

**Dissociable pathways for moving and static face perception begin
in early visual cortex: evidence from an acquired prosopagnosic**

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Keywords

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Highlights

- An acquired prosopagnosic with a right occipitotemporal lesion completed three fMRI experiments.
- Results showed an impaired response in his right OFA and right FFA.
- The response in his right pSTS was comparable with controls despite his prosopagnosia.
- These results suggest pSTS has functional inputs independent of the OFA.

Abstract

To investigate the functional connections between the core components of the face processing network we tested Herschel, an acquired prosopagnosic patient with a right ventral occipitotemporal lesion. In Experiment 1, Herschel, and control participants, were scanned with functional magnetic resonance imaging (fMRI) while viewing videos of moving faces, or static images taken from the videos. In Experiment 2, participants viewed videos of actors making facial expressions, or static images taken from the videos. In Experiment 3, participants viewed videos of moving faces presented in the left or right visual field. Results showed the neural response in Herschel's right occipital face area (OFA) was impaired for moving and static faces (Experiment 1), moving expressions (Experiment 2) and moving faces in the left visual field (Experiment 3). The response in Herschel's right fusiform face area (FFA) to moving and static faces was impaired in Experiment 1 only, in Experiments 2 and 3 Herschel's FFA response was not significantly different from controls. By contrast, the response in Herschel's right posterior superior temporal sulcus (rpSTS) to moving and static faces and expressions (Experiments 1 and 2) and the visual field response (Experiment 3) was not significantly different from control participants. Our results demonstrate there are cortico-cortical inputs to the pSTS from early visual cortex that are independent of the OFA, a conclusion inconsistent with established models of face processing.

1. Introduction

Detailed studies of neuropsychological patients exhibiting category-selective visual agnosias have provided seminal insights into high-level visual processing (Vaina et al., 1990, Moscovitch et al., 1997, Moro et al., 2008, Susilo et al., 2015) and this is especially true in the case of face perception (Sergent and Signoret, 1992, McNeil and Warrington, 1993, Barton et al., 2002, Rossion et al., 2003, Steeves et al., 2006, Riddoch et al., 2008, Dalrymple et al., 2011). Faces are complex visual stimuli that convey an individual's identity, emotions, state of mind and the direction of their attention. This wealth of information is processed by a network of face-selective areas distributed across the brain that have been linked together in models of face processing (Haxby et al., 2000, Calder and Young, 2005). These models propose there are two functionally distinct face processing pathways beginning in the occipitotemporal cortex. The ventral pathway includes the fusiform face area (FFA) (Kanwisher et al., 1997, McCarthy et al., 1997) and preferentially processes invariant facial aspects, such as identity (Grill-Spector et al., 2004, Rotshtein et al., 2005). The lateral pathway includes the face-selective area in the posterior superior temporal sulcus (pSTS) (Puce et al., 1996) and preferentially processes changeable facial aspects, such as facial expression and eye gaze direction (Andrews and Ewbank, 2004, Winston et al., 2004, Hoffman and Haxby, 2000). Despite these functional differences both pathways are thought to begin in the occipital face area (OFA) (Gauthier et al., 2000), an area that acts as the gateway for the extended face processing network (Haxby et al., 2000). In the current study we tested the hypothesis that the OFA is the sole entry point for the face network by testing Herschel, an acquired prosopagnosic patient with a lesion in his right ventral occipitotemporal cortex.

Herschel suffered two strokes and two transient ischemic attacks in 2008. Subsequent investigation revealed a lesion in his right ventral occipitotemporal cortex, the area of the brain

where the OFA and FFA are typically located. Behavioral testing demonstrated he was impaired at tasks measuring face matching, famous face recognition, face memory, learning new faces, gender discrimination and facial expression recognition (Rezlescu et al., 2012, Rezlescu et al., 2014). The aim of the current study was to systematically compare the functional responses of Herschel's core face-selective areas (OFA, FFA, pSTS) with control participants in three fMRI experiments. We hypothesized that if the OFA is the sole entry point for the face processing network, then the damage to Herschel's right OFA should impair the neural response in his right pSTS. However, if the functional profile of Herschel's right pSTS is comparable with controls, then it is likely that the right pSTS receives functional input from brain areas that are independent of the right OFA.

Neuroimaging studies of healthy participants demonstrate that the pSTS exhibits a greater response to moving faces than static faces, while the OFA and FFA show little or no preference for moving faces (Puce et al., 1998, LaBar et al., 2003, Fox et al., 2009, Schultz and Pilz, 2009, Pitcher et al., 2011a, Pitcher et al., 2019a). This preferential response to motion suggests that the pSTS is receiving functional input from the motion-selective brain area hMT+ (O'Toole et al., 2002). This hypothesis is consistent with anatomical studies in humans and macaques that report cortical connections between motion-selective areas and the STS (Gschwind et al., 2012, Ungerleider and Desimone, 1986b, Boussaoud et al., 1990). These cortical pathways project along the superior temporal sulcus across the lateral brain surface. Evidence for this lateral pathway was also demonstrated in our earlier combined transcranial magnetic stimulation (TMS) and fMRI study (Pitcher et al., 2014). TMS disruption of the right OFA and right FFA did not reduce the response to moving faces in the right pSTS, suggesting that the pSTS has functionally independent cortical inputs.

Likely alternate sources of functional input for the right pSTS are face-selective areas in the left hemisphere, notably the left pSTS. While evidence from different methodologies demonstrates that face processing is right lateralized (Kanwisher et al., 1997, Landis et al., 1986, Pitcher et al., 2007, Yovel et al., 2003), it is clear that face-selective areas in the left hemisphere are also important. For example, TMS delivered over the left pSTS impairs facial expression recognition, but to a lesser extent than TMS delivered over the right pSTS (Sliwinska and Pitcher, 2018). More recently, our dual-site TMS of the bilateral pSTS demonstrated that the right and left pSTS are functionally connected when recognizing facial expressions (Sliwinska et al., 2020). In this study, offline thetaburst TMS (TBS) delivered over the left pSTS prior to online TMS stimulation of the right pSTS doubled the size of the task impairment compared to TMS stimulation of the right pSTS alone.

To further investigate the functional connectivity between face areas across the two hemispheres we also conducted a visual field mapping fMRI study in which face videos were presented alternately in the two visual fields (Pitcher et al., 2020). Consistent with prior studies (Hemond et al., 2007, Kay et al., 2015) we observed a greater response for faces presented in the contralateral visual field in the FFA and the OFA. By contrast, we observed no visual field bias for faces in the pSTS. This lack of visual field bias in the pSTS is consistent with non-human primate studies reporting that motion-selective visual areas (MT, MST, FST) show an increasing representation of the ipsilateral visual field when moving anteriorly along the STS (Ungerleider and Desimone, 1986a). In humans, this suggests that the contralateral visual input into the pSTS comes from the ipsilateral hMT+, while the ipsilateral visual input comes from the contralateral hemisphere, possibly the contralateral pSTS. Because Herschel's lesion is in his right

occipitotemporal cortex (encompassing his right FFA and right OFA), we predicted that the visual field responses in Herschel's right pSTS would be comparable with normal participants.

