The role of holistic face processing in acquired prosopagnosia: evidence from the composite face effect

Article *in* Visual Cognition · December 2016

DOI: 10.1080/13506285.2016.1261976

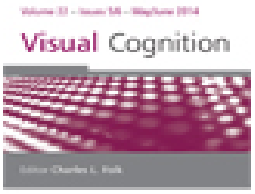
4 authors:

Dawn Finzi
Stanford University

Tirta Susilo
Victoria University of Wellington

Jason J.S Barton
University of British Columbia - Vancouver

Brad Duchaine
Dartmouth College



Visual Cognition

ISSN: 1350-6285 (Print) 1464-0716 (Online) Journal homepage: http://www.tandfonline.com/loi/pvis20

The role of holistic face processing in acquired prosopagnosia: evidence from the composite face effect

R. Dawn Finzi, Tirta Susilo, Jason J. S. Barton & Bradley C. Duchaine

VISUAL COGNITION, 2016
http://dx.doi.org/10.1080/13506285.2016.1261976

The role of holistic face processing in acquired prosopagnosia: evidence from the composite face effect

R. Dawn Finzi [a], Tirta Susilo [b], Jason J. S. Barton [c] and Bradley C. Duchaine [d]

[a]Department of Psychology, University of California, San Diego, CA, USA; [b]School of Psychology, Victoria University of Wellington, Wellington, New Zealand; [c]Departments of Medicine (Neurology) & Ophthalmology and Visual Sciences, University of British Columbia, Vancouver, Canada; [d]Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NH, USA

ABSTRACT

Faces are processed more holistically than other objects, and it has been suggested that the loss of holistic face processing causes acquired prosopagnosia. Support for this hypothesis comes from several cases who failed to show holistic face effects as well as the absence of reports of prosopagnosics with unequivocally normal holistic face perception. The current study examines the relationship between holistic face processing and prosopagnosia by testing seven acquired prosopagnosics with the face composite task, a classic measure of holistic face processing. To enhance the robustness of the findings, each prosopagnosic was tested with two versions of the composite task showing upright faces. We also tested an inverted condition to exclude the possibility that more general factors account for composite effects for upright faces. Four of the seven acquired prosopagnosic participants showed consistent upright face composite effects with minimal inverted face composite effects. We conclude that severe face processing deficits can co-occur with intact holistic face processing and that factors other than a loss of holistic processing contribute to the perceptual and recognition deficits in acquired prosopagnosia.

ARTICLE HISTORY
Received 30 June 2016
Accepted 6 November 2016

KEYWORDS
Acquired prosopagnosia; lesion patients; face processing; face perception; holistic perception

Faces are fundamental to human social interaction, and the ability to recognize other people from their faces is especially important. Much evidence suggests that face processing depends on different processes than do other types of visual recognition (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010; Duchaine & Yovel, 2015; McKone, Kanwisher, & Duchaine, 2007; Moscovitch, Winocur, & Behrmann, 1997; Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Tsao, Freiwald, Tootell, & Livingstone, 2006), and a number of studies have indicated that faces are processed more holistically than most other objects (Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). Our understanding of holistic face processing remains sketchy, but it involves a more unitary representation of the properties of the face than the part-based representations used for objects (Biederman, 1987) as well as a representation in which the perception of one facial feature influences the perception of another (Freiwald, Tsao, & Livingstone, 2009; Tanaka & Sengco, 1997). The role of local facial features is not dismissed in most accounts of holistic processing, but emphasis is placed on the perception of the integrated whole as opposed to independent representations of the components (Pomerantz, Sager, & Stoever, 1977; Rossion, 2009).

While a disproportionate inversion effect for faces was the first evidence used to argue that face processing depends on a more holistic representation (Diamond & Carey, 1986; Garrido, Duchaine, & Nakayama, 2008; McKone et al., 2007; Valentine, 1988; Yin, 1969; see Bruyer, 2011, for a meta-analysis), more direct evidence for holistic face processing comes from three experimental effects: the part-whole effect (Tanaka & Farah, 1993; Tanaka & Sengco, 1997), the gaze-contingent effect (Van Belle, De Graef, Verfaillie, Busigny, & Rossion, 2010; Van Belle, De Graef, Verfaillie, Rossion, & Lefèvre, 2010; Van Belle, Lefèvre et al., 2010), and the face composite effect (Rossion, 2013; Young et al., 1987). The most frequently studied of these effects is the face composite effect in which observers find it more difficult to recognize that the top halves of two face stimuli are identical when the top halves are aligned with two different bottom halves than when the top and bottom halves are misaligned (Hole, 1994; Young et al., 1987). This effect is robust for upright

CONTACT R. Dawn Finzi dfinzi@ucsd.edu Department of Psychology, University of California, 9500 Gilman Drive, La Jolla, San Diego, CA, USA 92093

faces but weak for inverted faces (Susilo, Rezlescu, & Duchaine, 2013; Young et al., 1987; see Rossion, 2013, for a review). The face composite effect for upright faces reflects the integration of the two halves into a unitary representation which generates the perception of an entirely new face (Young et al., 1987).

The face composite effect is a commonly used and robust measure of holistic processing of upright faces for several reasons (Maurer, Le Grand, & Mondloch, 2002; McKone et al., 2007; Rossion, 2013). First, the face composite effect reflects an illusion generated by an artificial whole-face percept (Figure 1. Composite illusion), which provides a strong phenomenological basis for the notion of holistic face processing. Second, because each face is divided clearly into a top half and a bottom half (by a small gap or lines at the face edge), the "part" that participants are asked to consider is clearly delineated as opposed to potentially more ambiguous parts such as "the eyes" in the part-whole task (Rossion, 2013). Third, the face composite effect is typically large (often around or above 20% for accuracy; e.g., Rossion & Boremanse, 2008; Susilo, Rezlescu, et al., 2013) and moderately reliable (DeGutis, Wilmer, Mercado, & Cohan, 2013; Susilo, McKone, & Edwards, 2010; Wang, Li, Fang, Tian, & Liu, 2012), making it a useful paradigm for measuring holistic processing in the individual participants.

1. Holistic face perception and prosopagnosia

The holistic nature of face perception has led researchers to propose that an absence of holistic processing may be at the root of prosopagnosia, an impairment in recognizing facial identity that cannot be attributed to low-level visual problems or general deficiencies in memory or intelligence (Benton, 1980; Bodamer, 1947; Hecaen & Angelergues, 1962; Rondot & Tzavaras, 1969). Support for this notion is provided by anecdotal descriptions of acquired prosopagnosic participants that suggest holistic face impairments. For example, patient WL was described by Spillmann, Laskowski, Lange, Kasper, and Schmidt (2000) as "unable to form a holistic percept of a given face that would have revealed its bearer's identity" and lacking in the ability "to create an integrated, unitary percept or a gestalt of a human face enabling him to assign identity to an individual". A decade earlier, patient LH was similarly described by Levine and Calvanio (1989) as "unable to get an immediate overview of a face … as a whole at a single glance". Patients have also described themselves in this way, with patient GG responding that he was no longer capable of building a "global picture" of faces when asked to describe his difficulties (Busigny et al., 2010).

Despite the popularity of this holistic perception account of prosopagnosia, only four acquired prosopagnosic participants have been tested with measures of holistic face processing (Busigny et al., 2010, 2014; Ramon, Busigny, & Rossion, 2010; Rezlescu, Pitcher, & Duchaine, 2012; Van Belle, De Graef, Verfaillie, Busigny et al., 2010). Consistent with the holistic account, three patients failed to show the face composite effect, and they also had deficits in other measures of holistic processing. Patient GG showed a complete absence of the face composite effect, though he possessed intact non-face object recognition and an intact ability to perceive objects as integrated wholes, illustrated by a normal Navon effect and perception of 3D figures (Busigny et al., 2010). Furthermore, he showed no inversion effect or part-whole advantage for faces. Similarly, patient PS lacked a face composite effect, failing to show a significant advantage for misaligned over aligned trials in either accuracy or response time, and did not display part-whole effects (Ramon et al., 2010). PS was also extensively tested with gaze-contingent measures and again failed to show holistic face processing as measured by these tasks (Van Belle, De Graef, Verfaillie, Busigny et al., 2010). A third case of acquired prosopagnosia, patient LR, presented with an atypical

Figure 1. The face composite illusion. Identical top-halves that are aligned with different bottom-halves appear to be different (left pair). This illusion disappears when the top- and bottom-halves are misaligned (right pair). Reproduced from Susilo, Rezlescu, et al. (2013) with permission.

face composite effect, where the identity of the bottom half of the face influenced the patient's judgment of the top half on both aligned *and* misaligned trials, contrary to normal controls (Busigny et al., 2014). In other tests of holistic processing, patient LR also did not show typical face inversion or part-whole effects. The only exception to date is patient Herschel, who exhibited a face composite effect in the normal range (Rezlescu et al., 2012; Herschel's data in Experiment 1 of the current report was presented in that paper). However, it is unclear whether Herschel's face composite effect results from holistic face perception because he was not tested with a control condition, such as inverted faces (McKone et al., 2013).

