

Acquired prosopagnosia with spared within-class object recognition but impaired recognition of degraded basic-level objects

Constantin Rezlescu¹, David Pitcher², and Brad Duchaine³

¹Department of Cognitive, Perceptual and Brain Sciences, University College London, London, UK

²Laboratory of Brain and Cognition, National Institute for Mental Health, Bethesda, MD, USA

³Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH, USA

We present a new case of acquired prosopagnosia resulting from extensive lesions predominantly in the right occipitotemporal cortex. 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. In contrast, Herschel's lateral occipital complex showed normal activation to objects. Behaviourally, Herschel is severely impaired with the recognition of familiar faces, discrimination between unfamiliar identities, and the perception of facial expression and gender. Notably, his visual recognition deficits are largely restricted to faces, suggesting that the damaged mechanisms are face-specific. 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 intact ability to name basic objects (except four-legged animals). Furthermore, Herschel displayed a normal face composite effect and typical global advantage and global interference effects in the Navon task, suggesting spared integration of both face and nonface information. Nevertheless, he failed visual closure tests requiring recognition of basic objects from degraded images. This abnormality in basic object recognition is at odds with his spared within-class recognition and presents a challenge to hierarchical models of object perception.

Keywords: Acquired prosopagnosia; Case study; Face perception; Domain specificity; Object recognition.

Acquired prosopagnosics (APs) are individuals that experience severe face recognition deficits following brain injury. Deficits in acquired prosopagnosia (AP) are varied, and different forms seem

likely to have particular unique neural correlates, so an understanding of AP has the potential to dramatically advance our understanding of face processing in normal brains. Here we report a

Correspondence should be addressed to Constantin Rezlescu, Department of Cognitive, Perceptual and Brain Sciences, University College London, 26 Bedford Way, London WC1H 0AP, UK. (E-mail: c.rezlescu@ucl.ac.uk).

This research was partly supported by a PhD fellowship from the AXA Research Fund to C.R. We thank Herschel for his participation and enthusiasm and Lucia Garrido and Nicole Whitty for help with running some of the tests.

The work of David Pitcher was authored as part of his official duties as an Employee of the United States Government and is therefore a work of the United States Government. In accordance with 17 USC, 105, no copyright protection is available for such works under US Law.

Constantin Rezlescu and Brad Duchaine hereby waive their right to assert copyright, but not their right to be named as co-authors in the article.

325

new case of acquired prosopagnosia, Herschel, a 56-year-old British man with a degree in astronomy, who contacted us in 2009 because of difficulties with face identification following two strokes. The current study aimed to investigate his prosopagnosia and contribute to the debate on face specificity, a central issue in visual recognition.

Are the mechanisms involved in face recognition different from those used in other types of visual recognition? If they are different, we should expect to find APs who are normal with object recognition (“pure” prosopagnosics). If face and other sorts of visual recognition depend on the same mechanisms, the brain damage responsible for prosopagnosia should always impair nonface object recognition. While most APs present severe deficits with faces *and* objects (e.g., Barton, 2008; Boutsen & Humphreys, 2002; Delvenne, Seron, Coyette, & Rossion, 2004; Gauthier, Behrmann, & Tarr, 1999; Levine & Calvanio, 1989; Steeves et al., 2006), the neuropsychological literature also describes APs that seem to be able to correctly identify nonface objects of different types (basic-level recognition) and of the same type (within-level recognition).

A recent paper, Busigny, Joubert, Felician, Ceccaldi, and Rossion (2010), included a detailed description of one such case along with a summary table of 13 other potentially “pure” cases, spanning 25 years of research on acquired prosopagnosia. But as Busigny, Joubert, et al. (2010) note, there is yet no irrefutable evidence for “pure” prosopagnosia. Damasio, Damasio, and van Hoesen (1982) pointed out that within-class discrimination (e.g., distinguish Car A from Car B) is more comparable to face recognition than basic object recognition (e.g., distinguish car from chair) is, and a careful examination of the 13 cases summarized in the table from Busigny, Joubert, et al. (2010) revealed that the ability to identify items within various highly homogeneous object categories was not rigorously tested in many of them. For example, Case 3 from Takahashi, Kawamura, Hirayama, Shiota, and Isono (1995) was tested for naming real basic objects (normal performance), but not for identification of any within-category items. The same can

be said about patient 009 (Barton, Cherkasova, Press, Intriligator, & O’Connor, 2004) and the unnamed patient tested by Wada and Yamamoto (2001), both of whom were able to name fruits, vegetables, and animals normally. Although some researchers (Barton et al., 2004; Schweinberger, Klos, & Sommer, 1995) argued for a parallel between these tests and face recognition, the basic-level recognition tests place demands on the cognitive system that are likely to be different from the individuation demands of face recognition. In addition, these basic-level tests typically produce ceiling effects in control participants, making the discovery of subtle impairments difficult.

Another problem is that some within-class recognition tests used in previous papers had issues that made the interpretation of results problematic. For example, De Renzi and colleagues assessed within-category discrimination in Patient 4 (De Renzi, 1986a) and V.A. (De Renzi, Faglioni, Grossi, & Nichelli, 1991) with two tests. One was a coin discrimination test, in which patients were required to sort local from foreign coins, and in the second test, the patients were successful at recognizing personal items from a set of similar items (e.g., their necktie from other neckties). However, it is not certain they would succeed with less familiar items, and it is impossible to gauge whether the tasks were as difficult as face tests that these patients scored poorly on. Even when sensitive tests for within-level recognition were used, APs often were tested with only one category of objects. Such was the case for patients Anna (De Renzi & di Pellegrino, 1998), W.B. (Buxbaum, Glosser, & Coslett, 1996), L.R. (Bukach, Bud, Gauthier, & Tarr, 2006), F.B. (Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008), and D.C. (Rivest, Moscovitch, & Black, 2009), who recognized exemplars normally from within one of the following categories: glasses, doors, novel objects, and dog breeds.

To summarize, many of the potentially face-specific cases of acquired prosopagnosia do not convincingly demonstrate accurate perception of visually similar exemplars within nonface categories. A rigorous documentation of cases with

normal exemplar discrimination for a wide array of objects is crucial to support claims that acquired prosopagnosia can result from deficits in face-specific mechanisms as the face specificity hypothesis entails. Below we present results from Herschel on perceptual and/or memory tests for cars, houses, tools, sunglasses, guns, horses, novel objects, human bodies, and hairstyles, making him one of the most thoroughly tested prosopagnosics for within-class object discrimination, along with P.S. (Busigny, Graf, Mayer, & Rossion, 2010) and G.G. (Busigny, Joubert, et al., 2010).

In addition to investigating nonface recognition, another way to address whether prosopagnosia can be face-specific is to test predictions of accounts of prosopagnosia that do not involve face-specific mechanisms. One such account is Levine and Calvanio's (1989) proposal that prosopagnosia arises as a result of a general impairment in visual configural processing, defined as "the ability to identify by getting an overview of an item as a whole in a single glance" (p. 159). If individuals have problems forming unified representations of objects from individual parts, they would be impaired with objects for which recognition by parts matching is difficult, and Levine and Calvanio (1989) suggest that faces are such a category. A testable prediction of this view is that prosopagnosics will be impaired with objects for which recognition is normally done by parts, but for which critical chunks have been occluded such as Mooney-type objects (Mooney, 1957). Indeed, patient L.H. performed poorly in tests of visual closure, in which he was required to identify objects or words presented under challenging viewing conditions (in incomplete form or with visual noise added, see Figure 5) (Levine & Calvanio, 1989). L.H., however, had a wider range of cognitive deficits, including basic-level object naming difficulties (Levine & Calvanio, 1989; Levine, Calvanio, & Wolf, 1980), which makes the interpretation of his results problematic. In contrast, several other APs with unimpaired object recognition showed normal performance in visual closure tasks (De Renzi, 1986a; De Renzi & Pellegrino, 1998; De Renzi et al., 1991; Henke, Schweinberger, Grigo, Klos, & Sommer, 1998;

Whitely & Warrington, 1977). Here we investigate whether Herschel's prosopagnosia is associated with a deficit in general configural processing that may pass undetected in usual object recognition, but become apparent in tests of visual closure. We also test Busigny, Joubert, et al. (2010) related but more specific claim that acquired prosopagnosia is necessarily linked to a deficit in face-specific (rather than general) configural processing.

CASE REPORT: HERSCHEL

Herschel is a 56-year-old (born 1956) right-handed British man. He holds a degree in astronomy (hence his patient name) and currently manages a science and technology team. Herschel contacted us through the Prosopagnosia Research Center website (www.faceblind.org) in October 2009 because he suffered from face recognition problems. In February 2008 he suffered a stroke that produced prosopagnosia, face-related visual anomalies ("mouths had tiger-like snarls"), severe navigation problems ("I could not navigate around the streets where I live"), and an upper left quadrantanopia. In June 2008 a second stroke produced a temporary loss of colour perception and upper right quadrantanopia. In August 2008 he suffered two transient ischaemic 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). Navigation abilities and colour perception largely returned, although Herschel says that they remain different from how they were before his strokes. Nevertheless, he seemed to effortlessly find his way around London and the inside of the building where he was tested, and he performed normally in our colour perception tests (see below). He is intellectually normal (see tests below) and continues to run his lab.

Neuroimaging findings

Whole-brain imaging was performed on a Siemens 1.5 Tesla MR scanner at the Birkbeck-UCL

Neuroimaging Centre (BUCNI) in January 2010. Functional data were acquired over four blocked-design functional runs each lasting 234 s using a gradient-echo echo planar imaging (EPI) sequence (23 slices, repetition time, TR = 2 s, echo time, TE = 50 ms, voxel size = 3 × 3 × 3 mm). In addition, a high-resolution anatomical scan (T1-weighted FLASH, TR = 12 ms; TE = 5.6 ms; 1-mm³ resolution) was acquired at the start of each scanning session for anatomically localizing functional activations. In addition to Herschel, we also scanned four male control subjects (age range 38–48 years).

Structural data (Figure 1) showed hydrocephalus with enlargement of the lateral ventricles, the third ventricle, the fourth ventricle, and the interpeduncular fossa. An extensive cyst located above the right tentorium cerebelli suppressed the right ventral and medial occipital lobe including occipitotemporal gyrus, occipital gyrus, and lingual gyrus. The cyst extended to the right hippocampal formation, but did not reach or affect the right amygdala. There was a very minor midline shift in the cerebellar vermis.

