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Title: Regions of visual cortex responding to tactile stimulation in an individual with longstanding low vision are not causally involved in tactile processing performance

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Abstract

Braille reading and other tactile discrimination tasks recruit the visual cortex of both blind and normally sighted individuals undergoing short-term visual deprivation. Prior functional magnetic resonance imaging (fMRI) work in patient 'S', a visually impaired adult with the rare ability to read both highly magnified print visually and Braille by touch, found that foveal representations of S's visual cortex were recruited during tactile perception, whereas peripheral regions were recruited during visual perception. Here, we test the causal nature of tactile responses in the visual cortex of S by combining tactile and visual psychophysics with repetitive transcranial magnetic stimulation (rTMS). First, we replicate this prior fMRI work in S. Second, we demonstrate that transient disruption of S's foveal visual cortex has no measurable impact on S's tactile processing performance compared to that of healthy controls – a pattern not predicted by the fMRI results. Third, stimulation of foveal visual cortex maximally disrupted visual processing performance in both S and controls, suggesting the possibility of preserved visual function within S's foveal cortex. Finally, stimulation of somatosensory cortex induced the expected disruption to tactile processing performance in both S and controls. These data suggest that tactile responses in S's foveal representation reflect unmasking of latent connections between visual and somatosensory cortices and not behaviourally relevant cross-modal plasticity. Unlike studies in congenitally blind individuals, it is possible that the absence of complete visual loss in S has limited the degree of causally impactful cross-modal reorganisation.

Significance statement

Prior fMRI work in patient 'S' identified that foveal portions of S's visual cortex respond more to tactile processing, whereas peripheral portions respond more to visual processing. Here, we tested whether this foveal processing was causally related to either tactile or visual processing. First, using fMRI we replicate prior work. Second, we demonstrate that TMS of the foveal representation and of somatosensory cortex interfered with visual and tactile discriminations respectively in controls and crucially also in S. The foveal representation in S, which is responsive

46 to tactile stimulation, does not however play a causal role in mediating S's ability to discriminate
47 Braille characters and likely reflects the unmasking of latent connections between visual and
48 somatosensory cortices.
49
50 **Introduction**
51 Whether or not human visual cortex reorganises functionally following deprived visual input is a
52 crucial question in visual neuroscience (Baseler et al., 2011; Cheung et al., 2009; Haak et al.,
53 2015; Sadato et al., 1996). In blind individuals, fMRI studies highlight visual cortex activity during
54 somatosensory tasks (Burton et al., 2002; Sadato et al., 1996) (e.g. Braille reading) and short-
55 term visual deprivation can lead to increased recruitment of visual cortex during somatosensory
56 tasks in normally sighted individuals (Kauffman et al., 2002; Merabet et al., 2007, 2008). Further,
57 somatosensory and auditory task-related activity has been reported in the lesion-projection-zone
58 (LPZ) of patients with macular degeneration (Masuda et al., 2021). Collectively, these fMRI data
59 suggest that some form of cross-modal plasticity is possible in visual cortex.
60 Whilst transient disruption of visual cortex via TMS impairs Braille reading performance in blind
61 individuals (Cohen et al., 1997), its detrimental impact appears to depend on the onset of
62 blindness, with little impact on Braille reading performance of individuals whose blindness occurs
63 after ~14 years of age (Cohen et al., 1997, 1999). Thus, despite considerable fMRI evidence
64 suggesting visual cortex is capable of cross-modal plasticity, whether or not such activity is
65 causally related to cross-modal performance is less clear and may depend on plasticity of the
66 brain that is only present early in life.
67
68 Prior fMRI work (Cheung et al., 2009), capitalized on the rare case of 'patient S', who despite
69 being visually impaired, is capable of both reading print visually and Braille by touch. In S, tactile
70 processing (e.g. Braille reading) selectivity recruited the foveal representation of visual cortex
71 whereas visual processing (e.g. viewing letter strings) recruited more peripheral portions. There
72 was no evidence of central-visual field loss in S, despite the loss of visual responses in the foveal
73 representation. The fact that the foveal representation was recruited during Braille reading in S
74 was interpreted as reflecting retinotopically specific cross-modal plasticity. Although it was argued
75 that in S, such reorganisation was optimal - since only those parts of visual cortex that were not
76 critical for S's remaining low-vision were recruited during somatosensory processing - whether or
77 not this somatosensory activity plays a causal role in S's tactile processing ability is unclear.
78
79 Here, we tested this prediction directly in S by pairing both tactile and visual psychophysics with
80 rTMS of the foveal representation of visual cortex (occipital pole [OP]), somatosensory cortex (S1)
81 and an occipital lobe control region (OC). First, our fMRI experiment replicated prior work in S by
82 demonstrating preferential recruitment of the foveal and peripheral representations of visual
83 cortex during tactile and visual stimulation, respectively (Cheung et al., 2009). Second, we report
84 that despite the pattern of fMRI data in S, transient disruption of OP via repetitive TMS (rTMS)
85 does not alter tactile performance beyond that observed in normally sighted controls. The
86 somatosensory-related activity within the foveal representation of visual cortex of S likely reflects
87 unmasked latent connections with somatosensory cortex rather than reflecting causally relevant
88 cross-modal reorganisation.
89