In this study, we examined the role of holistic processing in prosopagnosia by testing seven acquired prosopagnosic participants with the face composite task. We chose to use the standard composite design rather than the full design (Cheung, Richler, Palmeri, & Gauthier, 2008; Hole, 1994; Rossion, 2013; Young et al., 1987), because of concerns that the alternative design is not sensitive to holistic face processing. The full design generates composite effects for upright faces that are similar in size to composite effects for many stimuli that do not appear to generate composite illusions such as inverted faces (Richler, Mack, Palmeri, & Gauthier, 2011), cars (Bukach, Phillips, & Gauthier, 2010; Gauthier, Curran, Curby, & Collins, 2003), and novel objects (Gauthier & Tarr, 2002; Wong, Palmeri, & Gauthier, 2009) (see Rossion, 2013, for further explanation). The argument for the alternative design rests on the potential for spurious results due to response bias in the standard design. However, the inclusion of an inverted condition allows us to assess whether holistic effects found for upright faces result from response bias. If response bias was contributing to the composite effect, similar-sized composite effects would be expected for both upright and inverted faces.

In the standard design, only the trials with two stimuli that had the same top halves are used to compute the face composite effect (Le Grand, Mondloch, Maurer, & Brent, 2004; Robbins & McKone, 2007; Rossion, 2013). This is because the holistic account makes a clear prediction only for these "same-top-half" trials: the aligned condition should be less accurate than the misaligned condition when the bottom halves differ because perceptual integration of the top and bottom of aligned stimuli decreases the perceived similarity of the identical top halves. For different trials, however, the prediction of holistic processing is unclear. If the two bottom halves are very different, the added dissimilarity through holistic integration could make the judgment that the top halves are different more accurate in the aligned than in the misaligned condition. If the bottom halves are relatively similar, holistic processing could result in the different top halves in the aligned condition being erroneously perceived as similar, making performance in the aligned condition less accurate than in the misaligned condition. However, in the full design, all trials are analysed and the measure is the interaction between alignment and congruency, with congruency referring to the relation between the correct response for the target half (same or different) and same-different status of the task-irrelevant half.

Our study extended prior results in two ways. First, given the modest reliability of the composite task (DeGutis et al., 2013; Susilo, McKone, et al., 2010; Wang et al., 2012), we tested participants with two composite tasks, to ensure that our findings are consistent across repeated assessments. To increase the generalizability of our findings, these two tasks also used different face stimuli and slightly different paradigms (one task presented a gap between top and bottom halves, the other task used demarcating lines at the edge of the face).

Second, we tested participants with inverted faces to assess whether any upright face composite effects present in the acquired prosopagnosics might result from factors other than holistic face perception, such as unusually broad visuospatial attention (McKone et al., 2013; Susilo, McKone, Dennett, et al., 2010). The composite face task assumes that in the absence of holistic perception, visuospatial attention can be focused on the target half. However, if a participant is incapable of focusing attention solely on the target half, then a spurious face composite effect could occur. The use of inverted faces addresses this possibility, because if the participant has unusually broad visuospatial attention, he/she would show similar-sized composite effects for upright and inverted faces (McKone et al., 2013; Susilo, McKone, Dennett, et al., 2010).

Additionally, our use of inverted faces controls for concerns that acquired prosopagnosics may use a different strategic approach to the composite task, and that the composite face paradigm may not be a valid measure of holistic processing in prosopagnosia (DeGutis, Cohan, Mercado, Wilmer, & Nakayama, 2012). The use of a different strategy—such as focusing on the nose region only—can lead to the appearance of a composite effect, but it would produce similar effects for upright and inverted faces.

2. Methods and results

2.1. Participants

We tested seven acquired prosopagnosics referred to as Faith, Florence, Galen, Herschel, Kepler, Kili, and Sandy (mean age = 46.0 years; *SD* = 11.3). These participants contacted us through the Prosopagnosia Research Center website (www.faceblind.org). All patients had structural and functional MRI to characterize their lesions. Table 1 lists the causes of their lesions, the face-selective regions disrupted by their lesions, and previous papers that included their results. Ten age-matched individuals (seven female) with a mean age of 51.8 years (*SD* = 8.2) provided control data for the composite experiments.

To establish that these participants have face recognition deficits, we collected results from three tests of face memory and one test of face perception. Results on all four tests confirmed that the seven acquired prosopagnosic participants have severe face processing deficits (Figure 2). Below we briefly describe each test and the control data for each test.

In the famous faces test, participants were shown 60 photographs one-at-a-time of individuals from entertainment or politics familiar to most US or Canadian participants (Yovel & Duchaine, 2006), or to most Britons, depending on the participant. Two versions of the test were used as Herschel is British, while the rest of the prosopagnosic participants are American or Canadian. Participants were given unlimited time to identify by name the people depicted. Control participants varied depending on whether the US/Canadian or the UK version of the test was used. For the UK test, 16 middle-aged adults were used as the control group (*M* = 44.1 years), while for the US/Canadian test, 19 US/Canadian controls were used (*M* = 40.9 years).

Next we assessed them with the Cambridge Face Memory Test (CFMT), a widely used test of unfamiliar face recognition (Duchaine & Nakayama, 2006; Wilmer et al., 2012). While the results on tests with famous faces may be affected by variable exposure of participants to the faces in daily life, this test probes short-term familiarity for unfamiliar faces so exposure to the faces is equated. Control data were from 20 middle-aged controls (*M* = 45.1 years) (Duchaine, Yovel, & Nakayama, 2007).

Face memory abilities were additionally evaluated using an old-new test (Duchaine & Nakayama, 2005). During the study phase participants were first shown

Table 1. The demographic information, causes of their lesions, face-selective regions disrupted by their lesions, and previous papers their results have appeared in for each acquired prosopagnosia participant.

Patient	Age	Sex	Cause	Lesions	Disrupted core face-selective regions	Previous literature
Faith	52	F	Resection for tumour	R Occipito-Temporal lobe	Right OFA, right FFA, right pSTS-FA	Fox, Iaria, & Barton, 2009; Susilo, Yang, Potter, Robbins, & Duchaine, 2015
Florence	32	F	Resection for epilepsy	R Hippocampus, R Amygdala	All regions preserved	R-AT1 in Barton, Hanif, & Ashraf, 2009; Fox, Hanif, Iaria, Duchaine, & Barton, 2011; Fox, Iaria, Duchaine, & Barton, 2013; Florence in Rezlescu, Susilo, Barton, & Duchaine, 2013; Susilo, Yovel, Barton, & Duchaine, 2013; Rezlescu, Barton, Pitcher, & Duchaine, 2014; Susilo, Yovel, et al., 2013
Galen	32	M	Resection for AVM	R Occipito-Temporal lobe	Right OFA, right FFA	Susilo, Yovel, et al., 2013; Susilo, Wright, Tree, & Duchaine, 2015; Susilo, Yang, et al. 2015; Yang, Susilo, & Duchaine, 2016
Herschel	58	M	Stroke	R Occipito-Temporal lobe, R Hippocampus	Right OFA, FFA, pSTS-FA, left OFA	Rezlescu et al., 2012; 2014; Susilo, Yang, et al., 2015
Kepler	56	M	Stroke	R Inferior Occipito-Temporal lobe	Right OFA, right FFA	R-IOT1 in Dalrymple et al., 2011; Rezlescu et al., 2013
Kili	53	F	Stroke	R Occipital lobe	All regions preserved	CB2 in Das, Tadin, & Huxlin, 2014; Susilo, Yang, et al., 2015
Sandy	39	F	Resection for epilepsy/ peri-operative stroke	Occipital lobe	Not available	Rezlescu et al., 2013; Susilo, Yovel, et al., 2013

Note: Face-selective regions were determined from results from functional localizer scans that contrasted the response to faces with the response to objects.

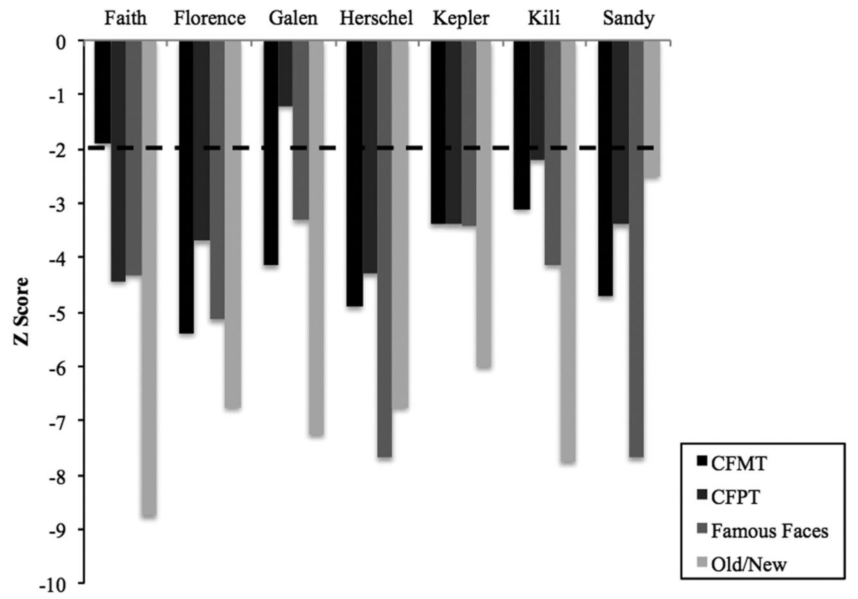


Figure 2. Face memory and perception *z* scores for the acquired prosopagnosic participants. The *z* scores on a Cambridge Face Memory Test (CFMT), Cambridge Face Perception Test (CFPT), famous face test and Old/New Recognition Test for each participant are displayed. The dashed line indicates two standard deviations below the control mean, the typical 95% cut-off in neuropsychological tests.

