



Citation for published version:

Pasqualotto, A, Furlan, M, Proulx, MJ & Sereno, MI 2018, 'Visual loss alters multisensory face maps in humans', *Brain Structure and Function*, vol. 223, no. 8, pp. 3731-3738. <https://doi.org/10.1007/s00429-018-1713-2>

DOI:

[10.1007/s00429-018-1713-2](https://doi.org/10.1007/s00429-018-1713-2)

Publication date:

2018

Document Version

Peer reviewed version

[Link to publication](#)

This is a post-peer-review, pre-copyedit version of an article published in *Brain Structure and Function*. The final authenticated version is available online at: <https://doi.org/10.1007/s00429-018-1713-2>

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Visual loss alters multisensory face maps in humans

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Citation at time of acceptance, and published version:

7

Pasqualotto, A., Furlan, M. U. A., Proulx, M. J., & Sereno, M. I. (in press). Visual loss alters

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multisensory face maps in humans. *Brain Structure & Function*.

9

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

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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. 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.

1 Introduction

2 Humans, like other primates, are predominantly visual animals. The adaptive importance of
3 vision is reflected in the extensive neural representation of visual information, with over half
4 of the primate brain responsive to visual stimulation (Felleman and Van Essen, 1991; Sereno
5 and Allman, 1991). In turn, experience with the visual world has been found to affect a
6 number of non-visual cognitive modules, such as spatial memory and representation
7 (Pasqualotto et al. 2013b; Guerreiro et al. 2015), semantic processing and memory (Bedny et
8 al. 2011; Pasqualotto et al. 2013a), multisensory integration (Cecchetti et al. 2015; Hötting
9 and Röder 2004), number representation (Castronovo and Seron 2007; Pasqualotto et al.
10 2014) and even olfactory perception (Araneda et al. 2016). The crucial role of visual
11 experience has been revealed by studies that tested people blind from birth, or congenitally
12 blind, in comparison with those who have acquired blindness (or late blind). It has been
13 documented that congenital blindness also has a profound effect on the physical structure of
14 the brain (Jiang et al. 2009; Pan et al. 2007; Qin et al. 2013), potentially giving rise to greater
15 individual differences in functional neuroanatomy as a function of visual experience.

16 The aim of this study is to investigate the role of visual experience on the multisensory
17 topographical maps representing stimuli delivered near/to the face, which were recently
18 discovered in human superior parietal cortex (Sereno and Huang 2006; Huang et al. 2012;
19 Huang et al. 2017). By adapting methods originally used to localise and characterise these
20 areas in non-human primates (Cooke and Graziano 2003; Graziano and Gandhi 2000), they
21 showed that these aligned maps used head-centred coordinates. This suggests that this
22 neocortical area provides a crucial system for mapping objects moving near/to the face.
23 Being able to align visual information with tactile information in such a way as to cancel the
24 effects of eye position is crucial for protecting the face from collision, on the one hand, or for
25 efficiently bringing food to the mouth, on the other. Given the fact that somatosensory

1 coordinates dominate over retinocentric (visual) coordinates in the anterior portion of the
2 intraparietal cortex (in contrast to more posteriorly located intraparietal areas where
3 retinocentric coding is dominant, Sereno and Huang, 2006) the authors surmised that areas
4 such as VIP (ventral intraparietal, see Colby et al. 1993) might best be thought of as a
5 somatosensory area with additional visual inputs. This suggests that the formation of tactile
6 maps in parietal cortex might proceed even in the absence of visual experience.

7 Here we assessed whether spatially organised somatosensory maps of the face in human
8 intraparietal cortex can develop independently of external visual stimulation, or whether they
9 require visual experience. Although there is still some disagreement on the exact homology
10 of VIP between human and non-human primates, there are several studies showing functional
11 equivalence in several cortical areas across humans and primates, included the posterior
12 parietal cortex (Bremmer et al. 2001; Culham and Kanwisher 2001; Sereno and Tootell
13 2005). Moreover, although different research groups tend to use different names to indicate
14 VIP (e.g. DIPSA, aIPS, etc.), **there is abundant literature** supporting the claim that human and
15 primate VIP are functionally overlapping (Culham et al. 1998; Orban et al. 2003; Astafiev et
16 al. 2003). Yet, in our study we will refer to the putative human VIP (hVIP) identified, among
17 the others, by Sereno and Huang (2006).