90 **Methods**
91
92 **Participants**
93 We report fMRI and behavioural measurements from 1 participant with 'low-vision' (Patient S; see
94 **Case Description**) and three control participants with normal vision (C1-3; 2 male and 1 female;
95 ages 21-35. Recruitment of low-vision patients who can still read visual print and are also expert
96 Braille readers for basic research is difficult. Prior work, on which this study is based, published
97 in *Current Biology,* focused on a case study of Patient S and compared fMRI response in S to
98 those of 4 healthy controls. In the current case study of S, we have therefore adopted methods
99 that enable us to perform measurements of single participants. All procedures adhered to
100 protocols based upon the declaration of Helsinki ethical principles for research involving human
101 participants. The ethics committees at the York Neuroimaging Centre and the Department of
102 Psychology at the University of York approved these experiments. All participants provided written
103 informed consent to participate in the experiment.
104
105 **MR Tactile and visual stimuli**
106 Tactile stimuli in the form of Braille letters [(a, l, q or x)] were delivered via piezoelectric stimulator
107 (max amplitude, 300ms). Eight presentations occurred during each 12s block. Visual stimuli
108 consisted of 100% contrast reversing ring patterns (radial frequency 0.16 cycles per degree,
109 reversal rate 6Hz). Ring stimuli extended to 15deg eccentricity. Each run consisted of 10 cycles
110 of 12s on 12s off stimulation using an interleaved paradigm (Visual, rest, Tactile, rest).
111
112 **Scanning Procedure**
113 All MRI data were acquired on a 3.0 Tesla GE Sigma HD Excite scanner. For structural data, two
114 multi-average, whole-head T1-weighted anatomical volumes were acquired for each subject
115 (repetition time = 7.8 ms, echo time = 3 ms, TI = 450 ms, field of view = 290 × 290 × 176, 256 ×
116 256 × 176 matrix, flip angle = 20°, 1.13 × 1.13 × 1.0 mm3). For functional data, gradient recalled
117 echo pulse sequences were used to measure T2* blood oxygen level–dependent data (repetition
118 time = 2,000 ms, echo time = 30 ms, field of view = 192 cm, 64 × 64 matrix, 39 contiguous slices
119 with 3-mm thickness). Images were read-out using an echo planar imaging (EPI) sequence.
120 Magnetization was allowed to reach a steady state by discarding the first five volumes.
121
122 **fMRI Data Analysis and Visualisation**
123 All anatomical and functional data were pre-processed and analysed using the Analysis of
124 Functional NeuroImages (AFNI) software (Cox, 1996) (RRID: SCR_005927). All images were
125 motion-corrected to the first volume of the first run (using the AFNI function *3dVolreg*). Following
126 motion correction, images were detrended (*3dDetrend*) and spatially smoothed (*3dmerge*) with a
127 3mm full-width-half-maximum smoothing kernel. Signal amplitudes were then converted into
128 percent signal change (*3dTstat*). To analyse the functional data, we employed a general linear
129 model implemented in AFNI (*3dDeconvolve*, *3dREMLfit*). The data at each time point were treated
130 as the sum of all effects thought to be present at that time and the time-series was compared
131 against a Generalized Least Squares (GSLQ) model fit with REML estimation of the temporal
132 auto-correlation structure. Responses were modelled by convolving a standard gamma function
133 with a 12s square wave for each stimulus block (Visual, Tactile). Estimated motion parameters

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134 were included as additional regressors of no-interest and fourth-order polynomials were included
135 to account for slow drifts in the MR signal over time. To derive the response magnitude per
136 condition, *t*-tests were performed between the condition-specific beta estimates and baseline. The
137 corresponding statistical parametric maps were aligned to the T1 obtained within the same
138 session by calculating an affine transformation (*3dAllineate*) between the motion-corrected EPIs
139 and the anatomical image and applying the resulting transformation matrices to the T1. In each
140 participant, the pre-processed functional data were projected onto surface reconstructions
141 (*3dvol2surf*) of each individual participant's hemispheres derived from the Freesurfer4 autorecon
142 script (http://surfer.nmr.mgh.harvard.edu/) using the Surface Mapping with AFNI (SUMA)
143 software (Saad & Reynolds, 2012).

