COGNITIVE NEUROPSYCHOLOGY, 0000, 00 (0), 000–000

Psychology Press
Taylor & Francis Group

Prosopagnosia as an impairment to face-specific mechanisms: Elimination of the alternative hypotheses in a developmental case

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For more than 35 years, researchers have debated whether face recognition is carried out by face-specific mechanisms or whether it involves more general mechanisms that are also used for objects. Prosopagnosic patients have furnished powerful evidence for face-specific mechanisms. Yet for each case that has been tested there have always been several untested alternative explanations that could account for the case. As such, each of these individuals has not been sufficiently tested to provide conclusive evidence for face-specific processes. Here we make a stronger argument with a single case of severe developmental prosopagnosia by exhaustively addressing all extant alternatives. We reject each in turn and thus eliminate all alternative accounts. Because this case is developmental in etiology the results also indicate that face recognition involves developmental mechanisms different from those producing other visual recognition mechanisms.

Face perception has played a central role in social interaction for millions of years in a wide range of species. Information from faces is used to infer emotional state (nonhuman primates: Darwin, 1872; human infants: Klinnert, Campos, Sorce, Emde, & Svejda, 1983), gender (human infants: Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002), attractiveness (macaques: Waitt et al., 2003; human infants: Rubenstein, Langlois, & Kalakanis, 1999), attentional focus (snakes: Burghardt, 1990; plovers: Ristau, 1991; macaques: Perrett & Mistlin, 1990; human infants:

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This work was supported by grants from NIH (F 32 MH64246–03 and R01 EY13602). Some of the images were provided courtesy of Mike Tarr (Brown University, Providence, RI). Special thanks to Anne Grossetete, Gayle Speck, Kerry Dingle, and Nancy Kanwisher for their contribution to this project.

http://www.psypress.com/cogneuropsychology
DOI:10.1080/02643290500441296

Papousek & Papousek, 1979), age, and physical prowess (adult humans: Fox, 1997). Possibly because of the richness of these social signals (Bruce & Young, 1998), faces have also become a primary means for individual identification in many species, and the primacy of the face for human identification is demonstrated by our use of faces for photographs, portraits, identification cards, and police sketches. Face recognition is also an important issue within cognitive neuroscience that has been approached with a wide variety of methods over the past forty years. Herein we investigate the nature of the mechanisms that humans use for the identification of individual faces by assessing the recognition abilities of an individual with lifelong face recognition impairments.

This bears on fundamental issues in cognitive neuroscience. Despite years of discussion, it remains a matter of debate whether the brain contains mechanisms that are specialized for processing information about domains described by natural kind terms (e.g., faces, animate beings, plants, language, children)—mechanisms often called domain specific (Caramazza & Mahon, 2003; Caramazza & Shelton, 1998; Hirschfeld & Gelman, 1994). Such mechanisms are typically contrasted with domain-general mechanisms or horizontal faculties that operate over a wide range of domains (Fodor, 1983; Tooby & Cosmides, 1992). The two abilities most often pointed to as products of domain-specific mechanisms are language and face recognition (Bruce & Young, 1986; Chomsky, 1980; Cowie, 1998; Fodor, 1983; Jackendoff, 1992; Pinker, 1994). Language, however, is a more difficult test case, because language appears to involve a number of mechanisms, and it is difficult to isolate one of these and determine if it is language specific. In contrast, the relative simplicity of face recognition makes it a more tractable ability to explore. A second, related, issue is whether the brain contains mechanisms specialized for social cognition. While research on social cognition has begun to flourish, it remains an open question whether any social computations are handled by mechanisms dedicated to social interaction.

In addition, because this case is developmental in nature, it provides a means to investigate the developmental processes that produce the mechanisms used for visual recognition. Unlike acquired dissociations, dissociations found in developmental cases are not only functional dissociations but also developmental dissociations. Thus, if this case is best accounted for by an impairment to face-specific mechanisms, it will indicate that these mechanisms are produced, at least in part, by developmental processes that are uninvolved in the development of other visual-recognition mechanisms. Our results also bear on a current theoretical debate about developmental disorders. Some have argued that developmental impairments in one mechanism will necessarily impact the functioning of other developing mechanisms (Thomas & Karmiloff-Smith, 2002) and so predict that residual normality, as it has been called, for other mechanisms should not exist. However, investigations of specific developmental disorders in other domains (e.g., dyslexia, dyscalculia, semantic amnesia, episodic amnesia) suggest that functionally unrelated mechanisms can develop normally (Landerl, Bevan, & Butterworth, 2004; Ramus et al., 2003; Temple & Richardson, 2004; Vargha-Khadem, Gadian, & Mishkin, 2001; Vargha-Khadem et al., 1997). Whether this is the case for visual recognition mechanisms remains to be determined. Apparently face-selective cases of developmental prosopagnosia indicate that other recognition mechanisms can develop normally (Duchaine & Nakayama, 2005; Nunn, Postma, & Pearson, 2001), but further evidence is necessary to draw firm conclusions.

Dissociations within visual recognition

Evidence from a number of sources indicates that some of the mechanisms used for face recognition are different from the mechanisms used for other types of visual recognition. Studies of prosopagnosics have shown that face and object recognition can dissociate even when task demands are equivalent and speed/accuracy trade-offs are ruled out (Duchaine & Nakayama, 2005; Farah, 1996).

Conversely, a number of patients have been reported who show normal (Moscovitch, Winocur, & Behrmann, 1997) or relatively spared (McMullen, Fisk, & Phillips, 2000) face recognition despite severe impairments with objects. Evidence from lesion studies, neurophysiology, and neuroimaging indicate that the inferior right temporal lobe is involved in face recognition (Barton, Press, Keenan, & O'Connor, 2002; Kanwisher, McDermott, & Chun, 1997; Kreiman, Koch, & Fried, 2000; Landis, Cummings, Christen, Bogen, & Imhof, 1986; McCarthy, Puce, Belger, & Allison, 1999; McCarthy, Puce, Gore, & Allison, 1997; Yin, 1970). Behavioural experiments using different methods have demonstrated that faces are processed in a more configural or holistic manner than many object classes including inverted faces (Freire, Lee, & Symons, 2000; McKone, Martini, & Nakayama, 2001; Tanaka & Farah, 1993; Tanaka & Sengco, 1997; Yin, 1969; Young, Hellawell, & Hay, 1987). Although these studies demonstrate that face recognition relies on different mechanisms from those for many other types of recognition, they do not demonstrate that the mechanisms are face specific.

To make this point more clearly, we display some of the potential architectures that might be used to process faces in Figure 1. For example, selective deficits could result from an architecture that contains a battery of mechanisms that are each specialized for a particular processing task such as parts-based processing, configural processing, individual item recognition, or expert processing. These mechanisms could be applied to any class depending on the properties of that class and/or an individual's experience with the class. Recognition of items from a particular stimulus class could activate one, some, or all of the mechanisms, and selective impairments could result from problems with a subset of these mechanisms. Visual recognition could also be performed by an array of domain-specific mechanisms that only operate on the class for which they are specialized. Of course, impairment to some of these mechanisms would produce selective dissociations. Finally, there could be a mixed architecture with a battery of more general-purpose mechanisms as well as domain-specific

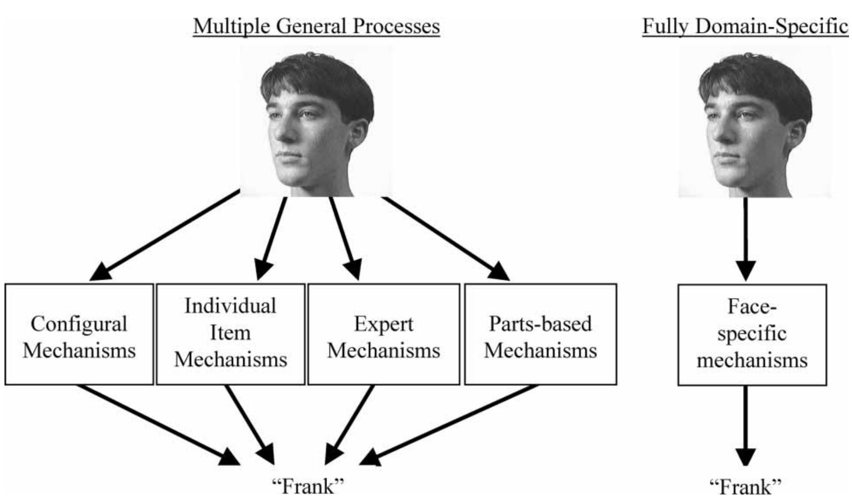

Figure 1. *Possible organizations for mechanisms involved with face recognition. For the multiple general process model, faces are recognized by a number of mechanisms that are also used with other object classes. Note that the battery of mechanisms included in the model that we present is only one of many possibilities. In a fully domain-specific model, upright face recognition depends almost exclusively on face-specific mechanisms. A hybrid organization is also a possibility; faces would be processed by both face-specific mechanisms and more general-purpose mechanisms. Impairments to any of these mechanisms could cause prosopagnosia.*

mechanisms. The more general mechanisms may contribute to the recognition of the classes for which domain-specific mechanisms exist, or they may be uninvolved in recognizing such items. Each of these architectures would lead to different patterns of dissociations, but current evidence does not clearly support a particular organization.

To draw firm conclusions, all alternative explanations must be addressed in a single case

Over the years, many explanations for prosopagnosia have been proposed, and we discuss each explanation below. All agree that some mechanisms in the visual system are not working properly, but they differ in how to characterize the domain of the impaired mechanisms and thus on what classes the mechanisms operate. Because the proposed classes differ, the hypotheses make different predictions about which nonface classes prosopagnosics will be impaired with. In many past studies of prosopagnosia, researchers have tested some of these predictions and have demonstrated that a single explanation for prosopagnosia cannot account for the observed pattern of normal object recognition and impaired face recognition. They have then often concluded that defective mechanisms proposed by one of the explanations are the best account of the case and the best account of prosopagnosia in general. However, there are many alternative explanations, and all of the alternatives have not been addressed in a single case. Until this is done, no one hypothesis is implicated as the best explanation, and so past cases do not provide strong evidence about the nature of the mechanisms performing face recognition in normal subjects.

To illustrate this issue, consider the following case: An individual with severe face recognition impairments shows normal or relatively spared recognition for individual televisions and individual lamps. This pattern would demonstrate that the individuation explanation could not account for this subject's prosopagnosia, because this explanation proposes that prosopagnosia is caused by impairment to mechanisms used for individual item recognition within any class. Comparable results have often been considered supportive of the face-specific explanation. However, though the results are consistent with the face-specific explanation, they are also consistent with a number of the remaining alternative explanations as well. For instance, there is little reason to believe that either object class (televisions or lamps) requires configural processing so the configural processing explanation remains a possibility. Similarly, subjects are unlikely to have significant visual expertise with either class so the expertise explanation may account for the face impairment. In fact, normal performance with televisions and chairs only eliminates the individuation explanation so the results are only a first step in ascertaining which explanation is the best account. To draw firmer conclusions, the predictions of the other alternatives must be tested as well.

Furthermore, each alternative must be tested in a single case. Above, we discussed that many possible architectures could give rise to the dissociations seen in previous cases of prosopagnosia, and for some of these architectures, face recognition relies on a number of different mechanisms. If multiple mechanisms contribute to face recognition, then impairment to any of these mechanisms could result in prosopagnosia, and there would be different varieties of prosopagnosia (Davidoff, 1986; Schweich & Bruyer, 1993). Therefore, past demonstrations that an explanation cannot account for a prosopagnosic's deficits does not rule it out as an explanation in another prosopagnosic. To provide support for a particular explanation, all explanations need to be addressed in a single case study. Before proceeding, we provide a list of the extant explanations of prosopagnosia to be addressed in the present study.

Here are the proposed explanations and their predictions:

Face-specific explanation. This account proposes that prosopagnosia results from an impairment to mechanisms specialized for faces—in particular, upright faces (Moscovitch et al., 1997). Because it suggests face-specific mechanisms, it makes no predictions about other impairments that should accompany impairments to face recognition. Although single subjects cannot provide evidence against it, the face-specific hypothesis predicts that some cases with face-specific impairments should exist, and it would be weakened if the field failed to find any selective cases (Gauthier, Behrmann, & Tarr, 1999).

