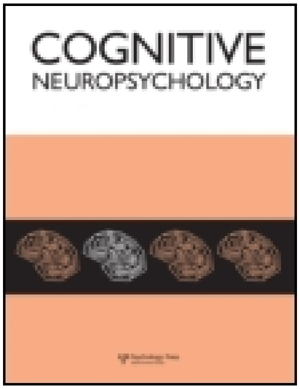

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Are faces special? A case of pure prosopagnosia

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Are faces special? A case of pure prosopagnosia

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The ability to recognize individual faces is of crucial social importance for humans and evolutionarily necessary for survival. Consequently, faces may be "special" stimuli, for which we have developed unique modular perceptual and recognition processes. Some of the strongest evidence for face processing being modular comes from cases of prosopagnosia, where patients are unable to recognize faces whilst retaining the ability to recognize other objects. Here we present the case of an acquired prosopagnosic whose poor recognition was linked to a perceptual impairment in face processing. Despite this, she had intact object recognition, even at a subordinate level. She also showed a normal ability to learn and to generalize learning of nonfacial exemplars differing in the nature and arrangement of their parts, along with impaired learning and generalization of facial exemplars. The case provides evidence for modular perceptual processes for faces.

Keywords: Prosopagnosia; Modular processing; Category specificity; Configural processing.

Prosopagnosia was first defined by Bodamer (1947) as the inability to recognize familiar faces. The ability to match unfamiliar faces (Bruyer et al., 1983) and to perceive facial expression (Hécaen, 1981) may be retained. Prosopagnosia can result from unilateral right hemisphere lesions[1] (e.g., Sergent & Signoret, 1992; Uttner, Bliem, & Danek, 2002), but more usually following bilateral lesions involving the ventral occipitotemporal cortex (e.g., Delvenne, Braithwaite,

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[1] There is also at least one report of prosopagnosia following a unilateral left hemisphere lesion (Mattson, Levin, & Grafman, 2000).

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Riddoch, & Humphreys, 2002; Rossion et al., 2003). As we note below, there is controversy about how specific the deficits are in such cases and whether any deficit for faces reflects factors such as the level of detail required to identify faces relative to other objects. This controversy is mirrored by arguments concerning the specificity of the neural substrates of face processing, based on data from functional neuroimaging. In this paper we present the case of a patient who, we argue, has a highly specific deficit for faces. This case provides evidence for the argument that faces are "special" for the human visual system.

Face specificity in prosopagnosia

Although acquired prosopagnosia was initially described as a face-specifc disorder, it is the case that many prosopagnosic patients have some difficulties with the visual processing of objects (e.g., Farah, Wilson, Drain, & Tanaka, 1995; Gauthier, Behrman, & Tarr, 1999; McNeil & Warrington, 1993). Furthermore, although a few patients have been reported with recognition deficits restricted to faces (Bukach, Bub, Gautier, & Tarr, 2006; De Renzi, Faglioni, & Spinnler, 1968; De Renzi & Pellegrino, 1998; Henke, Schweinberger, Grigo, Klos, & Sommer, 1998; Rossion et al., 2003; Wada & Yamamoto, 2001), the specificity of the deficit in these cases can be questioned. For instance, De Renzi and Pellegrino (1998) reported that their patient performed virtually at ceiling on a number of different picture-naming tests, but they did not formally assess naming of items from visually homogeneous categories. Similar arguments can also be made about the patients reported by Bukach et al. (2006), De Renzi (1986), and Wada and Yamamoto (2001). Henke et al. (1998) did assess whether their patient, M.T., could name fruits, vegetables, and cars, and performance on these items fell within the control range. Rossion et al. (2003) also assessed the ability of their patient P.S. to perform a physical identity-matching test with the homogeneous category of cars. P.S. was slower and less accurate than the controls on this task suggesting that the visual-processing deficit was not restricted to faces. On the other hand, Schiltz and colleagues (2006) assessed P.S. with a larger set of visually homogeneous categories (birds, ships, cars, chairs, and faces) using a two-alternative forced-choice matching task. A target stimulus was presented centrally followed by a pair of stimuli—a probe that was physically identical to the target and a distractor drawn from either the same or a different category. For all object categories apart from faces, P.S.'s performance fell within the control range, even when within-category discriminations were required. This is consistent with a face-specific deficit. However, since a physical matching task was required, the judgements may not have been made using high-level perceptual representations.