To measure the functional profile of Herschel's pSTS, we ran three separate fMRI experiments. In Experiment 1, participants viewed short videos, or static images taken from those videos of faces, bodies, objects and scenes. In Experiment 2, participants viewed short videos, or static images taken from those videos of actors making different facial expressions; these were taken from movies on the Internet. In Experiment 3, participants viewed short face videos presented in the two visual fields. Based on prior studies, we predicted a greater response to moving faces than static faces in the pSTS in Herschel and control participants in Experiments 1 and 2 (Puce et al., 1998, LaBar et al., 2003, Fox et al., 2009, Schultz and Pilz, 2009, Pitcher et al., 2011a). In Experiment 3, we predicted there would be a greater response for faces presented in the contralateral visual field in the bilateral FFA and OFA, but there would be no visual field bias in the bilateral pSTS (Pitcher et al., 2020). We hypothesized that if there are independent cortico-cortical connections from early visual cortex via hMT+ into the pSTS that bypass the OFA, then the pattern of responses in Herschel's right pSTS should be comparable with control participants (Figure 1).

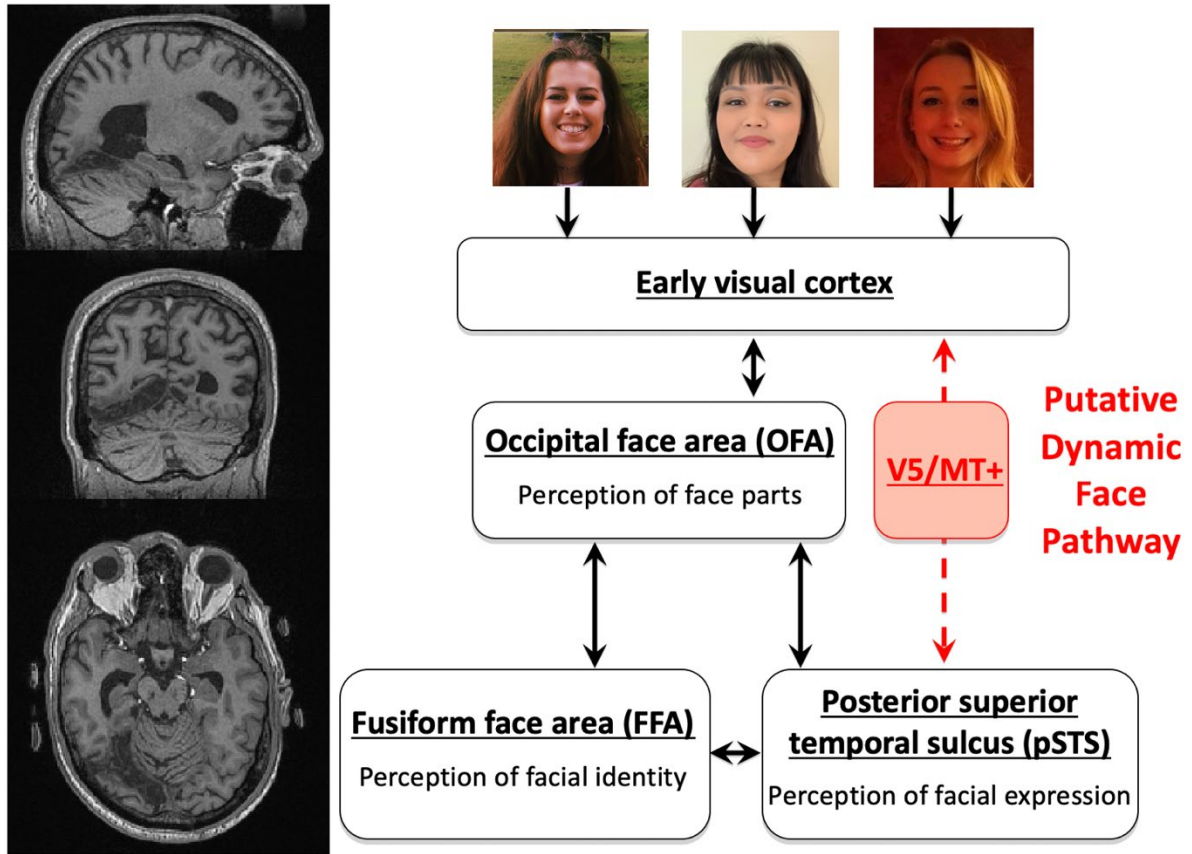


Figure 1. Left panel: structural MRI of Herschel’s lesion in the right ventral occipitotemporal cortex (images shown in radiological format). Right panel: the present study tests the hypothesis that dynamic face information reaches Herschel’s pSTS via a cortical pathway that projects via V5/MT+ and is independent of the OFA (represented by the dotted red line). This model was adapted from O’Toole et al., 2002.

2. Method

2.1.1 Patient Herschel

Herschel is a 62-year-old (born 1956) right-handed British man. He holds a degree in astronomy (he selected his own patient name in honor of his favorite astronomer) and currently manages a science and technology team. In February 2008, he suffered a stroke that caused severe face-related visual recognition impairments, severe navigation problems, and an upper left quadrantanopia. In June 2008, he experienced a second stroke that produced a temporary loss of

color perception and upper right quadrantanopia. In August 2008, he suffered two transient ischemic attacks that produced temporary loss of control of the left leg and temporary speech problems. Currently, he reports only face recognition difficulties and an upper visual field loss (complete left and two thirds right). Herschel's navigation abilities and color perception largely returned, although he reports that both are different since his strokes. Behavioral testing demonstrated that Herschel was severely impaired at recognizing familiar faces, discriminating between unfamiliar identities, and the perception of facial expression and gender (Rezlescu et al., 2012). He showed normal recognition memory for a wide variety of object classes in several paradigms, normal ability to discriminate between highly similar items within a novel object category, and an intact ability to name basic objects (except four-legged animals). Functional brain imaging revealed atypical activation of all core face areas in the right hemisphere, with reduced signal difference between faces and objects compared to controls (Rezlescu et al., 2012). Before participating in any studies Herschel gave informed consent as directed by University College London Ethics committee (Experiment 1) and the York Neuroimaging Centre Research Ethics Committee at the University of York (Experiments 2 and 3).

2.1.2 Control participants

In Experiment 1, we tested 9 right-handed participants (4 males, 5 females, 27 to 58 years old) with normal, or corrected-to-normal, vision and no history of neurological disorders. All participants gave informed consent as directed by the University College London Ethics committee and were paid for their time. In Experiments 2 and 3 we tested 10 right-handed male participants (40 to 65 years old) with normal, or corrected-to-normal, vision and no history of neurological disorders. All participants gave informed consent as directed by the York Neuroimaging Centre Research Ethics Committee at the University of York.