Individuation explanation. The individuation explanation proposes that face recognition deficits result from impairment to mechanisms used for the recognition of individual items from within a class (Damasio, Damasio, & Van Hoesen, 1982; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). It is often called the within-class hypothesis or the subordinate-level hypothesis, but following Moscovitch et al. (1997) we refer to it as the individuation hypothesis. Intuitions about "within class" and "subordinate level" usually lead researchers to consider them to refer to individual items, but neither term is clear about the specificity involved. Note, however, that individual item is not well suited to describe recognition of mass-produced artifacts that are identical in appearance (Henke, Schweinberger, Grigo, Klos, & Sommer, 1998), and most researchers have treated these as individual items for experiments addressing the hypothesis (Gauthier, Skudlarski, Gore, & Anderson, 2000; Henke et al., 1998; Sergent & Signoret, 1992). The individuation explanation predicts that impairment to the mechanisms used for individual-item object recognition will impair performance whenever recognition of individual items from a particular class is required.

Holistic explanation. Another alternative explanation for prosopagnosia is that it represents the malfunction of one of two hypothetical shape representation systems proposed to generate structural descriptions of objects (Farah, 1990). Farah's two-process theory was based upon her review of 99 cases of agnosia not attributable to lower level perceptual deficits. She found that there were cases with pure prosopagnosia, pure alexia (an inability to read words), alexia with object agnosia, prosopagnosia with object agnosia, and cases with all three deficits. However, she did not find any cases of pure object agnosia or any cases of alexia with prosopagnosia. This led Farah to postulate that there are two shape representation systems: One constructs structural descriptions for objects that are decomposable into numerous parts, and one constructs structural descriptions for objects that allow little shape decomposition and so must be represented as a complex whole. In her account, words are handled by the part-based system, faces are handled by the holistic system, and objects are handled by a combination of the two systems. Alexia results from a deficit in the part-based system whereas prosopagnosia is produced by damage to the holistic system. Different varieties of object agnosia are produced when one or both systems are malfunctioning. This proposal predicts that prosopagnosia will always be accompanied by deficits with object classes that allow little shape decomposition.

Configural processing explanation. Many results indicate that a key difference between face recognition and object recognition is that configural information in faces is represented in a more precise manner than it is in objects (Freire et al., 2000; Le Grand, Mondloch, Maurer, & Brent, 2001; Leder & Bruce, 1998). While configural processing has been defined in a number of ways, here we refer to it as representation of the spacing between features (Freire et al., 2000; Leder & Bruce, 2001; Le Grand et al., 2001). However, what produces this type of representation is unclear. It could result from the operation of face-specific mechanisms or domain-general configural mechanisms. Levine and Calvanio (1989) proposed that faces are processed by domain-general configural processing mechanisms, and they suggested that prosopagnosia results from impairment to these mechanisms. In many ways this proposal is similar to Farah's holistic hypothesis (Farah, 1990), but it places more emphasis on the configural nature of face representation. It of course predicts that prosopagnosics will fail with object tasks requiring configural processing.

Curvature explanation. The curvature hypothesis is the most recently proposed explanation for prosopagnosia. Two versions of this hypothesis have been discussed, and both suggest that impairments that leave individuals unable to represent items with curvature may result in prosopagnosia. One version proposes that the perception of any curved stimulus is impaired (Kosslyn, Hamilton, & Bernstein, 1995) whereas the more specific version proposes that it is the perception of geometric volumes made of curved surfaces that is impaired (Laeng & Caviness, 2001). Faces, of course, have many curved surfaces, and the hypothesis predicts that prosopagnosia caused by curvature deficits will also have impairments with object classes with substantial curvature.

Expertise explanation. The final explanation for prosopagnosia is one of the most commonly discussed possibilities, and it has been investigated with many different approaches. It contains elements of all of the other domain-general hypotheses except the curvature hypothesis, and so it attempts to account for many of the results discussed above. This explanation proposes that face recognition is performed by mechanisms that operate on classes for which subjects have developed expertise (Diamond & Carey, 1986; Gauthier & Tarr, 1997). It claims that expertise with a class is acquired when viewers must repeatedly recognize individual items from a visually homogeneous class that share a first-order configuration. This expertise allows subjects to represent items from expert classes in a configural or holistic manner. Because all expert classes are handled by the same expert mechanisms, this view predicts that when these mechanisms are defective subjects will have difficulty acquiring and/or using expertise for faces or any other object class. The amount of exposure needed for expertise development is a matter of debate. The rapid expertise view proposes that it can be acquired in hours (Gauthier & Tarr, 1997) whereas the extended view suggests that years of experience are required (Diamond & Carey, 1986).

Developmental prosopagnosia

Our prosopagnosic subject reports lifelong face recognition problems, and so he is classified as a developmental prosopagnosic. Because he knows of no events that may have caused brain damage, he may also be a congenital prosopagnosic, but because we do not know the developmental course that led to his face recognition problems, we prefer to classify him more conservatively as a developmental prosopagnosic. Until the last few years, there were few documented cases of developmental prosopagnosia, and so it appeared to be an extremely rare condition. However, there has been a sharp increase in the number of cases of developmental prosopagnosia coming to the attention of researchers recently. This seems to be primarily because the Internet and media have raised awareness of the condition, and the Internet has allowed prosopagnosic individuals to contact researchers easily. Our laboratory created a Web site four years ago to recruit prosopagnosic subjects, and we have been contacted by more than 450. Few of these individuals acquired their prosopagnosia as adults so developmental prosopagnosia seems to be more common than acquired prosopagnosia.

There appear to be a number of possible routes to developmental prosopagnosia. These include genetic conditions (de Haan, 1999; Duchaine & Nakayama, 2005), early brain damage (Barton, Cherkasova, Press, Intrilligator, & O'Connor, 2003; Michelon & Biederman, 2003), and possibly early visual problems such as infantile cataracts (Le Grand et al., 2001; Le Grand, Mondloch, Maurer, & Brent, 2003) or severe myopia. A number of problems are commonly associated with developmental prosopagnosia, and, not surprisingly, many of the associated deficits are handled by brain areas in the vicinity of areas involved with face recognition. However, for each ability that is sometimes impaired, some developmental prosopagnosics have been shown to perform normally. Some show deficits with other types of face processing such as emotion recognition (Ariel & Sadeh, 1996; de Haan & Campbell, 1991; Duchaine, 2000; Kracke, 1994) and gender discrimination (Ariel & Sadeh, 1996; de Haan & Campbell, 1991; Jones & Tranel, 2001). Many, though not all (Bentin, Deouell, & Soroker, 1999; Duchaine & Nakayama, 2005; Nunn et al., 2001) developmental prosopagnosics have trouble with nonface object recognition (Ariel & Sadeh, 1996; Duchaine & Nakayama, 2005; Laeng & Caviness, 2001; McConachie, 1976), but usually this affects only exemplar recognition (a particular car, a particular horse), not basic-level recognition (cars or horses, in general). About one third of those who have contacted us have difficulties with everyday large-scale navigation (Duchaine, Parker, & Nakayama, 2003b), and approximately one fifth report that they have trouble understanding speech in noisy settings. In addition, many individuals with autism-spectrum disorder have problems with face perception (Barton, Cherkasova, Hefter, Cox, O'Connor, & Manoach, 2004; Cipolotti, Robinson, Blair, & Frith, 1999; Duchaine, Nieminen-von Wendt, New, & Kulomaki, 2003a).

EDWARD

Edward is a 53-year-old married right-handed man who has PhDs in theology and physics. He currently works as a physicist in a magnetic resonance research laboratory, and his interests in magnetic resonance imaging and prosopagnosia led to our collaboration. He recalls face recognition difficulties during childhood, such as problems recognizing his father. Edward is unaware of any head trauma that may have caused his prosopagnosia. While discussing his prosopagnosia recently with his sister, she reported that she had difficulties with facial identity and emotion as a teen especially in stressful situations but she reports no problems as an adult.

Despite his difficulties, Edward is able to manage in most social situations, and we believe that his object recognition provides him with an alternative means that many other prosopagnosics with agnosia cannot use as proficiently. For individual recognition, he reports using context, hair, body types, facial hair, gait, voices, and distinctive facial features. Edward's problems with faces extend to aspects of face perception other than identification. Below we present data showing that he has problems recognizing expressions and gender from the face. His wife has told him that he sometimes fails to notice subtle facial expressions (though we note that such complaints are commonly heard by nonprosopagnosic spouses as well!). Recordings done with magnetoencephalography show that Edward, unlike normal subjects, fails to show a face-selective M170 signal (Harris, Duchaine, & Nakayama, 2005), and he also does not show any face-selective voxels when face activation is compared to object activation (Yovel, Duchaine, Nakayama, & Kanwisher, 2005).

Edward has scored normally on all tests dependent on early visual processes. He performed normally on the Pelli–Robson test of contrast sensitivity (Pelli, Robson, & Wilkins, 1988), and he also was in the normal range on the low-level visual tests (Tests 1–5) from the Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993). On a demanding visual spatial attention test involving tracking of multiple objects (Pylyshyn & Storm, 1988), Edward scored normally. He also had no difficulty naming 100 common objects from Snodgrass and Vanderwart's (1980) set of line drawings.

Edward's face perception

Face recognition

First we demonstrate that Edward is impaired with different aspects of face perception including, most importantly, face recognition. Edward was tested individually. Our first testing session was in May 2002, and the most recent was in January 2005. Controls were also tested individually, and because the composition of the control groups varied we present information about each control group prior to discussing test results. In some cases, we used age- and education-matched controls. However, we often used undergraduate and graduate student controls because Edward scored in the normal range even when compared to these younger subjects.

Famous face identification. Edward and the control subjects were presented with 23 famous faces (Duchaine, 2000). Most of these images were in colour, and they had been cropped so that little of the hair was visible (See Figure 2 Panel A for examples). Each image was presented for 10 s, and subjects were asked to provide the name or other uniquely identifying information (e.g., movie role, political office).

Results and comment. Edward's performance was compared to that of a group of 17 male and female subjects between the ages of 55 and 64 years. Edward was able to identify only three faces whereas the control average was 18.0 (*SD* = 3.3). Figure 2 Panel B shows the scores sorted from worst to best for Edward (black column) and each control subject. This figure makes it clear that Edward's correct identification of only three of the faces was far worse than any of the control subjects. Among the approximately 40 developmental prosopagnosics who have been assessed with this test, Edward's score is one of the worst. It was particularly striking that Edward failed to identify Bill Clinton, because nearly all of the developmental prosopagnosics we have tested are able to identify him. After completing the test, we asked Edward about his exposure to the individuals that he was unable to name. He was confident that he had significant exposure to 18 of the 23 individuals.

The three faces that Edward correctly identified were Michael Jackson, Ronald Reagan, and Martin Luther King Jr. His comments suggested that he might not have identified these faces through normal means. He uncertainly identified Michael Jackson by his formerly telltale strands of hair on his forehead. Edward correctly identified Reagan and King, but afterward reported that we used well-known images that he had seen before in situations in which he was aware of their identity. Thus he may have recognized the image rather than the face.

Edward's famous face results suggest that he has a severe face recognition deficit. However, all subjects have different amounts of exposure to famous faces so we tested him with a test of unfamiliar-face recognition in which exposure was equivalent for all subjects.

Cambridge Face Memory Test. The Cambridge Face Memory Test is a recently designed test from our laboratory. We are distributing it free of charge if used for research, and it is fully described in Duchaine and Nakayama (in press).