In another test of the specificity of the deficit, Sergent and Signoret (1992) noted that two of their three prosopagnosic patients were able to distinguish their own possessions from distractors belonging to the same basic-level category (see also De Renzi, 1986). Furthermore, the patient who had the most severe face-processing problem performed at a level higher than that of controls when identifying cars, a category with which this particular patient had expertise. Sergent and Signoret conclude that the perceptual processes underlying the identification of faces are dissociable from similar processes with other objects. Similar arguments have been made from cases of developmental prosopagnosia (e.g., Avidan, Hasson, Malach, & Berhmann, 2005; Barton, Cherkasova, Press, Intriligator, & O'Connor, 2003; Behrmann & Avidan, 2005; Behrmann, Avidan, Marotta, & Kimchi, 2005; Duchaine, 2000; Duchaine & Nakayama, 2005, 2006; Duchaine, Nieminen-von Wendt, New, & Kulomaki, 2003; Nunn, Postma, & Pearson, 2001). For example, Nunn's subject was able to name objects from three categories with homogeneous exemplars (cars, flowers, and famous buildings) at a control level. Duchaine and Nakayama (2005) report the results of an extensive series of tests with 7 developmental prosopagnosics using an old/new recognition memory paradigm for faces and for six other object categories. A total of 4 of these individuals showed marked differences in performance between faces and stimuli from the other categories, and, for other categories, performance fell within the normal range. Duchaine, Yovel, Butterworth, and Nakayama (2006) found similar results with a further developmental prosopagnosic (Edward). Edward fell within 2 standard deviations of the control mean for all nonface categories apart from natural scenes, while old/new recognition performance with faces was far below the control mean.

These results suggest that prosopagnosia can be highly specific, in both acquired and developmental cases. This conclusion, though, is limited by the relatively small numbers of categories explored when patients name objects from homogeneous categories and by the use of physical identity matching and old/new recognition tasks, which might depend on relatively low-level representations of stimuli.

Functional imaging

Other evidence for the specificity of face processing comes from studies using functional brain imaging. Numerous studies have identified brain regions that respond more to face images than to other objects. Most notably, the lateral, middle fusiform gyrus has been labelled as the "fusiform face area" (FFA) on the basis of it showing increased activation to faces compared with other objects (Henson et al., 2003; Kanwisher, McDermott, & Chum, 1997; Spiridon & Kanwisher, 2002), though this region is not unique in showing high responsivity to faces (a characteristic also of neurons in the so-called occipital face area; see Kanwisher and Yovel, 2006, for a discussion of the relative properties of FFA and the occipital face area). The relations between these different regions have been assessed through imaging studies with prosopagnosic patients. Steeves et al. (2006) reported one patient with bilateral ventral lateral occipital cortex lesions who showed greater activation in the FFA when viewing faces than when viewing scenes, despite having a severe prosopagnosia (see also Avidan et al., 2005; Hasson, Avidan, Deouell, Bentin, & Malach, 2003; Rossion et al., 2003). This suggests a distributed network for face processing, with regions outside the FFA being necessary for face recognition. This is also indicated by data from Schiltz et al. (2006). Their prosopagnosic patient had occipital lesions along with a structurally intact FFA (see Rossion et al., 2003). Despite the FFA being intact, there was reduced recovery from functional magnetic resonance imaging (fMRI) adaptation in the FFA for faces relative to other objects. Recovery from adaptation can serve as a fine-grained marker of the involvement of particular populations of neurons in the processing of the adapted stimulus. In this case, occipital damage seemed to limit responsivity in the FFA, providing evidence for areas outside this region being critical for any face-specific responses in the FFA. More recently, Sorger, Goebel, Schiltz, and Rossion (2007) in a detailed analysis of patient P.S. (Rossion et al., 2003), argue that the critical lesion for prosopagnosia is the right inferior, occipital gyrus and that the exact role of FFA remains unknown.