10 target faces, each presented twice. They were then shown 50 faces sequentially, 20 of which were the 10 "old" faces each appearing twice, and 30 of which were "new" faces. Participants were given unlimited time to indicate which faces were old (previously seen) and which were new. Nine participants between 52 and 59 years old ($M = 56.1$ years; five female) were used as controls.

Face identity perception was evaluated with the upright items from the Cambridge Face Perception Test (CFPT; Duchaine, Germine, & Nakayama, 2007). In this task, participants sort morphed images containing different proportions of the target faces (28%, 40%, 52%, 64%, 76%, and 88%) based on their similarity to the target. Twenty-one middle-aged participants served as controls ($M = 46.5$ years) (Duchaine et al., 2007).

2.2. Experiment 1a: Composite task 1 with upright faces

2.2.1. Stimuli and procedure

Our stimuli and procedure were adapted from the face composite task first used in Experiment 2 of Susilo, McKone, et al. (2010). Example stimuli can be seen in Figure 1. Stimuli were created from 60 original faces (32 female) with neutral expressions, seen in front-view greyscale. The original faces were grouped into sets according to sex and skin tone, and composite faces were created from top and bottom halves from different faces within these sets. Composites included a line on the bottom edge of the top half and the top edge of the bottom half to divide the two halves. The two halves of each composite were either aligned into an intact face or misaligned by moving the bottom half to the right by half a face. To cover hair cues, a black ski-cap was pasted electronically onto the images. When viewed from 80 cm, aligned composites subtended 4.0 degrees of visual angle vertically and 3.1 degrees horizontally and misaligned composites subtended 4.0 degrees vertically by 4.6 degrees horizontally. For testing, a composite image was paired with another composite that had either the same top half or a different top half: the bottom half always differed between the two. The full set consisted of 90 pairs of composite faces representing four conditions (30 *aligned/same-top*, 30 *misaligned/same-top*, 15 *aligned/different-top*, 15 *misaligned/different-top*).

On each trial, a pair of composite faces was presented sequentially, with the first stimulus (the target) appearing for 200 ms, followed by a black screen for 400 ms, and then the second stimulus (the probe) for 200 ms. Participants were told to indicate whether the two top-halves in a pair were the same or different, while ignoring the bottom-halves. Six practice trials were provided. Both upright and inverted trials were included in the block, with 90 trials for each orientation, and each composite pair presented only once in each orientation. The upright and inverted trials were randomly mixed. The upright data are discussed as Experiment 1a, and the inverted data presented as Experiment 1b.

The face composite effect in accuracy was calculated for each participant by subtracting the mean accuracy on *aligned/same-top* trials from that on *misaligned/same-top* trials. A positive face composite effect would result from lower accuracy in the *aligned/same-top* condition, with alignment leading to the illusion that the top half differed between the target and the probe stimuli. To compare each prosopagnosic participant's face composite effect against that of the controls, we ran *t*-tests designed for single-case analysis using the SINGLIMS software (Crawford & Garthwaite, 2002; Crawford & Howell, 1998).

We also analysed response times (RT) to determine if any face composite effects could be attributed to speed-accuracy trade-offs. For each participant, we calculated an RT face composite score by subtracting the mean RT of *misaligned/same-top* trials from the mean RT of *aligned/same-top* trials. This value would be negative if a speed-accuracy trade-off was creating faster but less accurate responses on aligned trials: if this was both negative and outside the normal range of performance, we would conclude that a speed-accuracy trade-off may be creating a spurious impression of holistic perception.

2.2.2. Results

The age-matched controls showed an upright face composite effect at the group level, ranging from 0 to 0.60 in individuals ($M = 0.28$, $SD = 0.23$, $t_9 = 3.84$, $p = .004$). This confirmed that the task used in Experiment 1 does produce face composite effects in participants with normal face processing. We then analysed our prosopagnosic participants' results at the individual level (Figure 3). Five participants, Galen, Florence, Herschel, Kili, and Sandy, had composite effects ranging from 0.10 to 0.37, within the control range, (all $ps > 0.4$). Two participants, Faith and Kepler, did not show the face composite effect, with difference scores of −0.03 and 0 respectively.

If speed-accuracy trade-offs were responsible for accuracy differences indicative of a face composite effect, then those participants would also be faster on aligned than misaligned trials. At the individual level (Figure 4), this was not the case for four of the five prosopagnosic participants with normal face composite effects for accuracy (Galen, Florence, Herschel, and Kili). The fifth prosopagnosic participant with a normal face composite effect for accuracy, Sandy, was faster on aligned than misaligned trials (Figure 5), but not significantly so compared to controls (RT face composite score = −98 ms, $t_9 = -1.176$, $p = 0.27$). Overall, these results indicate that the face composite effects in accuracy are not due to unusual speed-

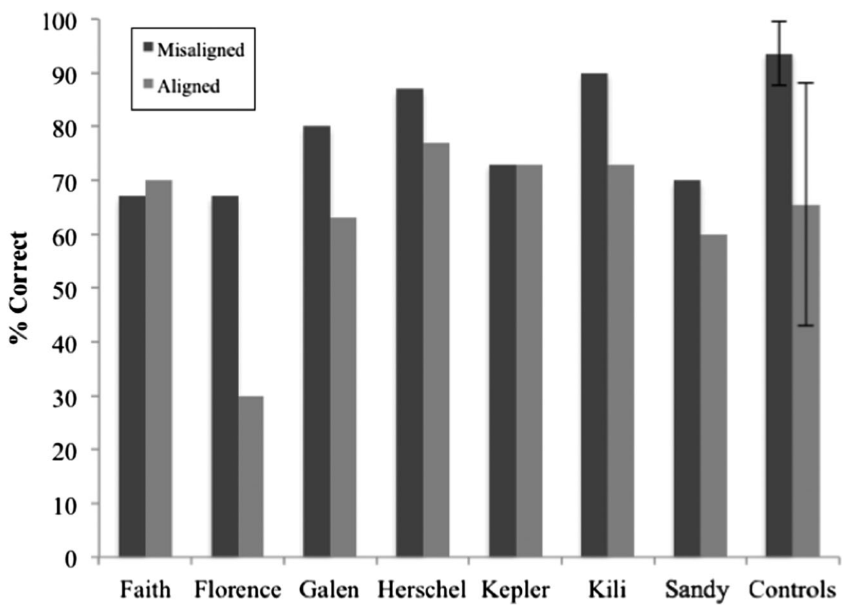


Figure 3. Experiment 1a: Accuracy for individual participants with acquired prosopagnosia, and mean for control group, on aligned and misaligned trials. Error bars represent one standard deviation.

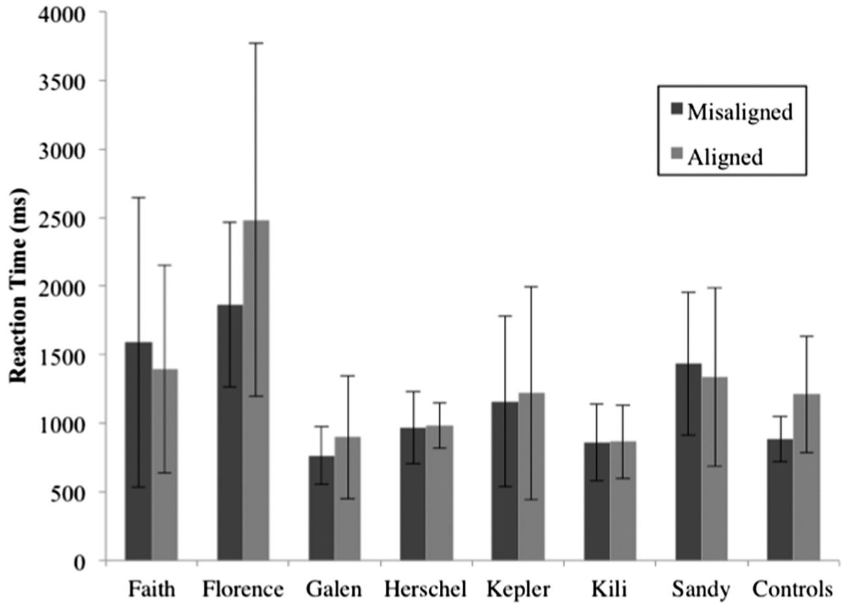


Figure 4. Experiment 1a: Response times for individual participants with acquired prosopagnosia, and mean RT for control group, on aligned and misaligned trials. Error bars represent one standard deviation.