To identify category-selective regions in the visual cortex, we used a dynamic functional localizer (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011). Stimuli were 3-second movie clips of faces, bodies, scenes, objects, and scrambled objects. Each functional run contained two sets of five consecutive dynamic stimulus blocks (faces, bodies, scenes, objects, or scrambled objects) sandwiched between rest blocks, making 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. To focus attention, participants were instructed to press a key whenever the subject of the movie clip was repeated twice in a row (1-back task).

Functional imaging data were analysed using FSL (Smith et al., 2004). 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, Bannister, Brady, & Smith, 2002). The images were then smoothed with a 5-mm FWHM (full width at half maximum) Gaussian filter and pre-whitened to remove temporal autocorrelation (Woolrich, Ripley, Brady, & Smith, 2001). The resulting images were entered into a subject-specific general linear model with five conditions of interest corresponding to the five categories of visual stimuli (faces, bodies, scenes, objects, and scrambled objects). Blocks were convolved with a double-gamma canonical hemodynamic response function (Glover, 1999) 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. Functional images were then registered to each participant's individual structural scan using a 12-degrees-of-freedom affine transformation (Woolrich et al., 2001).

The last two functional runs were used to define category-selective regions of interest (ROIs) within each participant. We identified face regions by contrasting faces greater than objects, body regions by contrasting bodies greater than objects, scene regions by contrasting scenes greater than objects, and object regions by contrasting objects greater than scrambled objects. The same statistical threshold ($p = 10^{-3}$, uncorrected) was used for all participants. Within each functionally defined ROI, we then calculated the magnitude of response (percentage signal change, or PSC, from a fixation baseline) to the conditions of the four stimulus categories (faces, bodies, scenes, objects, and scrambled objects), using the data collected from the first two runs. All of the data used to calculate PSC were independent of the data used to define the ROIs.

Although we could identify all core face areas in Herschel's right hemisphere, a comparison between Herschel's and controls' activation levels to different stimulus categories revealed an atypical pattern for Herschel (Figure 2). In all face areas, his absolute PSCs to faces were below those of controls, as were the relative increases in PSC from objects to faces. We note that the differences are not statistically significant (all $ps > .13$), although we also point out the limited statistical

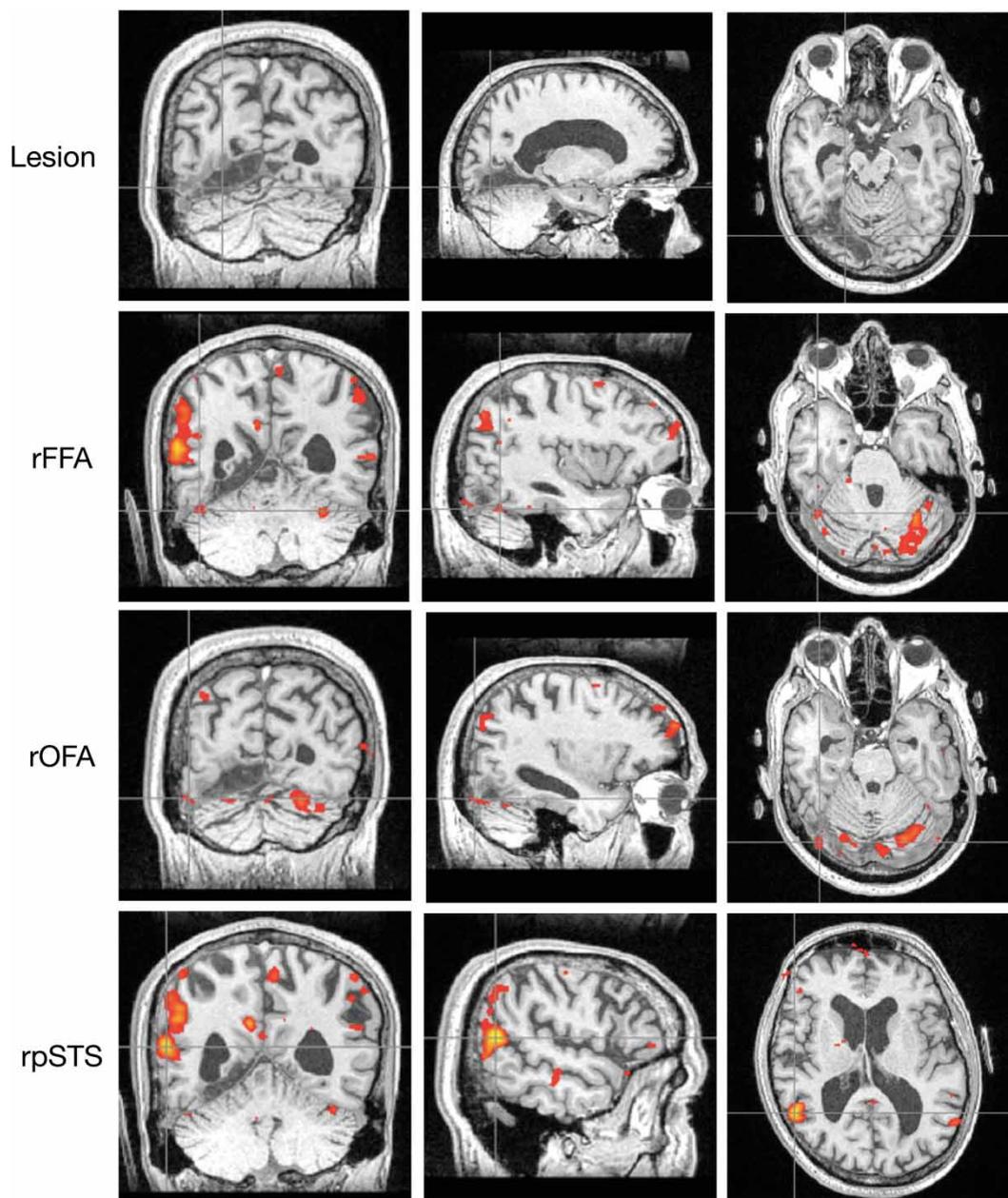
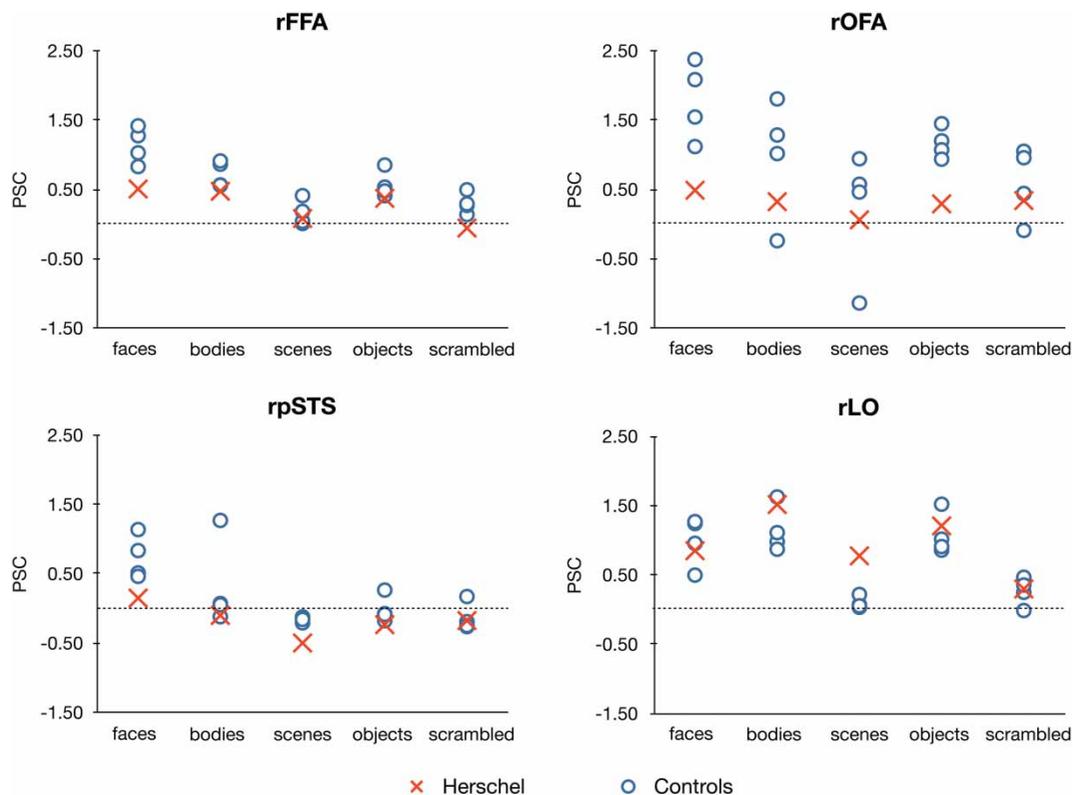


Figure 1. Structural and functional imaging of Herschel showing lesion location and activation of right fusiform face area (rFFA), right occipital face area (rOFA), and right posterior superior temporal sulcus (rpSTS). Images are shown in radiological orientation (right hemisphere on the left). To view a colour version of this figure, please see the online issue of the Journal.



	Herschel	Control 1	Control 2	Control 3	Control 4
rFFA	42, -42, -28	42, -34, -25	42, -42, -28	38, -46, -20	40, -44, -18
rOFA	44, -80, -16	43, -82, -16	40, -80, -10	38, -88, -14	44, -82, -14
rpSTS	58, -52, 16	59, -41, 8	52, -48, -2	60, -36, 4	50, -42, 2

Figure 2. Magnitude of response (percentage signal change, PSC, from a fixation baseline) in the right hemisphere face and object areas to five stimulus categories (faces, bodies, scenes, objects, and scrambled objects). Below, MNI (Montreal Neurological Institute) coordinates for peak activations (during the face localizer) in the face areas. rFFA = right fusiform face area. rOFA = right occipital face area. rpSTS = right posterior superior temporal sulcus. rLO = right lateral occipital cortex. To view a colour version of this figure, please see the online issue of the Journal.

power provided by such a small control group. The levels of activation in the left fusiform face area (FFA) and left superior temporal sulcus (STS) were similar to those in the right hemisphere. We could not identify a left occipital face area (OFA) in Herschel, but one control did not show a left OFA as well. Herschel also failed to show a right parahippocampal place area (rPPA) as this region of cortex was damaged by his stroke. The other category-selective regions targeted by our functional localizer (Pitcher et al.,

2011) were present, including the lateral occipital complex (LOC). Herschel's activation to objects in the LOC was comparable to that seen in controls, suggesting spared functional mechanisms for object recognition.

General neuropsychological assessment

We tested Herschel on his general intellectual and low-level visual abilities, to exclude them as possible causes of his reported difficulties with faces.