The test has three stages. In the introduction, subjects are introduced to the six target individuals that they will attempt to recognize throughout the test (See Figure 3A). Target individuals are

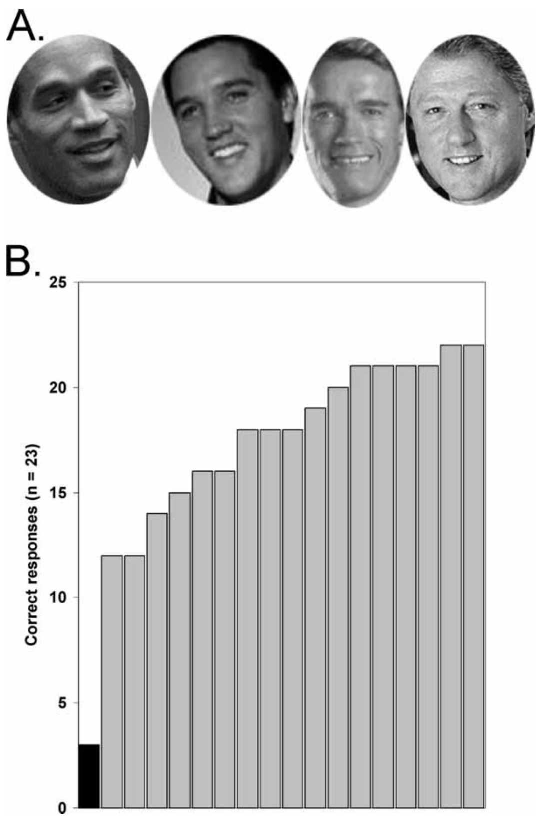

Figure 2. *Famous-face test. Panel A shows examples from the famous-face test. Panel B shows scores on the famous-face test for Edward (black) and each age-matched control subject (grey). The scores have been sorted from worst to best.*

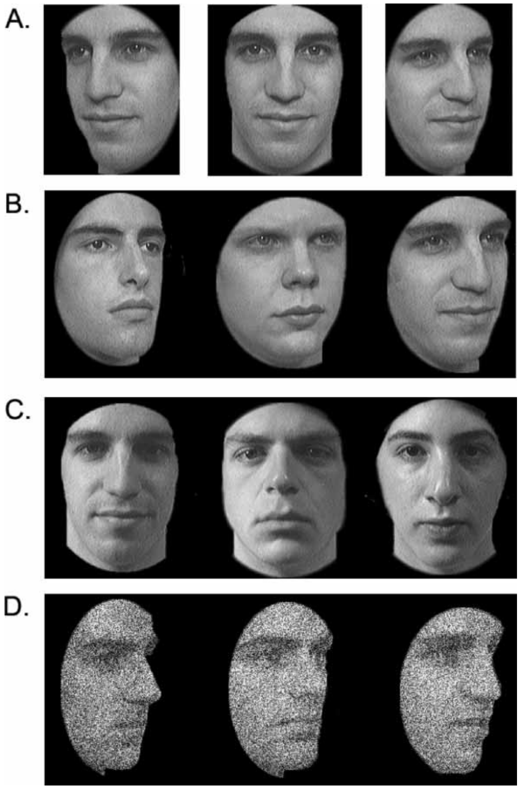

Figure 3. *Sample stimuli from the Cambridge Face Memory Test. None of these items was used in the test. In the test, test faces are numbered 1, 2, and 3 from left to right, but we omitted this to save space. Panel A shows study views of a target face. Study views are presented for 3 s each. Panel B displays a test item from the introduction. Face 3 is the same image as the rightmost study view in Panel A. Panel C shows an item from the novel images section (Face 1 is the target). Panel D displays a test item from the novel images with noise section (Face 3 is target).*

introduced one at a time by presenting a three-quarter left profile, a frontal view, and a three-quarter right profile for 3 seconds each. All of the faces throughout the test have been cropped so that no hair is visible. Following the three study faces, subjects are simultaneously presented with three faces photographed in identical poses and under identical lighting. Two are distractors, and the other is one of the study views presented seconds before (Figure 3B). Subjects are to choose the target face. Two more items are then presented consisting of the two other study views along with two distractors. This procedure is repeated for the five other target faces so there are 18 test items in the introduction.

Following this, there are two sections: novel images and novel images with noise. During the novel images section, subjects are tested with 30 trials, each of which consists of the presentation of a target with two distractors (Figure 3C). In this section and in the novel images with noise section, any of the six target faces can be presented so these items are much more difficult than the introduction items. In addition, all of the images are novel views in which the pose and/or lighting differ from the study views. In the novel images with noise sections, Gaussian noise was added to the 24 test items (Figure 3D). There are a total of 72 possible points on the test (18 + 30 + 24).

Results and comment. Figure 4 shows the cumulative scores for Edward and 9 age-matched and education-matched control subjects (average age 46.5, *SD* = 7.7). The plot is divided into the three sections of the test (introduction, novel images, novel images with noise). As is apparent

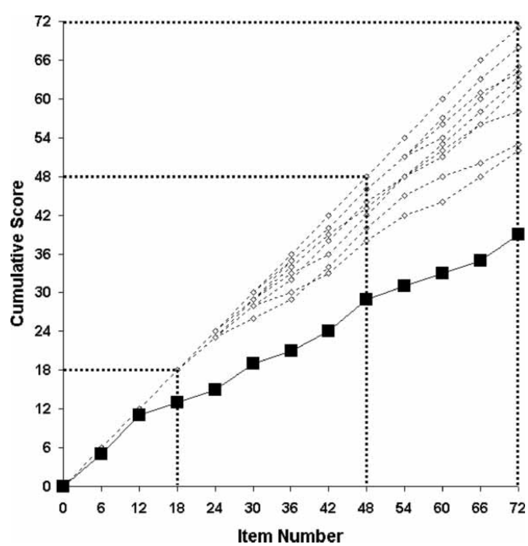

Figure 4. *Cumulative scores for Edward (black square) and 9 age- and education-matched control subjects (open diamonds). The plot is divided into the tests three sections: introduction, novel images, and novel images with noise.*

from the figure, Edward had more difficulty with all parts of the test than the control subjects did. In the introduction the correct test choice was identical to study images that subjects had just viewed, yet Edward was able to respond correctly on only 13 of the 18 items. In contrast, our control subjects made no errors in this section. On the 30 novel images, Edward scored 13 while controls averaged 26, and on the 24 novel images with noise, Edward scored 10 compared to the controls' average of 18. His total score of 39 was 3.5 standard deviations below the control average of 62.8 ($SD = 6.8$). Edward's errors were distributed fairly evenly between all of the faces. There were 12 test items for each of the six target faces, and the number of errors that Edward made per face ranged between 3 and 7.

These results make it clear that Edward is worse than control subjects even when all subjects are provided with identical exposure to the faces. In later sections, we present face recognition results that further demonstrate Edward's face recognition impairment. A number of these experiments demonstrate that Edward is impaired with facial identity even in tasks with minimal memory demands (Duchaine, Dingle, Butterworth, & Nakayama, 2004).

Face detection

Most prosopagnosics (de Gelder & Rouw, 2000; Duchaine, 2000; Duchaine et al., 2003a) score normally when asked to detect the presence of faces or discriminate between faces and nonfaces. We investigated Edward's ability to detect faces with two tests.

Face detection. Two-tone faces were created for this experiment by adjusting the threshold controls in Adobe Photoshop. This left a face in which the darker areas were black, and the lighter areas were white (see Figure 5). Faces were composed of black areas for the major features (irises, eyebrows, lips, bottom of nose) while the rest was white. Each test image contained one of these faces surrounded by a large field of individual features drawn from other faces that served to make the facial configuration more difficult to perceive.

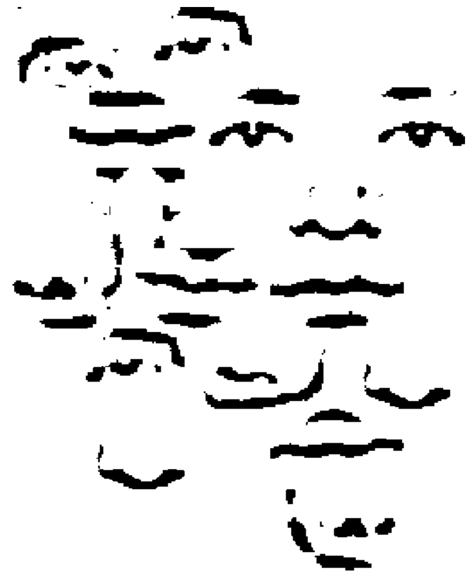

Figure 5. *Example of a stimulus from the face detection task. The stimulus was presented for 150 ms, and subjects indicated whether the face was on the left or on the right.*

The face was placed on either the left or the right side of the test image. A total of 90 of these images were presented to subjects for 150 ms each, and subjects indicated with a key press whether the face was on the right or the left. Subjects were run on two blocks of upright trials and two blocks of inverted trials.

Results and comment. A total of 16 controls between the ages of 35 and 45 years averaged 87.2% ($SD = 6.0$). Edward's score of 91.2% was slightly above the control mean. This indicates that he can detect upright faces normally. In addition, it demonstrates that he can perceive briefly presented displays. He was also in the normal range with inverted faces. His average was 78.9% while the controls averaged 69.4%. Thus, both Edward and the controls showed large inversion effects with face detection. Next we test his face detection with a different method.

Face decision. In this test (Duchaine et al., 2003a), subjects decided whether an image showed a normally configured face or a scrambled face. Both types of faces were created by pasting features from hand-drawn faces into face outlines. Features were placed in the typical locations for the normally configured faces whereas they were misplaced in scrambled faces. There were 30 of each type, and the faces were presented for 100 ms. A total of 23 controls between 35 and 45 years of age averaged 93.2% ($SD = 7.1$). Edward's score of 88.3% placed him within one standard deviation of the control mean.

Results and comment. Edward's normal scores on both of these tests demonstrate that he has no difficulty categorizing a face as a face. His difficulties only become obvious when he is asked to do finer processing of faces.

Emotion perception tests

In addition to his problems with facial identity, Edward reports difficulties with emotion recognition so we assessed his abilities with three tests of emotion recognition. His scores for the tests were compared to those for a group of 14 subjects who ranged in age from 55–64 years.

Emotion hexagon. In this test (Duchaine et al., 2003b), we presented faces created by morphing between four individuals from Ekman and Friesen's emotion face set (Ekman & Friesen, 1976). After Calder, Young, Perrett, Etcoff, and Rowland (1996), our morph sequence was happy–surprise–fear–sadness–disgust–anger–happy, and we presented five morph proportions: 90–10, 70–30, 50–50, 30–70, and 10–90. This created 120 images (4 individuals × 6 morph series × 5 morphs per series). Subjects were presented with each image twice in a random order, and they were asked to label the predominant emotion with one of the six emotion labels.

Results and comment. We did not analyse the 50–50 morph trials, because they did not have a predominant emotion. The black square in Figure 6 shows the average percent correct for the control subjects, and the error bars display two standard deviations above and below the control mean. Performance at chance would be

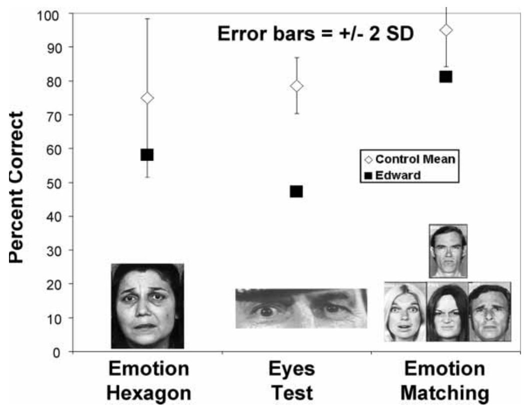

Figure 6. *Performance on three tests of emotion recognition. The open diamond displays the control mean for each test, and the error bars represent 2 standard deviations above and below the control mean. The black squares are Edward's percent correct for each test. Images below the scores show examples from each test.*

16.7%. Edward's score of 58.4% correct was 1.4 standard deviations below the control mean of 75% ($SD = 11.7$).

Eyes Test. Baron-Cohen and his colleagues designed the Eyes Test to assess advanced theory of mind (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). Subjects were presented with the eye region of a face along with four emotion state words on a computer. They were asked to pick the word that best described the eye region. There were 36 items.

Results and comment. Figure 6 shows that Edward's percent correct was far out of the normal range. In fact, his score was more than seven standard deviations below the mean. Whereas the controls chose correctly on 78.6% of the items ($SD = 4.1$), Edward was correct on only 47.2% items. This test clearly revealed the emotion recognition deficits that Edward reported.