Although neurons external to the region may be necessary for the sensitivity of cells within the FFA, there is evidence that the FFA is specifically recruited when face identity is derived. Grill-Spector, Knouf, and Kanwisher (2004), for example, found that the FFA showed increased activation when briefly presented faces could be detected, although there was no correlation between the FFA response and success in car identification in car experts. Yovel and Kanwisher (2005) compared the response to upright and inverted faces in three cortical areas strongly activated by faces. They found higher responses to upright than to inverted faces in the FFA and the superior temporal sulcus, but only in the FFA was differential activation to upright over inverted faces found to correlate with behavioural matching responses to upright and inverted faces. Face identification is highly sensitive to inversion (Yin, 1969), and the increased FFA activation for upright over inverted faces may reflect responsivity to the configural identity of the faces. Other work has indicated that the differences in activity between the processing of faces and objects tend to be greater in the right than in the left FFA (Allison, Puce, Spencer, & McCarthy, 1999; Kanwisher et al., 1997; McCarthy, Puce, Belger, & Alllison, 1999; Rossion et al., 2000), matching the neuropsychological evidence on prosopagnosia after unilateral right hemisphere damage (e.g., De Renzi, 1986). High-resolution studies on the monkey also suggest that there is considerable neural specificity in FFA. Tsao, Freiwald, Tootell, and Livingstone (2006) demonstrated patches in the macaque temporal lobe where nearly 100% of visually responsive neurones were strongly face selective. Similarly, in human fMRI, Spiridon, Fischl, and Kanwisher (2006) found that selectivity for faces had disappeared 4 mm from the standardly defined border of FFA.

Studies of the effects of expertise have been used to argue against there being functional specialization of neural regions for faces. Unlike many objects that we identify, faces are recognized at a subordinate level (individual people), a task requiring perceptual expertise. It may be that the processes and neural substrates of face recognition are not unique to faces, but rather reflect our perceptual expertise at a subordinate level. Nevertheless, if expertise is acquired for other stimuli, then similar processes and neural regions may be recruited. Work by Gauthier and colleagues has suggested this. For example, in their studies the acquisition of expertise with novel objects ("greebles") led to increased activation in the right fusiform gyrus, matching the data for faces; in contrast, novices in greeble recognition failed to show similar levels of activation (Gauthier, Tarr, Andersen, Skudlarski, & Gore, 1999). Similarly, Gauthier, Skudlarski, Gore, and Andersen (2000) report a greater increase in the right FFA response for cars and birds than for control objects in car and bird experts (Gauthier et al., 2000; see also Xu, Liu, & Kanwisher, 2005, for similar results in a magnetoencephalography, MEG, study).

There is a continuing debate about the expertise hypothesis. Robbins and McKone (2007) found no evidence for face-like processing in dog experts in three behavioural tasks that are commonly used to support the configural processing of faces (e.g., the effects of inversion, same/different matching using aligned or nonaligned composite stimuli, and the effects of contrast reversal on same/different matching). In a critical review of the literature, Robbins and McKone fail to find evidence for configural/holistic processing in objects of expertise (see also McKone, Kanwisher, & Duchaine, 2007). These conclusions, however, are strongly disputed by Gauthier and Bukach (2007).

The view from functional imaging, then, is consistent with some degree of neural specialization for face processing. Here we present neuropsychological evidence that is consistent with this argument.

The present study

We report the case of an acquired prosopagnosic patient (F.B.) who has a unilateral right hemisphere lesion and whose deficit is confined to faces. We believe that F.B. is an important case for several reasons:

1. Her deficit is highly selective to faces and does not extend to other categories of object. Only two cases have been previously reported where naming of items from visually homogeneous categories has been spared (one of these being a case of developmental prosopagnosia; Henke et al., 1998; Nunn et al., 2001).
2. Up until now there have been few reports of cases of prosopagnosia resulting from unilateral right hemisphere lesions (e.g., Barton, Press, Keenan, & O'Connor, 2002; Landis, Regard, Bliestle, & Kleihues, 1988; Marotta, Genovese, & Behrmann, 2001; Sergent & Signoret, 1992; Sergent & Villemure, 1989; Uttner et al., 2002; Wada & Yamamoto, 2001). F.B. adds to this number.
3. F.B. showed a normal rate of learning when asked to associate a name to nonface stimuli that had similar parts and differed only in the spatial arrangement of those parts. This learning also generalized across variations in image quality and viewpoint. In contrast, her ability to learn to associate faces with names was impaired, and when learning took place there

was poor generalization. As we discuss in the Introduction to Experiment 3, prior data on new learning in prosopagnosia are mixed, and few studies have examined generalization when learning does take place. The contrast between F.B.'s learning of faces and with other sets of visually homogeneous objects supports the specificity argument.

CASE HISTORY

F.B., a former store detective, suffered an embolization of a right posterior inferior arteriovenous malformation (AVM) at the age of 30 years, which resulted in a marked difficulty in recognizing faces. An MRI showed that there was damage to the right fusiform, right inferior temporal, right middle temporal, and right inferior occipital gyri. There were no indications of left hemisphere language (see Figure 1). We should note here that prosopagnosia is usually associated with bilateral lesions and that only a few cases of unilateral right-side lesions have been observed (e.g., De Renzi, 1986; Landis, Cummings, Christen, Bogen, & Imbof, 1986; Sergent & Villemure, 1989; Uttner et al., 2002).

F.B. did not complain of any other cognitive deficit other than an extreme difficulty in recognizing familiar people out of an expected context. She attempted to compensate for her problem by focusing on cues such as clothing, hair, or voice. As a result of her deficit, F.B. was unable to continue working as a store detective and instead enrolled at a university to study English Literature. During the course of the reported investigations F.B. successfully graduated with a first-class degree. Where relevant, F.B.'s data are compared with those of her husband, S.B., who was 32 years old and had a similar educational background to that of F.B.

NEUROPSYCHOLOGICAL INVESTIGATIONS

Since F.B.'s main complaint was a difficulty in the recognition of familiar faces, we placed an emphasis on tests of face and object recognition in our initial neuropsychological investigations. We examined F.B.'s ability to name famous faces, and, in order to determine whether her deficit was specific to faces, we also assessed her ability to distinguish by name different exemplars from categories where the individual members are visually similar (e.g., flowers, dogs, etc.). We examined F.B.'s performance using standardized clinical batteries of visual object processing, and we also assessed her ability to access the semantic system from vision.

Face processing

F.B. was presented with 30 famous faces to name and was unable to name any of them. Prior to testing, we determined with F.B.'s husband that all the presented faces were known to F.B. We then examined whether she retained any sense of familiarity for pictures of famous people. She was shown 100 faces (50 familiar celebrities

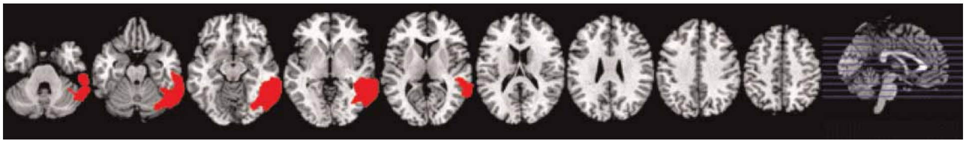

Figure 1. *Lesion reconstruction for F.B. from MRI scan. Lesions have been drawn in MRICRon (http://www.sph.sc.edu/comd/rorden/micron/) onto ch2bet, a scalp-stripped version of the average of 27 T1-weighted scans from the same individuals (displayed at www.bic.mni.mcgill.ca/cgi/icbm_view). The whole brain (right) shows the nine slices used. Left of the slice represents the left hemisphere. The lesion was confined to the right hemisphere and involved the fusiform gyrus, inferior temporal gyrus, middle temporal gyrus, and inferior occipital gyrus. (Figure can be viewed in colour online.)*

and 50 unfamiliar people) and was asked to decide which were familiar but was unable to do so. When she was asked to guess, she declined stating that none of the faces seem familiar at all.