Table 1. General neuropsychological assessment of Herschel, showing normal general cognitive skills (A and B) and normal low-level vision (C and D)

A. General cognitive skills				B. Digit Span Memory			Controls	
	Herschel	Max		Herschel	<i>M</i>	<i>SD</i>		
Abbreviated Ravens	11	12	98th percentile	Scaled score	11	10	3.0	
National Adult Reading	57	61	high upper range					
C. Low-level vision				D. Recognition Battery			Controls	
	Herschel	Max/normal		Herschel	<i>M</i>	<i>SD</i>		
Visual acuity	20/19	20/20	normal	Length Match	28	26.9	1.6	
Contrast sensitivity (Michelson)	0.95%	0%	normal	Size Match	28	27.3	2.4	
Ishihara Color Perception Test	8	8	normal	Orientation Match	27	24.8	2.6	
Munsell Hue Text	23	0	upper range	Position of Gap	37	35.1	4.0	

Consistent with his reports, he scored within the normal range for all these tests (see Table 1 for detailed results). Herschel was in the 98th percentile for his age group at the Abbreviated Raven's Matrices, a test designed to measure abstract reasoning, and was in the high range for Digit Span Memory Forward (score 12) and Backward (score 7), demonstrating his normal working memory. His language skills were also intact: He correctly recognized 57 out of the 61 words presented in the National Adult Reading Test (he did not know how to pronounce: *epergne, vivoace, talipes, synecdoche*).

Herschel suffers from a full upper left and partial right quadrantanopia, but his low level vision is otherwise normal. His visual acuity, contrast sensitivity, and colour perception are all in the upper ranges. His visuospatial perceptual skills were assessed using the Birmingham Object Recognition Battery of tests (Riddoch & Humphreys, 1993), and he discriminated line length, size, orientation, and position of gap normally.

Face processing abilities

Next we performed a series of tests to experimentally confirm his deficits in recognizing facial identity and to determine whether he also had deficits with evaluations of facial expressions and facial gender. In all following experiments, significance of test scores differences between Herschel and

controls was assessed using Crawford's modified *t* test for single case studies (Crawford & Howell, 1998). Results are summarized in Figure 3.

Experiment 1: Famous face recognition

In a *Famous Faces* test (Duchaine & Nakayama, 2005), participants were presented with 60 photographs of people familiar to most Britons, cropped so that only faces were visible. Each face was displayed for 3 s, and participants named the individual or provided uniquely identifying information. We compared Herschel to a middle-aged control group of 16 UK adults ($M = 44.1$ years).

Herschel identified only 3 out of the 60 faces presented, more than 7 standard deviations below controls ($M = 47.3$, $SD = 6.2$; $t = 6.93$, $p < .001$). To verify that the personalities presented were familiar to Herschel, we asked him afterwards which individuals were sufficiently known to him to allow recognition; he confirmed that he knew 48 of the famous people presented.

Experiment 2: Face matching

The *Face Matching* task is designed to test the ability to match unfamiliar faces for identity across different viewpoints. In contrast to the *Famous Faces* test, performance does not rely on long-term memory. Participants were presented with a target face (frontal view) for 400 ms, followed immediately by three faces presented

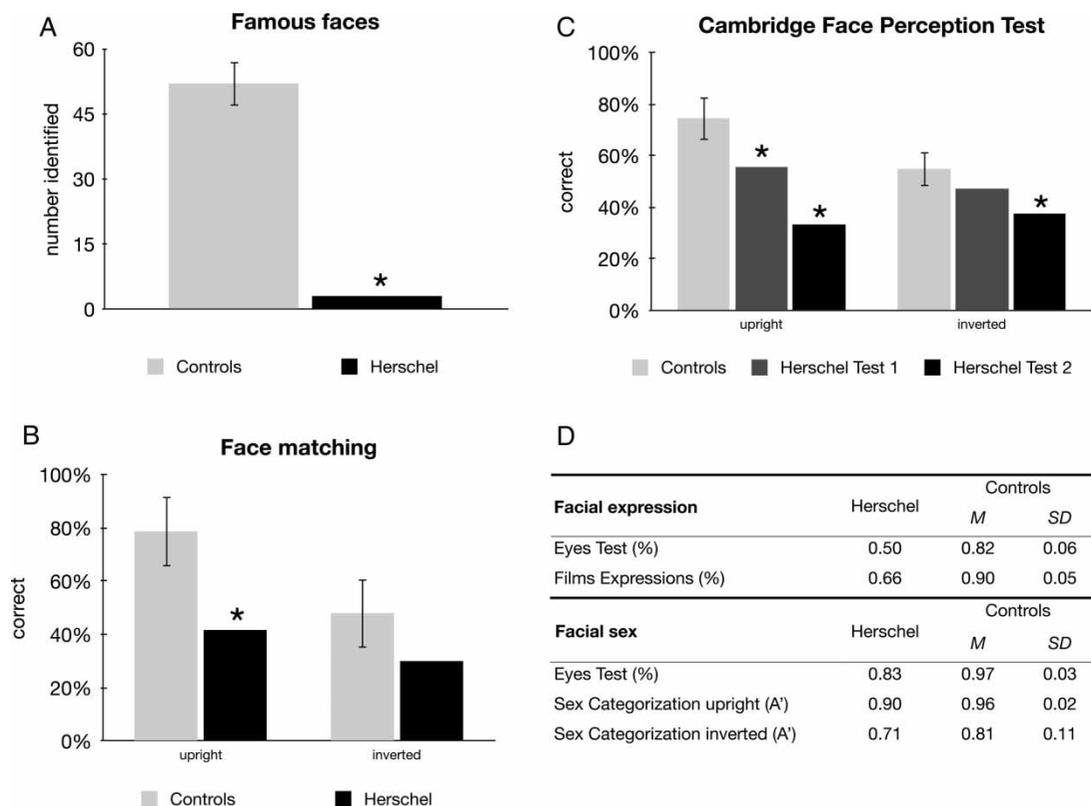


Figure 3. Face processing assessment: Herschel was severely impaired with: (A) face recognition; (B) face matching; (C) face perception; (D) inferring emotional and sex information from faces. Error bars show ± 1 standard deviation. Stars show significant differences (using Crawford's modified *t* test) between performance of Herschel and that of controls.

simultaneously as half-profiles for 2,000 ms. Participants chose which one of the three test faces was the same individual as the target face. The stimuli were all male faces, with their hair completely covered by a standard black cap, so that judgements were based on facial features. Sixty trials with upright faces and 60 trials with inverted faces were randomly interleaved. Ten age-matched participants (6 female, age range: 47–61 years old, $M = 53.6$ years) provided control data.

Herschel's accuracy at matching upright faces was 41.8% (chance level 33.3%), or 2.8 standard deviations below that of controls ($M = 78.7\%$, $SD = 13.2\%$; $t = 2.67$, $p = .026$). He scored slightly below chance for inverted faces: 30.0%

compared to the average 48.0% ($SD = 13.1\%$; $t = 1.31$, $p = .223$) achieved by control participants. Herschel's inversion effect of 11.8% was the lowest from all participants and substantially lower than controls' average of 30.7% ($SD = 14.0\%$), although the difference was not statistically significant ($t = 1.29$, $p = .230$).

Experiment 3: Face perception

The results above demonstrate Herschel's problems with recognizing the identity of previously seen faces. It is possible that his pronounced prosopagnosia is due to an inability to remember faces, while his perception of faces is still normal. To test this possibility, we used the *Cambridge Face Perception Test* (CFPT; Duchaine, Germine,

& Nakayama, 2007; Duchaine, Yovel, & Nakayama, 2007). In it, participants have one minute to sort six test faces according to their similarity to a target face. Test faces are morphed images containing different proportions of the target face: 28%, 40%, 52%, 64%, 76%, and 88%. There are eight trials with upright faces and eight trials with inverted faces, presented in a random order. The final accuracy score represents the percentage of correct sorts using the formula: $100 \times 1 - (\text{sum of deviations from the correct ordering for each trial}/\text{maximum deviations possible})$. Chance performance is 35.6%. The control data came from 21 age-matched participants (mean age = 46.5 years).

We tested Herschel twice with the CFPT, once in October 2009 and once in September 2011. His scores for upright faces were outside the normal range on both occasions: 55.6% and 33.3%, respectively, whereas controls' mean score was 74.5% ($SD = 8.5\%$; $t = 2.17$, $p = .042$; and $t = 4.74$, $p < .001$, respectively). These results indicate a perceptual component in Herschel's prosopagnosia. The lower score in the repeated test may be due to Herschel's acknowledgment of the difficulty of this test for him after the first session; as a result he might have not tried as hard the second time. Indeed, a comparison of the average time taken per trial (each trial had a time limit of one minute, but could be ended sooner) revealed that Herschel spent more time sorting the faces in the first session ($M = 44.9$ s) than in the second session ($M = 37.9$ s; paired-samples t test: $t(7) = 2.36$, $p = .051$). When asked to sort inverted faces, Herschel performed comparably to controls in the first session: 47.2% compared to 54.9% ($SD = 6.8\%$; $t = 1.11$, $p = .282$), and significantly worse than controls in the second session: 37.5% ($t = 2.50$, $p = .021$). This drop in performance from Session 1 to Session 2 is consistent with a general decrease in attention/effort during the second session.

Experiments 4 and 5: Facial expression recognition

Many APs also have difficulty extracting other information from faces, such as expressions and age (Fox, Hanif, Iaria, Duchaine, & Barton,

2011; Sergent & Signoret, 1992). We assessed Herschel's ability to recognize expressions with two tests. Control data were provided by nine age-matched male participants (age range: 41–55 years, mean age 46.8 years).

In the *Eyes Test* (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001), participants are presented with the eye region of a face along with four emotion state words. In 36 trials, they choose the word that best describes what the person is thinking or feeling. Herschel proved to be impaired at this task, scoring more than 2 standard deviations below control data. He matched the eye region with the correct adjective in 50% of trials, whereas controls' average was 82.2% ($SD = 6.4\%$; $t = 4.77$, $p = .001$).

The second task was the *Films Facial Expression Task*. In this task, participants are asked to identify subtle facial expressions captured from 18 obscure foreign films. In each of the 58 trials, participants see a word describing an emotional state, followed by three static images of the same actor/actress portraying different facial expressions. Images are presented for 500 ms. Participants indicate which of the three images best matches the target emotional adjective (see Garrido et al., 2009, for more details). Herschel was severely impaired at this task too; he could recognize the expression in only 65.5% of the clips, while controls' average performance was 89.8% ($SD = 5.4\%$; $t = 4.27$, $p = .003$).

