Face perception is category-specific: Evidence from normal body perception in acquired prosopagnosia

Tirta Susilo a,⇑, Galit Yovel b, Jason J.S. Barton c, Bradley Duchaine a

a Department of Psychological and Brain Sciences, Dartmouth College, United States
b School of Psychological Sciences & Sagol School of Neuroscience, Tel Aviv University, Israel
c Departments of Medicine (Neurology) & Ophthalmology and Visual Sciences, University of British Columbia, Canada

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Does the human visual system contain perceptual mechanisms specialized for particular object categories such as faces? This question lies at the heart of a long-running debate in face perception. The face-specific hypothesis posits that face perception relies on mechanisms dedicated to faces, while the expertise hypothesis proposes that faces are processed by more generic mechanisms that operate on objects we have extended experience with.

Previous studies that have addressed this question using acquired prosopagnosia are inconclusive because the non-face categories tested (e.g., cars) were not well-matched to faces in terms of visual exposure and perceptual experience. Here we compare perception of faces and bodies in four acquired prosopagnosics. Critically, we used face and body tasks that generate comparable inversion effects in controls, which indicates that our tasks engage orientation-specific perceptual mechanisms for faces and bodies to a similar extent. Three prosopagnosics were able to discriminate bodies normally despite their impairment in face perception. Moreover, they exhibited normal inversion effects for bodies, suggesting their body perception was carried out by the same mechanisms used by controls. Our findings indicate that the human visual system contains processes specialized for faces.

1. Introduction

A fundamental issue in cognitive science concerns the extent to which the human mind consists of processes specialized for particular object categories. This issue motivates the long-running debate about the nature of face perception. According to the face-specific hypothesis, face perception is carried out by mechanisms specialized for faces (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Tanaka & Farah, 1993; Yin, 1969). According to the expertise hypothesis, faces are analyzed by more generic mechanisms for objects with which we have extended experience (Diamond & Carey, 1986; Gauthier & Tarr, 1997; McGugin, Gatenby, Gore, & Gauthier, 2012). Here we contrast the two hypotheses by examining body perception when face perception is impaired in acquired prosopagnosia (Bodamer, 1947).

Previous studies that have investigated the nature of face processing using acquired prosopagnosia have typically compared perception of faces and a variety of non-face objects (e.g., Busigny, Graf, Mayer, & Rossion, 2010; Farah, Klein, & Levinson, 1995; Moscovitch, Winocur, & Behrmann, 1997; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008). While dissociations between perception of faces and non-faces suggest that faces are processed differently than most objects, they do not distinguish between the face-specific hypothesis and the expertise hypothesis because (i) both hypotheses agree that faces are processed by mechanisms different from those used for objects (i.e., most of us are experts with faces but not objects), and (ii) the non-face categories tested (e.g., cars, chairs) are not matched to faces in terms of perceptual
experience. To discriminate between the two hypotheses, faces need to be compared with an object category for which participants have similar amounts of perceptual experience. Only then will the expertise hypothesis predict an association between faces and non-faces in all prosopagnosics, while the face-specific hypothesis suggest dissociations can occur in some prosopagnosics.

Here we used bodies as a comparison category, because faces and bodies share two theoretically important characteristics. First, both faces and bodies produce inversion effects (i.e. worse discrimination of visual stimuli presented upside-down) larger than those for other objects (the face inversion effect, *Yin, 1969*; the body inversion effect, *Reed, Stone, Bozova, & Tanaka, 2003*). This is important because inversion effects indicate orientation-specific processing and are considered a marker of perceptual expertise. Most critical for our study, inversion effects for faces and bodies can be similar in size (*Robbins & Coltheart, 2012a; Yovel, Pelc, & Lubetzky, 2010*), which indicates that faces and bodies can engage orientation-specific mechanisms to a similar extent. Second, faces and bodies exhibit consistent first-order configurations (i.e., fixed spatial relations between eyes, nose, and mouth for faces; arms, torso, and legs for bodies), which have been suggested to be necessary for the development of visual expertise for particular object categories (*Diamond & Carey, 1986*).