We assessed F.B.'s recognition memory with a standardized test (the Warrington Recognition Memory Test, WRMT; Warrington, 1984) for faces and words. F.B. was at chance for faces (21/50 correct) while she performed near ceiling for words (49/50 correct). The difference in performance between faces and words was highly significant, $\chi^2(1) = 37.3$, $p < .001$. Age-matched controls do not perform differently with the two stimulus types (mean for faces = 43.8, *SD* 3.6; mean for words 45.8, *SD* 3.6, for the 30–34-year-old age group). F.B.'s performance with words was normal, while her performance on faces was impaired.

We also assessed F.B. on some tests of face processing that did not require matching to memory, including same/different matching of unfamiliar faces, age judgements, sex judgements, expression analysis, and tests of covert recognition. Since access to stored memories for individual faces was not required, these tests provide data on whether F.B.'s perceptual processing was spared for the structural, and perhaps other, properties of faces.

Matching unfamiliar faces

Pairs of grey-level faces ($3 \times 3^\circ$) were presented sequentially on a Macintosh computer using SuperLab. The first face was presented for 1,500 ms on a white background; there was then a blank interstimulus interval (ISI) of 500 ms followed by a second face exposed for 2,000 ms. For "same" faces, either a physically identical view was shown, or a three-quarter view. F.B. was required to respond with key presses for "same" both when the two faces were both physically identical and when they were different views of the same face. "Different" responses were made when the faces were of different people. The speed of responding was not stressed. Two age-matched controls performed at ceiling on this task (100% correct). There were a total of 104 trials presented in one block. Condition was randomized over the block. F.B. scored 100% (24/24) correct for physically identical faces, for different-view–same-person faces she scored 1/48, and for different-person views she was at ceiling (100%, 72/72 correct). She was able to match identical images of faces but was poor at matching across rotations to a three-quarter view. Control performance (F.B.'s husband) was at ceiling. Reaction times were not analysed since the instructions only stressed the accuracy of performance.

Recognition of emotion

The Emotional Hexagon Test uses faces from the Ekman and Friesen (1976) set that have been manipulated to produce images of graded difficulty. A maximum score is 120. Young, Perrett, Calder, Sprengelmeyer, and Ekman (2002) provide control data with a mean score of 109.16/120 and a cut-off of 94. F.B. scored 99/120, and her performance was within the normal range. Reaction times are not standardly measured, and they were not recorded here.

Age judgements

F.B. was shown 59 faces (34 familiar and 25 unfamiliar) chosen by the experimenters to reflect a range of ages (based on data provided by a group of control participants; there were 5 faces below 30 years, 13 faces 30–39 years, 18 faces 40–49 years, 13 faces 50–59 years, and 10 faces 60–69 years). The task was to rate each face for age. F.B. tackled this task with confidence and completed two sets of rating on different days of testing. All 34 familiar faces were individuals whom F.B. had confirmed she was familiar with prior to her injury, but none of them was recognized as familiar during the age-rating sessions. Five other age-matched judges were also asked to provide age ratings for the entire set of faces. There was a significant correlation between the two sets of ratings furnished by F.B., $r(57) = .91$. These two sets were collapsed to provide a mean score for each face, which was correlated with the mean rating provided by the other five judges. Again, a significant relationship was observed between F.B.'s ratings and those of the controls, $r(57) = .94$. Analysed across items there was no reliable difference between F.B.'s ratings and the mean of the control ratings: F.B.'s mean rating was 46.0 years, and that for the controls was 45.9 years, $t(58) = 0.162$.

Sex classification

F.B.'s ability to classify the sex of faces was assessed using images where both the hair and the external features were removed, making classification decision contingent solely on an analysis of the internal features. A total of 96 images (48 female and 48 male) were presented one at a time on a computer screen for 1,500 ms. Accuracy of decision was stressed more than reaction time (RT), but RTs were recorded. F.B. made a two-alternative key press according to the judged sex of the face. There was then a 1,000-ms interval followed by another face. F.B. performed very accurately with these impoverished faces under speeded response conditions, scoring 94/96 correct. Her RTs were all made within 1 s.