Experiments 6 and 7: Facial gender recognition

We assessed Herschel's ability to judge the sex of the faces with two tests. The first was the *Eyes Test* described in the previous section (same control participants); after choosing the expression of each pair of eyes, participants also indicated the sex of the eyes. Herschel was correct on 83.3% of trials, which was significantly less than the controls' average of 96.9% ($SD = 2.8\%$; $t = 4.61$, $p = .002$).

The second was the *Sex Categorization* task. In this task, 60 upright faces and 60 inverted faces are presented for 500 ms in a fixed, randomized order, and subjects have to categorize them as male or female. Faces were cropped below the

eyebrows so participants had to rely on other information. Control data were provided by 9 age-matched participants (age range 52–59 years, mean age = 56.1 years; 5 female). Performance was measured with A' (MacMillan & Creelman, 1991), a bias-free measure that varies between .5 and 1.0, with higher scores indicating better discrimination ability between male and female faces. Herschel was mildly impaired with the upright faces ($A' = .90$, controls: $A' = .96$, $SD = .02$; $t = 2.85$, $p = .022$). His results were not significantly different from those of controls with inverted faces ($A' = .71$; controls: $A' = .81$, $SD = .11$; $t = 0.86$, $p = .414$).

Specificity of Herschel's prosopagnosia: Faces versus objects

The results of the experiments above demonstrate that Herschel has severe face processing problems and suggest that they result from deficits to high-level visual mechanisms. We next examine whether these deficits affect only face processing or extend to other objects.

According to an influential view of object recognition (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976), objects are first categorized at a basic level (e.g., a car, a chair) and then identified as a specific exemplar from within that category (e.g., my car). We assessed Herschel's basic-level object recognition with a reduced set of the Snodgrass and Vanderwart (1980) image set and his within-level object recognition with three other tests.

Experiment 8: Basic-level object recognition

For most people, identifying objects at a basic level happens instantaneously and effortlessly. Thus, it is perhaps not surprising that previous tests of basic object recognition suffered from ceiling effects, with normal participants consistently achieving maximum scores. These tests may be useful for detecting pathological performance, but unfortunately they are not suitable for uncovering finer deficits, potentially affecting individuals that do not report object recognition problems in everyday life, such as Herschel. We

therefore created a more sensitive test for basic object identification to more subtly probe the functioning and organization of Herschel's visual recognition system.

Basic object recognition is often assessed using the Snodgrass and Vanderwart (1980) picture set. The set includes 260 black-and-white line drawings of diverse common objects. Based on the norms published in Snodgrass and Vanderwart (1980), we selected a subset of 82 pictures, half of which were living (e.g., zebra, arm, leaf) and half of which were nonliving (e.g., umbrella, glass, chair) objects. Familiarity and complexity were matched across the two groups. To increase the difficulty of this simple recognition task, we presented each stimulus for only 50 ms, followed by a pattern mask. After the presentation, participants had unlimited time to name the object. Seven age-matched participants (4 female, age range: 51–66 years, $M = 56.7$ years) provided control data.

Herschel correctly identified 72.0% of the objects presented, which was slightly below the average score for controls ($M = 77.0\%$, $SD = 12.7\%$, range: 52.4–93.9%; the difference was not significant: $t = 0.37$, $p = .725$). A closer examination of Herschel's results revealed that a disproportionate number of errors were made for the 15 images depicting mammals, of which he identified only 7 (his 46.7% performance was significantly below normal range: controls' $M = 81.9\%$, $SD = 14.3\%$, range: 53.3%–93.3%; $t = 2.30$, $p = .061$), while for the rest of the images his performance was in line with that of controls (77.6% compared to 75.9%, $SD = 12.7\%$, range 52.2–94.0%). Furthermore, Herschel was the only one to score lower for mammals (46.7%) than for nonmammals (77.6%), while controls scored on average 6.0% better with mammals than with nonmammals. Interestingly, for most missed items, he seemed to correctly identify the stimuli at a superordinate level (as mammals), but mistook, for example, a bear for a cat, a deer for a cow, a donkey for a dog, and a zebra for a horse. These results and Herschel's low score on the horse old–new test (but still within normal range, see next experiment) raise the possibility

that Herschel has a deficit with a particular type of object—mammals—even though he is normal with a wide range of other objects.

Basic-level object recognition (e.g., fork vs. spoon) is generally considered to be easier than face recognition, and, thus, a difference in recognition abilities for faces versus basic objects in acquired prosopagnosia may simply reflect a difference in cognitive demands rather than face specificity. It has been argued (e.g., Damasio et al., 1982) that because face recognition involves discriminating highly similar exemplars within the same category (Face A vs. Face B), it must be compared with discrimination of other objects within the same category (e.g., Car A vs. Car B).

Experiment 9: Old–new discrimination of faces versus nonface objects

In the *Old–New Recognition Memory Test* (Duchaine & Nakayama, 2005), participants first see 10 target items from within the same object category, with each item presented twice. They are then presented with 50 items, 20 targets (10×2), and 30 nontargets and must discriminate between targets (old) and nontargets (new). We tested Herschel with nine different old–new tests: cars, horses, houses, tools, natural landscapes, sunglasses, guns, and two separate face tests (for details about the stimuli see Duchaine & Nakayama, 2005). Control data were provided by nine age-matched participants (age range 52–59 years, mean age = 56.1 years; 5 female).

As can be seen in Figure 4A, Herschel was severely impaired with Faces 1 ($A' = .85$ compared to average A' for controls: $M = .95$, $SD = .03$; $t = 3.16$, $p = .013$) and Faces 2 ($A' = .68$ compared to average A' for controls: $M = .95$, $SD = .04$; $t = 6.40$, $p < .001$). With horses, he performed at the lower end of the normal range ($A' = .86$ compared to average A' for controls = $.94$, $SD = .04$; $t = 1.66$, $p = .135$). For all the other categories, Herschel's performance was normal (all $ps > .31$). His normal performance with objects could not be attributed to speed/accuracy trade-offs (see Figure 4B).

Experiments 10, 11, and 12: Memory for faces versus hairstyles versus cars

The *Cambridge Face Memory Test* (CFMT) was developed to detect prosopagnosia (Duchaine & Nakayama, 2006) and has been shown to have good psychometric properties (Bowles et al., 2009; Wilmer et al., 2010). In this test, participants study six target faces and then must recognize them in 72 three-option forced-choice trials. The trials vary in difficulty, with the three images presenting faces in views and lighting conditions that are the same or different to those studied. Some trials also had images with visual noise added. A score of 24 represents chance-level performance. Our control participants were 20 age-matched individuals (average age = 45.1 years). Herschel had severe difficulties with this task, scoring well outside the normal range: 31 correct responses compared to controls' average score of 59.6 ($SD = 7.6$, see Figure 4C; $t = 3.67$, $p = .002$).

Using the same procedure as the CFMT, we tested Herschel with two other nonface stimulus classes: hairstyles and cars (Figure 4C). The *Cambridge Hair Memory Test* (CHMT) presented male hairstyles cut out from head shots from the same image set as the set that the faces used in the CFMT were drawn from. Like the CFMT, the 72 test items presented the hairstyles in views and lighting that were the same as and different from those studied and with and without added noise. Control participants were 20 undergraduate students from Dartmouth College (15 female, age range 18–27 years old, $M = 19.5$ years, $SD = 2.1$). Herschel's score was comparable to those of the young controls: 44 versus a control average of 50.85 ($SD = 6.05$; $t = 1.10$, $p = .283$).

The *Cambridge Car Memory Test* (CCMT) replaced faces with cars (Dennett et al., 2012). Because males were found to score higher than females on this task, we compared Herschel's performance to that of the 60 males from a larger mixed pool of young adults (age range 18–35 years, $M = 20.63$, $SD = 2.88$). As with hairstyles, Herschel's score with cars was well within the normal range; he scored 54, only slightly below the control mean ($M = 57.43$, $SD = 8.31$; $t = 0.41$, $p = .684$).

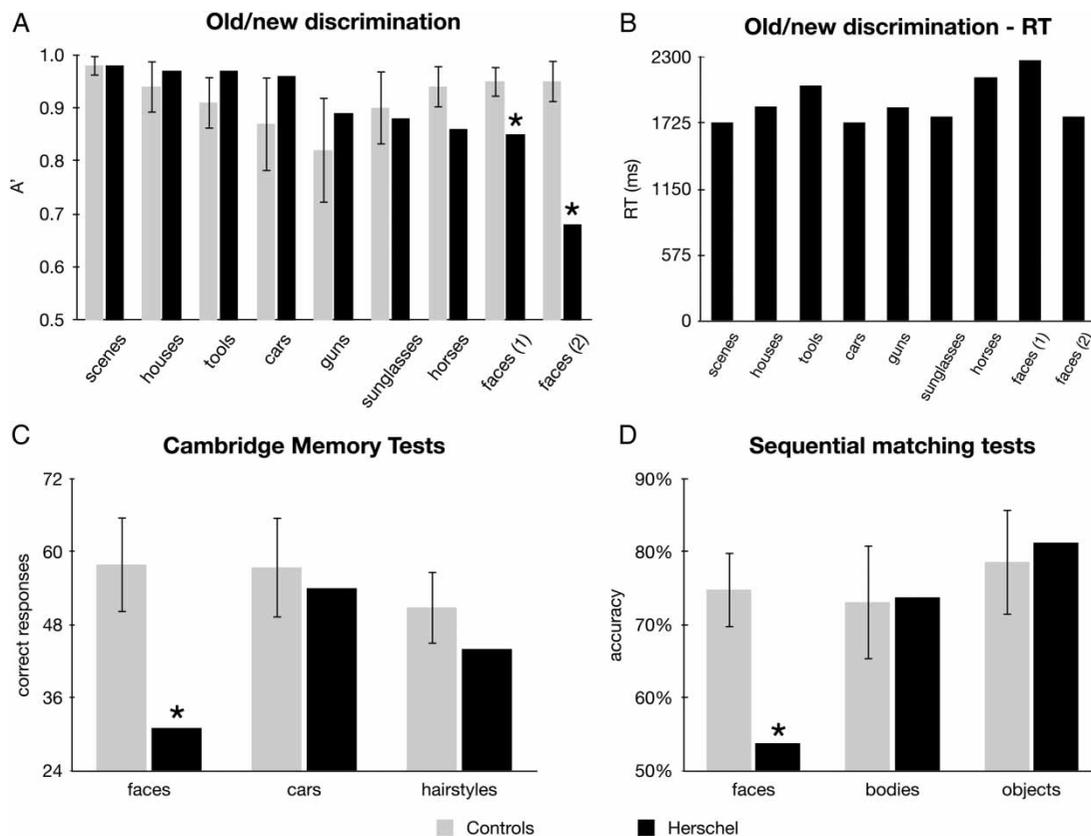


Figure 4. Specificity of Herschel's prosopagnosia: He was markedly impaired with faces but normal with nonface stimuli in tests of learning, memory, and sequential matching. RT = reaction time. Error bars represent ± 1 standard deviation. Stars show significant differences using Crawford's modified t test.