Our study consisted of three steps. We first confirmed that our face and body tasks generate comparable inversion effects in controls. This step ensured that our tasks engage orientation-specific processing of faces and bodies to a similar extent, a critical factor in contrasting the face-specific and the expertise hypotheses. Next we compared how the prosopagnosics discriminate among exemplars of upright faces and of upright bodies. Finally we examined whether the prosopagnosics who were able to discriminate upright bodies as accurately as controls also showed normal-sized inversion effects for bodies, which would suggest that their body perception was generated by the same mechanisms used by controls. The status of the body inversion effect in acquired prosopagnosia is of additional interest because there is some evidence that the body inversion effect might involve face-selective rather than body-selective neural mechanisms (*Brandman & Yovel, 2010*).

### 2. Method

#### 2.1. Participants

We tested four acquired prosopagnosics, namely Florence, Sandy, Grace, and Galen, as part of our broader investigation of prosopagnosia. Table 1 shows their performance on tests of face recognition.

Florence is a right-handed nurse born in 1982. She was 29 years old when tested. In 2006, Florence noticed problems with face recognition following a right amygdalo-hippocampectomy. Functional MRI scans showed bilateral activations in her fusiform face area, occipital face area, and superior temporal sulcus. In 2008 she underwent a second surgery that removed the anterior third of her right temporal lobe, sparing the core face areas previously identified. Florence did not complain of visual impairments other than prosopagnosia, and she performed normally on within-class recognition of objects including hairstyles, cars, and abstract paintings. In *Fox, Hanif, Iaria, Duchaine, and Barton (2011)*, Florence was referred to as R-AT1.

Sandy is a right-handed woman born in 1975. She was 36 years old when tested. Sandy became prosopagnostic after a right hippocampal resection in 2003 during which she had a stroke in the occipital lobe and she lost her left visual field completely. She complained of severe difficulties recognizing faces, including herself in the mirror and her children in the school, and reported that she relies heavily on gait and walking sound to identify people. Sandy also complained of object recognition problems, such as finding her car when other cars in the parking lot have similar colors. Sandy was impaired on tests of visual closure, eye gaze perception, facial expression recognition, and hairstyle recognition. Sandy reported no general memory problems.

Grace is a right-handed pharmacist born in 1968. She was 43 years old when tested. Grace acquired prosopagnosia after a brain biopsy of the right temporal lobe in 1982 to treat herpes simplex viral encephalitis. Grace complained about difficulties in face recognition and relies on non-face cues like voice, hairstyle, glasses, and gait to identify people. In addition to her prosopagnosia, Grace was also impaired on tests of color perception, visual closure, and basic object recognition from line drawings. Structural MRI scans showed a lesion in the right anterior temporal lobe extending to the middle fusiform and inferior temporal gyri, as well as a small lesion in the middle aspect of the left fusiform gyrus. She was referred to as B-OT/AT1 in *Dalyrmple et al. (2011)*.

Galen is a right-handed physician born in 1982. He was 29 years old when tested. Galen became prosopagnostic in 2004 following a craniotomy for an arteriovenous malformation in his right temporal lobe. He complained of difficulties recognizing faces, including celebrities and people who are related or have similar appearances and reported using contextual cues to identify people. Galen previously experienced a left-superior quadrantanopia, but a recent examination showed his low-level abilities in the

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**Table 1**

| Face recognition ability (z-scores) of the acquired prosopagnosics. In the Cambridge Face Memory Test (CFMT, *Duchaine & Nakayama, 2006*), participants study six target faces and then select which of three presented faces is a target face. In the Cambridge Face Perception Test (CFPT, *Duchaine, Yovel, & Nakayama, 2007*), participants sort six faces based to their similarity to a target face simultaneously presented in a different view. In the Queen Square Face Identity Test (*Garrido et al., 2009*), participants make a same/different identity judgment on two sequentially presented faces that always differ in expression. All z-scores are more than two standard deviations below the mean (except Galen’s z-score on the CFPT), indicating severe impairment in face processing. All z-scores were computed using control means in the cited references. |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|
| Florence | Sandy | Grace | Galen |
| Cambridge Face Memory Test | −4.66 | −4.29 | −3.53 | −3.78 |
| Cambridge Face Perception Test | −3.65 | −3.38 | −3.24 | −1.26 |
| Queen Square Identity Test | −4.33 | −2.77 | −2.31 | −2.33 |
The main experiment used a task developed by Yovel et al. (2010), in which participants made same/different judgments on 144 sequentially presented pairs of headless bodies, faceless bodies, and faces, shown in different blocks (Fig. 1). Body pairs differed in terms of, the position of the arms, legs, and heads (in the faceless bodies). Face pairs differed in terms of eyes, nose, and mouth. For each of the three categories, upright and inverted trials (72 each) were interleaved in a pre-determined random order. Headless bodies were tested first, faceless bodies second, and faces last to ensure that poor face discrimination was not due to unfamiliarity with the paradigm and that normal body discrimination was not confounded by practice effects. Dependent measures were $d'$-prime and response time. Inversion effects were computed as $[\text{upright } d' - \text{inverted } d']$ and as $[\text{upright RT} - \text{inverted RT}]$. (Note that we also computed inversion effects in a relative manner: $[(\text{upright } d' - \text{inverted } d')]/(\text{upright } d' + \text{inverted } d')]$ and $[(\text{upright RT} - \text{inverted RT})]/(\text{upright RT} + \text{inverted RT})$; as presented in Supplementary Figure, we found similar results for all prosopagnosics and thus came to the same conclusion.)