Emotion matching. This test assesses the ability to categorize emotional expressions as the same despite changes in the models portraying the emotions. Subjects were briefly presented with a target face from the Ekman and Friesen set (Ekman & Friesen, 1976) portraying surprise, disgust, happiness, or neutrality. Following this, they were presented with three faces simultaneously. Each face portrayed a different emotional expression, and the individual used in the preceding target photo was not presented. One of the individuals portrayed the same emotion as that of the target model, and subjects were to choose which of the three faces depicted the same emotion as that of the target image. There were 8 trials for each of the four emotions for a total of 32 trials.

Results and comment. The control subjects correctly matched 95% ($SD = 5.3$) of the items so this test suffers from ceiling effects. Despite these ceiling effects, Edward's percent correct of 81% placed him 2.6 standard deviations below the control mean, and his score was lower than that of any of the controls (See Figure 6). On five of his six errors, the target face portrayed disgust. Taken together, these three tests indicate that Edward does, in fact, have difficulties with the recognition of facial expressions of emotion. Next we examine Edward's gender discrimination ability.

Gender discrimination

College-age male and female faces were cropped so that little or no hair was visible. The 35 images were briefly presented, and subjects categorized them as male or female.

Results and comment. Edward's performance was compared to 22 college-age control subjects. Controls found this task easy. Scores ranged between 33 and 35, and the control mean was 34.5 ($SD = 0.7$). Edward's score was 29. Although Edward was able to categorize most of the faces successfully, it is clear that he has gender discrimination problems.

Summary of face perception experiments

These experiments show that Edward has problems not only with face recognition but also with face processing more generally. However, he had no difficulties with face detection tasks. We have also recently collected data showing that Edward makes atypical attractiveness judgments when asked to sort faces in order of attractiveness (Sadr, Duchaine, & Nakayama, 2004).

TESTING PREDICTIONS OF THE ALTERNATIVE EXPLANATIONS

Next we present six experiments that test the predictions of the explanations for prosopagnosia.

Old–new discriminations

The first set of experiments compare Edward's individual item recognition for faces to seven nonface classes. Old–new recognition memory tests with 10 target items and 30 nontargets are used for all of the classes. The nonface classes include horses, cars, guns, sunglasses, tools, houses, and natural scenes. A wide range of object classes was used, because a number of experiments have suggested that nonface classes may be recognized by dissociable mechanisms (Cipolotti et al., 1999; Duchaine et al., 2003a; Farah, McMullen, & Meyer, 1991; Sartori & Job, 1988). These dissociations have often been segregated roughly as animate objects, inanimate objects, and places. By including classes from each of these categories, we increase the chances of discovering impairments with classes other than faces.

His performance with the nonface recognition tests tests three explanations. The individuation hypothesis predicts that prosopagnosics will show impairments with tests of individual item recognition. Consequently, normal performance by Edward with some or all of the nonface classes would be inconsistent with this hypothesis. The holistic explanation claims that prosopagnosia is caused by impairment to mechanisms used to represent complex parts that must be represented holistically (Farah, 1990). Although the hypothesis is not explicit about what classes other than faces consist of complex parts, Farah does mention animals as a likely candidate. Consideration of our nonface classes shows that the cars and horses are at least as nondecomposable as the faces. Therefore, Edward's performance with cars and horses appears to be a test of the holistic hypothesis. Lastly, the curvature hypothesis predicts that Edward will have impairments with any class for which curved surface representation is important. The horses, cars, guns, and sunglasses all have curved surfaces so normal performance with these classes would be inconsistent with the curvature hypothesis.

Method

Control participants

A total of 17 graduate students (9 women and 8 men) served as controls for the old/new recognition memory tests, and their mean age was 27.8 years with a range from 24 to 34. Each control participant produced a score for each old/new test except for 4 instances out of a possible 136 (17 controls × 8 tests). The control results showed no significant sex differences for any of the tests, and in fact the means for each sex were quite similar.

Stimuli

In each test, 40 items from within a category were used. Of these, 10 items were target items, and they were shown during the study phase of the experiment; 30 items were nontargets that were presented along with the target items during the test phase. See Figure 7 for examples.

Faces. Greyscale yearbook photographs of women's faces were cropped so that very little or no hair was visible. In order to achieve a fairly standard pose, some of the images were flipped or rotated. All of the images were the same size.

Cars. The cars used in these greyscale photographs had all conspicuous ornaments removed, and they were placed on a white background facing the same direction. Each car was categorized into one of three styles (compact, sedan, truck), and they were divided proportionally into target cars and nontarget cars. The sizes of the cars were adjusted so that they were the proper size relative to the other cars.

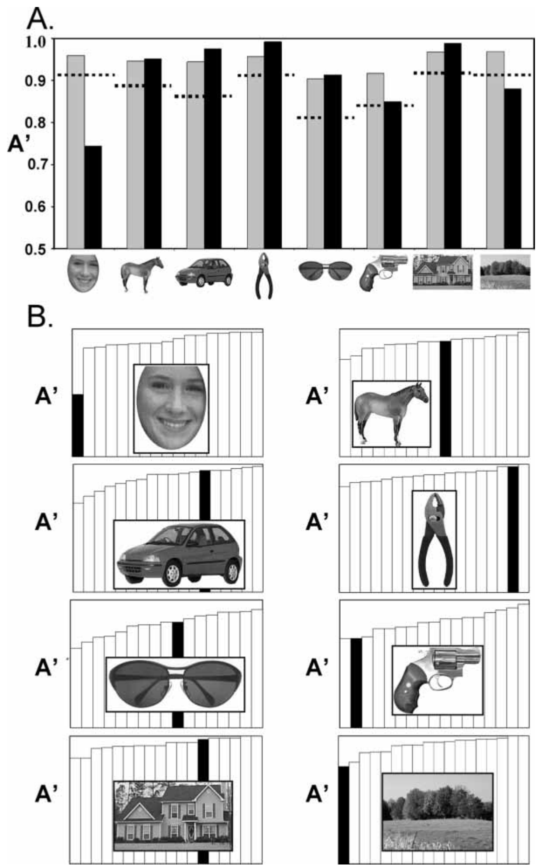

Figure 7. *Performance on the old–new discriminations. Panel A displays the average A′ scores for the controls (grey bars) and Edward's A′ score (black bars). Dashed lines indicate the point 2 standard deviations below the control mean. Panel B shows individual A′ scores for each test. Edward's score is in black, and the control scores are in white. Each set of scores has been sorted from worst to best. The images labelling the class for each test are items drawn from the test.*

Tools. Eight tool images were drawn from five categories (saws, hammers, pliers, wrenches, and screwdrivers), and these greyscale items were presented on a white background. Two items from each category were chosen as targets, and all items from particular categories were presented with a similar orientation and size.

Guns. Colour images of handguns were used. All conspicuous decorations were erased, and the guns were presented in the same orientation and were scaled similarly.

Horses. The images for this test consisted of colour photographs of model horses made by Breyer Animal Creations placed on a white background. The photographs presented a side view of the horses, and their poses and sizes were similar.

Sunglasses. Each colour image consisted of a pair of sunglasses in a standard pose on a white background.

Natural landscapes. Greyscale photographs of natural landscapes that did not have any man-made structures were used. Eight landscapes were chosen from each of the following five categories: beaches, lakes, meadows, mountains, and deserts. Two images were chosen from each category to serve as targets, and six served as nontargets. All images were the same size.

Houses. The colour photographs used in this test contained typical-looking houses photographed from the front with some of the yard surrounding the house visible. The sizes of the images were similar.

Procedure

Participants were tested individually in a normally lit room and were seated approximately 40 cm from the monitor. Prior to each test, instructions were given both verbally and on the monitor to ensure that participants understood the procedure. For the study portion, participants were presented with the 10 target items for 3 s per item. The 10 items were cycled through twice so that control performance would be high enough that we would be better able to identify impaired performance. The target images were identical throughout each task. During the test phase, participants were presented with items one at a time and were asked to respond whether an item was a target item (old) or a nontarget item (new) as quickly as possible with a mouse click. A total of 50 test items were presented consisting of 20 target items (10 targets $\times$ 2 presentations) and 30 nontargets (30 nontargets $\times$ 1 presentation). The order of the stimuli remained the same for all participants.

Results

A′ was used as the measure of discrimination in the following comparisons. It is a bias-free measure that varies between 0.5 and 1.0 with higher scores indicating better discrimination (Macmillan & Creelman, 1991). Unlike d′, A′ values can be computed when zero values are present.

Figure 7 Panel A shows Edward's A′ score along with the mean A′ for the control subjects. Dashed lines were placed two standard deviations below the control mean. As is evident, Edward's A′ score for faces was far below the control mean. In contrast, all of his A′ scores for nonface objects were within two standard deviations of the control mean except for his natural scenes score, which was just out of the normal range. Note that the mean A′ for the controls for faces was as high as or higher than the mean A′ for the other classes. This demonstrates that the nonface tests were at least as difficult as the face test, and a number were more difficult than the face test. As a result, Edward's normal performance cannot be due to the nonface tests being less demanding than the face test.

In Figure 7 Panel B we present individual A′ scores for Edward and the controls for each class. Individual scores have been sorted from least to best, and Edward's score is in black whereas the controls' scores are white. Consideration of the face test scores shows that Edward's score was far below that of even the lowest scoring control subject. However, when we consider the other tests, we see that Edward is scoring much better. For example, for the horse test, Edward's A′ score is right in the middle of the scores of the control subjects. For the other tests, Edward's score was well within the normal range with the exception of his natural scenes score, and this presentation of the results demonstrates that his natural scenes score is not an outlier from the control group.

Earlier we discussed that measurement of response times is critical to demonstrate that a dissociation is not the result of speed/accuracy

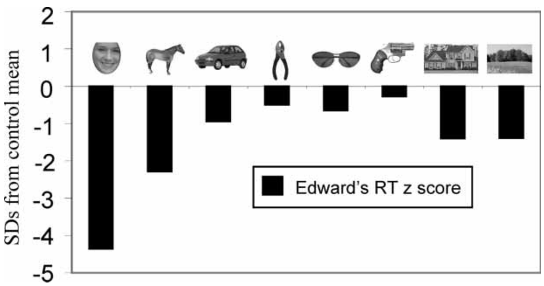

Figure 8. *The z scores for Edward's average response time on each old–new discrimination. Scores below zero are longer than the mean control response time.*

trade-offs. Thus, it could be that apparently selective deficits in prosopagnosia are due to their propensity to take more time with nonface tasks, thus elevating their performance (Gauthier et al., 1999). To address this issue, we present z values computed from the response times for Edward on each test in Figure 8. These were computed by subtracting Edward's score from the control average so that any of Edward's response times longer than the control mean would be negative z values. For speed/accuracy trade-offs to account for dissociation seen in Edward's A′ scores, his object response times need to be longer than those of the control group. His z score for the face test was more than four standard deviations longer than the mean response time. Inspection of his z scores for the nonface tests shows that none of his nonface z scores were as low as his face z score. In fact, nearly all of them were just slightly below the control mean. In addition, the actual length of his face response times was also longer than any of the nonface response times. Hence differentiated speed/accuracy trade-offs between face and nonface tasks cannot explain Edward's pattern of A′ results.

Comment

Edward's performance with faces for both A′ and response time was far worse than that of the controls. In contrast, his performance with the nonface classes was quite good. His results are the clearest demonstration in the literature that a prosopagnosic can perform normally on comparable nonface tests. Not only were his accuracy scores in the normal range but his response times were as well. This is especially impressive considering that Edward is a 53-year-old while the controls were in their twenties and thirties.

His results are clearly inconsistent with the individuation explanation. All of the tasks involved individual item recognition yet he only had substantial difficulties with the face test. His normal performance with horses and cars suggests that the holistic explanation also cannot account for his prosopagnosia. Finally, many of the nonface classes had curved surfaces (horses, cars, guns, sunglasses) yet Edward was normal with these classes. As a result, the curvature account does not appear to be an appropriate explanation for his face recognition difficulties. In the other experiments discussed below, we present more results that reinforce our conclusions about these three explanations.