Experiments 13, 14, and 15: Matching for faces versus matching for bodies and objects

The previous experiments indicate that Herschel has a selective impairment in remembering previously learned faces. We next tested Herschel on three matching tasks with more limited memory demands (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009). In these tasks, participants see a target image for 500 ms, followed by a mosaic mask for 250 ms and a test image for 500 ms. Participants decide whether the test and the target images are the same or different (50% chance level). To avoid matching based on low-level visual cues, the test image was displayed in a slightly different position on the screen than the target.

Herschel completed one matching test for bodies, one for objects and one for faces (in this order). FantaMorph 3.0 software (Abrosoft, 2002) was used to make 10 morph series between 20 pairs of stimuli for each category. Pairs of images were then drawn from the morph series to create 80 unique experimental trials for each category (40 same, 40 different). Within each block, the trial order was randomized. The original faces were created using FaceGen Modeller 3.3 software (Singular Inversions, 2008); the bodies were created using Poser 8 software (Smith Micro Software, 2009); the objects were selected from the pairwise similar objects set presented in Tarr, Kersten and Bülthoff

(1998). More details on the stimuli are provided in Pitcher et al. (2009). Control data came from 8 age-matched participants (5 female, age range: 52–59 years, mean age = 56.0 years).

As can be seen in Figure 4D, Herschel scored close to chance level for faces (53.8% compared to controls $M = 74.8\%$, $SD = 5.2\%$; $t = 3.81$; $p = .007$), but within normal range for bodies (73.8% compared to controls $M = 73.1\%$, $SD = 7.9\%$; $t = 0.08$) and objects (81.3% compared to controls $M = 78.6\%$, $SD = 7.3\%$; $t = 0.35$).

The results in this section indicate that Herschel's high-level visual problems are largely restricted to faces. He performed normally with other object categories in recognition memory tests and sequential matching tasks. He seemed to have difficulties only with basic-level recognition of four-legged animals.

General and face configural processing

Abnormal visual general configural processing has been advanced as one of the possible causes of prosopagnosia (Levine & Calvanio, 1989). Indeed, many APs failed tests of visual closure (e.g., Bauer & Trobe, 1984; De Renzi, 1986a, 1986b; De Renzi et al., 1991; Lê et al., 2002; Levine & Calvanio, 1989) or other tests used to assess configural processing, such as the Navon hierarchical letters (e.g., Behrmann & Kimchi, 2003). However, most of these patients were also severely impaired with object recognition, making it difficult to know whether their results were due to a specific deficit in configural processing or to general object agnosia. Other researchers (Busigny, Joubert, et al., 2010) suggested that, while configural processing of nonface items may be spared, configural processing of faces is impaired in all cases of acquired prosopagnosia.

Visual closure tests are recognition tests that require the ability to reconstruct the whole from incomplete parts or shape information. This ability was considered by Levine and Calvanio (1989) to rely on general configural processing. All tests of visual closure present degraded images of objects or words, either by adding visual noise or by deleting essential parts.

Herschel was tested on four such tests, with a modified presentation procedure involving brief presentations so that the tasks depended more on normal recognition processes and less on the slow, visual problem-solving processes that can be used when stimuli are presented for long durations (Farah, 2004). Basic-level recognition (Rosch et al., 1976) was required in all tests, and given Herschel's good performance with most within-class object tests we expected he would perform normally in the tests of visual closure. In addition, we tested Herschel's configural processing of faces with the composite test.

Experiments 16, 17, and 18: Visual closure

The following three tasks are adapted from the Kit of Factor Referenced Cognitive Tests (Ekstrom, French, & Harman, 1976), previously used by Levine and Calvanio (1989) and Duchaine (2000) to assess visual closure in prosopagnosics. Pilot studies were conducted to remove the stimuli that were either always or never correctly identified. For the modified tests, the control participants were 9 age-matched participants (6 female, age range 47–61 years, $M = 53.0$ years). Two participants who were not native English-speakers (both male, age 47 and 48 years) were not run on the words test.

Modified Gestalt Completion Task (MGCT). The Gestalt Completion Task involves identifying a common object from a group of black blotches created by erasing parts of the object (see Figure 5A for examples of stimuli from all visual closure tests; images from MGCT are very similar to those from the Street test; Street, 1931). Each object was shown for 500 ms followed by a pattern mask for 250 ms, after which participants were required to say the name of the object. The original test had 20 items, but after the pilot test we kept only 16 for the main experiment. Herschel was severely impaired at this task; he was not able to identify even one object, while controls averaged 6.2 ($SD = 2.5$; range: 4–12; $t = 2.35$, $p = .046$).

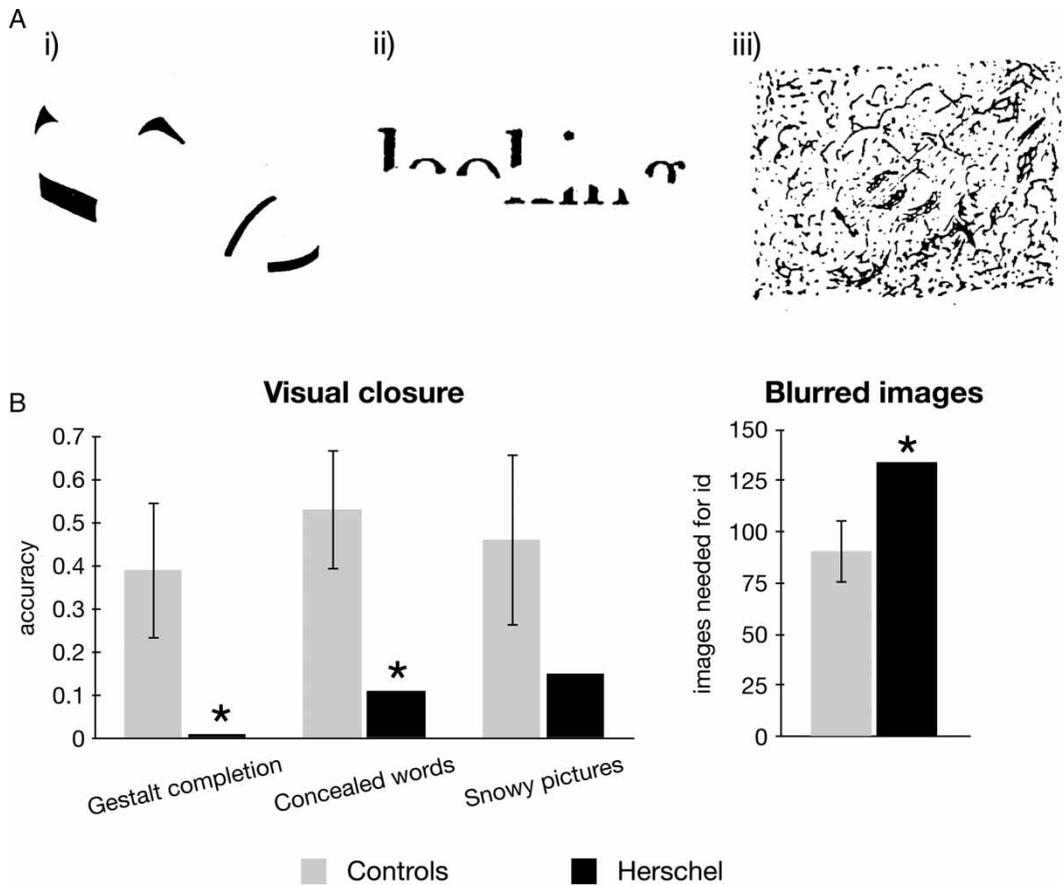


Figure 5. (A) Examples of stimuli presented in the visual closure tests: (i) Modified Gestalt Completion Task (MGCT), (ii) Modified Concealed Words Task (MCWT), (iii) Modified Snowy Pictures Task (MSPT). The objects/word depicted are: shoe, looking, and guitar. (B) Herschel was impaired at two tests of visual closure and in the lower range at the other. He was also impaired at the blurred images test. Error bars represent ± 1 standard deviation. Significant differences (using Crawford's modified t test) between Herschel and controls are marked with an asterisk.

Modified Concealed Words Task (MCWT). The Concealed Words Task is similar to the above test, except that objects are replaced with words: Participants must identify common words from their fragments. The occluded words were shown for 1,500 ms, followed by a pattern mask for 250 ms, and after the pilot study we kept 28 of the original 50 stimuli. Again, Herschel was severely impaired, recognizing only three words; his score was more than 3 standard deviations below that of controls ($M = 14.9$, $SD = 3.9$; range: 10–20; $t = 2.85$, $p = .029$).

Modified Snowy Pictures Task (MSPT). In this task, participants had to identify a line drawing of an object degraded by a snow-like pattern. The snowy pictures were shown for 1,000 ms followed by a pattern mask for 250 ms, then a blank screen for 500 ms. There were 24 items in the original version of this test, and we used 13 of the items after the results of the pilot study. Herschel could name the objects presented in only two snowy pictures, while controls managed to recognize an average of 6.0 objects ($SD = 2.7$; range: 2–9; $t = 1.41$, $p = .198$).

Experiment 19: Blurred objects

We created a modified version of the Blurred Pictures Task (MBPT) presented in Viggiano, Costantini, Vannucci, and Righi (2004). The original set of stimuli consists of 62 basic-level objects, each object with 10 images varying in contrast, from extremely blurry to crystal clear. The test trial starts with the most blurred image of an object for 250 ms, then the second most blurred image for 250 ms, and so on, until the participant correctly identifies the object or all 10 images are displayed. After that, the images of the next object are presented. The onset of each image is controlled by participants, and participants have unlimited time to provide an answer. The score is calculated by adding the number of images displayed before each object is recognized; higher scores represent worse recognition performance. In a pilot study, we used the same procedure as that in Experiments 16–18 to select 27 stimuli for our main experiment. The control data came from 7 age-matched participants (6 female, age range: 48–61 years, $M = 54.0$ years). Herschel needed a total of 134 images to recognize the selected objects, while controls needed on average 90.6 images ($SD = 15.7$; range: 73–109; $t = 2.59$, $p = .041$).

Together (see Figure 5B), Herschel's scores suggest an impaired ability to recognize basic objects from impoverished visual stimuli, in contrast to his normal performance when nonliving objects were presented unobstructed. His visual recognition system appears to be impaired at inferring the actual form of objects when this information is incomplete.