2.2 Stimuli

2.2.1 Experiment 1 – Moving and static faces

Participants viewed dynamic and static stimuli from five different categories (faces, bodies, scenes, objects and scrambled objects). These stimuli were used in previous fMRI studies of face perception (Pitcher et al., 2011a, Pitcher et al., 2019a).

Dynamic stimuli. Dynamic stimuli were 3-second movie clips of faces, bodies, scenes, objects and scrambled objects. There were sixty movie clips for each category in which distinct exemplars appeared multiple times. Movies of faces and bodies were filmed on a black background, and framed close-up to reveal only the faces or bodies of 7 children as they danced or played with toys or adults (who were out of frame). Fifteen different locations were used for the scene stimuli which were mostly pastoral scenes shot from a car window while driving slowly through leafy suburbs, along with some other films taken while flying through canyons or walking through tunnels that were included for variety. Fifteen different moving objects were selected that minimized any suggestion of animacy of the object itself or of a hidden actor pushing the object (these included mobiles, windup toys, toy planes and tractors, balls rolling down sloped inclines). Within each block stimuli were randomly selected from within the entire set for that stimulus category. This meant that the same actor or object could appear within the same block.

Static stimuli. Static stimuli were identical in design to the dynamic stimuli except that in place of each 3-second movie we presented three different static images taken from the beginning, middle and end of the corresponding movie clip. Each still image was presented for one second with no

inter stimulus interval (ISI), to equate the total presentation time with the corresponding dynamic movie clip.

hMT+ localizer. hMT+ was localized using an on/off block design to identify parts of the brain that respond more strongly to coherent dot motion than random dot motion. Stimuli were presented in 12 alternating blocks of coherent and random motion (11.43 sec each). In both conditions, 150 white dots (dot diameter: 0.04 degrees, speed: 5.0 degrees/sec) appeared in a circular aperture (diameter: 9 degrees). During blocks of coherent motion, dots changed their coherent direction every second to avoid adaptation to any maintained direction of motion. The dots in the incoherent condition changed every second but the changes were not coordinated with each other to generate the appearance of random motion. Participants were instructed to focus on a red fixation dot presented at the center of the screen. hMT+ was identified using a contrast of activation evoked by coherent dot motion greater than that evoked by random dot motion (noise).

2.2.2. Experiment 2 – Moving and static facial expressions

Participants viewed dynamic and static stimuli of actors making one of five different facial expressions (anger, happiness, fear, sadness and surprise).

Dynamic stimuli. Eighty 2-second video clips were taken from Internet video platforms (e.g., YouTube, Vimeo). Videos were parts of movies, television shows and homemade clips. 16 clips were found for each of the 5 expressions. The relevant parts of the videos were screen captured and each clip was cropped down to the two seconds of the clip showing a face presenting that particular expression. Only clips presenting clear faces with an obvious expression were used.

Static stimuli. Static stimuli were identical in design to the dynamic stimuli except that in place of each 2-second movie we presented a static image taken from a movie clip used for the dynamic stimuli. We selected an image in which the facial expression was most prominent. Each static image was presented for two seconds with no ISI, to equate the total presentation time with the corresponding dynamic movie clip.

2.2.3. Experiment 3 – Visual field responses in face areas

Visual field responses in face-selective regions were mapped using the same 3-second video clips of dynamic faces described in the dynamic stimuli section above (Pitcher et al., 2011a). Videos were presented at 12×13 degrees of visual angle but were shown centered in the two visual hemifields at a distance of 8 degrees from fixation to the center of the stimulus (Figure 2).



Figure 2. A static image taken from the hemifield visual field mapping stimulus used in Experiment 3. 3-second videos of children interacting with an adult (offscreen) were shown in the left or right visual hemifield. Participants maintained fixation on a centrally presented cross.

2.3 Brain Imaging

Scanning for Experiment 1 was performed using a Siemens 1.5 Tesla MR scanner at the Birkbeck-UCL Neuroimaging Centre at University College London. Functional images were recorded with a Siemens 12-channel phased array head-coil using a gradient-echo EPI sequence (23 interleaved slices, repetition time (TR) = 2000 sec; echo time (TE) = 50 msec; voxel size = $3 \times 3 \times 3$ mm; and a 0.6mm interslice gap). Slices were aligned with the anterior/posterior commissure. In addition, a high-resolution T-1 weighted MPAGE anatomical scan were also acquired for anatomically localizing functional activations.

Scanning for Experiments 2 and 3 was performed using a 3T Siemens Magnetom Prisma MRI scanner (Siemens Healthcare, Erlangen, Germany) at the York Neuroimaging Centre. Functional images for the main and localisation tasks were recorded using a gradient-echo EPI sequence (35 interleaved slices, repetition time (TR) = 2000 msec, echo time (TE) = 30 msec; voxel size = $3 \times 3 \times 3$ mm) providing whole brain coverage. Slices were aligned with the anterior to posterior commissure line. T-1 weighted MPAGE anatomical scan were also acquired for anatomically localizing functional activations.

2.4 Procedure

2.4.1 Experiment 1 – Moving and static faces

Functional data were acquired over 6 blocked-design functional runs lasting 234 seconds each. Each functional run contained three 18-second rest blocks, at the beginning, middle, and end of the run, during which a series of six uniform colour fields were presented for three seconds each. Each run contained two sets of five consecutive stimulus blocks

(faces, bodies, scenes, objects or scrambled objects) sandwiched between these rest blocks, to make two blocks per stimulus category per run. Each block lasted 18 seconds and contained stimuli from one of the five stimulus categories. The order of stimulus category blocks in each run was palindromic (e.g. fixation, faces, objects, scenes, bodies, scrambled objects, fixation, scrambled objects, bodies, scenes, objects, faces, fixation) and was randomized across runs. Functional runs presented either movie clips (the four dynamic runs) or sets of static images taken from the same movies (the two static runs). For the dynamic runs, each 18-second block contained six 3-second movie clips from that category. For the static runs, each 18-second block contained 18 one-second still snapshots, composed of six triplets of snapshots taken at one second intervals from the same movie clip. Participants were instructed to watch the movies and static images but were not asked to perform any overt task. At the end of the session a T1-weighted structural brain scan was also collected to anatomically localise the functional data for each participant.

2.4.2 Experiment 2 – Moving and static facial expressions

Functional data were acquired over 8 blocked-design functional runs lasting 176 seconds each. Each functional run contained six 16-second rest blocks during which a grey screen was presented. Between these rest blocks five stimulus blocks were shown. Each stimulus block presented different actors portraying the same facial expression (anger, fear, happy, sad and surprise). Facial expressions were always presented in the same order. Functional runs presented either movie clips (the four dynamic runs) or static images taken from the same movies (the four static runs). For the dynamic runs, each 16-second block contained eight 2-second movie clips from that category. For the static runs, each 16-second block contained eight two-second still snapshots taken from the corresponding movie clip.

Participants were instructed to watch the movies and static images but were not asked to perform any overt task.