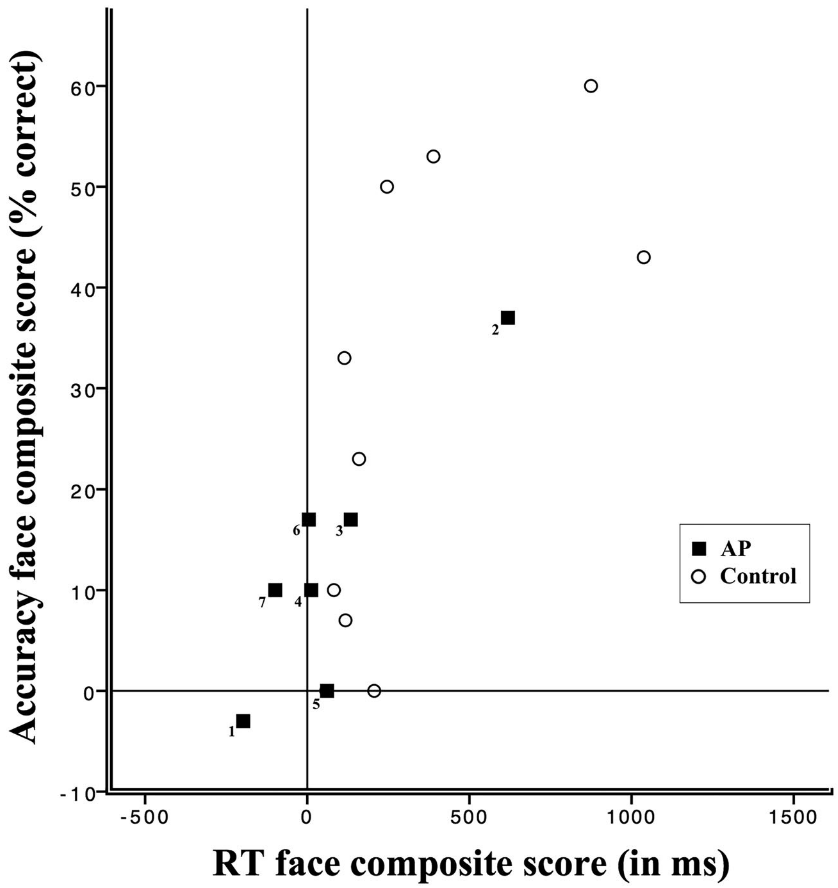


Figure 5. Experiment 1a: Individual RT face composite scores plotted against face composite effects (FCE) for accuracy. Acquired prosopagnosic (AP) participants are labelled with numbers as follows: 1 = Faith, 2 = Florence, 3 = Galen, 4 = Herschel, 5 = Kepler, 6 = Kili, and 7 = Sandy. For those participants who displayed positive face composite effects for accuracy, but negative RT face composite scores (top-left quadrant), speed-accuracy trade-offs may be responsible for the face composite effects. Here, only Sandy's score fulfils these criteria.

accuracy trade-offs between the aligned and misaligned conditions.

2.3. Experiment 1b: Composite task 1 with inverted faces

McKone et al. (2013; see also Susilo, McKone, Dennett, et al., 2010) have argued that upright face composite effects provide evidence for holistic processing only if participants also show little or no composite effect for inverted faces. Otherwise the disrupted performance in the aligned condition may result from factors that are not specific to face processing, such as the proximity of the two halves or unusually broad visuospatial attention. Thus, we tested for the presence of composite effects with inverted faces.

2.3.1. Stimuli and procedure

Data for both upright and inverted faces were collected during the protocol described in Experiment 1a, with the same faces used in upright and inverted trials, in random order. Here we present the results for the inverted trials.

2.3.2. Results

As expected, the age-matched controls did not display an inverted face composite effect ($M = 0.00$, $SD = 0.07$, $t_9 = 0.14$, $p = .89$). Additionally, when compared to the upright face composite effects from Experiment 1a, a repeated measures ANOVA (Orientation: upright, inverted) found that the inverted scores, as measured by percent correct, were significantly smaller the upright scores ($F(1,8) = 20.46$, $p = .001$, $\eta_p^2 = .70$). This was also true for RT face composite scores, with inverted RT scores significantly different from upright RT scores ($F(1,8) = 15.60$, $p = .003$, $\eta_p^2 = .63$).

Four of the five acquired prosopagnosic participants who showed face composite effects for upright stimuli in Experiment 1a, Herschel, Galen, Kili, and Sandy, had inverted face composite effects ranging from −0.07 to 0.10, which are within the normal range (all $ps > 0.1$, Figure 6), as well as being smaller than their corresponding upright FCEs from Experiment 1a. Faith, who lacked a face composite effect for upright faces in Experiment 1a, also lacked an inverted face composite effect (0.03) ($t_9 = -0.742$, $p = 0.447$). Two acquired prosopagnosic participants, Florence and Kepler, showed large inverted face composite effects (0.20) that differed from controls ($t_9 = 2.471$, $p = 0.018$). While Kepler did not show a normal composite effect in Experiment 1a (FCE = 0.00), Florence did show a normal effect (FCE = 0.37). Her inverted face composite effect indicates that Florence's apparently normal face composite effect may be driven by factors other than holistic face processing such a broad visuospatial attention, so her upright results should be interpreted cautiously.

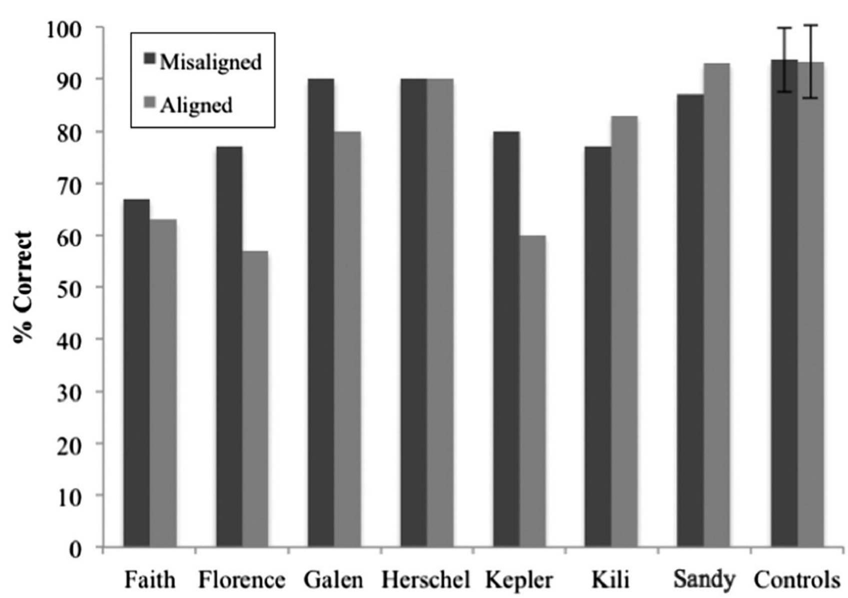


Figure 6. Experiment 1b: Accuracy for individual participants with acquired prosopagnosia, and mean for control group, on aligned and misaligned inverted trials. Error bars represent one standard deviation.

Inverted RT face composite scores for all prosopagnosic participants (Figure 7) ranged from −192 ms to 224 ms, but were within the normal range (all $ps > 0.05$). Faith, Florence, and Kili had negative inverted RT face composite scores of −192 ms, −112 ms, and −42 ms respectively, indicating faster responses on aligned trials, but none were abnormal compared to controls (all $ps > 0.1$).

2.4. Experiment 2: Composite task 2 with upright faces

2.4.1. Stimuli and procedure

In Experiment 2, we tested the seven prosopagnosic participants with a different composite task to examine whether we would find results similar to Experiment 1a. This composite task was created with the stimuli used in tasks assessing the face composite effect in patients GG, PS, and LR (Busigny et al., 2010, 2014; Ramon et al., 2010). Five female faces were used to create the stimuli. All images were cropped to remove external features and converted to greyscale. A three-pixel gap was inserted between the top and bottom face parts and was located above the upper limit of the nostril. This gap was identical to that used in Busigny et al. (2014) and ensured that the border separating the top and bottom halves of the face could be easily identified in the aligned condition (Rossion, 2013; Rossion & Retter, 2015). The full set of stimuli consisted of 180 composite pairs. Among these 180 pairs, each identity was represented equally as the first stimulus (target stimulus) and used as the second stimulus (probe stimulus) six to eight times. In each trial, the probe stimulus was 5% larger than the target stimulus to make strategies based on matching of low-level properties more difficult.

The task consisted of six trial types, two alignment conditions (aligned, misaligned) as in Experiment 1, but now with three target-probe pairing conditions (same-top, different-top, and same-both). The "same-top" condition is identical to the "same" condition in Experiment 1. In it, the top halves of the two faces in a trial were identical and the bottom halves were different. In the "different-top" condition, both the top and bottom halves of the target were from different identities than those of the probe. In the "same-both" condition, both the top and bottom halves of the probe had the same identity as the target. This third pairing condition was included to control for general effects of misalignment (for a discussion of the rationale see Rossion, 2013). Previous research has shown that performance on these "same-both" trials, where the bottom half does not change from target to probe, is not significantly affected by the alignment of the two halves of the face (Busigny et al., 2010; Jiang, Blanz, & Rossion, 2011).