Experiment 20: Navon hierarchical letters

We also tested Herschel's configural processing using a Navon task (Navon, 1977). The Navon hierarchical letters are compound letters consisting of a number of small capital Ss or Hs (local letters) configured to form either a global S or a global H (Figure 6A). The letters can be consistent (the global and local letters are identical) or inconsistent (the global and local letters are different). When asked to identify either the local or global letters, participants typically show an advantage

for global processing (faster identification of global letters) and an interference effect (slower identification when global and local letters are inconsistent; Behrmann, Avidan, Marotta, & Kimchi, 2005; Navon, 1977).

Herschel and 14 control participants (average age = 41.7 years) were tested in two back-to-back sessions, and the order of the blocks within a session was local, global, global, and local for a total of 384 trials. The local and global letters were consistent on half the trials and inconsistent on the other half (Figure 6A). Herschel performed normally in this task (Figure 6B). He was on average faster for global than for local trials, and he showed the typical global interference effect (he also showed a large local interference effect). He was 100% accurate for all trials (controls averaged 98%). These results suggest that Herschel does not have a global processing deficit.

Experiment 21: Composite faces

Herschel's configural face processing was assessed with the composite faces test (Young, Hellawell, & Hay, 1987). The version we used was adapted from Susilo et al. (2010). Composite stimuli were created by combining top halves and bottom halves of different faces. Participants were presented pairs of composites sequentially (first stimulus for 300 ms, blank screen for 400 ms, second stimulus for 300 ms) and were asked to say whether the top halves matched. Half of all trials presented aligned composites, with the top halves and bottom halves neatly arranged to form new faces, and the other half presented misaligned composites, with the top halves shifted to one side (left or right) compared to the bottom halves. Holistic face processing should make trials with aligned faces more difficult because of automatic processing of bottom halves. The bottom halves in each pair were always different, while the top halves were the same (60 trials) or different (30 trials). We analysed only "same" trials because "different" trials are difficult to interpret (Robbins & McKone, 2007). The composite effect (indicating holistic face processing) was measured as the difference in performance between misaligned and aligned "same" trials.

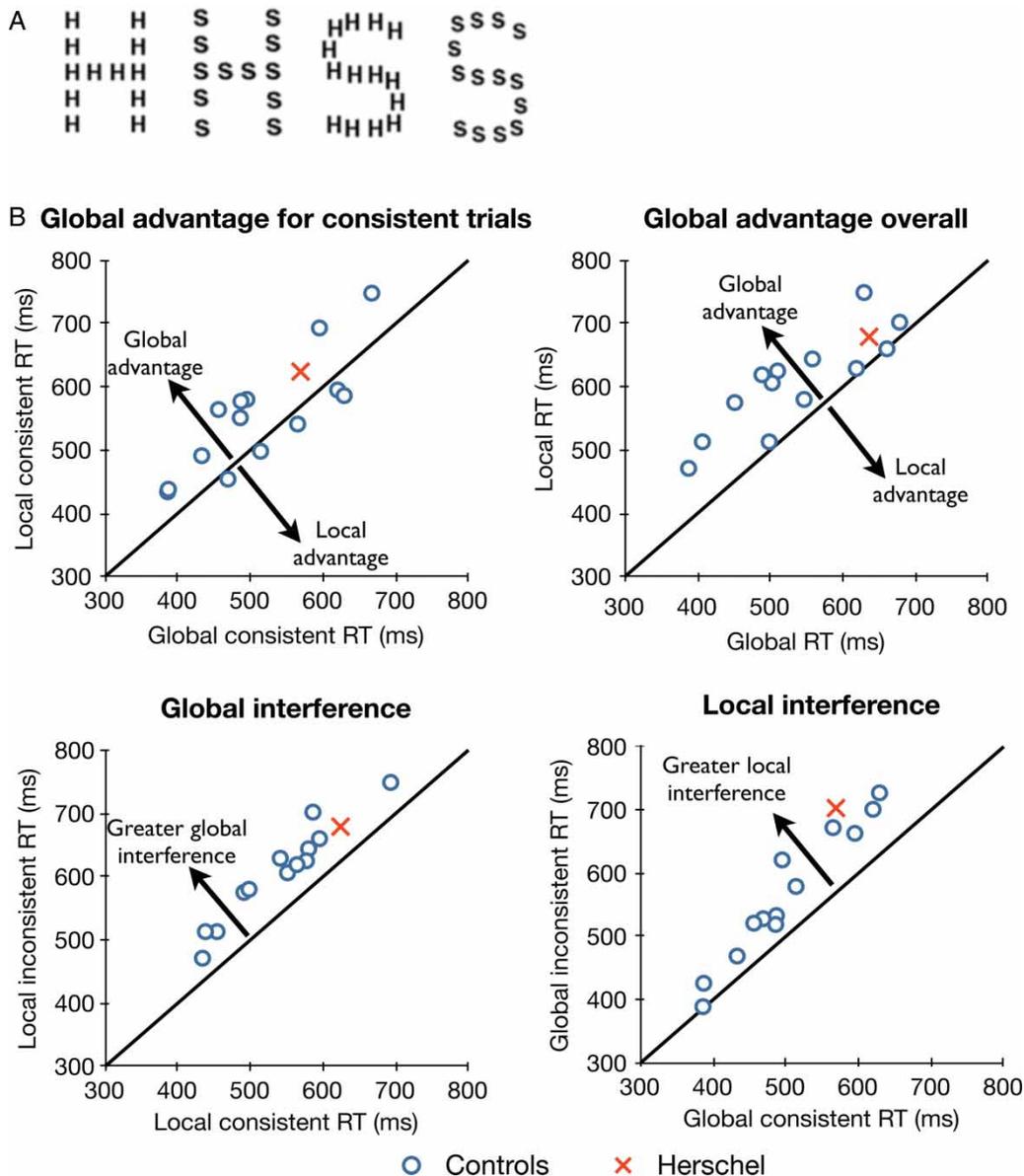


Figure 6. (A) The compound stimuli used in the global–local Navon task. (B) Individual reaction times (RTs; averaged across the two sessions) of controls and Herschel on the global–local task. Each circle represents one control participant. Herschel is represented by a red \times . The diagonals in the top figures separate participants who showed a global advantage from those who showed a local advantage; the larger the distance to the diagonal the higher the respective advantage. The diagonals in the bottom figures represent points for which there is no global/local interference. The larger the distance to the diagonal the higher the global/local interference. Herschel showed the largest local interference, but it was not significantly different from that of controls, and his global interference and global advantage were comparable to those of controls. To view a colour version of this figure, please see the online issue of the Journal.

Herschel was correct on 90% of the misaligned “same” trials and on 70% of the aligned “same” trials. Seven controls (age range: 49–56 years, mean age 54.3 years; 4 female) averaged 95.2% and 73.3%, respectively. Herschel’s composite effect of 20% was not significantly different from controls’ average composite effect of 21.9% ($t = 0.11, p = .919$), indicating normal configural/holistic face processing.

DISCUSSION

We have presented a new case of acquired prosopagnosia that displays an interesting and surprising cognitive profile. Herschel is a 56-year-old British man with a degree in astronomy. Following two strokes, he suffered extensive lesions in the occipito-temporal cortex, especially severe in the right occipital cortex. Despite his intellect, he was unable to recognize famous faces, remember faces previously shown to him, or match or order faces based on similarity. Herschel was also impaired with facial expressions and facial gender judgements. In contrast, he showed normal memory for a wide variety of objects in several paradigms and normal ability to discriminate between highly similar items within a novel object category; he was also successful with fine discrimination between human bodies. Furthermore, he was normal at recognizing basic-level objects (with the exception of mammals) in brief presentations when the images were intact. Interestingly though, when visual noise was added or parts information was removed from the images, Herschel had substantial difficulties identifying objects at the basic level. His general global processing (measured with the Navon task) and his holistic face processing (measured with the composite test) were normal.

Normal within-class object recognition in prosopagnosia

Faces play a vital role in our daily interactions, and considerable evidence indicates that the brain contains mechanisms dedicated to face recognition (Duchaine, Yovel, Butterworth, & Nakayama,

2006; Farah, 1996; Kanwisher, McDermott, & Chun, 1997; McNeil & Warrington, 1993; Moscovitch, Winocur, & Behrmann, 1997; Tsao, Freiwald, Tootell, & Livingstone, 2006). However, not all researchers share this view. One alternative possibility is that the brain uses the same mechanisms to recognize both faces and objects (Damasio et al., 1982). This view predicts that prosopagnosics will show impairments with any nonface object task of comparable complexity and within-class similarity to faces.

Herschel’s lesions appear to have selectively affected mechanisms used for face processing, leaving object recognition largely intact. Experiments 9–15 showed a clear dissociation between performance with faces and other objects. Herschel recognized unfamiliar cars, houses, horses, tools, sunglasses, and guns normally, but he was severely impaired with faces. He scored within the normal range in challenging tasks measuring the ability to distinguish between highly similar members of complex natural classes (cars and hairstyles). His within-class discrimination of bodies and novel objects created to match faces for complexity and similarity was also normal, in stark contrast with his face skills. Herschel demonstrated these dissociations in a variety of paradigms: The Cambridge memory tests were memory based, while the matching tests were perceptual in nature. These results suggest that his severe prosopagnosia is not associated with deficits relating to within-level recognition of nonface objects.

Herschel’s results mirror results from other patients with acquired prosopagnosia who could learn and/or discriminate between visually similar exemplars of various, complex nonface objects. P.S. was normal at discriminating between highly similar novel shapes and between exemplars of common object classes—such as cars, dogs, cups, shoes—parametrically manipulated for similarity (Busigny, Graf, et al., 2010). G.G. performed in the normal range for within-category discrimination of birds, boats, cars, and chairs (Busigny, Joubert, et al., 2010). The case of W.J. reported by McNeil & Warrington (1993) is also quite remarkable; following the

stroke that led to severe prosopagnosia, he became a farmer and could accurately identify his own sheep and learn unfamiliar sheep from face photographs. The normal performance at fine-grained discrimination of nonface objects or nonhuman faces displayed by these cases supports the specificity of mechanisms implicated in human face processing.