Face-selective ROIs were identified using the dynamic face localiser task described above (Pitcher et al., 2011a). Data were acquired over four runs using a block-design runs, lasting 234 sec each. The number of localizer runs was increased to 4 runs for Experiments 2 and 3 in order to successfully localize the core face-selective areas (OFA, FFA and pSTS) in all participants. At the end of the session a T1-weighted structural brain scan was also collected to anatomically localise the functional data for each participant. In addition, we also collected a T1-FLAIR scan was acquired to improve co-registration of the functional and structural scans.

After exiting the scanner, all participants were asked to identify the emotions of the dynamic (40 items) and static stimuli (40 items). Moving and static stimuli were presented over 4 blocked design runs (2 moving, 2 static). The same stimuli from the scanner session were used (2-second videos or 2-second static images taken from the videos) but unlike in the scanner session the expressions were interleaved. The interleave constituted of a 5-second gap between each presentation during which the participant verbally named the expression being presented.

2.4.3 Experiment 3 – Visual field responses in face areas

Functional data were acquired over 6 blocked-design functional runs lasting 270 seconds each. There was a 10-second rest block at the beginning and end of each run. Participants fixated the center of the screen while 2-sec video clips of children performing

different facial expressions were shown in the two hemifields of the visual field (these are the same stimuli described in Experiment 1). Each functional run contained ten 16-sec blocks during which eight videos were shown. A 10-second rest block was included after each visual mapping block during which a blank black screen was shown. This was included to allow the haemodynamic response to return to baseline before the next visual mapping block began.

2.5 Data analysis

Functional MRI data from all three experiments were analysed using the fMRI Expert Analysis Tool (FEAT) included in the FMRIB (v6.0) Software Library (www.fmrib.ox.ac.uk/fsl). After deleting the first four volumes of each run to allow for T1 equilibrium, the functional images were realigned to correct for small head movements (Jenkinson et al., 2002). The images were then smoothed with a 5mm FWHM Gaussian filter and pre-whitened to remove temporal auto-correlation (Woolrich et al., 2001). Blocks were convolved with a double gamma “canonical HRF” to generate the main regressors. In addition, the estimated motion parameters were entered in as covariates of no interest, to reduce structured noise due to minor head motion. First-level functional results for each participant were registered to their anatomical scan and then to the Montreal Neurological Institute (MNI) 152-mean brain using a 12 degree-of-freedom affine registration. The T1-FLAIR scan was added as an expanded functional image to help aid registration (Jenkinson et al., 2002)

Face-selective ROIs were identified for each participant using a contrast of greater activation evoked by dynamic faces than that evoked by dynamic objects, calculating significance maps of the brain using an uncorrected statistical threshold ($p = 0.01$). We

identified face areas using anatomical landmarks, these were the bilateral: fusiform face area (FFA), occipital face area (OFA), posterior superior temporal sulcus (pSTS). The peak voxel of activation was identified for each area and a 5mm sphere was drawn around this point for individually for each participant. In addition to face-selective ROIs we also identified cortical regions selective for bodies, scenes and objects and motion. The extrastriate body area (EBA) (Downing et al., 2001) was identified using a contrast of dynamic bodies greater than dynamic objects. The lateral occipital area (LO) (Malach et al., 1995) was identified using a contrast of dynamic objects greater than dynamic scrambled objects. V5/MT+ (Watson et al., 1993) was identified using a contrast of coherent motion greater than random motion. Within each functionally defined ROI, we then calculated the magnitude of response (percent signal change from a fixation baseline) for the experimental data.

In order to test whether the responses in Herschel were different from control participants we used the single-case statistical methods for neuropsychology developed by Crawford and Howell (<https://homepages.abdn.ac.uk/j.crawford/pages/dept/SingleCaseMethodology.htm>). (Crawford et al., 1998, Karahalios et al., 2010).

No part of this study was pre-registered. The sample size of the control participants was determined prior to testing but no power analysis was performed. No data were excluded from analysis.

3.1 Results

3.1.1 Identifying ROIs

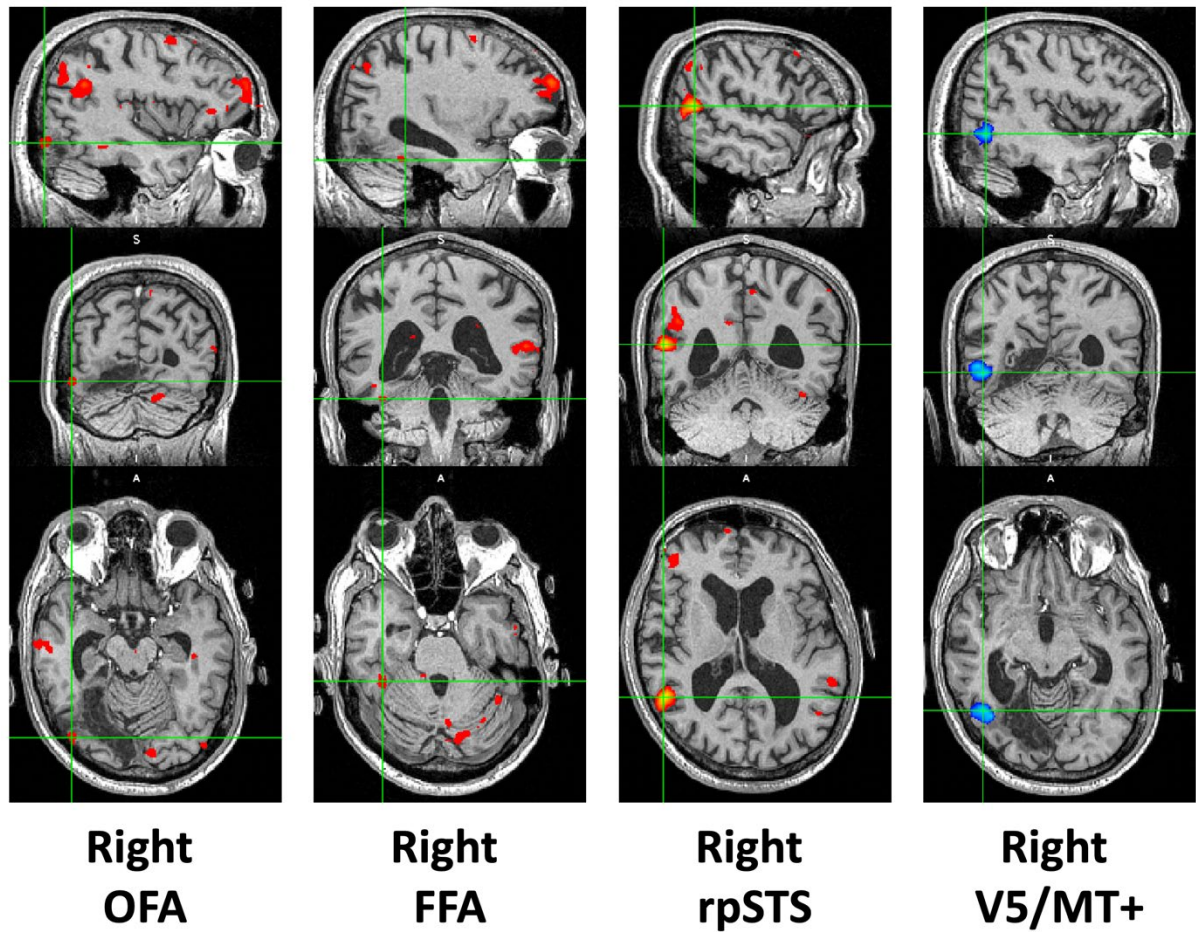


Figure 3. Functional imaging of Herschel's face areas (rOFA, rFFA and rpSTS) in orange and the motion-selective area V5/MT+ in blue. Images are shown in radiological format.