Presentation of these stimuli followed the procedure used in Experiment 1, with the first stimulus

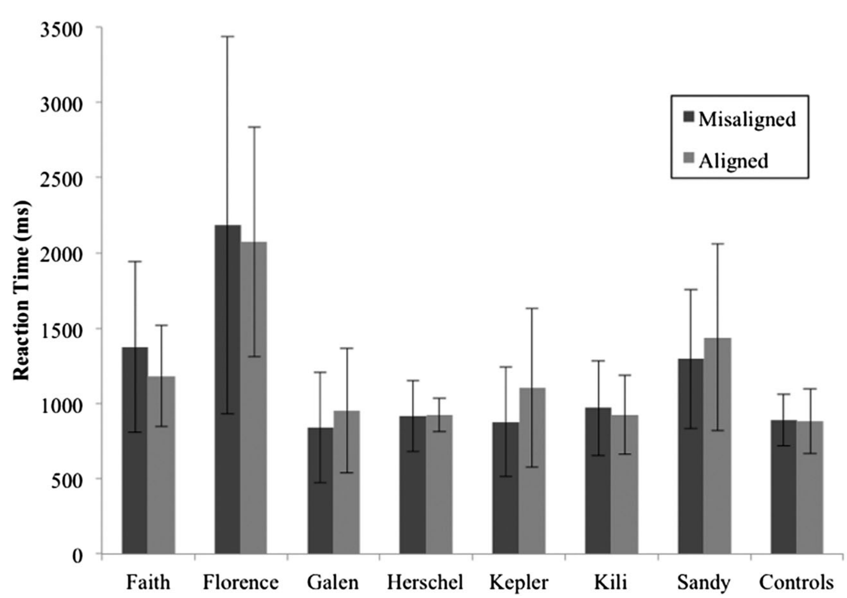


Figure 7. Experiment 1b: Response times for individual participants with acquired prosopagnosia, and mean for control group, on aligned and misaligned trials. Error bars represent one standard deviation.

(the target) appearing for 200 ms, followed by a black screen for 400 ms, and then the second stimulus (the probe) for 200 ms.

The face composite effect was calculated in the way as it was in Experiment 1 by subtracting mean accuracy in the *aligned/same-top* condition from mean accuracy in the *misaligned/same-top* condition. A corrected face composite effect that controls for general effects of misalignment is calculated by subtracting from the standard face composite effect the difference in mean accuracy between the *aligned/same-both* and *misaligned/same-both* conditions. The face composite effect of each prosopagnosic participant was compared to that of the controls by the same *t*-tests designed for single-case analysis as above.

As in Experiment 1, an RT face composite score was calculated to look speed-accuracy trade-offs.

2.4.2. Results

The age-matched controls showed a standard face composite effect ($t_9 = 3.93$, $p = .003$) that averaged 0.14 ($SD = 0.11$, range −0.03 to 0.3). This effect was smaller than the effect found in Experiment 1a ($t_9 = -2.51$, $p = .034$; Exp. 1 $d = 1.70$; Exp. 2 $d = 0.78$), but was comparable to the face composite effect in previous papers using this stimulus set (Busigny et al., 2010, 2014; Ramon et al., 2010).

At the individual level, the same five acquired prosopagnosic participants who showed face composite effects in Experiment 1a (Galen, Florence, Herschel, Kili, and Sandy) also showed face composite effects in the normal range in this experiment (all $ps > 0.5$) (Figure 8). Additionally, Kepler, who did not show a composite effect in Experiment 1a, had a face composite effect in Experiment 2 that was only slightly less than the control mean (Kepler's face composite effect = 0.13; $t_9 = -0.117$, $p = 0.909$). Faith, who had a slightly negative face composite effect in Experiment 1, had a negative face composite effect of −0.20 in this experiment ($t_9 = -2.877$, $p = 0.018$).

Incorporating the results of the same-both condition to give a corrected face composite effect resulted in a mean index of −0.14 ($SD = 0.13$) for controls, which is expected given that the alignment effect for the same-both condition should be around 0.

Based on this index, all prosopagnosic participants had a score which fell within the normal range (−0.2 to 0.07, all $ps > 0.08$). However, we will focus the remainder of our analysis on the uncorrected face composite effect, as those results are more conservative for our patients.

Four of the seven prosopagnosic participants had positive RT face composite scores ranging from 2 ms to 278 ms, indicating no speed-accuracy trade-off.

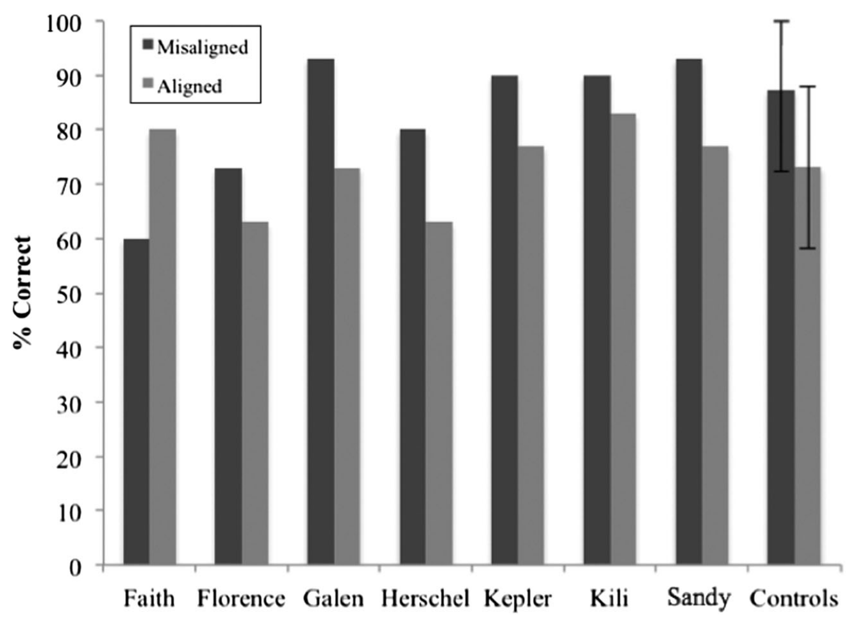


Figure 8. Experiment 2: Accuracy for individual participants with acquired prosopagnosia, and mean for control group, on aligned and misaligned trials. Error bars represent one standard deviation.

However, all of the prosopagnosic participants had RT face composite scores which were within the normal range (all $ps > 0.05$, Figure 9), including the three (Faith, Galen, and Kepler) who had negative RT face composite scores ($ps > 0.7$). Thus, while Galen and Kepler had results that might suggest a speed-accuracy trade-off, their RT face composite scores were closer to zero (indicating less of a speed-accuracy trade-off) than those of five control participants who also had a positive face composite effect in accuracy (Figure 10). Face composite effect results for both Experiment 1(a & b) and Experiment 2 can be seen in Figure 11.

2.5. Variability in the face composite effect between participants

The variability in the face composite effect between participants in our results, with some prosopagnosic participants showing robust composite effects while others did not, led us to consider whether differences in the severity of face recognition deficits or in the face areas damaged could explain our findings.

We first asked whether performance, as measured by z-scores (with a larger negative z-score indicating a worse deficit, Figure 2) on each of the four face recognition tests administered (CFMT, CFPT, Famous Faces, and Old/New) was correlated with either of the two upright face composite effects. Performance on the CFPT, the Famous Faces task, and the Old/New task was not correlated with face composite effects from Experiment 1 or Experiment 2 (all $ps > .187$). The lack of correlation with the CFPT is particularly relevant, as both the CFPT and the face composite effect are perceptual measures, whereas the CFMT, Famous Faces, and old/new task also involve memory processes. Performance on the CFMT was also not correlated with the face composite effect in Experiment 1 ($r(5) = -.69$, $p = .084$), but was negatively correlated with the face composite effect in Experiment 2 ($r(5) = -.77$, $p = .042$). This correlation could be interpreted to mean that more severe face recognition deficits are associated with stronger face composite effects, a paradoxical result. Given our small sample size, the borderline p-value, and the number of correlations tested (eight), we believe this effect is spurious. We also performed a grand correlation of the average z-score on all four face recognition tests versus the average face composite effect combining Experiments 1 and 2: this was not significant ($r(5) = -.07$, $p = .883$).