2.2. Stimuli and procedure

The main experiment used a task developed by Yovel et al. (2010), in which participants made same/different judgments on 144 sequentially presented pairs of headless bodies, faceless bodies, and faces, shown in different blocks (Fig. 1). Body pairs differed in terms of, the position of the arms, legs, and heads (in the faceless bodies). Face pairs differed in terms of eyes, nose, and mouth. For each of the three categories, upright and inverted trials (72 each) were interleaved in a pre-determined random order. Headless bodies were tested first, faceless bodies second, and faces last to ensure that poor face discrimination was not due to unfamiliarity with the paradigm and that normal body discrimination was not confounded by practice effects. Dependent measures were $d'$-prime and response time. Inversion effects were computed as $[\text{upright } d' - \text{inverted } d']$ and as $[\text{upright RT} - \text{inverted RT}]$. (Note that we also computed inversion effects in a relative manner: $[(\text{upright } d' - \text{inverted } d')]/(\text{upright } d' + \text{inverted } d')]$ and $[(\text{upright RT} - \text{inverted RT})]/(\text{upright RT} + \text{inverted RT})]$; as presented in Supplementary Figure, we found similar results for all prosopagnosics and thus came to the same conclusion.)

2.3. Statistical analysis

We used the $t$-test for single-case analysis (Crawford & Howell, 1998) to compare a case score against the control mean in a particular condition (e.g., Florence’s discrimination of upright faces). To compare each case’s difference scores (e.g., the difference between Florence’s discrimination of faces and her discrimination of faceless bodies) against the difference scores in controls, we used the Bayesian Standardized Difference Test (Crawford & Garthwaite, 2007). For all statistical analyses we report the estimated percentage of the control population that would perform worse than a case score or would exhibit a larger difference score in the predicted direction. Note that these estimated percentages directly correspond to $p$-values. Scores below a 5% cut-off were classified as abnormal.

3. Results

3.1. Did faces and bodies show comparable inversion effects in controls?

Fig. 2A shows that all conditions produced inversion effects in controls. Computed using the absolute index (i.e. $[\text{upright } d' - \text{inverted } d']$), the inversion effect for faces ($M = 1.28, \ SE = 0.21$) was comparable to that for faceless bodies ($M = 1.04, \ SE = 0.18$, $F(1,19) = 3.19, \ p = 0.09$, but larger than that for headless bodies ($M = 0.55, \ SE = 0.18$, $F(1,19) = 24.91, \ p < 0.001$). Computed using the relative index (i.e., $[(\text{upright } d' - \text{inverted } d')]/(\text{upright } d' + \text{inverted } d')]$, the inversion effect for faces ($M = 0.31, \ SE = 0.04$, $F(1,19) = 24.91, \ p < 0.001$) was again comparable to that for faceless bodies ($M = 0.26, \ SE = 0.03$, $F(1,19) = 1.52, \ p = 0.23$, and larger than that for headless bodies ($M = 0.16, \ SE = 0.07$, $F(1,19) = 4.9, \ p = 0.04$). Fig. 2B shows that there was no speed–accuracy trade-off: participants were slower to discriminate inverted than upright stimuli. This result replicates a previous finding (Yovel et al., 2010), and indicates that faces and faceless bodies, but not headless bodies, engage orientation-specific processes to a similar degree.