144

145 **TMS target localisation**
146 TMS target locations were defined in each participant individually. The occipital pole [OP] target
147 was defined according to the T1-weighted anatomical scan. The occipital control [OC] target was
148 defined as a fixed distance (~1cm) dorsal and anterior of that participants' OP target. Our team
149 has employed a similar approach previously in order to define close proximity control locations
150 relative to our primary target sites (Silson et al., 2013; Strong et al., 2017). The S1 target site was
151 defined as the voxel showing the largest response to tactile stimulation within the appropriate
152 portion of the somatosensory cortex.

153

154 **Psychophysical tasks and stimuli**
155 Tactile and visual thresholds were established in each individual participant prior to TMS
156 sessions. Note that due to S's low-vision the size of the visual stimuli differed from controls.
157 **Tactile threshold:** Braille letters (a, l, q or x) were delivered via piezoelectric stimulator. Each
158 stimulus comprised all 6 pins, which were raised to a minimum pedestal level of 2250 (max
159 available 4095) units. All pins were raised for 100ms, before a subset of these 6 pins were further
160 raised to represent the Braille letter. Participants had to detect the target letter as the pins raised
161 above the background 'noise'. Using a 4AFC paradigm with a 1 up 2 down staircase, the
162 maximum pin displacement was reduced while the noise pin amplitude was held constant to
163 establish a 71% correct threshold for letter detection. **Visual threshold:** Maximum luminance
164 visual letters (white, A, L, Q or X) were presented on a black background (15 degrees for S, 4
165 degrees for controls). Using a 4AFC paradigm with a 1 up 2 down staircase, the background
166 luminance was increased while the letter luminance was held constant to establish a 71% correct
167 threshold for letter detection.

168

169 **TMS Protocol.**
170 A train of four biphasic (equal relative amplitude) TMS pulses, separated by 50 ms (20 Hz) at 70%
171 of the maximum stimulator output (2.6 T) were applied to the participants' scalp using a figure-of-
172 eight coil (50-mm external diameter of each ring) connected to a Magstim Rapid2 stimulator
173 (Magstim). Participants were seated in a purpose-built chair with chin rest and forehead support.
174 The coil was secured mechanically and placed directly above each cortical target (occipital pole
175 [OP}, occipital control [OC], somatosensory cortex [S1]) with the handle oriented parallel with the
176 floor. The position of the coil was monitored and tracked in real time allowing the displacement
177 between the intended and actual site of rTMS delivery to be measured. Each participant

178 underwent eight sessions (2 tasks × (3 TMS sites + 1 no TMS)). Each TMS session contained 35
179 trials (5 training). Stimuli (both Tactile and Visual) were presented according to each participants'
180 specific threshold. rTMS pulses were delivered concurrently with the presentation of the test
181 stimulus. This temporal configuration was identical to that used in previous studies from our
182 laboratory where induced functional deficits were found to be maximized when rTMS was
183 delivered coincident with the stimulus onset.

185 **Resampling of rTMS data**
186 Our study lacked the power to compare S' behavioural performance to the average of the controls
187 as is commonplace. Instead, we adopted a bootstrapping and resampling procedure to
188 demonstrate that the impact of OP stimulation in S was not different from an expected distribution
189 of controls. For each control and session, we randomly sampled 80% of the experimental data
190 (24/30 trials) and calculated the percentage of correct responses. This procedure was then
191 repeated 10,000 times before averaging these values across control participants. Distributions of
192 the difference between conditions (e.g. S1 - OP tactile performance) were then created and
193 compared with the same calculation in S.

195 **Subjective observations from S**
196 We acquired subjective reports from S following rTMS sessions. Following S1 stimulation during
197 tactile processing S reported that "all pins felt the same", "Jaw reflex was a little distracting". S did
198 not report experiencing any tingling (i.e. tactile phosphenes) following S1 stimulation. Following
199 OC stimulation during tactile processing, S reported that "it was a little easier than before (S1),
200 but not great". Following OP stimulation during tactile processing S reported that "That was easier
201 than before (OC)".