In Experiment 1, face-selective ROIs were identified based on the data from two runs of the dynamic localizer using a contrast of moving faces greater than moving objects. While we were able to localize the OFA, FFA and pSTS in the right hemisphere of all participants, we were unable to successfully localise these same areas in the left hemisphere. We were able to identify the OFA, FFA and pSTS in Herschel's left hemisphere, but this was not the case for all of the controls. Across the nine control participants 5 had an OFA, 5 had an FFA and 6 had the pSTS. The EBA was identified using a contrast of moving bodies greater than

moving objects. LO was identified using a contrast of moving objects greater than moving scrambled objects. hMT+ was identified using a contrast of coherent motion greater than scrambled motion (localiser data for two control participants were not acquired due to technical issues). Herschel's functionally localised right OFA, right FFA, right pSTS and right hMT+ are shown in Figure 3.

In Experiments 2 and 3, the number of dynamic localiser runs was increased from two to four in order to more robustly identify face-selective areas. Face-selective ROIs were identified using a contrast of moving faces greater than moving objects. We were able to successfully localise the OFA, FFA and pSTS in both hemispheres in all participants.

3.1.2 Experiment 1

We compared the response profile of the core face-selective areas in the right hemisphere (OFA, FFA and pSTS) and the motion-selective area hMT+ to moving and static faces in Herschel with control participants (Figure 4). To confirm the pattern of differences between the pSTS and other face areas, we analyzed two interaction effects (patient/controls x ROI) using Crawford & Garthwaite's (2005) RSDT test. Comparing moving faces in rOFA and rpSTS gives $t(8) = 2.466$, $p=0.038$ (one-tailed). Comparing moving faces in rFFA and rpSTS gives $t(8)=1.86$, $p=0.049$ (one-tailed). This demonstrates a significant difference in response across the different ROIs for Herschel and controls.

To further test whether the neural responses across Herschel's ROIs were significantly lower than the control participants we used the single-case statistical methods for neuropsychology developed by Crawford and Howell (Crawford et al., 1998, Karahalios et al., 2010). The results of

this analysis are shown in Table 1. Results showed that Herschel exhibited an impaired response to moving faces in his right FFA and right OFA. There was also an impaired response to static faces in his right OFA but the difference in the right FFA did not reach significance ($p = 0.066$). This impaired response in the OFA and FFA is consistent with the lesion to Herschel's right ventral occipitotemporal cortex. By contrast, the response to moving and static faces in Herschel's right pSTS and in hMT+ was equivalent, or greater, to that of control subjects. There was also no difference in response to moving and static objects in right LO and between moving and static bodies in the right EBA.

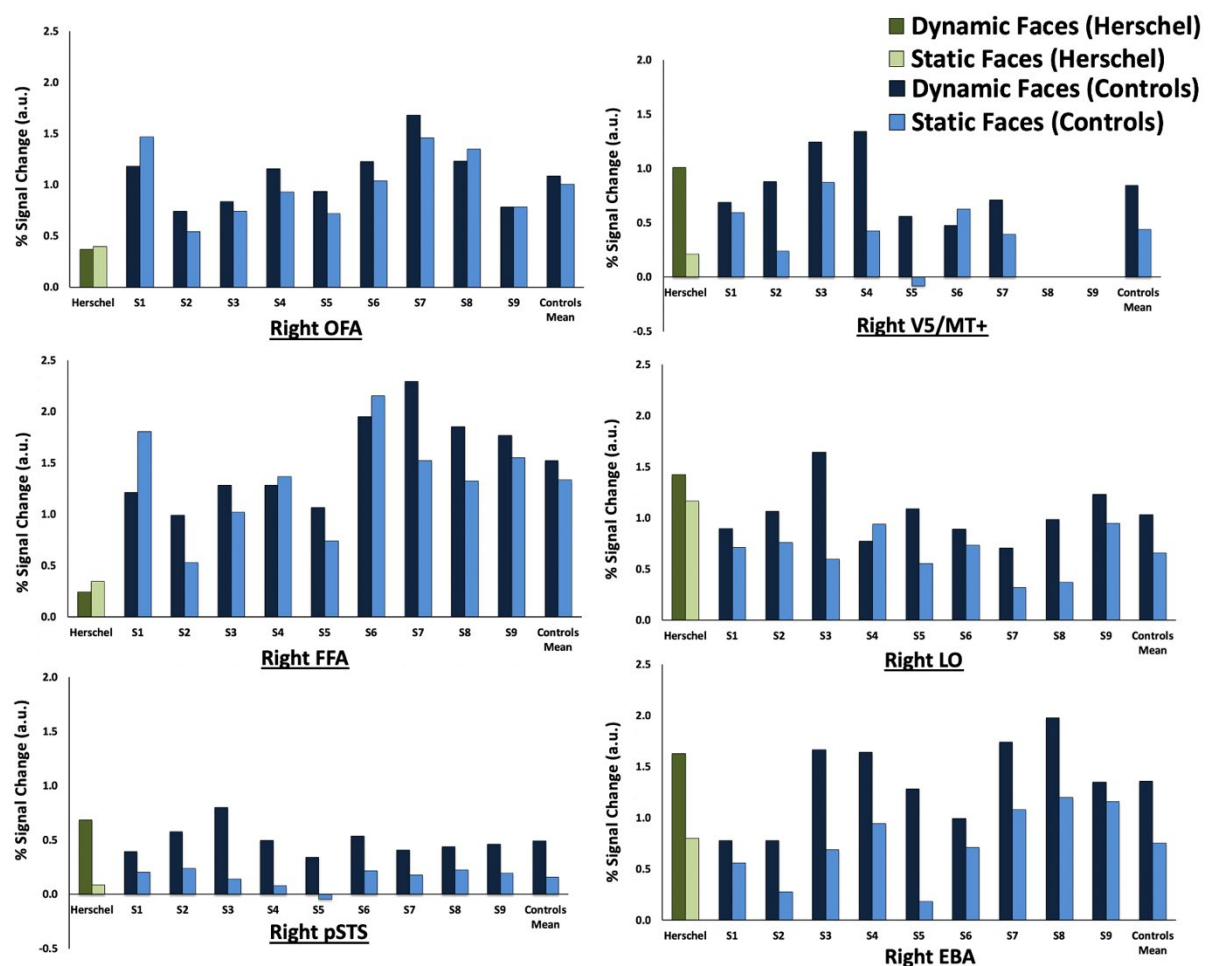


Figure 4. Percentage signal change data for the moving and static stimuli in the OFA, FFA, pSTS, hMT+, LO and EBA in the right hemisphere of Herschel and the control participants. Consistent with the location of his lesion in the right ventral occipitotemporal cortex we observed impaired

responses for moving and static faces in Herschel's OFA and an impaired response for moving faces in his FFA.