Normal basic-level recognition of nonliving objects

As noted in the introduction, it is possible that the normal basic-level object recognition reported for many cases of prosopagnosia in the literature was due to ceiling effects in basic-level tests. To avoid ceiling effects, Herschel was asked to identify objects from line drawings presented for only 50 ms, which made the task challenging even for control participants. Herschel's performance was in line with that of controls, with the exception of mammals, of which he identified only 47% (controls identified 82% of mammals on average). His results show a striking resemblance to those of patient R.M. (Sergent & Signoret, 1992), who was also severely impaired at recognizing "feline animals" (50% success rate) while being perfectly normal with other objects (success rate 96%). Selective deficits with living but not with nonliving objects have been noted to co-occur with prosopagnosia before (L.H.: Levine & Calvanio, 1989; Farah, McMullen, & Meyer, 1991; M.B.: Farah et al., 1991). The living–nonliving distinction has also been reported in many cases with semantic deficits (Caramazza & Shelton, 1998; Pillon & d'Honinckun, 2011; Warrington & Shallice, 1984), but Herschel's deficits may be due to category-selective visual problems. The existence of such a visual deficit would fit well with functional imaging studies demonstrating that lateral regions of the ventral visual stream show a stronger response to living objects than to tools (Chao, Haxby, & Martin, 1999; Noppeney, Price, Penny, & Friston, 2006). Future testing of his visual and semantic abilities with living objects will address this possibility.

Configural processing in prosopagnosia: Questions and an interesting hypothesis

One of the goals of our study was to examine Levine and Calvanio's (1989) suggestion that prosopagnosia is generated by a deficit in general-purpose configural processing. Face perception has been shown to rely on configural processing, but this could be face-specific configural processing or configural processing applied to many visual categories (Behrmann et al., 2005; Farah, 2004; Levine & Calvanio, 1989). Here we tested Herschel on three modified visual closure tasks used by Levine and Calvanio (1989) to measure general configural processing, which they defined as the ability to represent and recognize an object based on overall shape rather than the individual features. We also added a fourth test looking at Herschel's ability to recognize objects from blurred images. His configural face processing was examined with the composite faces test.

Herschel's normal performance on most within-category object tests led us to believe that he would score normally on the tests of visual closure, but he proved to be severely impaired in all tests: with objects, as well as with words; with images of objects occluded, obscured by visual noise or blurred (all his scores were statistically different from those of controls, with the exception of Snowy Pictures; in this test he recognized only two images, fewer than any control participant). His marked impairment at visual closure mirrors that of patient L.H. (Levine & Calvanio, 1989) and several other prosopagnosics (Bauer & Trobe, 1984; Benton & van Allen, 1972; De Renzi, Faglioni, & Spinnler, 1968). All these seem to point towards a general impairment with configural processing, consistent with the Levine and Calvanio (1989) hypothesis. However, no configural processing deficit was apparent in the Navon task; Herschel showed typical global advantage and global interference effects, challenging the generality of his configural problems. His normal Navon results mirror those of P.S., a well-documented case of acquired prosopagnosia with face-selective deficits (Busigny & Rossion, 2011). One interpretation of this dissociation in performance on tests

thought to measure configural processing is that there are two types of general configural processing: one that requires integration of visible local features and the other that requires integration of visible and occluded local features. In one case, there is no physical difference between the information available for the global versus local construct; in the other case, the global construct requires filling in.

While Herschel's prosopagnosia does not seem to be a result of deficits with general configural processing, it could still be linked to a face-specific configural processing deficit. However, Herschel displayed a normal-sized composite face effect, providing preliminary evidence that this is not the case. Further studies are needed to more firmly establish this finding as it would be inconsistent with a suggestion in Busigny, Joubert, et al. (2010) that acquired prosopagnosia cannot occur without abnormal holistic face processing.

It is conceivable that Herschel's poor results at the visual closure tests may be due to his left and right quadrantanopia; damaged upper visual fields may have caused Herschel to see fewer parts of the objects when they were presented for 250 ms. Considering that available visual information had already been reduced to the minimum necessary to allow recognition, further stimulus loss may have made the tasks extremely challenging for Herschel because of low-level deficits rather than recognition deficits. However, we believe this is not the case; Herschel was still unable to recognize the objects from the Gestalt Completion test and the Snowy Pictures test when we allowed him unlimited viewing time, which presumably could compensate for his visual field defect. He could not "see" the objects in the images even after we named them.

Another possibility is that the type of configural processing deficits that Herschel has (and that is apparent only in visual closure tests) disproportionately affects perception of living, dynamic objects, such as faces and animals (for which Herschel had different degrees of impairment). This may occur because Herschel cannot integrate the non-nameable features characterizing living things into a coherent whole (Levine & Calvanio, 1989) or because of other aspects specific to the

perception of living things. For example, constructing a flexible representation necessary to accommodate the dynamics of the second-order spatial relations between the features of a particular living item (e.g., a face must be recognized even when facial expressions modify the face parts and their spatial layout) may require some ability to correct the representation so it can be matched to memory representations. The absence of this ability would compromise recognition of living items, but would not be noticeable in normal object recognition tests, because no correction is required. Spatial relations between individual features of a nonliving object are expected to stay the same, and thus a static mental representation (allowing for differences in orientation, viewpoint, etc.) would be fine. The deficit would become apparent only when identification depends on reconstructing the spatial configuration of individual parts from incomplete images, as is the case in visual closure tests. It is also possible that Herschel's lesions disrupted lower level processes that are only required when any stimulus is degraded, regardless of its animacy.

Herschel's abnormal results in visual closure tests suggest impairments in the system responsible for object perception, impairments that were not apparent in object recognition tests with unaltered images of nonmammal objects (Experiment 8). This raises an interesting possibility: Within-class recognition or discrimination (for which Herschel was normal, see Experiments 9, 11, 12, 15) may not require intact basic-level recognition. In other words, visual recognition of objects appears not to follow the hierarchy implied by models of object processing (e.g., Rosch et al., 1976), with successful within-level discrimination necessarily dependent on a normal basic-level recognition stage. Perhaps only certain aspects of basic-level recognition are critical for the within-level recognition, which may still function normally despite impairments affecting basic-level recognition. Farah, Levinson, and Klein (1995) argued that prosopagnosic L.H., impaired with visual closure (Levine & Calvanio, 1989) and basic object recognition (Levine et al., 1980), similarly showed normal within-level discrimination. However, L.H. was tested with only one category of nonface objects (glasses), and

floor effects might have masked subtle impairments (he scored 63% with glasses while controls averaged 69%). In contrast, Herschel showed substantially better recognition of houses, horses, tools, sunglasses, guns (Experiment 9), cars (Experiments 9 and 12), hairstyles (Experiment 11), bodies, and novel objects (Experiment 15) than of faces (Experiments 9, 10, 13) in tests whose difficulty levels for faces and objects were well matched. Therefore, we believe Herschel is the first well-documented case to have intact within-object with compromised basic-level recognition.

CONCLUSION

The marked contrast in Herschel's performance with faces and nonface objects represents additional support for, at least partly, distinct processing for faces. While Herschel had difficulties in recognizing objects at a basic level under difficult conditions, he was very good at learning and discriminating between similar exemplars of several nonface object classes. His basic level recognition of objects was also fine, with the notable exception of mammals. Herschel's prosopagnosia does not appear to relate to a general or face-specific configural processing; even though Herschel failed to "see" objects beyond the sum of their (incomplete) individual parts in the visual closure tests, he showed normal configural processing in the Navon task and in the composite faces test. His atypical functional activation across the whole cortical face-selective network precludes us from linking his deficits to a particular face area.

Manuscript received 26 June 2012

Revised manuscript received 6 November 2012

Revised manuscript accepted 8 November 2012

First published online 7 December 2012

REFERENCES

Abrosoft Co. (2002). FantaMorph (Version 3.0) [computer software]. Beijing: Abrosoft. Available from <http://www.facegen.com>.

- Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The "Reading the Mind in the Eyes" Test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry*, *42*, 241–251.
- Barton, J. J. S. (2008). Structure and function in acquired prosopagnosia: Lessons from a series of 10 patients with brain damage. *Journal of Neuropsychology*, *2*, 197–225.
- Barton, J. J. S., Cherkasova, M. V., Press, D. Z., Intriligator, J. M., & O'Connor, M. (2004). Perceptual functions in prosopagnosia. *Perception*, *33*, 939–956.
- Bauer, R. M., & Trobe, J. D. (1984). Visual memory and perceptual impairments in prosopagnosia. *Journal of Clinical Neuro-ophthalmology*, *4*, 39–46.
- Behrmann, M., Avidan, G., Marotta, J. J., & Kimchi, R. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 1. Behavioral findings. *Journal of Cognitive Neuroscience*, *17*, 1130–1149.
- Behrmann, M., & Kimchi, R. (2003). What does visual agnosia tell us about perceptual organization and its relationship to object perception? *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 19–42.
- Benton, A. L., & van Allen, M. W. (1972). Prosopagnosia and facial discrimination. *Journal of the Neurological Sciences*, *15*, 167–172.
- Boutsen, L., & Humphreys, G. W. (2002). Face context interferes with local part processing in a prosopagnosic patient. *Neuropsychologia*, *40*, 2305–2313.
- Bowles, D. C., McKone, E., Dawel, A., Duchaine, B., Palermo, R., Schmalzl, L., ... Yovel, G. (2009). Diagnosing prosopagnosia: Effects of ageing, sex, and participant–stimulus ethnic match on the Cambridge Face Memory Test and Cambridge Face Perception Test. *Cognitive Neuropsychology*, *26*, 423–455.
- Bukach, C. M., Bud, D. N., Gauthier, I., & Tarr, M. J. (2006). Perceptual expertise effects are not all or none: Spatially limited perceptual expertise for faces in a case of prosopagnosia. *Journal of Cognitive Neuroscience*, *18*, 48–63.
- Busigny, T., Graf, M., Mayer, E., & Rossion, B. (2010). Acquired prosopagnosia as a face-specific disorder: Ruling out the general visual similarity account. *Neuropsychologia*, *48*, 2051–2067.
- Busigny, T., Joubert, S., Felician, O., Ceccaldi, M., & Rossion, B. (2010). Holistic perception of the individual face is specific and necessary: Evidence from