203 **Results**

205 **Foveal recruitment during somatosensory processing**
206 First, blood-oxygen-level-dependent (BOLD) fMRI was employed to localise tactile and visual
207 responses in S and three normally sighted controls (C1-C3). **Figure 1**, shows the contrast of
208 Visual *versus* Tactile overlaid onto surface reconstructions of both hemispheres for S (**Figure 1A**)
209 and a representative control (C2, **Figure 1B**). In S, tactile responses are evident at the occipital
210 pole in both hemispheres and throughout somatosensory cortex, whereas visual responses are
211 restricted to more anterior portions of visual cortex that represent the periphery (Wandell et al.,
212 2007). No such somatosensory related activity was observed in the visual cortex of C2. Indeed,
213 visual and tactile responses were restricted to visual and somatosensory cortices, respectively -
214 a pattern replicated in C1 and C3 **(Figure 1C)**.

216 To confirm the replication of prior work (Cheung et al., 2009), three contiguous regions of interest
217 (ROIs) were defined that divided primary visual cortex (V1) into foveal (< 4 deg eccentricity),
218 parafoveal (> 4 < 8 deg) and peripheral (> 8deg) portions using eccentricity data from an
219 independent group-average dataset derived from 29 healthy volunteers. **Figure 1D** shows the
220 median response (given by the t-value for Visual *versus* Tactile) within each ROI for S and all
221 three controls. In S, foveal responses are negative, reflecting tactile recruitment with both

222 parafoveal and peripheral responses becoming increasingly positive (visual recruitment). In
223 contrast, all three controls show positive responses, reflecting visual recruitment in all ROIs that
224 increase in magnitude with increasing eccentricity.
225
226 **TMS target locations**