	Right OFA		Right FFA		Right pSTS		Right EBA		Right LO		Right hMT+	
	Moving Faces	Static Faces	Moving Faces	Static Faces	Moving Faces	Static Faces	Moving Faces	Static Faces	Moving Faces	Static Faces	Moving Faces	Static Faces
Herschel	0.2	0.3	0.4	0.4	0.7	0.1	1.5	0.8	1.4	1.2	1.0	0.2
Control Mean	1.5	1.3	1.1	1.0	0.5	0.2	1.5	0.8	1.0	0.6	0.8	0.4
Control STDEV	0.5	0.5	0.4	0.4	0.1	0.1	0.6	0.4	0.3	0.5	0.3	0.3
Sample Size	9	9	9	9	9	9	9	9	9	9	7	7
p Value	0.014*	0.05*	0.047*	0.07	0.12	0.3	0.43	0.47	0.1	0.14	0.33	0.24
Population Below Score	1%	5%	5%	7%	88%	30%	56%	53%	89%	85%	67%	25%

Table 1. The results of the statistical analysis performed on the percentage signal change data in Experiment 1. We observed impaired responses for moving and static faces in Herschel's right OFA and an impaired response for moving faces in his right FFA.

3.1.3 Experiment 2 – Moving and static facial expressions

In Experiment 2, we compared the neural response to moving and static facial expressions in the core face-selective areas of both hemispheres in Herschel and control participants. The data for each participant is shown in Figure 5. The results of the single case neuropsychology analysis are shown in Table 2. This analysis showed a significantly lower response to moving faces in Herschel's right OFA. While the response to static faces in the right OFA and to moving and static faces in the Herschel's right FFA were both low they were not significantly different than controls. However, as in Experiment 1, the response to moving and static faces in Herschel's right pSTS was comparable with controls. This pattern was confirmed by an analysis of two interaction effects (patient/controls x ROI) using Crawford & Garthwaite's (2005) RSDT test: Comparing moving faces in rOFA and rpSTS gives $t(10) = 2.558$, $p = 0.014$ (one-tailed); Comparing moving faces in rFFA and rpSTS gives $t(10)=2.121$, $p=0.029$ (one-tailed). We observed no significant differences in the face-selective areas in the left hemisphere.

After exiting the scanner, all participants were asked to name the emotions of the dynamic and static stimuli. The same stimuli from the scanner session were used (2-second videos or 2-second static images taken from the videos), but unlike in the scanner session the expressions were interleaved. Results (Herschel: 70%; Controls 81%, $SD = 4.5\%$) showed that Herschel was able to correctly identify fewer moving facial expressions than control participants ($t = -2.35$, $p = 0.022$). Results (Herschel: 70%; Controls 79%, $SD = 3.38\%$) also showed that Herschel was also able to identify fewer static facial expressions than control participants ($t = -2.74$, $p = 0.011$).

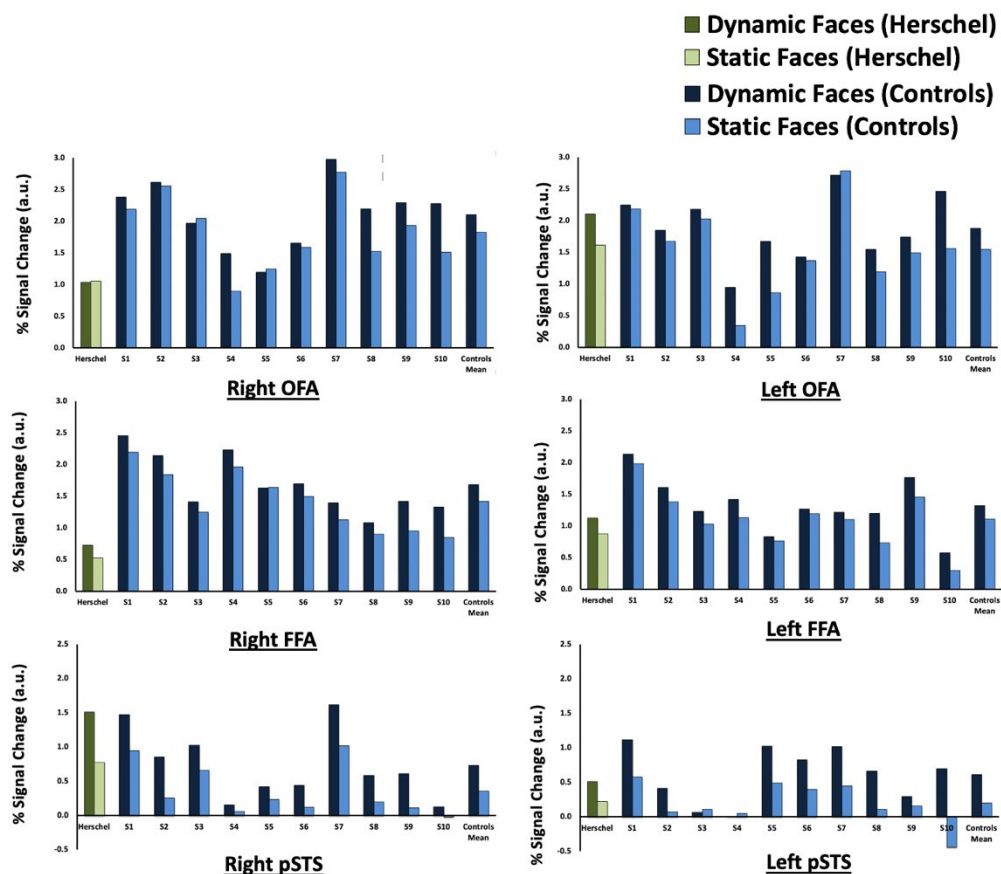


Figure 5. Percent signal change data for the dynamic and static face stimuli in the bilateral FFA, OFA and pSTS. Results showed that an impaired response to dynamic and static faces in Herschel's right OFA, right FFA and left pSTS compared to age-matched controls. However, the

response to dynamic and static faces in Herschel's left OFA, left FFA and right pSTS was not significantly different from controls.