The meaning of Edward's low score with the natural scenes is unclear to us, and we plan to conduct more tests with similar stimuli. He reports neither navigational difficulties nor difficulties recognizing places, and he performed normally on a famous-places test. Neuropsychological (Carlesimo, Fadda, Turriziani, Tomaiuolo, & Caltragirone, 2001; Incisa de la Rocchetta, Cipolotti, & Warrington, 1996; Whiteley & Warrington, 1978) and neuroimaging (Aguirre, Zarahn, & D'Esposito, 1998; Epstein, De Yoe, Press, Rosen, & Kanwisher, 2001; Epstein & Kanwisher, 1998) studies indicate that place recognition involves specialized mechanisms that differ from those used for face and object recognition. Thus, if further experiments show that Edward's scene recognition is impaired, this may be due to problems with mechanisms unrelated to his prosopagnosia.

Face matching: Upright and inverted

Inverted- and upright-face recognition has been contrasted in many experiments, because inverted faces are an almost ideal control class for upright faces. They are identical to upright faces except for orientation so they are matched on many dimensions that have been considered critical for face recognition. They have equivalent curvature, second-order configural information, complexity, and within-class similarity. As a result, comparing upright- and inverted face performance allows researchers to look into the importance of these dimensions as factors underlying our impressive abilities with faces.

In the next experiment, we use upright faces and inverted faces to examine whether the explanations involving curvature, holistic representation, configural processing, and individuation can account for Edward's face recognition impairments. If Edward is impaired with upright faces in this paradigm all of these hypotheses predict that he will also be impaired with inverted faces. However, if he is out of the normal range with upright faces and in the normal range with inverted faces, this will indicate that these hypotheses cannot account for his prosopagnosia.

The previous face recognition experiment demonstrated that Edward has impairments with face memory tests, but these difficulties could result from perceptual problems, memory problems, or a combination of perceptual and memory problems. To compare upright and inverted face recognition, we use a sequential face matching test. Subjects must match faces presented only a few hundred milliseconds apart, and so the memory demands are minimal. If Edward has difficulties with the upright faces in this paradigm it will demonstrate that his impairments with faces do not only involve long-term memory for faces.

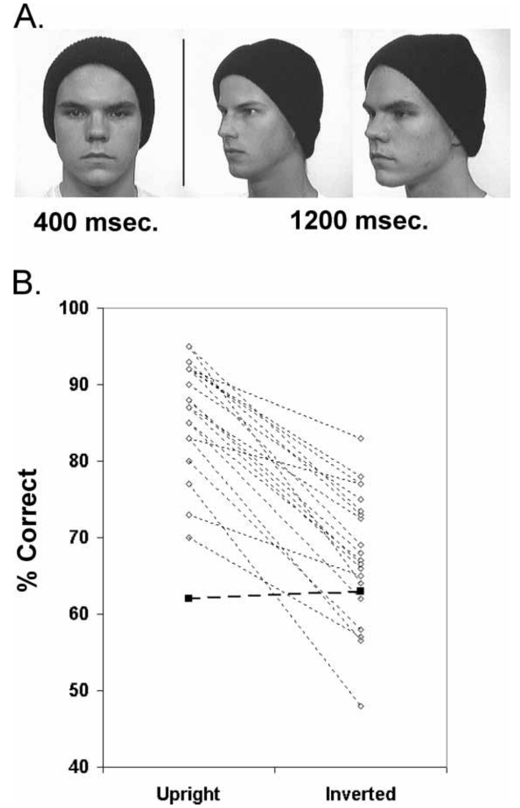

Figure 9. *Sequential face matching. Panel A shows a target face and two test faces. The test face on the right is the correct answer. The difference between upright presentation and inverted presentation can be experienced by rotating the page. Panel B shows the percent correct for upright and inverted trials. Controls are represented by open diamonds, and a dashed line connects each subject's upright and inverted scores. The black squares show Edward's scores.*

Method

Control participants

The controls consisted of 10 men and 10 women between 35 and 45 years of age.

Stimuli

Images consisted of full-frontal and three-quarter-profile shots of Caucasian college-age men wearing black ski hats so that their hair was not visible (See Figure 9 Panel A).

Procedure

On each trial, a frontal shot was presented for 400 ms, after which 2 three-quarter views were presented side by side for 1,200 ms. Subjects indicated which of the 2 three-quarter views matched the frontal shot with a key press. There were 120 trials; half consisted of upright faces, and half consisted of inverted faces. The upright and inverted trials were interleaved.

Results

Figure 9 Panel B displays the percent correct for Edward (filled black square) and the controls. It is immediately apparent that Edward shows a different pattern from that of the controls. There are three significant things to note in these results. First, Edward's upright percent correct is well out of the normal range. The controls averaged 86.4% (SD = 7.0) ranging from 70.0% to 95.0% while Edward responded correctly to only 61.7%. Second, Edward's inverted score is well within the normal range. The controls inverted average was 69.6% (SD = 7.1) with a range from 56.7% to 83.3%, and Edward's percent correct was 63.3%. Lastly, the figure makes it clear that unlike every control subject, Edward showed no advantage for the upright faces. The average difference for the controls between upright and inverted was 16.8% (SD = 8.3). The differences ranged from 6.6% to 31.6% so Edward's −1.6% difference is very atypical. Edward's response times for upright and inverted trials were in the normal range and were similar in length (upright = 973 ms, inverted = 1,017 ms).

Follow-up experiment

Because chance performance was 50% correct in the face matching experiment, we wanted to be sure that Edward's normal performance with inverted faces was not due to floor effects. To test this possibility, we created another face matching task involving only inverted faces. Again a frontal shot was presented for 400 ms, but three test faces rather than two were presented for 3,000 ms. With three test faces, chance performance was 33%. There were a total of 120 trials. Six college-age controls averaged 51.3% (SD = 13.1), and their range was 29 to 64. Edward's score of 53% placed him in the midst of the controls and 20% above chance.

Comment

Edward manifested a severe deficit with upright faces in this matching paradigm. In contrast, he was well within the normal range with inverted-face matching. Because the inverted faces are identical as a stimulus class to upright faces, his poor performance with upright faces cannot be attributed to any aspect of upright faces shared by the inverted faces. These include curvature, the complexity of the face, or the type of second-order configural information present in the face, and so these results are inconsistent with the curvature hypothesis, the holistic hypothesis, and the configural processing hypothesis. Later experiments investigate whether Edward manifests difficulties after he and controls have had extensive experience with classes with these characteristics. In addition, the inverted trials required individual item recognition so the results are also consistent with the individual item hypothesis.

For years, it has been recognized that normal subjects apply a qualitatively different type of processing to upright faces than that used with inverted faces or other objects (Moscovitch et al., 1997; Yin, 1969; Young et al., 1987). However, Edward's nearly identical performance with upright and inverted faces indicates that he processes upright and inverted faces in the same manner. Similar results were reported for EP, another developmental prosopagnosic (Nunn et al., 2001). Because Edward's upright score and inverted scores were comparable to the inverted scores for the control participants, he may apply to all faces processes that normal subjects apply to inverted faces. He does not treat upright faces as a special class.

This test also placed few memory demands on Edward yet he was far out of the normal range. Consequently, the results demonstrate that Edward's problems with face recognition do not lie solely with long-term memory for faces, and they are consistent with the notion that Edward has perceptual problems with faces. An experiment discussed later reinforces this possibility.

Tests of visual closure

When the configural processing explanation was first proposed, tests of visual closure were used to assess configural processing in a prosopagnosic (Levine & Calvanio, 1989). These tests required subjects to identify basic-level objects and words from images in which portions of the objects had been deleted or occluded. Because individual parts are meaningless in these images, subjects had to rely on the general configuration of the object. As mentioned above, this type of configural processing is not comparable to second-order configural processing applied to faces. Nevertheless, because this has been a commonly discussed explanation of prosopagnosia, we test Edward with the tests of visual closure. The three tests were drawn from the Kit of Factor-Referenced Cognitive Tests (Ekstrom, French, & Harman, 1976), and these are the same tests as those that were used in the paper proposing the configural processing hypothesis (Levine & Calvanio, 1989).

Control subjects
Norms were drawn from the manual for the battery of tests in the Kit of Factor-Referenced Cognitive Tests (Ekstrom et al., 1976). Edward was compared with a sample of young adults.

Results

In the Gestalt Completion Test (which is very similar to the Street Test), subjects must identify a common object from a group of black blotches created by deleting parts of the object (See Figure 10 Panel A for examples from the three tests). Figure 10 Panel B presents Edward's scores and the control subjects' scores. Edward's score of 14 is close to the control mean of 15.2 (SD = 3.6). In the Concealed Words Test, in which subjects identify words based on fragments of a printed word, Edward scored 24 whereas controls averaged 23.6 (SD = 6.4). Finally, on the Snowy Pictures Test, subjects must identify objects from an outline drawing that is partly obliterated by snow-like splatters. Edward's score of 12 places him above the control mean of 5.7 (SD = 3.0). In summary, Edward scored at or above the mean on the three tests of visual closure.

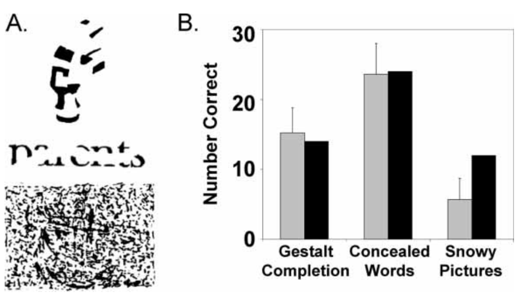

Figure 10. *Test of visual closure. Panel A displays practice items from the Gestalt Completion Test (hammer), Concealed Words Test (parents), and Snowy Pictures (anchor). Panel B shows the control mean in grey, and error bars represent 1 standard deviation. Edward's scores are in black.*

Comment
Edward performed very well on the tests of visual closure. However, these tests do not require the second-order configural processing that upright face recognition involves. Next we present results from a test that involved second-order configural processing in a nonface object class.

Discrimination of second-order spacing changes and part changes: Faces and houses

The configural processing explanation proposes that prosopagnosia results from impairment to domain-general configural processing mechanisms. To investigate whether Edward's abilities are consistent with these predictions, we compare his ability to process second-order configural information in faces and houses. The domain-general configural processing hypothesis predicts that he will have comparable deficits with faces and houses. We use a paradigm that has recently been used to look at sensitivity to two types of change in faces (Freire et al., 2000; Le Grand et al., 2001) and more recently faces and houses (Yovel & Kanwisher, 2004). Second-order configural processing is examined by presenting faces or houses that vary in the spacing of the parts, while part processing is assessed with faces or houses that vary only in the parts themselves.

If Edward has difficulty with the faces in this paradigm, the house results are also relevant to other explanations of prosopagnosia. Both tasks require individual item discrimination so normal performance with houses would be inconsistent with the individuation hypothesis. The faces and houses (See Figure 11) also appear to be similar in their decomposability (ease with which they

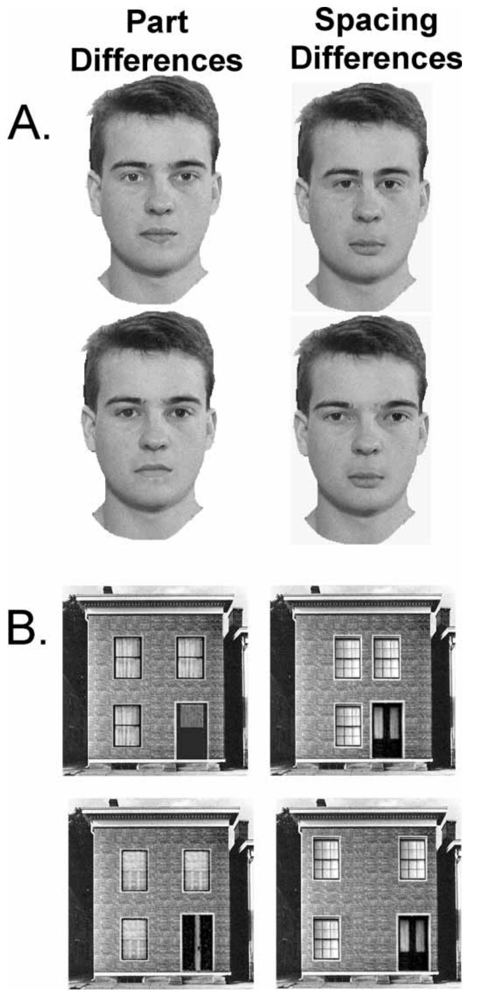

Figure 11. *Examples drawn from the face and house discrimination task with part difference versions on the left and spacing difference versions on the right. Panel A shows versions of Jeff. The changes were always made to the eyes and the mouth. Panel B displays versions of the house with changes made to the windows and the door.*

can be divided into parts) so should be similar in their need to be represented holistically (Farah, 1990). Hence the house results also provide a test of the holistic explanation.