3.2. How did the prosopagnosics discriminate faces and bodies in the upright orientation?

Table 2 (condition scores) shows that all prosopagnosics, except Sandy, were statistically impaired with faces but normal with faceless bodies and headless bodies on both $d'$-prime and RT. However, given that a statistically

1 The inversion effect for faceless bodies was trending smaller than that for faces ($p = 0.09$), but two previous studies using the same task found no such trend ($p = 0.54$ in Brandman & Yovel, 2012; $p > 0.3$ in Yovel et al., 2010). Based on all available data we would argue that our task generates statistically comparable inversion effects for faces and faceless bodies.
impaired score and a non-impaired score may not be significantly different (Crawford & Garthwaite, 2007), we next assessed whether the differences between discrimination of faces and bodies in the prosopagnosics were statistically abnormal compared to the same differences in controls.

### 3.3. Was the difference between discrimination of faces and faceless bodies abnormal?

The difference scores in Table 2 show that the d-primes for Florence, Grace, and Galen were significantly worse for faces than for faceless bodies. Florence and Galen were also significantly different on RT. Critically, all three prosopagnosics exhibited normal-sized inversion effects for faceless bodies on both d-prime and RT (Table 2 inversion effects, Fig. 3). Normal discrimination of and normal-sized inversion effects for faceless bodies indicates that despite their prosopagnosia, Florence, Grace, and Galen processed faceless bodies like controls did.

### 3.4. Was the difference between discrimination of faces and headless bodies abnormal?

The difference scores in Table 2 also show that all prosopagnosics performed worse with faces than with headless bodies on d-prime. As above, Florence and Galen also
showed a dissociation for RT. Florence, Sandy, and Grace showed normal-sized inversion effects for headless bodies on both $d'$-prime and RT (Table 2 inversion effects, Fig. 3C). These results indicate that perception of headless bodies can be spared in prosopagnosia, although it does not distinguish between the face-specific and the expertise hypotheses because the inversion effect for headless bodies in controls was smaller than that for faces to start with.

3.5. Did the prosopagnosics who show normal body inversion effects also show normal face inversion effects?

The idea that body inversion effects might rely on mechanisms for face rather than body perception (Brandman & Yovel, 2010) predicts that prosopagnosics who showed normal body inversion effects should also show normal face inversion effects. Is this the case? Our data suggest not. While Florence, Grace, and Galen showed face inversion effects in the normal range on $d'$-prime, Florence and Galen exhibited a clear speed/accuracy trade-off: they were much slower with upright faces than with inverted faces (Table 2 inversion effects, Fig. 3A). As a result, their data are difficult to interpret. In contrast, Florence and Galen showed normal-sized inversion effects for faceless bodies on both $d'$-prime and RT, thus indicating a dissociation between their inversion effects for faces and for faceless bodies.

3.6. Was discrimination of bodies easier than discrimination of faces?

- None of our results can be accounted by easier discrimination of bodies than of faces. In fact controls were better at discriminating faces than both faceless bodies, $t(19) = 2.90$, $p < .01$, and headless bodies, $t(19) = 8.08$, $p < .0001$. This means that three of four prosopagnosics performed normally on body tasks that are more challenging than the face task they had impairments with.
4. Discussion

In this study we addressed whether faces are processed by specialized mechanisms (face-specific hypothesis) or by more generic mechanisms for objects we have extended experience with (expertise hypothesis). We did so by comparing perception of faces and bodies in acquired prosopagnosia, because faces and bodies engage orientation-specific perceptual mechanisms and exhibit consistent first-order configurations among their parts. Controls exhibited comparable inversion effects for faces and faceless bodies. Three of four prosopagnosics were able to discriminate bodies as well as controls and showed normalized body inversion effects. Their results indicate body perception can be normal when face perception is impaired, consistent with the face-specific hypothesis.

Our findings add to the literature on acquired prosopagnosics who performed normally with non-faces. Termined “pure” prosopagnosics (for a review of 13 existing cases see Busigny et al., 2010), these participants are often considered evidence that faces are processed by dedicated mechanisms, especially when the face and non-face tasks are matched for task demands, equated in difficulty, and free of speed/accuracy trade-offs. However, such dissociations do not discriminate between the face-specific and the expertise hypotheses because it is unclear whether the prosopagnosics had extensive experience with the non-face categories tested. In contrast, our use of bodies as a comparison category allows us to tease apart the two hypotheses because faces and bodies share theoretically-important characteristics mentioned above.