18 We used a similar procedure to that used by Sereno and Huang (2006), but here we tested
19 congenitally blind participants (i.e. without visual experience), and late blind participants. **In**
20 **their articles Sereno and collaborators reported that when sighted individuals perceived**
21 **tactile stimuli delivered to the face they exhibited the activation of the primary and secondary**
22 **somatosensory cortices (S1 and S2, respectively), but also temporo-parietal areas such as the**
23 **posterior superior temporal sulcus (pSTS), the medio-temporal cortex (MT/MST), and the**
24 **lateral and ventral intraparietal cortices (LIP and VIP, respectively). Finally, they reported**

1 activation of frontal areas such as the dorsolateral prefrontal cortex (DLPFC) and the frontal
2 eye fields (FEF) (Huang and Sereno 2018; Huang et al. 2017 Experiment 1, 2018).

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

19 Method

20 Participants

21 We tested ten right-handed blind participants; five congenitally blind (four males) and five
22 late blind participants (four males), see Table 1. The average age for the congenitally blind
23 group was 50.4 (SD 16.5) and 51.8 (SD 10.5) for the late blind group. On average, late blind
24 participants lost vision at 18.6 years of age. They were screened for MRI contraindications

1 according to standard procedures and written consent was obtained. The procedure was
2 approved by the ethics committee at Birkbeck University of London. We did not include any
3 sighted group because the very same apparatus ('dodecapus') and empirical question had
4 already been extensively investigated in sighted participants by Sereno and collaborators (e.g.
5 Huang and Sereno 2007; Huang et al. 2012). Additionally, the aim of the present work is to
6 investigate the effect of visual experience, thus we tested congenitally and late participants
7 only as this between group comparison provides the necessary contrast to assess the impact
8 of developmental visual experience.

9 Apparatus and procedure

10 Participants were placed into the scanner with twelve MR-compatible plastic air tube nozzles
11 (Huang and Sereno 2007) arranged in a circle around the outer edge of the face as numbers are
12 arranged on the clock-face (see Figure 1). Participants were told to attend the 'air-puffs' emitted
13 by the air tubes, which were delivered from computer-controlled valves to produce light tactile
14 stimulation by adjusting the driving pressure from a compressed cylinder of medical-grade air.
15 Air-puffs were perceived as light, slightly cool touches on a localised region of the face. Face
16 stimulation consisted of four series of air-puffs (two clockwise and two counter-clockwise
17 series), each lasting 520 seconds. Each series included 8 full circles, each of them lasting 64
18 seconds, for a total of 512 seconds of stimulation. Within each runs, eight seconds 'blank
19 'preceded the stimulation.

20 *Data acquisition.* Standard echoplanar images were collected on a 1.5-Tesla Siemens Avanto,
21 with a 32-channel coil (20 coils remaining after removing the top). Functional data were
22 acquired using a T2*-weighted gradient-recalled echo-planar imaging (EPI) sequence (260
23 volumes per scan, 3.2 mm³ voxel size, flip angle 90° , TE=39 ms, TR=2000 ms, 64x64 matrix,
24 bandwidth 1474 Hz/pixel). Structural data were acquired using a T1-weighted 3D anatomical

1 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
2 190 Hz/pixel).

3 *Data analysis.* Data were analysed using Brain Voyager QX 2.3 (BrainInnovation, The
4 Netherlands). The first four volumes were discarded to allow image intensity to stabilise.
5 Three-dimensional motion correction and slice time correction were performed. The data were
6 temporally high pass filtered at 3 cycle/run ($\sim 0.01 \text{ Hz}$). The pre-processed EPI scans were then
7 co-registered with the anatomy. Finally, both functional and anatomical data were normalised
8 and aligned into Talairach space. The temporal phase of the response to the rotating sequence
9 of air-puffs at each voxel was obtained by fitting a model to the time-series. Phase was taken
10 as an indicator of air-puff position in terms of polar angle. Given the timing of the stimulation
11 (i.e., 64 seconds) and the duration of the TR (i.e., 2 seconds), a full cycle lasted 32 TRs and all
12 of them were used as lags in the phase-encoding mapping. A colour scale (red to blue to green,
13 see Figure 1) was used to illustrate the phase of the 8 cycles per scan response, which
14 corresponds to a particular position around the face. For each participant, data from different
15 runs were averaged and projected on an inflated representation of the grey matter. Then all the
16 data were averaged separately for each group, in order to investigate what regions were
17 consistently activated by the stimulation. A spatial threshold of 50 mm^2 and a statistical
18 threshold ($R^2 = 0.22$) were applied to the inflated brain in order to remove spurious activations.