227 **Figure 2A** shows the three TMS target locations in S, overlaid onto posterior and lateral partially
228 inflated surface reconstructions of the right hemisphere, along with the contrast of Visual *versus*
229 Tactile. The OP target site (black dot), which was defined according to the T1-weighted
230 anatomical scan, can be seen to overlap the tactile responses (at the selected statistical
231 threshold). The OC target (green dot) was defined as a fixed distance (~1cm) dorsal and anterior
232 of our OP target. Our team has employed a similar approach previously in order to define close
233 proximity control locations relative to our primary target sites (Silson et al., 2013; Strong et al.,
234 2017) . The S1 target site (yellow dot) was defined as the voxel showing the largest response to
235 tactile processing.
236
237 To confirm that our anatomical OP target was within tactile responding cortex in S, we defined a
238 region-of-interest (ROI) around the OP target site (500 vertices) and calculated the mean
239 response from this ROI across all 10 tactile and visual fMRI blocks. **Figure 2B** shows the mean
240 response (plus s.e.m) and highlights the preferential recruitment of this region during tactile
241 processing in S. **Figure 2C** shows the median response (t-value) from this OP ROI for both S and
242 all three controls. Whereas in S, a negative response is observed, reflecting tactile recruitment,
243 the opposite pattern is observed in each control. Thus, the pattern of fMRI responses not only
244 confirm prior work in S (Cheung et al., 2009), but also, highlight that responses in the foveal cortex
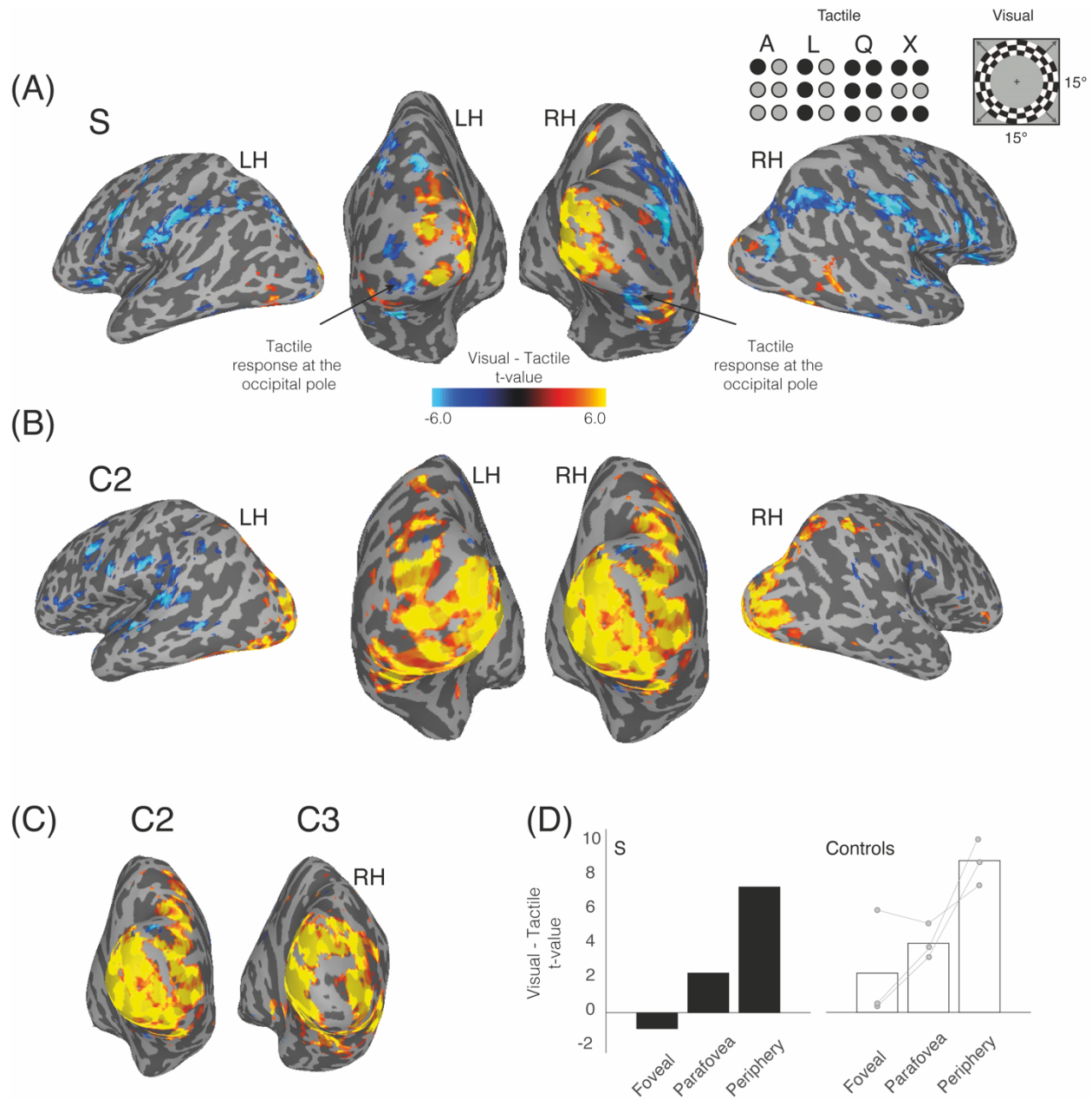245 of S are the opposite to those observed in normally sighted controls.
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Figure 1. Tactile responses in foveal cortex of S.