We then asked whether damage to the three areas of the core face network in the right hemisphere, the occipital face area (OFA), fusiform face area (FFA) and posterior superior temporal sulcus (pSTS-FA) predicted whether a face composite effect would be found. A linear regression testing whether the involvement of 0, 1, 2, or 3 face areas in the right hemisphere correlated with the magnitude of the face composite effect showed that presence or absence of the rOFA,

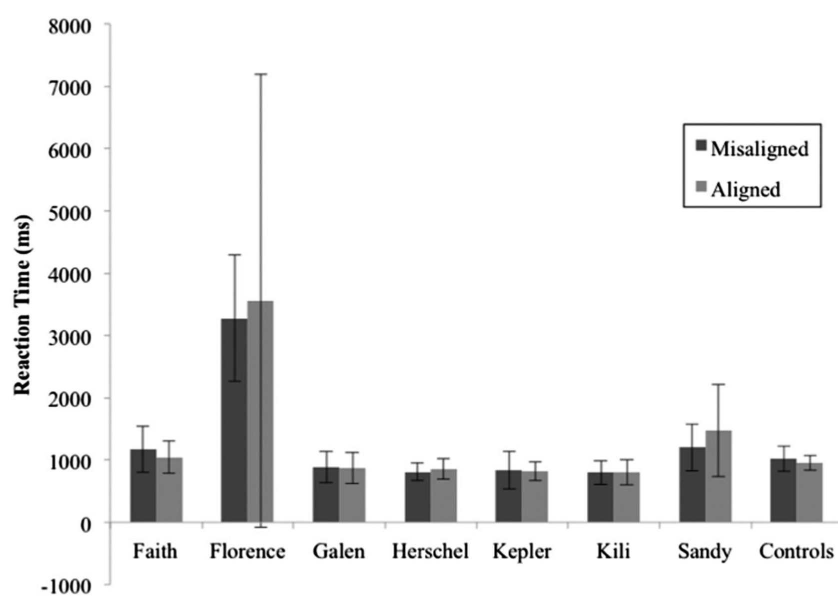


Figure 9. Experiment 2: Response time for individual participants with acquired prosopagnosia, and mean for control group, on aligned and misaligned trials. Error bars represent one standard deviation.

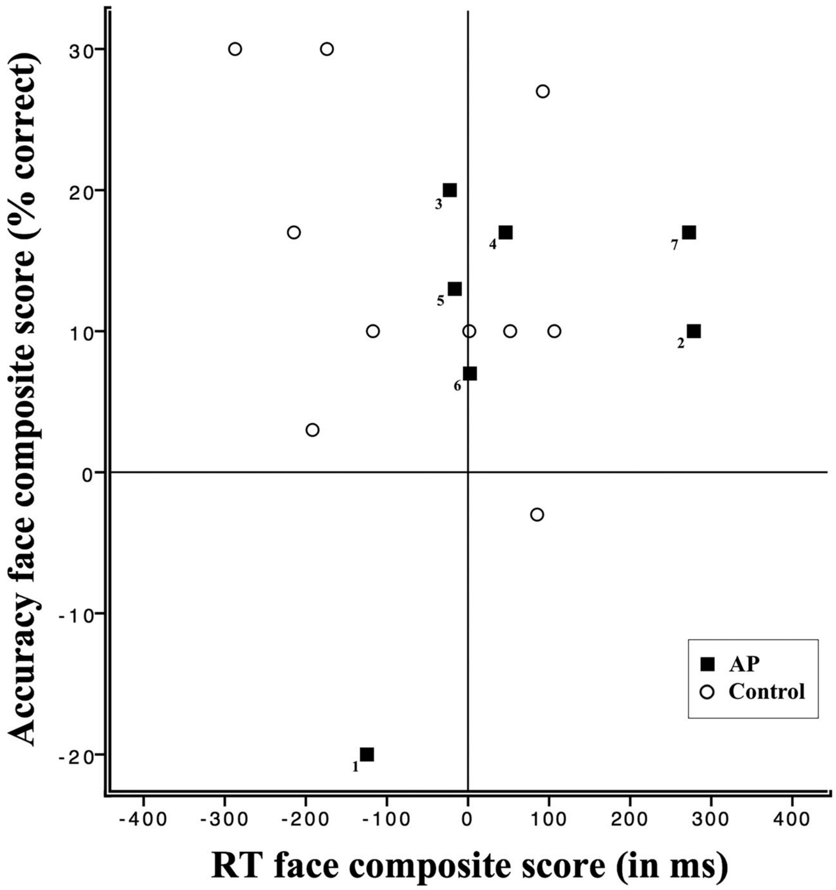


Figure 10. Experiment 2: Individual RT face composite scores plotted against face composite effects (FCE) for accuracy. Acquired prosopagnosic participants are labelled with numbers as follows: 1 = Faith, 2 = Florence, 3 = Galen, 4 = Herschel, 5 = Kepler, 6 = Kili, and 7 = Sandy. For those participants who displayed positive face composite effects for accuracy, but negative RT face composite scores (top-left quadrant), speed-accuracy trade-offs may be responsible for the face composite effects. While Sandy's score falls in that quadrant in Experiment 1a, in Experiment 2 she displays a large positive RT face composite score. Of the other acquired prosopagnosic participants, only Galen and Kepler show potential speed-accuracy trade-offs, and less so than a number of control participants (i.e., Galen and Kepler's negative RT face composite scores are greater—closer to zero—than those of five control participants).

rFFA or the right pSTS-FA did not significantly predict the face composite effects found in Experiment 1. A second linear regression with regards to the magnitude of the face composite effect in Experiment 2 found that the status of these three face areas did predict 97% of the variance in Experiment 2 face composite effects ($R^2 = .97$, $F(2,3) = 23.2$, $p = .042$), with absence of the right pSTS-FA significantly predicting lower face composite effects ($\beta = -.365$, $p = .016$). However, this is difficult to interpret as it is driven by an outlier: only one prosopagnosic participant, Faith, is missing her right pSTS-FA, and she displayed an anomalous negative face composite effect of −0.2 in Experiment 2. Finally, presence or absence of the rOFA, rFFA or the right pSTS-FA did not significantly predict the combined face composite effect derived from averaging the results of Experiment 1 and 2.

3. Discussion

We investigated the relationship between holistic face processing and acquired prosopagnosia using two versions of the face composite task with upright faces as well as an inverted control condition. Five of seven acquired prosopagnosic participants tested showed consistent face composite effects on both upright versions of the composite task. Response times in these five prosopagnosic participants were similar to those of controls, and speed-accuracy trade-offs were not a consistent nor convincing

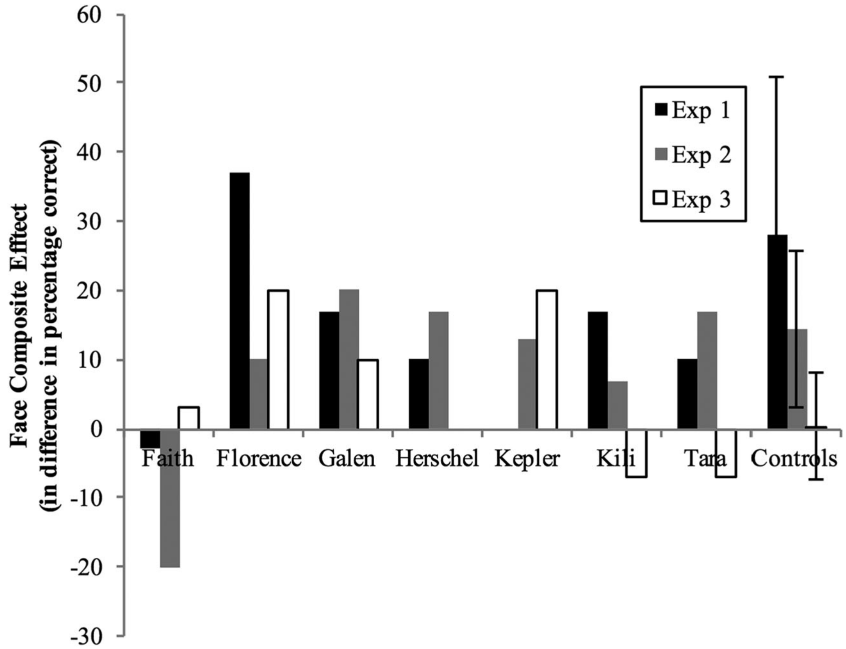


Figure 11. Experiments 1a, 1b & 2: Face composite scores for individual participants with acquired prosopagnosia, and mean for control group. Error bars represent one standard deviation.

explanation of their face composite effect results. Four of these prosopagnosic participants also showed reduced face composite effects for inverted faces that were comparable to controls, which indicates that their face composite effects found with upright faces do not result from more general factors. Together these findings demonstrate that holistic face processing can remain intact in at least some individuals with acquired prosopagnosia.

Previous research on the face composite effect in acquired prosopagnosia has found absent or atypical face composite effects in three cases (Busigny et al., 2010, 2014; Ramon et al., 2010). Patient GG showed a complete absence of a face composite effect, with no difference between performance on aligned and misaligned trials for either accuracy or RT (Busigny et al., 2010). Testing of patient PS focused on RT, as this proved to be the most consistent manifestation of the detrimental effect of aligned task-irrelevant bottom halves in the version of the composite task used: unlike controls, PS showed no composite effect with regards to RT (Ramon et al., 2010). Finally, patient LR had an atypical face composite effect. His accuracy was influence by the bottom half in both the aligned *and* misaligned conditions, whereas his RTs showed no effect of alignment (Busigny et al., 2014). These findings have led to suggestions that holistic face processing deficits are responsible for impaired face perception. The results for Faith and Kepler parallel these previous reports and add to the evidence that acquired prosopagnosia can be accompanied by deficits in holistic face processing.