Our study is the first to report a dissociation between face and body perception in acquired prosopagnosia. Case FM was impaired with perception of both faces and bodies (Moro et al., 2012). The well-known case PS showed typical fMRI activation in body-selective areas to emotional body stimuli, but her behavioral performance with bodies was not assessed (Peelen, Lucas, Mayer, & Vuilleumier, 2009). A few studies examined face and body perception in developmental prosopagnosia and found mixed results (e.g., Duchaine, Yovel, Butterworth, & Nakayama, 2006; Righart & De Gelder, 2007). Crucially, however, none of these studies demonstrated that the body tasks used generated face-size inversion effects in controls. It thus remains possible that normal body perception observed in developmental prosopagnosics did not depend on orientation-specific mechanisms to a similar extent as faces did.

Our result agrees with evidence from single-cell, functional imaging (fMRI), and transcranial magnetic stimulation (TMS) studies. The existence of face-selective neurons has long been reported (Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982), and recent investigations have established that these neurons are functionally organized in a network of face-selective patches (Moeller, Freiwald, & Tsao, 2008). Functional imaging studies have found separate cortical areas selective for faces and bodies in humans (de Gelder et al., 2010; Peelen & Downing, 2007), and TMS studies have indicated the causal involvement of some of these areas in discrimination tasks only for their preferred category (Pitcher et al., 2009; Urgesi, Berlucchi, & Aglioti, 2004). Our finding complements these data by showing a cognitive dissociation between face and body perception. While direct mapping between behavioral performance and lesion location is beyond the scope of the present study, future studies of acquired prosopagnosia are likely to benefit from obtaining functional scans to body and body part stimuli.

What is the nature of the orientation-specific mechanisms for faceless bodies that were spared in our prosopagnosics? Given their face-size inversion effects, these mechanisms might perform holistic computations similar to those in face perception. Consistent with this possibility, perception of body parts benefits from the presence of the whole body (Seitz, 2002), just like perception of face parts benefits from the context of the whole face (i.e., the part-whole effect, Tanaka & Farah, 1993). Perception of one-half of bodies can be influenced by the unattended half (Robbins & Coltheart, 2012b, but see Soria Bauser, Suchan, & Daum, 2011), similar to the composite face effect (Young, Hellaowell, & Hay, 1987). Future studies can use these paradigms to further clarify whether normal body perception in acquired prosopagnosia is holistic in nature.

A recent study however suggests that the face-size inversion effect for faceless bodies might not be driven by body perception mechanisms, but instead by face detection mechanisms (Brandman & Yovel, 2012). This study compared the size of inversion effects for several body conditions including faceless bodies, heads with shoulders, heads only, and bodies from the back. Only faceless bodies and heads with shoulders generated face-size inversion effects; other conditions produced smaller inversion effects. In a second experiment, different body conditions were flashed for 17 ms each, and participants were asked whether they saw a face. Interestingly, participants were more likely to report seeing a face in the same two conditions that produced face-size inversion effects, namely faceless bodies and heads with shoulders. The authors interpreted these results as evidence that the face-size inversion effects in bodies are generated by face detection mechanisms.

Although our data are not inconsistent with the potential involvement of face detection mechanisms (we did not systematically assess face detection ability of the prosopagnosics), it is worth noting that face-size inversion effects were obtained for faceless bodies and bodies with shoulders, not for heads only (Brandman & Yovel, 2012). This means two things: (i) there has to be some body parts in the stimuli (shoulders at the minimum) for the face-size inversion effects to emerge, and (ii) these body parts have to be processed normally. A participant with impaired shoulder perception, for example, would be expected to process faceless bodies abnormally, and thus would fail to exhibit normal inversion effects. The fact that our prosopagnosics exhibited normal inversion effects for faceless bodies implies that their ability to process all aspects of faceless bodies was normal.

Regardless of the underlying mechanisms, the body inversion effect indicates that bodies, unlike most non-face objects, are processed by perceptual mechanisms that are very sensitive to orientation and are therefore a suitable category for distinguishing between the expertise and the
face-specific hypotheses. No prosopagnosia studies to date have used a task where the non-face category is comparable to faces in terms of sensitivity to orientation, and thus our study offers a critical piece of evidence that is inconsistent with the notion that prosopagnosia is an impairment affecting the processing of objects with which we have extended experience. Rather, our findings suggest prosopagnosia can be a category-specific deficit that is restricted to faces, which indicates the human mind contains processes specialized for particular object categories.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2013.06.004.

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