(A) Tactile and visual stimuli presented during fMRI are displayed inset. The contrast of Visual - Tactile is overlaid onto lateral and posterior partially inflated surface reconstructions of both hemispheres in S (LH=left hemisphere, RH=right hemisphere). Hot-colours represent visually evoked responses, cold-colours represent tactile evoked responses (*p*<0.0001, uncorrected). Tactile responses are evident at the occipital pole in both hemispheres. **(B)** Same as (A) but for a representative control (C2). No tactile responses are evident within visual cortex. **(C)** The contrast of Visual – Tactile is overlaid onto posterior views of the right hemisphere in the additional control participants (C1, C3). No tactile responses are evident at the occipital pole or within visual cortex. **(D)** Bars represent the mean response (t-value) within foveal, parafoveal and peripheral portions of early visual cortex in S (black bars) and the average of controls (white bars). Individual data points are plotted and linked for each control. Negative values represent larger

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263 responses during tactile processing, positive values represent larger responses during visual processing.
264 In S, foveal cortex responds more to tactile over visual processing with the opposite pattern evident in
265 parafoveal and peripheral portions. In controls, all portions show the anticipated larger responses during
266 visual processing.
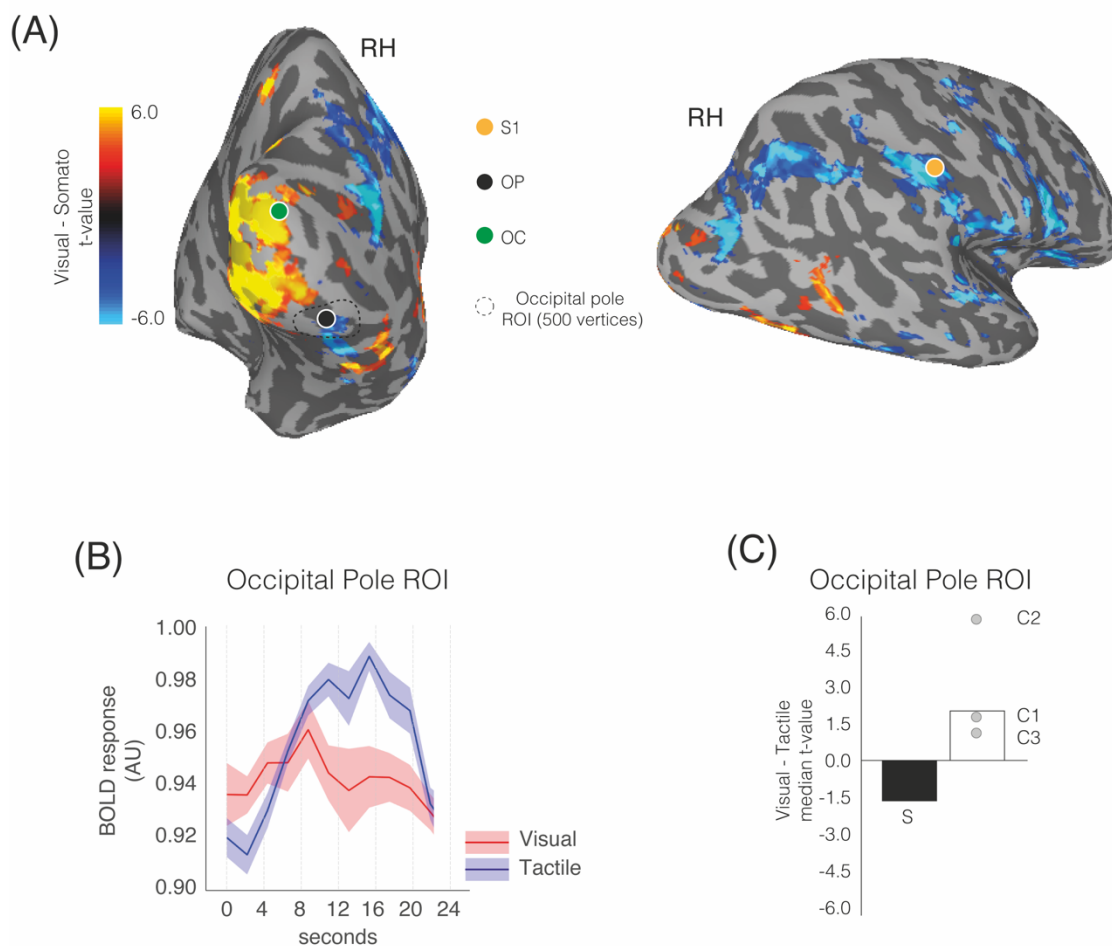
267 **Figure 2. TMS target sites in S and fMRI responses from the occipital pole.**
268 **(A)** Posterior and lateral views of the right hemisphere of S are shown with the contrast of Visual - Tactile
269 overlaid (*p*<0.0001, uncorrected). The occipital pole [OP] target site (black dot) can be seen to overlap
270 tactile responses. The occipital control [OC] target site (green dot) is located dorsal and anterior of the OP.
271 The somatosensory [S1] target site (yellow dot) can be seen to overlap tactile responses within the hand-
272 representation of somatosensory cortex. The OP ROI encompassing the OP target site is shown by the
273 black outline. **(B)** Lines represent the mean (plus s.e.m) response within the occipital pole ROI across all
274 tactile (blue-line) and visual (red-line) fMRI blocks in S. The OP ROI selectively responds to tactile over
275 visual processing. **(C)** Bars represent the mean response within the OP ROI in S (black bar) and the
276 average of controls (white bars). Individual data points are plotted and labelled for each control. Whereas
277 in S, the OP ROI shows a negative response reflecting selective recruitment during tactile processing, all
278 three controls show the opposite pattern, reflecting the expected selective recruitment during visual
279 processing.
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281
282

rTMS of OP has no measurable impact on tactile processing performance in S

Figure 3A shows tactile performance in S and controls for all four conditions. These data reveal a strikingly similar pattern of performance across TMS conditions in S and controls - not predicted on the basis of the fMRI data. In S, tactile performance was maximally impaired (relative to noTMS baseline) following rTMS of S1 and to a lesser extent OC. Critically however, rTMS of OP had little to no detrimental impact on S's tactile performance compared to the no TMS condition. On average controls showed a largely similar pattern with tactile performance maximally impaired following S1 stimulation but no clear detrimental impact of either OP or OC stimulation. Bootstrapping analyses indicate the impact of OP relative to S1 stimulation on tactile performance in S fell within the expected distribution of results in controls **(Figure 3B)**. Similarly, the impairment in tactile processing induced by TMS of S1 in S relative to noTMS baseline was of a similar magnitude to what could be expected from controls (**Figure 3C**).