19 [Table 1 about here]

20 [Figure 1 about here]

21 Results

22 *Late blind participants.* In order to inspect how sensory information delivered on the face is
23 mapped on the cortex, and how these maps are affected by visual experience, we used the

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

13 Thus, considering the entire group of late blind individuals, it seems that there is no evidence
14 of topographic maps of the face in intraparietal cortex, and in particular in hVIP. Is it the
15 same when we look at single brains? Indeed, topographic maps are sparsely present in the
16 intraparietal cortex of late blind participants. In fact, only late blind No 3 (right hemisphere)
17 and late blind No 5 (left hemisphere) **presented** topographic maps in correspondence of hVIP
18 (see Figure 3 the late blind side). On the other hand, late blind participants **presented** robust
19 phase activation of the primary motor/somatosensory cortices (late blind No 1, 2, 3, and 5),
20 occipital cortex (late blind No 1, 4, and 5 [right hemisphere]), prefrontal cortex (late blind No
21 2 [right hemisphere] and 4 [left hemisphere]), and MST (late blind No 3) (see Figure 3 late
22 blind side).

23 *Congenitally blind participants.* Overall, congenitally blind participants **presented** different
24 activations with respect to late blind participants. **However, also in this case the** activation was
25 asymmetrical, with the right hemisphere showing a wider set of areas on which the stimulus

1 was mapped. On the left hemisphere, similarly to late blind participants, the brain regions
2 sensitive to the stimulation were located around the inferior portion of the precentral sulcus,
3 more specifically on a posterior portion of cortex commonly identified as the primary motor
4 cortex (M1) controlling the face (Penfield and Boldrey 1937), and an anterior portion
5 commonly associated with the premotor cortex (pMC, Rizzolatti et al. 2002). On the right
6 hemisphere, stimuli were mapped along the precentral sulcus both anteriorly (premotor cortex,
7 pMC; Rizzolatti et al. 2002) and posteriorly (primary motor cortex, M1; Kakei et al. 1999),
8 along the central sulcus both anteriorly (primary motor cortex, M1) and posteriorly (primary
9 somatosensory cortex, S1; McCarthy et al. 1993), and the medial superior temporal area (MST,
10 the large area near the superior temporal sulcus, STS; Takemura et al. 2002), see Figure 2b and
11 Table 3.

12 Again, considering an entire group, in this case congenitally blind individuals, it seems that
13 that there is poor evidence of topographic maps of the face in the intraparietal cortex, especially
14 hVIP. However, looking at single participants, we discovered that several of them possessed
15 topographic maps in the intraparietal cortex; in particular, congenitally blind No 1 (left
16 hemisphere), congenitally blind No 2 (bilaterally), congenitally blind No 3 (bilaterally), and
17 congenitally blind No 5 (right hemisphere) (see Figure 3, congenitally blind side).
18 Additionally, congenitally blind participants presented robust phase activation of the primary
19 motor/somatosensory cortices (congenitally blind No 1 [right hemisphere], 2, 3, 4 [right
20 hemisphere], and 5), occipital cortex (congenitally blind No 1 [left hemisphere], 2, 3 [left
21 hemisphere], and 4 [left hemisphere]), prefrontal cortex (congenitally blind No 1 and 2), and
22 medial superior temporal area, and MST (congenitally blind No 1 and 5 [right hemisphere])
23 (see Figure 3, late blind side).

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

4 [Figure 2 about here]

5 [Table 2 about here]

6 [Table 3 about here]

7 [Figure 3 about here]

8 Discussion

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

22 Another interesting result is that we found phase activity in MST, which plays a role in
23 movement pursuit (both real and apparent) and optic flow perception (Kourtzi and Kanwisher

