, Qin W, Liu Y, Zhang Y, Jiang T, Yu C (2013). Altered white matter integrity in the congenital and late blind people. Neural Plast 2013:128236

Acknowledgements

This work was supported by a Marie Curie IEF (grant number: PIEF-GA-2010-274163) and a grant from the EPSRC (EP/J017205/1).

Legends

Figure 1: The experimental apparatus.

Figure 2: (a) Group averaged polar angle maps. The maps obtained with the sensory stimulation were averaged across the late blind participants using the normalized 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).

Figure 3: Brain hemispheres of each late and congenitally blind participant; hVIP area is indicated

Table 1: Details of the participants (PP): ‘Uni’ means ‘university level’, and ‘Sec’ means ‘secondary school level’. ‘Y’ means ‘yes’ and ‘N’ means ‘no’. ‘L/D’ means ‘light/darkness sensitivity’. Aetiology abbreviations: ‘RoP’, retinopathy of prematurity and ‘Ret pigm’, retinitis pigmentosa.

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).

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