Impact of TMS on visual processing performance in S and controls

Figure 3D shows visual performance in S and controls for all four conditions. In S, visual performance was impaired slightly (relative to noTMS baseline) following rTMS of both OP and OC, but not S1 (which caused a slight increase in performance). In controls, performance was severely impaired following OP stimulation with much smaller decreases following stimulation of OC and S1, respectively - as was predicted for foveally presented small letter stimuli. Bootstrapping analyses indicate that the effect of OP stimulation on S's visual performance is smaller than what could be expected compared to both stimulation of OC (**Figure 3E)** and the noTMS baseline (**Figure 3F**). The differential impact of OP stimulation on visual performance between S and controls likely reflects the fact that in S visual stimuli were required to be very large (~15 deg) extending much further into the periphery, whereas the targeted OP region represents foveal visual field positions.

Figure 3. Impact of TMS on tactile and visual performances in S and controls.
(A) Examples of the Braille letters presented during both psychophysics and rTMS sessions. **(B)** Schematic of visual stimuli presented during both psychophysics and rTMS sessions. During S's rTMS sessions, letters were highly magnified (15 dva), white and presented on a black background (BG luminance = 0). In controls, letters were smaller (4 dva), and presented on a background luminance determined through psychophysical testing. Note, the figure indicates a BG luminance of 0.9 for illustrative purposed only (see Supplementary data for BG luminance thresholds in C1-C3). **(C)** Bars represent tactile performance (% correct) across conditions (noTMS, S1, OC & OP) in S (solid bars) and the average of controls (faded bars). Individual data points are plotted and linked for each control. The pattern of results is strikingly similar across S and controls. In both, performance is maximally disrupted (relative to noTMS baseline) following TMS of S1, as expected. In S, rTMS of OC caused a slight drop in performance, but crucially rTMS of OP had little to no impact on tactile performance in either S or controls. **(D)** Distribution represents the bootstrapped difference in performance between TMS of S1 - OP in controls (negative values represent a larger drop in performance following rTMS of S1). The red-dashed line indicates the same difference in S. Crucially, this difference falls not only within the distribution of expected differences from controls, but also towards the left-hand edge of the distribution (i.e. the maximum difference that could be expected in controls). This reflects the fact that the impact of OP stimulation in S on tactile performance is as small as could be reasonably anticipated in controls **(E)** Same as (D) but for S1 - noTMS baseline. Again, the result in S falls within that expected from controls. **(F)** Bars represent visual performance (% correct) across conditions (noTMS, S1, OC & OP) in S (solid bars) and the average of controls (faded bars). Individual data points are plotted and

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347 linked for each control. Unlike tactile performance, the pattern of results is more varied between S and
348 controls. In both, performance is maximally disrupted (relative to noTMS baseline) following TMS of OP,
349 but the magnitude of this disruption is larger for controls than for S. In S, rTMS of S1 caused an increase
350 in performance, but had little to no impact in controls. **(G)** Distribution represents the bootstrapped
351 difference in performance between TMS of OP - OC in controls (negative values represent a larger drop in
352 performance following rTMS of OP). The red-dashed line indicates the same difference in S. The difference
353 observed in S falls beyond that expected in controls. **(H)** Same as (G) but for OP - noTMS baseline. Again,
354 the result in S falls outside that expected from controls.
355

356 **Discussion**
357 Our measurements suggest that the somatosensory related activity within the foveal
358 representation of visual cortex of S plays little to no causal role in S's tactile processing
359 performance, and more likely reflects unmasking of latent connections between the
360 somatosensory and visual cortices that are typically suppressed in normally sighted individuals
361 (Masuda et al., 2021).
362

363 The pattern of TMS results in S during Braille reading were largely indistinguishable from those
364 of the control participants, with stimulation of S1 inducing the largest detrimental impact to
365 somatosensory processing. Critically, OP stimulation in S did not induce the reduction in tactile
366 performance predicted on the basis of the fMRI experiments conducted here and in prior work
367 (Cheung et al., 2009). That the foveal confluence of S preferentially responds to tactile over visual
368 information was confirmed and yet the TMS data suggest that such activity is not causally related
369 to tactile performance. In this regard, the pattern of TMS results in S are consistent with those of
370 individuals with late-onset blindness (Cohen et al., 1999) This prior work demonstrated that TMS
371 of occipital cortex induced tactile deficits in both congenitally blind (Cohen et al., 1997) and early-
372 blind individuals but not those whose blindness occurred after 14 years of age (Cohen et al.,
373 1999), suggesting a critical time-frame in which functionally relevant reorganisation of visual
374 cortex occurs. Although S's loss of visual function began at approximately six years of age, and
375 thus within that timeframe, he nevertheless retains visual function. Indeed, S has a full visual field
376 with no evidence of a central scotoma despite the very low-resolution ventral vision (Cheung et
377 al., 2009). It is possible that this preserved peripheral visual function or his age when he lost vision
378 has prevented the foveal representation in visual cortex taking on a causal role in tactile
379 performance as is clearly the case in congenitally and early-onset blind individuals (Cohen et al.,
380 1997, 1999; Sadato et al., 2002).
381