Control participants
A total of 18 college-age students and young adults participated as controls.

Stimuli
The base stimuli consisted of a male face ("Jeff") and a house. The base stimuli were modified to create stimuli that differed in one of two ways. Spacing variants were created by changing the location of the features. For faces, the spacing of the eyes and the distance between the mouth and the nose were varied while house spacing changes involved the windows and the door. Part variants were created by substituting the features of the stimuli with features from other face/ house images while keeping the spacing of the parts as similar as possible. The replaced parts were the eyes, the mouth, the windows, and the door. Four variants of each type were created for each stimulus so there were 16 stimuli (2 stimuli × 2 types × 4 variants). The original face and house stimuli were also included and were paired with modified stimuli.

Procedure
Participants took part first in the face experiment and then in the house experiment. Trials with spacing changes and part changes were presented in a random order. Participants were informed that some trials would involve changes while others would not, but they were not told what sort of changes would occur. There were a total of 80 trials for each experiment with an equal number that were same or different and an equal number of spacing and part trials. Subjects were introduced to each experiment with five practice trials.

Trials consisted of stimulus presentation for 250 ms followed by a 1,000-ms interstimulus interval with a fixation cross. The second stimulus was then presented for 250 ms. Subjects indicated whether or not a change occurred with a key press.

Results

Figure 12 displays scatter plots with the results for the controls and Edward. As expected, the scatter plot for the face experiment clearly shows that Edward performed much worse than the control subjects for both the spacing and the part trials. Controls averaged 84.2% (SD = 7.9) for the spacing items while Edward was correct on only

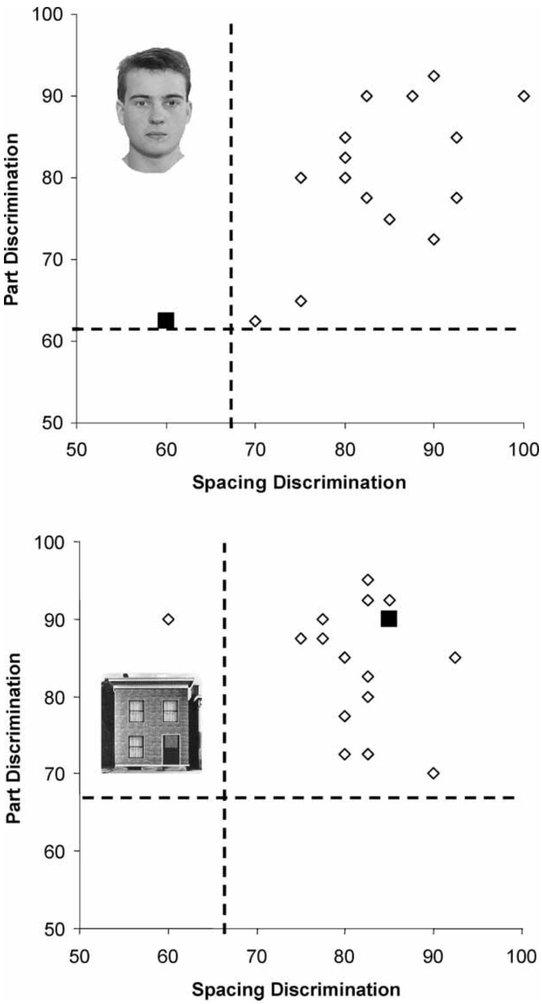

Figure 12. *Plots for Edward (black square) and control subjects (open diamonds) for the face and house tests. Percent correct for configural items is shown on the x axis and for feature items on the y axis. The tests were same–different tasks so chance was 50% correct. Dashed lines display 2 standard deviations below the mean.*

60% of the spacing items. Edward's score is 3.0 standard deviations below the mean. Similarly, the control mean for the part items was 80.3% (*SD* = 9.0), and Edward scored only 62.5%. Edward's score is two standard deviations below the mean.

Edward's response times with faces were normal. Controls averaged 501 ms (*SD* = 53) on the spacing trials, and Edward averaged 458 ms. On the face part trials, the control mean was 480 ms (*SD* = 93), and Edward's mean was 455 ms.

The house results quite clearly demonstrate that Edward has normal sensitivity to both types of house change. Contrary to the predictions of the configural processing explanation, his percent correct for the house spacing items of 85% was slightly higher than the control mean of 80.7% (*SD* = 7.3). Similarly, his score of 90% on the house part items was slightly higher than the control mean of 84.0% (*SD* = 8.0).

As with faces, Edward's house response times were normal. Controls averaged 436 ms (*SD* = 91) on spacing trials while Edward averaged 471 ms. On the part trials, the control mean was 483 ms (*SD* = 68), and Edward's mean was 514.

Comment

Edward's normal performance with the house configural items demonstrates that he does not have a problem representing second-order configural information for objects in general, and so these results are inconsistent with the configural-processing hypothesis. In a recent paper, Behrmann and colleagues used the Navon task (Navon, 1977) to investigate configural processing in five developmental prosopagnosics (Behrmann, Avidan, Marotta, & Kimchi, 2005). They found that some of these prosopagnosics did not process the global stimuli, which require spatial integration, normally whereas others showed normal configural effects. We believe that the house test used in our experiment provides a more direct comparison to configural processing in faces, but we plan to test Edward with a Navon task in the near future. The house results are also inconsistent with the individual item hypothesis and the holistic hypothesis.

An interesting aspect of Edward's face performance is his poor sensitivity with both spacing and part changes. Dissociations between spacing and part discrimination have led some to suggest that the special processing applied to upright faces may be limited to configural representation (see Maurer, Le Grand, & Mondloch, 2002, for a review). According to this view, the parts of a face are processed by domain-general mechanisms regardless of a face's orientation, but the configuration in upright faces is processed by a face-specific mechanism. This view predicts that individuals with face-specific deficits will have difficulty with configural processing but will perform normally with part changes. Edward's performance with objects indicates that his other recognition mechanisms are normal so his results are inconsistent with this prediction. His results are, however, consistent with models in which the entire face is represented holistically (Farah, Wilson, Drain, & Tanaka, 1995; Tanaka & Sengco, 1997; Yovel & Kanwisher, 2004), and parts and configuration are not processed separately (Yovel & Duchaine, in press; Yovel & Kanwisher, 2005).

Because this test is a matching task with minimal memory demands, these results support our previous conclusion that Edward's prosopagnosia involves a poor perceptual representation of the face. He may also have memory problems with faces that contribute to his difficulties, but his apparent perceptual difficulties make that difficult to determine.

Greeble training

The previous experiments demonstrate that Edward's face recognition problems are not elicited by stimulus properties considered important for face recognition (curvature hypothesis, holistic hypothesis, configural processing hypothesis) or the task demands of face recognition (individual item hypothesis). However, none of the experiments discussed so far have addressed the expertise hypothesis. The expertise hypothesis contends that some of the stimulus properties just mentioned are important as are task demands, but it also claims that substantial experience with an object class is necessary for special processing to occur (Diamond & Carey, 1986). After enough experience recognizing individual items from an object class with the same first-order configuration, observers begin to represent objects from the expert class in a configural or holistic manner.

The amount of experience necessary for this to occur is a matter of debate, and this has led us to refer to one view as the rapid expertise hypothesis and the other as the extended expertise hypothesis (Duchaine et al., 2004). Whereas the rapid-expertise hypothesis claims that expertise requires 10 hours or less to emerge, the extended view has suggested that it requires years. Regardless of the temporal issue, both hypotheses predict that an individual who cannot acquire expertise with faces will also be unable to acquire expertise with other object classes. Edward's performance with upright and inverted faces suggests that his years of experience with upright faces have not led to the development of any expertise with them. As a result, the expertise view predicts that Edward will also be unable to develop expertise with nonface classes.

The rapid expertise hypothesis claims that expertise can be activated in laboratory-based training in 10 hours or less when trained with an artificial stimulus class known as greebles (See Figure 13; Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998). However, a close inspection of the results supporting these claims raises questions about this conclusion (McKone & Kanwisher, 2005). The

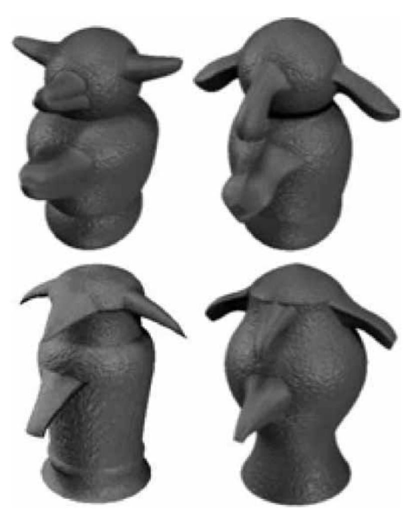

Figure 13. *Examples of greebles. The two greebles in the top row are in the same family, because they share a similar body shape.*

rapid expertise hypothesis predicts that Edward will perform similarly to the control subjects in the early training sessions, because in early sessions neither Edward nor the controls will process the greebles with expert mechanisms. However, in the later sessions, it predicts that Edward's performance will not improve like the controls, because they will be becoming greeble experts. To investigate Edward's performance in the greeble training, we designed a set of greeble training sessions nearly identical to those in a recent paper (Gauthier & Tarr, 2002), and we compared Edward and a group of age-matched control subjects in a recent paper (Duchaine et al., 2004) that we review next; we also present further relevant results.

As their criterion for expertise, Gauthier and colleagues have used response times for correct family and individual verification trials that presented consistent label–greeble pairs (trial types are discussed below). When family verification response times and individual verification response times are not significantly different, it has been claimed that subjects have become experts. This criterion was based on two previous findings. Tanaka and Taylor (1991) found that bird experts, but not bird novices, showed equivalent response times for basic-level verifications and subordinate-level verifications. Similarly, Tanaka (2001) found that subordinate verification (e.g., Bill Clinton) was as fast as basic verification (face). With greebles, it is claimed that individual recognition is a subordinate-level categorization while family recognition is a basic-level categorization. We have serious reservations with this as a measure of expertise, but because it is been used as a criterion we compare Edward's verification response times to determine whether he meets this criterion.

Control participants
Our six age- and education-matched control participants all had graduate degrees, and their average age was 48 ($SD = 10.2$). All showed a normal inversion effect on the sequential face-matching task described above and performed normally on the famous faces test (Duchaine et al., 2004). These results demonstrate that they have normal expertise with faces.

Stimuli
A total of 30 greyscale greebles were used in the experiment. Figure 13 shows examples of greebles used in the training, and all had the same first-order configuration. Thus, as with faces, subjects are forced to rely on second-order configural differences and feature differences. There are five greeble families, and greebles in the same family share the same general body shape.

Procedure
There were eight training sessions. In the first session, subjects were introduced to five greebles and the five greeble families. They were given practice and feedback with the greebles. In each of the first four sessions, five individual greebles were introduced so that after four sessions subjects were familiar with 20 different greebles. Subjects' knowledge of the greebles was assessed with two types of trial. In verification trials, a label is presented (either an individual name or a family name) for 600 ms after which a greeble is presented. The greeble remains visible until the subject indicates whether or not the label and the greeble are consistent. On naming trials, subjects are presented with a greeble and identify it by pressing the letter key corresponding to the first letter of its name. In the final four sessions, subjects were not introduced to any new greebles, but we continued to assess their knowledge with naming and verification trials. The first four sessions each took approximately one hour, and the last four sessions each took about 15 minutes.