Overall, F.B. showed a marked deficit in face recognition, which does not extend to the processing of non-identity-related aspects of face processing. Another case of acquired prosopagnosia has been reported to have normal processing of facial emotion (e.g., Young, Newcombe, de Haan, Small, & Hay, 1993), as have two cases of developmental prosopagnosia (Duchaine, Parker, & Nakayama, 2003; Nunn et al., 2001). However, it is possible that emotion judgements in such cases are based on an abnormal strategy where attention is paid to local detail rather than facial configuration. Baudouin and Humphreys (2006) reported accurate discrimination of emotion in a patient with acquired prosopagnosia and agnosia, but, unlike control participants, performance was relatively little affected by altering the configuration of the facial features. This may also have been the case here with F.B. Local information about the shape of the mouth or the tilt of the eyebrows may have been sufficient for emotion categorization.

A rather different approach to examining whether perceptual processing of faces is spared is to examine whether a patient shows covert recognition of faces that cannot be identified overtly. Covert recognition may be taken as indicating that perceptual processing is operating to a level that sustains access to stored knowledge (McNeil & Warrington, 1991). F.B.'s covert recognition of faces was tested in several ways: by presenting faces from the same category together in a face identification task (Sergent & Signoret, 1992); by testing whether name familiarity judgements were affected by prior presentation of a matching or mismatching face; and by testing whether occupation decisions to a name were affected by a simultaneously presented face (identical, related, or unrelated by name; De Haan et al., 1987).

Covert Recognition I (Sergent & Signoret, 1992)

F.B. was presented with sets of six grey-level images of faces made up of people who would have previously been recognized by her (confirmed by her husband). There were six sets where all the people were from the same category (actors belonging to the same TV show, politicians, and members of the UK royal family), along with a similar number where the same faces were presented in unrelated sets. F.B. failed to recognize any of the faces, irrespective of whether they were grouped in related or unrelated sets.

Covert Recognition II (De Haan et al., 1987)

This involved familiarity judgements to names, preceded by famous faces that were either closely related or unrelated to the names. F.B. was tested on two occasions. In each session she received 40 trials, 20 with a familiar name and 20 (fillers) with an unfamiliar name. On all trials, the target words were preceded by a photograph of a famous face. For trials with familiar names, there were 10 occasions where the name was preceded by a highly related face (e.g., Prince Charles–Princess Diana, David Beckham–Victoria Beckham) and 10 where the face was unrelated (Prince Charles–Victoria Beckham). The related items in the first session were used as unrelated items in the second session, and vice versa. The faces were $3 \times 3^\circ$. Each face was presented for 1,000 ms and was followed immediately by the word, which remained until the response was made. All trials were fully randomized. F.B. responded by key press, and there was an intertrial interval of 500 ms following the response. F.B.'s average reaction time to names preceded by related faces was 764 ms, and it was 816 ms to names preceded by unrelated faces. This difference was far from significant ($F < 1.0$). There were no errors to famous names and just one to an unfamiliar name (classified as familiar).

Covert Recognition III (De Haan et al., 1987)
In this study, F.B. was asked to perform a name categorization task: Was this the name of a politician or an actor? A single grey-level image (3 × 3°) of one of four politicians or four actors were presented on a Macintosh computer using SuperLab. An auditory name followed the presentation of each face. There were three conditions: one where the face and name were the same person (Tony Blair–Tony Blair), one where the face and name came from the same category (John Prescott–Tony Blair), and one where they came from different categories (Robert Redford–Tony Blair). Each face was presented four times in each condition within one block, and F.B. was presented with two blocks of trials (192 trials in total). F.B.'s average RT when the face and the name were identical was 917 ms, it was 875 ms when the face and name came from the same category, and it was 943 ms when the stimuli came from different categories. These differences did not approach significance ($F < 1.0$). She made two errors, with identical and related faces.