1 2000; Uesaki and Ashida 2015). Additionally, recent studies have suggested that MST is also
2 multisensory (Beer et al., 2013; Greenlee et al. 2016). In our experiment, participants were
3 required to attend to 12 air-puffs delivered to the face by following a serial order, thus
4 producing an ‘apparent movement’ of the tactile stimulation around the face. In fact, air-puff
5 number 1 **ceased** its air flow when air-puff number 2 began its air flow, air-puff number 2
6 **ceased** its air flow when air-puff number 3 began its air flow and so on, thus simulating the
7 movement of the tactile stimulus from location to location (for the equivalent visual illusion
8 see Sherrick and Rogers, 1966). Therefore, the fact that we found a trend showing that MST
9 is more active in congenitally blind (both as a group **and** as single participants) than late blind
10 participants, suggests that this brain area can develop without visual experience, but it is
11 impaired by the loss of vision. **As a matter of fact, studies by Sereno and colleagues testing**
12 **sighted participants showed the involvement of MT/MST (Huang and Sereno 2018; Huang et**
13 **al. 2017 Experiment 1, 2018).**

14 These phenomena can be explained by taking into consideration the existence of ‘sensitive
15 periods’ during the early phase of human development when brain plasticity is at its peak.
16 During sensitive periods the brain can better adapt to environmental conditions (Hensch
17 2005; Sadato et al. 2002). **The role of sensitive periods is highlighted by studies on**
18 **congenitally blind people who regained vision after the end of the sensitive period. Although**
19 **these studies are rather rare, the consensus is that the brain is only partially able to utilise the**
20 **new visual input (Ackroyd et al. 1974; Carlson et al. 1986; Fine et al. 2003).** In our case,
21 people born blind spent their sensitive period without any visual input, and the brain adapted
22 to this condition; this is **shown** by the existence of topographic maps in congenitally blind
23 participants. On the other hand, people born sighted spent their sensitive period with visual
24 input, and the brain adapted to this condition; yet, *after* the end of the sensitive period these
25 people lost vision and their brain was not fully able to adapt to this new condition; this is

1 **shown** by the lack of well-established topographic maps in late blind participants. Our
2 conclusion is supported by a recent study reporting that late blind participants **exhibited** white
3 matter atrophy on a larger scale than congenitally blind participants (Wang et al. 2013).

4 **Although late blind individuals possessed** sparsely organised topographic maps in the
5 intraparietal cortex, it is extremely unlikely that they had trouble perceiving the air-puffs, or
6 had problems localising them (all participants reported that the air-puffs were salient stimuli
7 occurring around their faces). In fact, late blind individuals can perform the vast majority of
8 tasks at the same level as sighted individuals (e.g. Papadopoulos et al. 2011; Pasqualotto and
9 Newell, 2007). Therefore, it is likely that to track tactile stimuli delivered to the face late
10 blind participants were using mechanisms that did not involve intraparietal topographic maps.

11 In fact, looking at the topographic maps **displayed** in Figure 2a (group maps), we can notice
12 that the late blind participants exhibit topographic maps in correspondence of the primary
13 motor cortex (M1), in particular at the level of the area representing the face (Kakei et al.
14 1999), and the premotor cortex (Rizzolatti et al. 2002). The single-subject view offers further
15 indications of how late blind participants monitored tactile stimuli. In particular the occipital
16 activation **exhibited** by some late blind participants suggests that they might use visual
17 imagery (Kosslyn et al. 1999), while prefrontal activation suggests that they might use
18 conscious strategies (see Figure 3 late blind side). This suggests that, instead of intraparietal
19 topographical maps, different brain networks were used by late blind participants to monitor
20 tactile stimuli delivered on the face, and they were thus unable to show the same
21 compensatory plasticity as the congenitally blind. **In particular, the involvement of motor**
22 **areas (e.g. M1), and the strong hemispheric lateralisation in both late and congenitally blind**
23 **participants is likely to support compensatory plasticity; in fact, Sereno and colleagues did**
24 **not find the activation of motor areas and strong lateralisation in sighted participants**

1 performing tactile perception tasks (Huang and Sereno 2018; Huang et al. 2017 Experiment
2 1, 2018).

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

17 Finally, an important limitation of our study is the small number of participants that,
18 nevertheless, allowed us to draw some cautious conclusions, which are consistent with the
19 available literature and represent a seminal work for future studies. Yet, using a single-
20 subject design can be a strength too, because it eliminates the danger of averaging across
21 important individual differences and obtain a misleading map (Fadiga 2007; Smith and Little
22 2018). In fact, our participants were highly variable in their brain activations and
23 neuroanatomy, and in many cases we could only explain the results by looking at the single-
24 subject views (e.g. topographical maps in congenitally blind's hVIP). Our study suggests that

- 1 changes in sensory experience have strong effects across many levels of the cortical
- 2 hierarchy.

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Acknowledgements

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

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