- an extensive case study of acquired prosopagnosia. *Neuropsychologia*, 48, 4057–4092.
- Busigny, T., & Rossion, B. (2011). Holistic processing impairment can be restricted to faces in acquired prosopagnosia: Evidence from the global/local Navon effect. *Journal of Neuropsychology*, 5, 1–14.
- Buxbaum, L. J., Glosser, G., & Coslett, H. B. (1996). Relative sparing of object recognition in alexia-prosopagnosia. *Brain and Cognition*, 32, 202–205.
- Caramazza, A., & Shelton, J. R. (1998). Domain-specific knowledge systems in the brain: The animate-inanimate distinction. *Journal of Cognitive Neuroscience*, 10, 1–34.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, 2, 913–919.
- Crawford, J. R., & Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. *Clinical Neuropsychologist*, 12, 482–486.
- Damasio, A. R., Damasio, H., & Van Hoesen, G. W. (1982). Prosopagnosia: Anatomic basis and behavioural mechanisms. *Neurology*, 32, 331–341.
- Delvenne, J.-F., Seron, X., Coyette, F., & Rossion, B. (2004). Evidence for perceptual deficits in associative visual (prosop)agnosia: A single-case study. *Neuropsychologia*, 42, 597–612.
- Dennett, H. W., McKone, E., Tavashmi, R., Hall, A., Pidcock, M., Edwards, M., & Duchaine, B. (2012). The Cambridge Car Memory Test: A task matched in format to the Cambridge Face Memory Test, with norms, reliability, sex differences, dissociations from face memory, and expertise effects. *Behavioral Research Methods*, 44, 587–605.
- De Renzi, E. (1986a). Current issues on prosopagnosia. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. Young (Eds.), *Aspects of face processing* (pp. 243–252). Dordrecht, The Netherlands: Martinus Nijhoff.
- De Renzi, E. (1986b). Prosopagnosia in two patients with CT scan evidence of damage confined to the right hemisphere. *Neuropsychologia*, 24, 385–389.
- De Renzi, E., & di Pellegrino, G. (1998). Prosopagnosia and alexia without object agnosia. *Cortex*, 34, 403–415.
- De Renzi, E., Faglioni, P., Grossi, D., & Nichelli, P. (1991). Apperceptive and associative forms of prosopagnosia. *Cortex*, 27, 213–221.
- De Renzi, E., Faglioni, P., & Spinnler, H. (1968). The performance of patients with unilateral brain damage on face recognition tasks. *Cortex*, 4, 17–34.
- Duchaine, B. (2000). Developmental prosopagnosia with normal configural processing. *Neuroreport*, 11, 79–83.
- Duchaine, B., Germine, L., & Nakayama, K. (2007). Family resemblance: Ten family members with prosopagnosia and within-class object agnosia. *Cognitive Neuropsychology*, 24, 419–430.
- Duchaine, B., & Nakayama, K. (2005). Dissociations of face and object recognition in developmental prosopagnosia. *Journal of Cognitive Neuroscience*, 17, 249–261.
- Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for neurologically intact individuals and investigation of its validity using inverted face stimuli and prosopagnosic individuals. *Neuropsychologia*, 44, 576–585.
- Duchaine, B., Yovel, G., Butterworth, E., & Nakayama, K. (2006). Prosopagnosia as an impairment to face-specific mechanisms: Elimination of the alternative hypotheses in a developmental case. *Cognitive Neuropsychology*, 23, 714–747.
- Duchaine, B., Yovel, G., & Nakayama, K. (2007). No global processing deficit in the Navon task in 14 developmental prosopagnosics. *Social Cognitive and Affective Neuroscience*, 2, 104–113.
- Ekstrom, R., French, J. W., & Harman, H. H. (1976). *Manual for Kit of Factor-referenced Cognitive Tests*. Princeton, NJ: Educational Testing Service.
- Farah, M. J. (1996). Is face recognition “special”? Evidence from neuropsychology. *Behavioural Brain Research*, 76, 181–189.
- Farah, M. J. (2004). *Visual agnosia: Disorders of object recognition and what they tell us about normal vision*. Cambridge, MA: MIT Press.
- Farah, M. J., Levinson, K. L., & Klein, K. L. (1995). Face perception and within-category discrimination in prosopagnosia. *Neuropsychologia*, 33, 661–674.
- Farah, M. J., McMullen, P. A., & Meyer, M. M. (1991). Can recognition of living things be selectively impaired? *Neuropsychologia*, 29, 185–193.
- Fox, C. J., Hanif, H. M., Iaria, G., Duchaine, B. C., & Barton, J. J. S. (2011). Perceptual and anatomic patterns of selective deficits in facial identity and expression processing. *Neuropsychologia*, 49, 3188–3200.
- Garrido, L., Furl, N., Draganski, B., Weiskopf, N., Stevens, J., Tan, G. C. Y., ... Duchaine, B. (2009). Voxel-based morphometry reveals reduced grey matter volume in the temporal cortex of developmental prosopagnosics. *Brain*, 132, 3443–3455.

- Gauthier, I., Behrmann, M., & Tarr, M. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience*, *11*, 349–370.
- Glover, G. H. (1999). Deconvolution of impulse response in event-related BOLD fMRI. *NeuroImage*, *9*, 416–429.
- Henke, K., Schweinberger, S. R., Grigo, A., Klos, T., & Sommer, W. (1998). Specificity of face recognition: Recognition of exemplars of non-face objects in prosopagnosia. *Cortex*, *34*, 289–296.
- Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *NeuroImage*, *17*, 825–841.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Lê, S., Cardebat, D., Boulanouar, K., Hénaff, M.-A., Michel, F., Milner, D., ... Démonet, J. F. (2002). Seeing, since childhood, without ventral stream: A behavioural study. *Brain*, *125*, 58–74.
- Levine, D. N., & Calvanio, R. (1989). Prosopagnosia: A defect in visual configural processing. *Brain and Cognition*, *10*, 149–170.
- Levine, D. N., Calvanio, R., & Wolf, E. (1980). Disorders of visual behavior following bilateral posterior cerebral lesions. *Psychological Research*, *41*, 217–234.
- Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. New York, NY: Cambridge University Press.
- McNeil, J. E., & Warrington, E. K. (1993). Prosopagnosia: A face-specific disorder. *Quarterly Journal of Experimental Psychology: Human Experimental Psychology*, *46A*, 1–10.
- Mooney, C. M. (1957). Age in the development of closure ability in children. *Canadian Journal of Psychology*, *11*, 219–226.
- Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special in face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, *9*, 555–604.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353–383.
- Noppeney, U., Price, C. J., Penny, W. D., & Friston, K. J. (2006). Two distinct neural mechanisms for category-selective responses. *Cerebral Cortex*, *16*, 437–445.
- Pillon, A., & d'Honincthun, P. (2011). A common processing system for the concepts of artifacts and actions? Evidence from a case of a disproportionate conceptual impairment for living things. *Cognitive Neuropsychology*, *28*, 1–43.
- Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple dissociation of faces, bodies, and objects in extrastriate cortex. *Current Biology*, *19*, 319–324.
- Pitcher, D., Dilks, D. D., Saxe, R. R., Triantafyllou, C., & Kanwisher, N. (2011). Differential selectivity for dynamic versus static information in face-selective cortical regions. *NeuroImage*, *56*, 2356–2363.
- Riddoch, M. J., & Humphreys, G. W. (1993). *BORB: Birmingham Object Recognition Battery*. Hove, UK: Lawrence Erlbaum Associates.
- Riddoch, M. J., Johnston, R. A., Bracewell, R. M., Boutsen, L., & Humphreys, G. W. (2008). Are faces special? A case of pure prosopagnosia. *Cognitive Neuropsychology*, *25*, 3–26.
- Rivest, J., Moscovitch, M., & Black, S. (2009). A comparative case study of face recognition: The contribution of configural and part-based recognition systems, and their interaction. *Neuropsychologia*, *47*, 2798–2811.
- Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, *103*, 34–79.
- Rosch, E., Mervis, C. B., Gray, W., Johnson, D., & Boyes-Braem, P. (1976). Basic objects in natural categories. *Cognitive Psychology*, *8*, 382–439.
- Schweinberger, S. R., Klos, T., & Sommer, W. (1995). Covert face recognition in prosopagnosia: A dissociable function? *Cortex*, *31*, 517–529.
- Sergent, J., & Signoret, J. L. (1992). Varieties of functional deficits in prosopagnosia. *Cerebral Cortex*, *2*, 375–388.
- Singular Inversions. (2008). FaceGen Modeller (Version 3.3) [computer software]. Toronto, ON: Singular Inversions.
- Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E., Johansen-Berg, H., ... & Matthews, P. M. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *Neuroimage*, *23*, S208.
- Smith Micro Software. (2009). Poser (Version 8) [computer software]. Aliso Viejo, CA: Smith Micro Software.

- Snodgrass, J. G., & Vanderwart, M. (1980). A standardized set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, *6*, 174–215.
- Steeves, J. K., Culham, J. C., Duchaine, B. C., Pratesi, C. C., Valyear, K. F., Schindler, I., ... Goodale, M. A. (2006). The fusiform face area is not sufficient for face recognition: Evidence from a patient with dense prosopagnosia and no occipital face area. *Neuropsychologia*, *44*, 594–609.
- Street, R. F. (1931). *A Gestalt completion university*. New York, NY: Teachers College of Columbia University.
- Susilo, T., McKone, E., Dennett, H., Darke, H., Palermo, R., Hall, A., ... Rhodes, G. (2010). Face recognition impairments despite normal holistic processing and face space coding: Evidence from a case of developmental prosopagnosia. *Cognitive Neuropsychology*, *27*, 636–664.
- Takahashi, N., Kawamura, M., Hirayama, K., Shiota, J., & Isono, O. (1995). Prosopagnosia: A clinical and anatomical study of four patients. *Cortex*, *31*, 317–329.
- Tarr, M. J., Kersten, D., & Bülthoff, H. H. (1998). Why the visual recognition system might encode the effects of illumination. *Vision research*, *38*, 2259–2276.
- Tsao, D. Y., Freiwald, W. A., Tootell, R. B., & Livingstone, M. S. (2006). A cortical region consisting entirely of face-selective cells. *Science*, *311*(5761), 670–674.
- Viggiano, M. P., Costantini, A., Vannucci, M., & Righi, S. (2004). Hemispheric asymmetry for spatially filtered stimuli belonging to different semantic categories. *Cognitive Brain Research*, *20*, 519–524.
- Wada, Y., & Yamamoto, T. (2001). Selective impairment of facial recognition due to a haematoma restricted to the right fusiform and lateral occipital region. *Journal of Neurology, Neurosurgery and Psychiatry*, *71*, 254–257.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, *107*, 829–854.
- Whiteley, A. M., & Warrington, E. K. (1977). Prosopagnosia: A clinical, psychological, and anatomical study of three patients. *Journal of Neurology, Neurosurgery & Psychiatry*, *40*, 395–403.
- Wilmer, J. B., Germine, L., Chabris, C. F., Chatterjee, G., Williams, M., Loken, E., ... & Duchaine, B. (2010). Human face recognition ability is specific and highly heritable. *Proceedings of the National Academy of Sciences*, *107*, 5238–5241.
- Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of fMRI data. *NeuroImage*, *14*, 1370–1386.
- Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception*, *16*, 747–759.