Results

Figure 14 shows the percent correct for Edward and the control subjects. We have scaled the percent correct for the naming and individual verification panels to reflect the number of greebles known in each session (5, 10, 15, 20). For example, in Session 1, only 5 of the 20 (25%) individual greebles had been introduced so we scaled the maximum percent correct to 25%. Figure 14

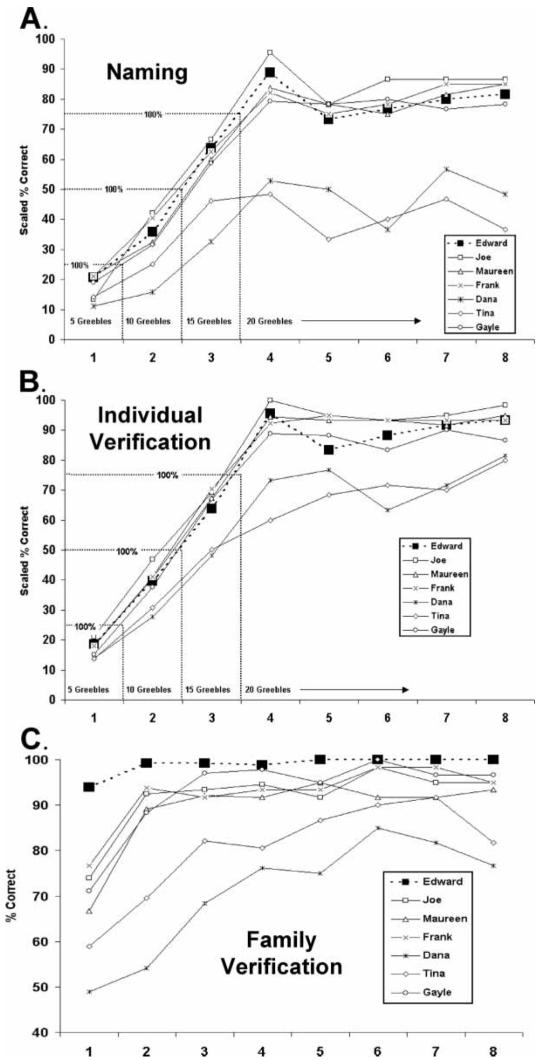

Figure 14. *Greeble training accuracy results. Percent correct for the three types of trial assessing greeble knowledge. For the naming trials (Panel A) and the individual verification trials (Panel B), we have scaled the scores to reflect the number of named greebles at each point in the training. For example, subjects had only been introduced to 5 of the 20 greebles in Session 1 so we divided their percent correct by 4 and placed the 100% level for Session 1 at 25% of the total percent correct. Panel C displays the family verification trials.*

Panel A displays the percent correct for the naming trials, and it is clear that, contrary to the predictions of the rapid expertise hypothesis, Edward's performance is normal. In fact, his score is comparable to that of our best performing subjects and considerably better than that of two of the control subjects. Figure 14 Panel B shows the results for the individual verification trials, and again it is clear that Edward is performing normally. Finally, Edward's family verification in Figure 14 Panel C was better than that of any of the control subjects. Edward's response times for all three trial types were in the normal range so speed/accuracy trade-offs cannot explain his normal accuracy (See Duchaine et al., 2004, for details).

Figure 15 displays Edward's response times, and arrows indicate the sessions in which the two types of response time were not significantly different from one another (Session 1, $p = .69$; Session 3, $p = .09$; Session 4, $p = .10$; Session 6, $p = .27$; Session 7, $p = .19$). Edward met this criterion for expertise in Sessions 1, 3, 4, 6, and 7. Thus, at least according to this criterion, Edward is a greeble expert.

Comments

Edward's results were clearly inconsistent with the rapid-expertise hypothesis (Duchaine et al., 2004). He was as good as our best control subjects with all

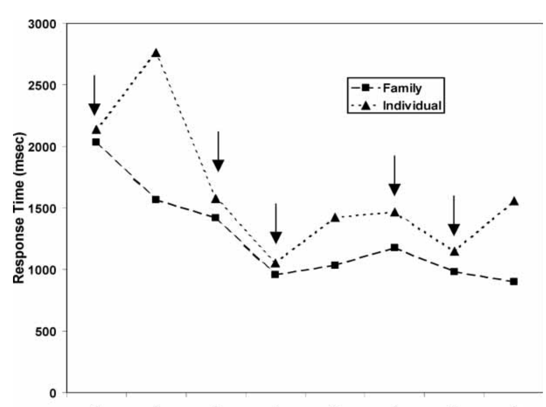

Figure 15. *Comparison of Edward's response times for individual verification trials and family verification trials. In particular, the responses were drawn from trials in which the label and greeble were consistent, and the subject responded correctly. The arrows point to sessions in which Edward's response times for the two trial types were not significantly different.*

three tasks assessing greeble knowledge, and his response times were comparable to those of the control subjects. He also met the criterion for expertise involving response time. This contrasts sharply with his face recognition abilities. Despite a lifetime of experience with upright faces, he appears to have not developed any expertise with them.

In our discussion of the interpretation of these results (Duchaine et al., 2004), we considered two explanations. One possibility is that Edward was able to acquire expertise with the greebles with the same speed as that of the control subjects. On this account, expertise with greebles and expertise with faces rely on separate mechanisms. Both types of mechanism operate normally in the control subjects, but for Edward only the mechanisms used with greebles operate normally. However, we favour a second interpretation, because we do not believe that past research has demonstrated that subjects process greebles in a qualitatively different fashion after training (Duchaine et al., 2004; McKone & Kanwisher, 2005). We believe that neither Edward nor the controls developed face-like expertise in the greeble training.

Past discussions of greeble expertise have relied on a number of different measures to argue for the presence of expertise. While Gauthier and colleagues have considered the response time comparison an important measure of expertise, we have empirical and theoretical concerns about it. In the only paper displaying individual data during greeble training (Gauthier et al., 1998), the session at which each of the 12 subjects met this criterion was highlighted; 2 met it in the fourth session, 2 in the third, 1 in the second, and 1 in the first session. Edward met it in the first session. Thus, many subjects achieve the criterion after very little training. Furthermore, regardless of the object classes used, response time with the two types of verification will surely depend on the amount of practice with each type and the similarity between individuals and between families. With more practice with individual identification, one would expect that subjects would more quickly meet the criterion while more practice with family identification would cause them to reach it more slowly. When we consider similarity it is apparent that if the individual greebles were more similar to one another, then individual response times would be increased, and the criterion would have been more difficult to meet whereas decreased similarity would have the opposite effect. Thus this criterion is strongly influenced by the parameters of the experiment, and so it is a very questionable measure of a qualitative shift in recognition processes.

Previous results from behavioural experiments purportedly showing configural processing after training are also unpersuasive (McKone & Kanwisher, 2005). While some experiments have shown the predicted effects, other experiments have shown null effects or effects in the opposite-to-predicted direction. A thorough discussion of each experiment investigating configural effects after greeble training is presented in McKone and Kanwisher (2005). Also, as mentioned earlier, there is no evidence that training leads to inversion effects for greebles nor is there clear evidence that training improves performance with new sets of greebles. The neural effects that are claimed to indicate that greeble training leads to expertise are also not convincing (McKone & Kanwisher, 2005). It has not been shown that training leads to increased fusiform activations in functional magnetic resonance imaging. Training also does not increase the magnitude of the N170 in face-selective electrodes (Rossion, Curran, & Gauthier, 2002), and training appears to affect left- but not right-lateralized processes whereas face-selective ERPs tend to be right lateralized or bilateral (Bentin, McCarthy, Perez, Puce, & Allison, 1996).

Because the evidence does not demonstrate that training activates different mechanisms, there is little reason to believe that Edward or the controls have greeble expertise (Duchaine et al., 2004). Instead, they simply used object recognition mechanisms throughout the training. Percent correct did improve during the training, but it is not surprising that practice with the task and the object–name pairs improved performance. Given

Edward's normal performance with objects in other experiments, we would not expect him to have any difficulties with the greebles if greeble performance relies solely on object recognition mechanisms. Regardless of which interpretation of Edward's results is correct, the results are clearly inconsistent with the rapid expertise hypothesis.

Matching across different views: Upright bodies and human faces

The greeble training demonstrates that the rapid-expertise explanation cannot account for Edward's prosopagnosia, but the results do not bear on the other version of the expertise explanation. The extended expertise explanation suggests that the acquisition of expertise with a class requires years of experience with it (Carey, 1992; Diamond & Carey, 1986). However, despite the prominence of this hypothesis, it remains unclear what nonface classes are processed with such mechanisms so testing this explanation is challenging.

Above, we discussed the many lines of evidence that are consistent with the view that upright faces are processed by face-specific mechanisms. This evidence includes behavioural experiments with normal subjects using a wide variety of methods including the inversion effect (Diamond & Carey, 1986; Yin, 1969), composite effect (Hole, 1994; Young et al., 1987), part–whole effect (Tanaka & Farah, 1993; Tanaka & Sengco, 1997), and similarity ratings (Leder & Bruce, 1998). The extended expertise explanation predicts that expert categories will also show these effects, but among these many effects, only inversion effects in recognition memory have been found with experts. Diamond and Carey (1986) found that dog show judges showed face-sized inversion effects. However, a recent study of Labrador experts did not replicate this effect. The Labrador experts had an average of 21 years of experience, but experts and novices showed comparably sized, small inversion effects, and neither group showed a composite effect (Robbins & McKone, 2005). This effect has not been found with any other classes. In addition, inversion effects do not provide a direct test of whether a class is being processed in a configural or holistic manner, and memory in general tends to be better when subjects are familiar with the memoranda (McKone & Kanwisher, 2005). In the only published, direct test of configural processing in experts, experts did not show part–whole effects for biological cells, Rottweilers, or cars (Tanaka, 1996; cited in Tanaka & Gauthier, 1997). Hence, there is little behavioural support for the expertise hypothesis.

However, a recent paper showed comparably sized inversion effects for faces and the positions of body parts in a same–different paradigm (Reed, Stone, Bozova, & Tanaka, 2003). In addition, bodies, like faces, produce selective activation in visual cortex (Downing, Jiang, Shuman, & Kanwisher, 2001; Peelen & Downing, 2005) and are more likely than most objects to capture attention (Downing, Bray, Rogers, & Childs, 2004). Expert processing for bodies appears reasonable given the conditions under which extended expertise is hypothesized to be acquired. Humans are, of course, constantly exposed to bodies, and bodies, like faces, are used to assess identity, gender, age, attractiveness, emotion, and intention. Second, bodies, like faces, share a common first-order configuration. Thus, bodies are currently the leading nonface candidate class to be processed by mechanisms used for extended expertise, and so we investigate Edward's ability to process bodies. To make the task analogous to a face matching task, the subjects are asked to match the identity of bodies that differ in terms of shape. The extended expertise explanation predicts that he will show impairments with bodies. Because bodies have curved surfaces the results are relevant to the curvature explanation, and because the matching requires individual recognition the results bear on the individuation explanation.

Control participants

A total of 10 participants (8 females, age range: 18–35 years) took part in the experiment.

Stimuli

Faces. Four photographs of four different men's faces were used in the experiment. Each face was presented in four different head rotations ranging from profile to three-quarter view. The outline of the face and the hair were covered to conceal nonfacial cues that might be used for recognition.

Bodies. Four headless male bodies were generated using Poser 4.0. The width and height of the torsos differed for each body, but the snug clothing was identical for all bodies. Four different trunk rotations were created for each body (see Figure 16).

Procedure

Subjects performed a two-alternative forced-choice task with either faces or bodies.

Faces and bodies were presented in different blocks. In both tasks, a stimulus was presented at the centre of the screen for 250 ms followed by two stimuli presented side by side with similar orientations. The orientations of the test stimuli always differed from the study image, but one of the stimuli matched the first stimulus on identity. Thus, subjects had to match the first and second stimuli based on identity across rotations. The two stimuli were presented on the screen until a response was made.