382 The finding that tactile responses in the foveal cortex of S play little to no causal role in S's tactile
383 performance offer the possibility that such cortical resources remain capable of high-resolution
384 visual analysis even in the absence of such an input from the retinogeniculate pathway (Cheung
385 et al., 2009). It is possible therefore that S's foveal representation could revert back to processing
386 high-resolution visual analysis if such retinogeniculate inputs could be restored (Fine et al., 2003)
387 - although prior sight-restorations studies offer mixed encouragement for this possibility (Fine et
388 al., 2003; Ostrovsky et al., 2006). Recent work in patients with macular degeneration (Masuda et
389 al., 2021) highlight the presence of both somatosensory and auditory related activity within the
390 LPZ during a one-back task, but not a passive condition. Such activity in the LPZ is considered to
391 be mediated by task-related feedback signals, rather than feedforward visual input. The pattern

392   of fMRI results in S could be interpreted in a similar manner, in that tactile responses within the
393   foveal representation could reflect task-related feedback from S1 (although distinguishing
394   feedforward from feedback signals definitively with fMRI is challenging due to the sluggishness of
395   the fMRI response). Nevertheless, it is possible that the reduced retinal input to foveal
396   representations in both S and patients with macular degeneration leads to an unmasking of pre-
397   existing connections between visual and other sensory cortices that are suppressed during
398   normal vision (Cheung et al., 2009; Masuda et al., 2021). Only one form of tactile perception (i.e.
399   Braille discrimination) was measured here, and although the pattern of rTMS results is striking, it
400   is nevertheless possible that some other form of tactile function (e.g. texture perception, tactile
401   acuity) might benefit from the tactile recruitment of foveal visual cortex.
402
403   At first glance, it may appear surprising that TMS of OP during visual processing induced a much
404   smaller decrement to performance in S than in controls. We believe however that this is accounted
405   for by considering the size of the visual stimuli presented to S with respect to the foveal visual
406   field representation of the targeted OP region. Placed in this context, it is not altogether surprising
407   that rTMS of S's OP induced a weaker deficit than TMS of OP in controls. It is likely that were it
408   possible to stimulate peripheral parts of V1 in S, a similar drop in performance would be observed
409   to that of OP stimulation in controls during visual perception. Additionally, we considered whether
410   differences in the accuracy of rTMS delivery could provide an alternative explanation for the
411   pattern of results reported here in S, and the critical finding that TMS of OP does not impact tactile
412   processing, in particular. To rule out this possibility, we analysed coil-displacement data acquired
413   during each rTMS trial - an index of stimulation error. We found no evidence for significant
414   variation is displacement as a function of either task or site. Thus, the lack of a detrimental impact
415   on tactile processing following rTMS of OP in S cannot be attributed to poor precision during rTMS
416   delivery.
417
418   In summary, our study of S demonstrates that whilst foveal portions of visual cortex respond
419   preferentially to tactile over visual stimulation, such activity does not causally influence tactile
420   processing performance. Although prior work interpreted S's responses in the foveal
421   representation as reflecting an optimal redistribution of cortical resources (Cheung et al., 2009),
422   our data suggests this pattern likely reflects the unmasking of latent connections between visual
423   and somatosensory cortex that are normally supressed by the feedforward visual input provided
424   to foveal cortex of normally sighted individuals (Masuda et al., 2021). We add weight to the view
425   that cortical responses in individuals with visual deficits that differ from those obtained from
426   controls are not always a signature of functional reorganisation.
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485 **Supplemental Data**

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487 **Table 1. Tactile and visual thresholds for S and controls**

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Participant	Tactile threshold delta (amplitude units)	Visual threshold (Background luminance / size dva)
S	440	0.000 / 15
C1	762	0.988 / 4
C2	731	0.985 / 4
C3	411	0.986 / 4

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