	Right OFA		Right FFA		Right pSTS		Left OFA		Left FFA		Left pSTS	
	Moving Faces	Static Faces	Moving Faces	Static Faces	Moving Faces	Static Faces	Moving Faces	Static Faces	Moving Faces	Static Faces	Moving Faces	Static Faces
Herschel	1.0	1.1	0.7	0.5	1.5	0.8	2.1	1.6	1.1	0.9	0.5	0.2
Control Mean	2.1	1.8	1.8	1.5	0.7	0.4	1.9	1.6	1.3	1.1	0.6	0.2
Control STDEV	0.5	0.6	0.7	0.7	0.5	0.4	0.5	0.7	0.4	0.5	0.4	0.2
Sample Size	10	10	10	10	10	10	10	10	10	10	10	10
<i>p</i> Value	0.046*	0.12	0.09	0.1	0.09	0.17	0.34	0.46	0.34	0.32	0.27	0.25
Population Below Score	5%	11%	9%	10%	91%	83%	65%	53%	35%	32%	27%	25%

Table 2. The results of the statistical analysis performed on the percentage signal change data in Experiment 2. We observed impaired responses for moving faces in Herschel's right OFA only.

3.1.4 Experiment 3 – Visual field responses in face areas

In Experiment 3, we compared the neural response to moving faces presented in the two visual fields in the core face-selective areas of both hemispheres in Herschel and control participants. The data for each participant is shown in Figure 6. As above, we analysed two interaction effects (patient/controls x ROI) using Crawford & Garthwaite's (2005) RSDT test. Comparing moving faces in LVF of rOFA and rpSTS gives $t(9) = 5.365$, $p = 0.0002$ (one-tailed). Comparing moving faces of LVF in rFFA and rpSTS gives $t(9) = 1.94$, $p = 0.0425$ (one-tailed). These results show reliable differences in the pattern of response in pSTS and both OFA and FFA. Further results of the single case neuropsychology analysis are shown in Table 3. This analysis showed a significantly lower response to faces in the left visual field in Herschel's right OFA. While the response to faces in the right visual field in the right OFA was low it was not significantly different

than controls. In the right FFA, there was no significant difference for faces in both visual fields, although the response for left visual field faces was low. By contrast, the responses for faces in both visual fields in Herschel's pSTS was significantly higher than that of control participants.

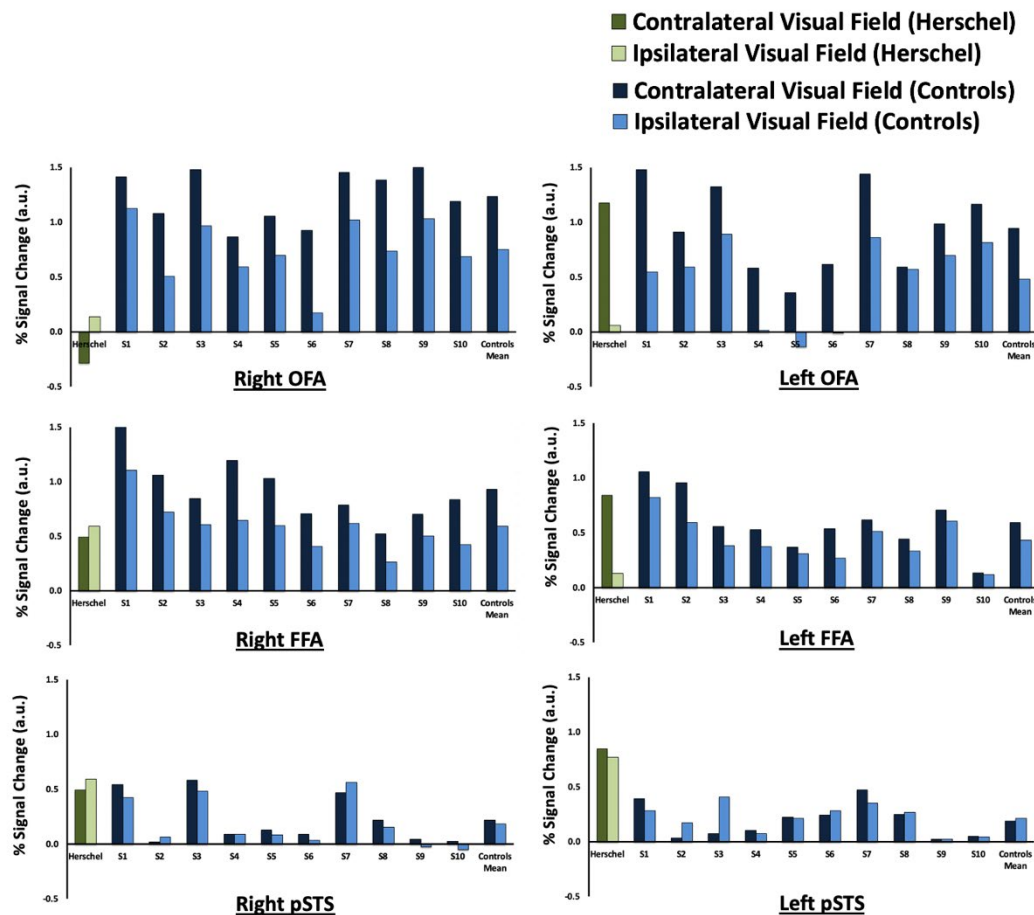


Figure 6. Percentage signal change data for face videos shown in the left and right visual field in the bilateral OFA, FFA and pSTS. Consistent with the lesion in Herschel's right ventral occipitotemporal cortex, we observed an impaired response to faces shown in his left visual field in bilateral OFA and FFA compared with controls. However, there was no impairment in the left visual response in the bilateral pSTS. There was an impairment in the right visual field in Herschel's rOFA only.

	Right OFA		Right FFA		Right pSTS		Left OFA		Left FFA		Left pSTS	
	Left Visual Field	Right Visual Field	Left Visual Field	Right Visual Field	Left Visual Field	Right Visual Field	Left Visual Field	Right Visual Field	Left Visual Field	Right Visual Field	Left Visual Field	Right Visual Field
Herschel	-0.3	0.1	0.5	0.6	0.5	0.6	0.1	1.2	0.1	0.8	0.1	0.2
Control Mean	1.2	0.8	0.9	0.6	0.2	0.2	0.5	1.0	0.4	0.6	0.2	0.2
Control STDEV	0.4	0.4	0.3	0.2	0.2	0.2	0.5	0.6	0.2	0.3	0.1	0.2

Sample Size	10	10	10	10	10	10	10	10	10	10	10	10
<i>p</i> Value	0.002*	0.07	0.1	0.5	0.02*	0.009*	0.2	0.38	0.09	0.2	0.22	0.4
Population Below Score	0%	7%	11%	50%	98%	99%	20%	61%	9%	80%	22%	59%

Table 3. The results of the statistical analysis performed on the percentage signal change data in Experiment 3. We observed impaired responses for faces in the left visual in Herschel's OFA and a significantly higher response than controls for faces in both visual fields in the rpSTS.