The normal holistic effects in four of the prosopagnosic participants tested here, however, demonstrate that normal face composite effects are present in some cases of acquired prosopagnosia and that the relationship between holistic face processing and prosopagnosia is more complex than previous results indicated. Our understanding of the neural basis of holistic face perception is limited (Schiltz & Rossion, 2006), but it is plausible that faces are represented holistically in multiple regions in the face processing network (Duchaine & Yovel, 2015; Haxby, Hoffman, & Gobbini, 2000). Disruption of one or several regions that represent faces holistically may disrupt the input to other regions, but the normal face composite effects in the four prosopagnosic participants suggest that holistic behavioural effects may persist because intact regions continue to represent the degraded input holistically.

The variability in holistic face perception in our acquired prosopagnosic participants mirrors the variability of holistic perception in developmental prosopagnosia. Participants with developmental prosopagnosia have been found to have impaired holistic face processing, but some also have face composite effects in the normal range (Palermo et al., 2011). A thorough case study of the developmental prosopagnosic SP revealed normal holistic processing for upright faces across three composite-face effect experiments (Susilo, McKone, et al., 2010). Similarly, a meta-analysis showed reduced face inversion effects in developmental prosopagnosic participants in 11 out of 14 studies (DeGutis et al., 2012), but again many developmental prosopagnosic participants had normal inversion effects. Interestingly, an examination of the part-whole effect in a large sample of developmental prosopagnosic participants suggests holistic effects may be found for some facial features but not others: DeGutis et al. (2012) found a normal holistic advantage for the mouth but an absence of a holistic advantage for the eye region. Whether such feature-specific holistic effects occur in acquired prosopagnosia is an open question.

Our findings raise the question of why some acquired prosopagnosic participants show normal holistic processing while others do not. We considered two hypotheses. One possibility is that prosopagnosics with milder face recognition deficits may show stronger holistic face perception. However, we found that performance on the standard face perception and face recognition tests generally failed to correlate with the face composite effect of either experiment, with the exception of a borderline paradoxical inverse correlation between the CFMT and the face composite effect in Experiment 1. Similarly, differences in damage to the core face network in the right hemisphere could not explain the variability. The status of the occipital face area (OFA), fusiform face area (FFA) or posterior superior temporal sulcus (pSTS-FA) did not correlate with the face composite effect in Experiment 1 or overall, while a modest predictive effect of the status of the right pSTS-FA for the face composite effect in Experiment 2 was dependent on an outlying value for Faith. Overall, though, our ability to address these hypotheses is limited by the small number of participants and further research is needed to probe the nature of these individual differences in holistic processing ability.

Our finding that holistic face processing capabilities in four of our acquired prosopagnosic participants are comparable to that of controls, suggests that other mechanisms are impaired in these prosopagnosic participants. We suggest three possibilities, though we note that these suggestions are speculative and different deficits may be present in different acquired prosopagnosics. One possibility is that the acquired prosopagnosics are impaired in part-based processing which could be either face-specific, such as for the eye region (Bukach, Grand, Kaiser, Bub, & Tanaka, 2008; Caldara et al., 2005), or category-general. A second possibility is impairment in generalization across view and/or other image changes. The diagnostic tests we used with the acquired prosopagnosics (namely the CFMT, CFPT and the famous face test) require the ability to generalize across face images, while the composite tasks test only one given view of a face (Susilo, McKone, Dennett, et al., 2010). While some of the acquired prosopagnosics we tested show normal holistic processing in single views, based on the composite task results, they may still be impaired on holistic processing across views. Finally, the face recognition deficits in these acquired prosopagnosics may be attributable to abnormal face space coding.

While we find consistent evidence of face composite effects in four of our prosopagnosic participants, it is unclear whether holistic face processing is fully intact in these four. The comparison of their face composite effects to that of the control group does not suggest any reduction in the magnitude of their holistic effects, but because we do not have composite data from pre-morbid testing, it is possible that they had even larger face composite effects prior to brain damage. Future work with larger samples could address this question, as could pre- and post-surgical testing. To draw firm conclusions however, such work will need to equate performance for controls and acquired prosopagnosic participants in the *misaligned/same-top* condition so that restrictions of range do not influence the results. It is also worth noting that while a large body of evidence exists in support of the holistic interpretation of the face composite effect (Hole, 1994; Maurer et al., 2002; McKone et al., 2007; Rossion, 2013; Young et al., 1987), some recent research has questioned this inference (Fitousi, 2015, 2016). However our study was motivated by the generally held position that the face composite effect measures holistic processing, and thus its presence in some acquired prosopagnosic participants suggests that deficits in face recognition abilities can coexist with normal holistic processing capabilities.

In summary, previous case studies had suggested that acquired prosopagnosia is always accompanied by an absence of holistic face perception. In contrast, we demonstrate that severe face recognition deficits can co-occur with robust holistic face processing. This dissociation indicates that factors other than a loss of holistic processing may contribute to perceptual dysfunction in acquired prosopagnosia. Our results also indicate that intact face processes maintain the capacity to represent faces holistically even when other regions in the face network are damaged.

Acknowledgments

We thank Faith, Florence, Galen, Herschel, Kepler, Kili, and Sandy for their interest and participation in this study. We also thank Constantin Rezlescu for his help with Testable.org.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by a grant to BD from the National Science Foundation [grant number 1634098]. JB is supported by a Canada Research Chair and the Marianne Koerner Chair in Brain Diseases.

ORCID

R. Dawn Finzi http://orcid.org/0000-0003-0636-7375

References

Barton, J. J., Hanif, H., & Ashraf, S. (2009). Relating visual to verbal semantic knowledge: The evaluation of object recognition in prosopagnosia. *Brain*, *132*(12), 3456–3466.

Benton, A. L. (1980). The neuropsychology of facial recognition. *American Psychologist*, *35*(2), 176–186.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, *94*(2), 115–117.

Bodamer, J. (1947). Die prosop-agnosie. *Archiv für Psychiatrie und Nervenkrankheiten Vereinigt mit Zeitschrift für die Gesamte Neurologie und Psychiatrie*, *179*(1-2), 6–53.

Bruyer, R. (2011). Configural face processing: A meta-analytic survey. *Perception*, *40*(12), 1478–1490.

Bukach, C. M., Grand, R., Kaiser, M. D., Bub, D. N., & Tanaka, J. W. (2008). Preservation of mouth region processing in two cases of prosopagnosia. *Journal of Neuropsychology*, *2*(1), 227–244.

Bukach, C. M., Phillips, W. S., & Gauthier, I. (2010). Limits of generalization between categories and implications for theories of category specificity. *Attention, Perception, and Psychophysics*, *72*, 1865–1874. doi:10.3758/APP.72.7.1865

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*(14), 4057–4092.

Busigny, T., Van Belle, G., Jemel, B., Hosein, A., Joubert, S., & Rossion, B. (2014). Face-specific impairment in holistic perception following focal lesion of the right anterior temporal lobe. *Neuropsychologia*, *56*, 312–333.

Caldara, R., Schyns, P., Mayer, E., Smith, M. L., Gosselin, F., & Rossion, B. (2005). Does prosopagnosia take the eyes out of face representations? Evidence for a defect in representing diagnostic facial information following brain damage. *Journal of Cognitive Neuroscience*, *17*(10), 1652–1666.

Cheung, O. S., Richler, J. J., Palmeri, T. J., & Gauthier, I. (2008). Revisiting the role of spatial frequencies in the holistic processing of faces. *Journal of Experimental Psychology: Human Perception and Performance*, *34*(6), 1327–1336.

Crawford, J. R., & Garthwaite, P. H. (2002). Investigation of the single case in neuropsychology: Confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia*, *40*(8), 1196–1208.

Crawford, J. R., & Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. The Clinical *Neuropsychologist*, *12*(4), 482–486.

Dalrymple, K. A., Oruc, I., Duchaine, B., Pancaroglu, R., Fox, C. J., Iaria, G., … Barton, J. J. (2011). The anatomic basis of the right face-selective N170 in acquired prosopagnosia: A combined ERP/fMRI study. *Neuropsychologia*, *49*(9), 2553–2563.

Das, A., Tadin, D., & Huxlin, K. (2014). Going beyond blindsight: Properties of recovered vision in cortically blind fields. *Journal of Vision*, *14*(10), 660–660.

DeGutis, J., Cohan, S., Mercado, R. J., Wilmer, J., & Nakayama, K. (2012). Holistic processing of the mouth but not the eyes in developmental prosopagnosia. *Cognitive Neuropsychology*, *29*(5-6), 419–446.

DeGutis, J., Wilmer, J., Mercado, R. J., & Cohan, S. (2013). Using regression to measure holistic face processing reveals a strong link with face recognition ability. *Cognition*, *126*(1), 87–100.

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, *115*(2), 107–117.

Duchaine, B., Germine, L., & Nakayama, K. (2007). Family resemblance: Ten family members with prosopagnosia and within-class object agnosia. *Cognitive Neuropsychology*, *24*(4), 419–430.

Duchaine, B., & Nakayama, K. (2005). Dissociations of face and object recognition in developmental prosopagnosia. *Journal of Cognitive Neuroscience*, *17*(2), 249–261.

Duchaine, B., & Nakayama, K. (2006). The Cambridge face memory test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia*, *44*(4), 576–585.

Duchaine, B., & Yovel, G. (2015). A revised neural framework for face processing. *Annual Review of Vision Science*, *1*, 393–416.

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*(2), 104–113.