The data provide no evidence for covert recognition, although covert recognition might be expected if F.B.'s perception of facial identity was spared (McNeil & Warrington, 1991). However, the results are consistent with F.B.'s lesion disrupting processing to such an extent that information about facial identity cannot be accessed even covertly. In sum, the results of these preliminary tests show that F.B. was severely impaired in face recognition (including recognition memory, in the Warrington memory test for faces); she was also poor at matching faces across viewpoint shifts. Processing of facial age, emotion, and gender was relatively good but there was no evidence of covert recognition for faces. The deficits in face matching as well as face recognition, and the lack of covert recognition, suggest a deficit at a perceptual level. In the next section we examine whether the deficit was specific to faces or whether it also affected other categories of items.

Visual object processing

Performance was assessed using three standardized tests:

1. The Birmingham Object Recognition Battery (BORB; Riddoch & Humphreys, 1993). This battery of tests can be used to assess visual processing of objects at a number of different levels: from low-level perception (matching for size, length, etc.), through figure–ground segmentation (the overlapping figures tests), object constancy (the unusual view tests), access to structural descriptions (object decision tests), stored semantic knowledge, and picture naming. F.B.'s data are presented in Table 1. Performance was good, and no impairment was apparent.

2. The Visual Object and Space Processing Battery (VOSP; Warrington & James, 1991). This battery assesses visual processing (a) of pictured objects (at a number of different levels and including tests for figure–ground perception, structural descriptions, object constancy, and picture naming), and (b) space perception (dot counting, position discrimination, number location, and cube counting). F.B.'s data are presented in Table 2. She scored either at ceiling or within the control range on the various subtests.

Table 1. *F.B.'s and control performance on subtests from the BORB*

		N	*F.B.*	*Controls*
Overlapping figures[a]	Letter pairs		1:1.1	1:1.2
	Letter triplets		1:1.1	1:1.1
	Line drawings		1:1.3	1.1.1[b]
Unusual views	Foreshortened	25	24	21.6 (2.6)
	Minimal feature	25	25	23.3 (2.0)
Picture naming		76	75	70.3 (3.2)

Note: Standard deviations in parentheses.
[a] The data are presented as a ratio of the time to name non-overlapping:overlapping stimuli. [b] Range 1:1.3.

Table 2. *F.B.'s and control performance on subtests from the VOSP*

	N	*F.B.*	*Controls*[a]
Shape detection	20	20	19.92 (0.33)
Fragmented letters	20	20	19.30 (0.8)
Picture naming	30	21	23.1 (4.1)
Object decision	20	17	18.6 (1.6)
Progressive silhouettes		10	9.8 (2.4)
Dot counting	10	10	9.9 (0.3)
Position discrimination	20	20	19.7 (0.8)
Number location	10	10	9.4 (1.1)
Cube analysis	10	10	9.3 (1.2)

Note: Standard deviations in parentheses.

[a] Data are reported in Warrington and James (1991).

3. The Pyramids and Palm Trees Test—picture-matching version (Howard & Patterson, 1992). This was used to test visual access to semantics. F.B. was given a two-alternative forced-choice test where she had to select which picture was most closely associated with a target picture (target = pyramid, choice items = palm tree and deciduous tree). F.B. scored close to ceiling (51/52; her husband, S.B., scored 49/52; the test manual indicates that normal controls score 98–99% correct and that no normal subject makes more than three errors).

Overall, F.B. performed at control levels on standardized tests of object and space processing. Her intact ability to match line drawings across different views stands in contrast to her ability to match faces with the same identity across different views.

We also found that the difficulty in naming faces did not extend to other categories of objects. On the McKenna (1997) Category-Specific Names Test F.B. performed at a similar level to her husband (S.B.) and within the reported control range. In this test four categories are presented: animals, fruits and vegetables, artefacts, and tools. There are 30 items in each category and range from commonly known to less familiar exemplars. These data are presented in Table 3.

F.B.'s performance did not differ from that of S.B. for any of the different categories (Fisher's exact *p*-value = .7, .7, 1.0, .7, for fruits and vegetables, animals, tools, and artefacts, respectively).

Table 3. *F.B.'s and control performance on the McKenna Category-Specific Names Test*

	N	*F.B.*	*S.B.*	*Controls*[a]
Fruit and vegetables	30	28	26	20.5 (4.4)
Animals	30	23	25	22.9 (5.3)
Praxic item	30	27	26	23.3 (3.6)
Nonpraxic items	30	26	24	20.7 (3.8)

Note: Standard deviations in parentheses.