4. Discussion

Influential models propose there are two functionally distinct pathways for face processing in the human brain (Haxby et al., 2000, Calder and Young, 2005). The ventral pathway, that includes the fusiform face area (FFA), preferentially processes invariant facial aspects such as identity. The lateral pathway, that includes the posterior superior temporal sulcus (pSTS), preferentially processes changeable facial aspects such as facial expression. Despite these functional differences, both pathways are thought to begin in the occipital face area (OFA). In the current study, we measured the neural response to moving and static faces in these face-selective areas in Herschel, an acquired prosopagnosic patient with a right ventral occipitotemporal lesion. Herschel and control participants were scanned using fMRI while viewing moving and static face stimuli (Experiment 1), moving and static facial expressions (Experiment 2) and moving faces in the left and right visual fields (Experiment 3). Results showed a reduced response in Herschel's right OFA and right FFA, compared with controls in all three experiments. However, the neural response to moving and static faces and the visual field responses in Herschel's pSTS were comparable with control participants.

This pattern of results suggests that the pSTS has functional cortico-cortical inputs that are independent of the FFA and OFA. This conclusion is inconsistent with established models

of face processing, which propose the OFA is sole source of face information for the pSTS (Haxby et al., 2000, Calder and Young, 2005, Pitcher et al., 2011b). The current data are consistent with the alternate hypothesis that the pSTS is part of an anatomically and functionally distinct lateral pathway with independent inputs from early visual cortex that includes the motion-selective area hMT+ (O'Toole et al., 2002).

The results of Experiment 1 demonstrated that the response to moving and static faces in Herschel's right pSTS was comparable with that of controls. This greater response to moving more than static stimuli was also seen in the bilateral pSTS for the facial expression stimuli presented in Experiment 2 in both Herschel and the control participants. Many prior neuroimaging studies have demonstrated that the pSTS shows a greater response to moving faces than static faces (Puce et al., 1998, LaBar et al., 2003, Fox et al., 2009, Schultz and Pilz, 2009, Pitcher et al., 2011a, Pitcher et al., 2019a) suggesting that a possible source of functional input into the pSTS is the motion-selective area hMT+ (O'Toole et al., 2002). An anatomical connection between motion-selective areas and the STS has been shown in both humans (Gschwind et al., 2012) and macaques (Ungerleider and Desimone, 1986a, Boussaoud et al., 1990). Neuropsychological patients with a face-selective pSTS, despite having lesions encompassing the brain area in which the FFA and OFA are typically located, also support the hypothesis that the pSTS has separate cortical inputs from other face-selective areas (Steeves et al., 2006, Dalrymple et al., 2011). Figures 3 and 4 demonstrate that Herschel has area hMT+ in his right hemisphere and that the response to moving and static faces in his hMT+ is comparable with that control participants (Table 1). This result, combined with the normal response to faces in Herschel's pSTS is consistent with the hypothesis that there is a functional pathway from early visual cortex that projects into the

pSTS via hMT+ that is independent of the ventral OFA and FFA (O'Toole et al., 2002, Gschwind et al., 2012, Pitcher, 2014, Duchaine and Yovel, 2015, Pitcher et al., 2017).

Additional likely sources of functional input into the right pSTS are face-selective areas in the left hemisphere. For example, a recent dual-site TMS study demonstrated that disruption of the bilateral pSTS doubled accuracy impairment on an expression recognition compared to disruption of the right pSTS alone (Sliwiska et al., 2020). This is also consistent with our study that mapped the neural responses in face-selective areas to faces presented in different parts of the visual field (Pitcher et al., 2020). Results from this study demonstrated a greater response for faces in the contralateral visual field more than ipsilateral visual field in the bilateral OFA and FFA, a finding consistent with prior studies (Hemond et al., 2007, Kay et al., 2015). By contrast, there was no visual field for faces presented in any part of the visual field in the bilateral pSTS. The results of Experiment 3 replicate and extend the findings of our earlier study by demonstrating that there is no visual field bias in Herschel's bilateral pSTS despite the impaired contralateral visual field response in his right OFA. At least part of the contralateral visual field response in Herschel's right pSTS and right FFA must come from the left hemisphere. The contralateral visual advantage for faces in the FFA observed in control participants is absent in Herschel's right FFA, presumably because of the damage to earlier visual areas in the right hemisphere, including his right OFA. However, we observed an equal response to faces in the contralateral and ipsilateral visual fields in the bilateral pSTS in both Herschel and in control participants. This result is further consistent with an anatomically distinct pathway running from early visual cortex along the STS that is independent of the ventral pathway that includes the OFA and FFA.

Despite the comparable neural response for faces in Herschel's pSTS, he is still profoundly prosopagnosic. Prior testing demonstrated he was impaired at face matching, famous face recognition, face memory, learning new faces, gender discrimination and facial expression discrimination (Rezlescu et al., 2012, Rezlescu et al., 2014). In the current study, all participants were asked to name the emotions expressed by the actors in the videos in Experiment 2 after they exited the scanner. Results showed that Herschel's performance at naming dynamic and static expressions was significantly lower than control participants. It therefore seems likely that despite having separate functional inputs from early visual cortex the ventral and lateral face processing pathways share information at higher levels (e.g. between the FFA and pSTS). For example, TMS delivered over the right occipital face area of neurologically normal experimental participants has been shown to impair facial expression recognition (Pitcher et al., 2008). In addition, our prior combined TMS / fMRI study demonstrated that transient disruption of the right pSTS impaired the response to static faces in the right FFA (Pitcher et al., 2014). These results, combined with prior examples of acquired prosopagnosic patients with lesions to single face-selective areas (Rossion et al., 2003) demonstrates that typical face recognition is dependent on the functional integrity of all the nodes in the face processing network.

In Experiment 2 there were no significant differences between moving and static recognition for either the control participants or for Herschel, despite the normal neural responses in his right pSTS. This suggests that while the pSTS preferentially responds to moving more than static face stimuli the accurate processing of moving face information is still dependent on the ventral face areas like the FFA (Bernstein & Yovel, 2015; Yovel &

O'Toole, 2016). fMRI studies show that information that facilitates identification of expressions and identity can be decoded from both the FFA and the pSTS (Said et al., 2011; Hahn et al., 2017). This is also consistent with behavioural evidence showing that motion information can aid the identification of both facial expressions (Trautmann et al., 2009; Lander & Butcher, 2015) and facial identity (Lander et al., 1999).

In conclusion, the results of the current study demonstrate a comparable response in Herschel's right pSTS with that of control participants. This normal response is interesting because the response in Herschel's right OFA and right FFA is impaired, a result consistent with the lesion to his right occipitotemporal cortex and his behavioural face recognition impairments. The pattern of neural responses across the face-selective areas in Herschel is consistent with recent evidence that has proposed the existence of functionally and anatomically distinct pathway along the lateral brain surface. This pathway projects from early visual cortex, via the motion-selective area hMT+, into the superior temporal sulcus and preferentially responds to moving, more than static faces.

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Transparency statement

We report how we determined our sample size, any data exclusions (of which there were none), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

Data and Materials Availability

Data and materials are available at <https://osf.io/8hq3x/files/>. Due to lack of physical institutional access caused by the COVID-19 pandemic, the complete data were not able to be deposited in the archive at the point of article acceptance. The complete dataset will be deposited in the linked archive as soon as access is possible.

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