Fitousi, D. (2015). Composite faces are not processed holistically: Evidence from the garner and redundant target paradigms. *Attention, Perception, & Psychophysics*, *77*(6), 2037–2060.

Fitousi, D. (2016). Comparing the role of selective and divided attention in the composite face effect: Insights from Attention Operating Characteristic (AOC) plots and cross-contingency correlations. *Cognition*, *148*, 34–46.

Fox, C. J., Hanif, H. M., Iaria, G., Duchaine, B. C., & Barton, J. J. (2011). Perceptual and anatomic patterns of selective deficits in facial identity and expression processing. *Neuropsychologia*, *49*(12), 3188–3200.

Fox, C. J., Iaria, G., & Barton, J. J. (2009). Defining the face processing network: Optimization of the functional localizer in fMRI. *Human Brain Mapping*, *30*(5), 1637–1651.

Fox, C. J., Iaria, G., Duchaine, B. C., & Barton, J. J. (2013). Residual fMRI sensitivity for identity changes in acquired prosopagnosia. *Frontiers in Psychology*, *4*, 756.

Freiwald, W. A., Tsao, D. Y., & Livingstone, M. S. (2009). A face feature space in the macaque temporal lobe. *Nature Neuroscience*, *12*(9), 1187–1196.

Garrido, L., Duchaine, B., & Nakayama, K. (2008). Face detection in normal and prosopagnosic individuals. *Journal of Neuropsychology*, *2*(1), 119–140.

Gauthier, I., Curran, T., Curby, K. M., & Collins, D. (2003). Perceptual interference supports a non-modular account of face processing. *Nature Neuroscience*, *6*, 428–432. doi:10.1038/nn1029

Gauthier, I., & Tarr, M. J. (2002). Unraveling mechanisms for expert object recognition: Bridging brain activity and behavior. *Journal of Experimental Psychology: Human Perception and Performance*, *28*(2), 431–446.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*(6), 223–233.

Hecaen, H., & Angelergues, R. (1962). Agnosia for faces (prosopagnosia). *Archives of Neurology*, *7*(2), 92–100.

Hole, G. J. (1994). Configurational factors in the perception of unfamiliar faces. *Perception*, *23*(1), 65–74.

Jiang, F., Blanz, V., & Rossion, B. (2011). Holistic processing of shape cues in face identification: Evidence from face inversion, composite faces, and acquired prosopagnosia. *Visual Cognition*, *19*(8), 1003–1034.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2004). Impairment in holistic face processing following early visual deprivation. *Psychological Science*, *15*(11), 762–768.

Levine, D. N., & Calvanio, R. (1989). Prosopagnosia: A defect in visual configural processing. *Brain and Cognition*, *10*(2), 149–170.

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, *6*(6), 255–260.

McKone, E., Davies, A. A., Darke, H., Crookes, K., Wickramariyaratne, T., Zappia, S., … Fernando, D. (2013). Importance of the inverted control in measuring holistic face processing with the composite effect and part-whole effect. *Frontiers in Psychology*, *4*, 33.

McKone, E., Kanwisher, N., & Duchaine, B. C. (2007). Can generic expertise explain special processing for faces? *Trends in Cognitive Sciences*, *11*(1), 8–15.

Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object Agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, *9*(5), 555–604.

Palermo, R., Willis, M. L., Rivolta, D., McKone, E., Wilson, C. E., & Calder, A. J. (2011). Impaired holistic coding of facial expression and facial identity in congenital prosopagnosia. *Neuropsychologia*, *49*, 1226–1235.

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*(4), 319–324.

Pomerantz, J. R., Sager, L. C., & Stoever, R. J. (1977). Perception of wholes and of their component parts: Some configural superiority effects. *Journal of Experimental Psychology: Human Perception and Performance*, *3*(3), 422–435.

Ramon, M., Busigny, T., & Rossion, B. (2010). Impaired holistic processing of unfamiliar individual faces in acquired prosopagnosia. *Neuropsychologia*, *48*(4), 933–944.

Rezlescu, C., Barton, J. J., Pitcher, D., & Duchaine, B. (2014). Normal acquisition of expertise with greebles in two cases of acquired prosopagnosia. *Proceedings of the National Academy of Sciences*, *111*(14), 5123–5128.

Rezlescu, C., Pitcher, D., & Duchaine, B. (2012). Acquired prosopagnosia with spared within-class object recognition but impaired recognition of degraded basic-level objects. *Cognitive Neuropsychology*, *29*(4), 325–347.

Rezlescu, C., Susilo, T., Barton, J. J., & Duchaine, B. (2013). Normal social evaluations of faces in acquired prosopagnosia. *Cortex*, *50*, 200–203.

Richler, J. J., Mack, M. L., Palmeri, T. J., & Gauthier, I. (2011). Inverted faces are (eventually) processed holistically. *Vision Research*, *51*, 333–342. doi:10.1016/j.visres.2010.11.014

Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, *103*(1), 34–79.

Rondot, P., & Tzavaras, A. (1969). La prosopagnosie après vingt années d'études cliniques et neuropsychologiques. *Journal de Psychologie Normale et Pathologique*, *66*, 133–165.

Rossion, B. (2009). Distinguishing the cause and consequence of face inversion: The perceptual field hypothesis. *Acta Psychologica*, *132*(3), 300–312.

Rossion, B. (2013). The composite face illusion: A whole window into our understanding of holistic face perception. *Visual Cognition*, *21*(2), 139–253.

Rossion, B., & Boremanse, A. (2008). Nonlinear relationship between holistic processing of individual faces and pictureplane rotation: Evidence from the face composite illusion. *Journal of Vision*, *8*(4), 1–13.

Rossion, B., & Retter, T. L. (2015). Holistic face perception: Mind the gap! *Visual Cognition*, *23*(3), 379–398.

Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipito-temporal cortex. *Neuroimage*, *32*(3), 1385–1394.

Spillmann, L., Laskowski, W., Lange, K. W., Kasper, E., & Schmidt, D. (2000). Stroke-blind for colors, faces and locations: Partial recovery after three years. *Restorative Neurology and Neuroscience*, *17*(2), 89–103.

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*(8), 636–664.

Susilo, T., McKone, E., & Edwards, M. (2010). Solving the upside-down puzzle: Why do upright and inverted face aftereffects look alike? *Journal of Vision*, *10*(13), 1–1.

Susilo, T., Rezlescu, C., & Duchaine, B. (2013). The composite effect for inverted faces is reliable at large sample sizes.

Susilo, T., Wright, V., Tree, J. J., & Duchaine, B. (2015). Acquired prosopagnosia without word recognition deficits. *Cognitive Neuropsychology*, *32*(6), 321–339.

Susilo, T., Yang, H., Potter, Z., Robbins, R., & Duchaine, B. (2015). Normal body perception despite the loss of right fusiform Gyrus. *Journal of Cognitive Neuroscience*, *27*(3), 614–622.

Susilo, T., Yovel, G., Barton, J. J., & Duchaine, B. (2013). Face perception is category-specific: Evidence from normal body perception in acquired prosopagnosia. *Cognition*, *129*(1), 88–94.

Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology Section A*, *46*(2), 225–245.

Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory & Cognition*, *25*(5), 583–592.

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.

Valentine, T. (1988). Upside-down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology*, *79*(4), 471–491.

Van Belle, G., De Graef, P., Verfaillie, K., Busigny, T., & Rossion, B. (2010). Whole not hole: Expert face recognition requires holistic perception. *Neuropsychologia*, *48*(9), 2620–2629.

Van Belle, G., De Graef, P., Verfaillie, K., Rossion, B., & Lefèvre, P. (2010). Face inversion impairs holistic perception: Evidence from gaze-contingent stimulation. *Journal of Vision*, *10*(5), 1–13.

Van Belle, G., Lefèvre, P., Laguess, R., Busigny, T., De Graef, P., Verfaillie, K., & Rossion, B. (2010). Feature-based processing of personally familiar faces in prosopagnosia: Evidence from eye-gaze contingency. *Behavioural Neurology*, *23*, 255–257.

Wang, R., Li, J., Fang, H., Tian, M., & Liu, J. (2012). Individual differences in holistic processing predict face recognition ability. *Psychological Science*, *23*(2), 169–177.

Wilmer, J. B., Germine, L., Chabris, C. F., Chatterjee, G., Gerbasi, M., & Nakayama, K. (2012). Capturing specific abilities as a window into human individuality: The example of face recognition. *Cognitive Neuropsychology*, *29* (5-6), 360–392.

Wong, A. C. N., Palmeri, T. J., & Gauthier, I. (2009). Conditions for facelike expertise with objects becoming a Ziggerin expert—but which type? *Psychological Science*, *20*(9), 1108–1117.

Yang, H., Susilo, T., & Duchaine, B. (2016). The anterior temporal face area contains invariant representations of face identity that can persist despite the loss of right FFA and OFA. *Cerebral Cortex*, *26*(3), 1096–1077.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, *81*(1), 141–145.

Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception*, *16*(6), 747–759.

Yovel, G., & Duchaine, B. (2006). Specialized face perception mechanisms extract both part and spacing information: Evidence from developmental prosopagnosia. *Journal of Cognitive Neuroscience*, *18*(4), 580–593.