Results

The results for the face and body matching tasks are displayed in Figure 17. As expected, Edward had great difficulty with the face matching task. His score of 69.4% correct is 3 standard deviations below the control average of 90.4% ($SD = 6.1$). In contrast, his percent correct with bodies was the second best among all subjects. Edward's percent correct was 93.1%, and the control average was 89.2% ($SD = 3.7$). His response times for both faces and bodies were in the normal range. With faces, controls averaged 1,018 ms ($SD = 309$) while Edward averaged 1,271 ms; with bodies, controls averaged 957 ms ($SD = 286$), and Edward averaged 1,062.

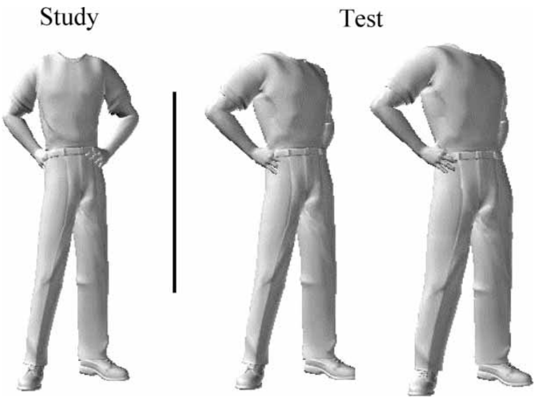

Figure 16. *Examples from the body-matching test. Subjects briefly viewed the study body and then chose the test body that matched the study body.*

Comment

Edward showed a clear dissociation between impaired face matching and normal body matching. His normal body perception is consistent with his report that he often uses body shape to determine identity and his avid interest in gymnastics and figure skating. Because human bodies are a good candidate for the application of visual expertise, Edward's results appear to be inconsistent with the extended expertise explanation. The results are consistent with other cases demonstrating that face recognition and nonface expert recognition are neuropsychologically dissociable. RM, who had extensive experience with cars, maintained his ability with cars after losing his face recognition abilities and was able to identify the makes and models of more cars than could any controls (Sergent & Signoret, 1992). Conversely, CK, an object agnosic with normal face recognition, was an expert with toy soldiers and planes yet he lost his abilities with these classes (Moscovitch et al., 1997). Perhaps most troubling for expertise explanations is that there are no cases with a selective association between face recognition and nonface expert recognition. In summary, there is currently no neuropsychological support for a common mechanism for faces and nonface expert categories.

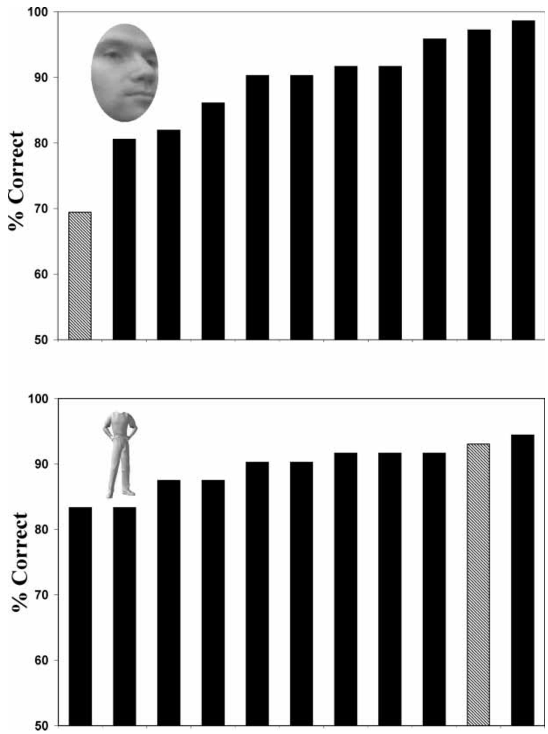

Figure 17. *Percent correct for each subject for face and body matching. Black columns are controls, and the hashed column is Edward.*

GENERAL DISCUSSION

We have tested all of the alternative explanations of prosopagnosia in a man with severe developmental prosopagnosia. Our experiments have shown that Edward has impairments with many types of face processing ability (identity, emotions, gender, attractiveness), yet he performed normally on nearly every test of nonface recognition with which we assessed him. These tests were designed to test the different accounts of prosopagnosia, and in Table 1 we present a list of the tests conducted with Edward. His results were inconsistent with all of the alternative explanations. As a result, it appears that none of the existing alternative explanations of prosopagnosia can account for Edward's prosopagnosia. Note that these results do not demonstrate that these explanations could not account for other cases of prosopagnosia, but they do demonstrate that they cannot explain his case.

Edward performed normally with face detection and showed a typical inversion effect so it appears that he has no trouble categorizing a visual stimulus as a face. However, his impairment affects a wide range of later face processing tasks. Thus, his processing difficulties are early in the face processing stream after face categorization but before face representations are processed by the separate mechanisms that have been hypothesized to underlie our ability to perform different face processing tasks (Bruce & Young, 1986). In Bruce and Young's influential model, Edward's impairment would be in the structural encoding stage.

When acquired prosopagnosics have defective structural encoding, it results from damage to the mechanisms normally performing this encoding. However, in Edward's case, this explanation seems unlikely. Because his performance with upright and inverted faces was nearly identical in the matching task, it appears that he processes

Table 1. *Evidence against the explanations for prosopagnosia*

	Individuation	*Curvature*	*Holistic*	*Configural*	*Rapid exp.*	*Expanded exp.*
Old–new discriminations	X	X	X			
Inverted face matching	X	X	X			
Tests of visual closure				X		
House discrimination	X		X	X		
Greeble training					X	
Body matching	X	X			X	X

Note: An X indicates that the results from an experiment were inconsistent with an explanation. Exp. = expertise.

these two classes with the same mechanisms. His inverted performance was in the normal range, and so it seems that his recognition systems treat upright faces in the same way that normal subjects treat inverted faces. He simply never developed the mechanisms that normally perform this special structural encoding. Instead Edward's visual system processes both orientations with more general-purpose recognition mechanisms that operate in a less configural manner than the mechanisms processing upright faces.

In the Introduction, we discussed the many architectures potentially involved with face recognition and visual recognition more generally. Consideration of both Edward's results and CK's results (Moscovitch & Moscovitch, 2000; Moscovitch et al., 1997) demonstrate the importance of face-specific mechanisms for face recognition. CK can identify faces as well as normal subjects can despite severe damage to the mechanisms used with nonface objects. Conversely, Edward's famous face performance indicates that he has almost no ability to identify faces despite the fact that the mechanisms that he uses for object recognition appear to be normal. Their cases suggest that face recognition is not the product of a number of mechanisms, one of which is face specific, but instead it is carried out entirely or nearly entirely by face-specific mechanisms.

Theorists discussing domain-specific mechanisms have often pointed to face recognition as an ability likely to be carried out by domain-specific mechanisms (Cowie, 1998; Fodor, 1983; Jackendoff, 1992; Tooby & Cosmides, 1992), and our findings with Edward provide firm support for this notion. However, these mechanisms can be characterized in a more precise fashion. A number of the alternative explanations for prosopagnosia tested with Edward are also domain-specific hypotheses. The holistic explanation suggested that objects that are difficult to decompose into parts are processed by mechanisms specialized for processing such objects. Similarly, the curvature explanation proposed specialized mechanisms for objects with significant curved surfaces. Neither nondecomposable objects nor curved objects are categories that we naturally carve the world into, but they are domains nonetheless. In contrast, faces are a category used in everyday categorization. To capture this distinction between types of domain, we can say that Edward's results provide evidence for a cognitive specialization for a natural category. That some cognitive mechanisms are specialized to process natural categories makes biological sense. We use these natural categories in everyday thought, because these are categories that affect our functioning in an enduring, systematic manner. In other words, they matter to us so we think about them. Cognitive mechanisms are created, whether phylogenetically or ontogenetically, in response to categories that matter, so it seems likely that other cognitive specializations are also consistent with our natural categories.

Developmental inferences

The existence of face-specific mechanisms leaves open the important question of the developmental mechanisms that give rise to these mechanisms. Previous cases of developmental prosopagnosia have indicated that face, object, and scene recognition are developmentally dissociable (Duchaine & Nakayama, 2005; Lerner et al., 2003; Nunn et al., 2001), but the nature of the disorder was unclear in the previous cases. In Edward's case, the evidence implicates a face-specific impairment and so indicates that he failed to develop these mechanisms despite developing normal object recognition mechanisms. Although face and object mechanisms may share a number of developmental mechanisms, Edward's developmental dissociation indicates that their construction involves different developmental mechanisms. However, Edward's results reveal little about how these developmental processes work, because retrospectively it is difficult to determine where the developmental process went awry in congenital cases. Prospective studies of children from families with genetic prosopagnosia and face perception problems caused by early brain damage, cataracts, and other known etiologies hold more promise. In addition, developmental cases similar to CK's agnosia without prosopagnosia would be highly informative. Given that there appear to be a number of specialized visual recognition mechanisms (Aguirre et al., 1998; Downing et al., 2001; Epstein, DeYoe, Press, Rosen, & Kanwisher, 2001; Epstein & Kanwisher, 1998; Grossman et al., 2000; Peelen & Downing, 2005), it will be interesting to see how these fractionate developmentally.

These developmental questions are central issues, but they are difficult to approach. Although congenital prosopagnosia and other congenital agnosias are likely to be powerful means to understand visual recognition mechanisms and their developmental basis, this approach depends on fortuitous dissociations caused by uncertain developmental events. Another converging method to examine these questions involves studying nonhuman primates raised under controlled conditions, and this approach circumvents some of the limitations of human developmental neuropsychology. For example, Mineka and colleagues found that laboratory-raised macaques develop intense fears to objects with reptilian properties (e.g., snakes, crocodiles) when they view another macaque behaving fearfully in the presence of the object (Cook & Mineka, 1989; Mineka & Cook, 1993). In contrast, they do not develop intense fears under identical conditions when an object does not have reptilian properties (e.g., flower, rabbit). Macaques were also used in a study that looked at the responses of monkeys raised in isolation to a variety of still images (Sackett, 1966). While the infants did not respond differentially to some images of monkeys (neutral adults, fearful adults, withdrawing adults) or control stimuli, they made revealing responses to photographs of threatening adults and neutral infants. In particular, the infants showed high rates of disturbance behaviours when presented with images of threatening adults. They also played significantly more when presented with threatening adults or infants. Because the macaques in these two experiments had no experience with snakes or other monkeys, it seems that their responses must result from the operation of evolved specializations coupled to motivational mechanisms. Though rarely used by vision researchers, similar methods hold great promise as a means of understanding the computational and developmental organization of recognition mechanisms.

In the Introduction, we mentioned the debate concerning developmental cognitive disorders and whether specific developmental cognitive disorders exist. Thomas and Karmiloff-Smith (2002) contend that specific developmental disorders should not exist, because developmental impairments to one system will necessarily affect the operation of other mechanisms. Because neighbouring brain regions perform object recognition and face recognition (Grill-Spector, 2004), they are especially likely to be developmentally interdependent. Nevertheless, Edward's normal object recognition and impaired face recognition indicate that developmental visual disorders can be quite specific, and defective developmental processes affecting particular visual mechanisms do not necessarily influence the development of other visual mechanisms. This is contrary to theoretical arguments against residual normality and consistent with other cases showing selective dissociations in developmental disorders and early brain damage such as dyslexia (Ramus, 2002; Ramus et al., 2003), semantic memory dysfuntion (Temple & Richardson, 2004), acalculia (Landerl et al., 2004), and episodic memory dysfunction (Vargha-Khadem et al., 1997; Vargha-Khadem et al., 2001).

Summary

We have addressed all of the existing alternative explanations of prosopagnosia, and we have rejected each of these accounts. Edward's remarkably restricted impairment with upright faces is best accounted for by the face-specific explanation, which claims that prosopagnosia results from defective face-specific mechanisms. This explanation for prosopagnosia is consistent with evidence from behavioural experiments, neuroimaging, neuropsychology, and neurophysiology that also suggests that the human brain contains face-specific mechanisms. Furthermore, because his case is developmental in nature, it indicates that face and nonface mechanisms are created, at least in part, by different developmental processes.

Manuscript received 8 March 2005
Revised manuscript received 10 October 2005
Revised manuscript accepted 20 October 2005
PrEview proof published online day month year

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