[a] The data from 400 controls are reported by McKenna (1997).

We also presented F.B. and S.B. and 5 age-matched controls with our own sets of pictured items. Each picture was printed in colour on an A4 sheet and was presented for naming. The categories were blocked in the test session. The categories were: birds ($N = 20$), flowers ($N = 20$), vegetables ($N = 16$), and fruits ($N = 19$). The data are presented in Table 4.

F.B.'s performance did not differ from that of S.B. for any of these categories of items (Fisher's exact *p*-value = 1.0, .4, 1.0, .3, for birds, flowers, vegetables, and fruit, respectively) nor did it differ from that of the 5 controls (Fisher's exact *p*-value = 1.0, .24, 1.0, 1.0, for birds, flowers, vegetables, and fruit, respectively).

Nothing informative could be gleaned from the errors. Generally F.B. made "don't know" responses. Of the total of 22 errors she made, S.B. also failed 13 of the same items. He also made similar responses.

The data reported in this section clearly demonstrate the specificity of F.B.'s deficit: She showed no problems in processing or identifying objects. This held even when some of the categories tested (birds, flowers) required naming at

Table 4. *F.B.'s and control performance in naming items from visually homogeneous categories*

		% Correct		
	N	*F.B.*	*S.B.*	*Controls*
Birds	20	85.0	90.0	89.0
Flowers	20	90.0	70.0	72.0
Vegetables	16	93.8	100	95.6
Fruit	19	94.7	84.2	94.7

the subordinate rather than the basic level. It could be argued that the colour of our pictured items may have provided nonshape cues that may have been helpful in the identification of the categories assessed. We do not think this is the case, however. For instance, a number of our flower exemplars were yellow (tulips, irises, crocuses, daffodils, water lilies, and sunflowers). F.B. made no errors with these particular items. F.B. also performed virtually at ceiling with the line drawings from BORB where no diagnostic colour was available. These drawings include equal numbers of artefacts and living things, with living things including items from visually homogeneous categories (fruit vegetables, animals, insects). No case of acquired prosopagnosia has yet been reported where other visually homogeneous categories of item have been so extensively tested and where performance has been shown to be in the normal range. Also, although naming times were not explicitly measured in these tests, F.B. named pictures of objects fluently, and there were no indications of any clinical deficit.

EXPERIMENTAL INVESTIGATIONS

Our experimental investigations focused on configural processing and whether we could demonstrate such processing in F.B. Many authors have argued that the critical difference between object and face processing is the greater importance of configural information for the recognition of faces relative to objects (De Gelder & Rouw, 2000a, 2000b; Farah, Klein, & Levinson, 1995). A deficit in processing configural information may therefore be characteristic of a core perceptual problem underlying prosopagnosia in a patient.

EXPERIMENT 1

Takane and Sergent (1983) and also Sergent (1984) asked subjects to match line drawings of faces, which were either identical or differed in the shape of one, two, or three of the facial features (e.g., hair, eyes, jaw; see Figure 1). They found that subjects were faster to detect differences between faces differing in two or three features than could be predicted from their response latencies in the single-feature conditions. Accordingly they argued that matching was not based on the serial comparison of features, but rather that configural information concerning the relations between features was encoded producing faster reaction times than those found for even the most discriminable single features. This proposal was supported by a multidimensional scaling analysis, which produced solutions including dimensions reflecting the relations among features.

Takane and Sergent's (1983) procedure provides one means of assessing the configural processing of faces. It was adopted for use with F.B. here. Her performance was compared with that of 8 age-matched controls (5 males, 3 females, mean age 34.5 years).

Method

Examples of the stimuli are shown in Figure 2. The stimuli were eight line drawings of faces. Across the faces, the hair, the eyes, and the jaw could each take on two values (see Figure 2). Other facial attributes were constant (e.g., nose, mouth, ears). The faces were 4 cm high and 2.5 cm wide, and they appeared in black and white.

There were 7 different types of "different" trials (3 in which faces differed by one feature, 3 where they differed by two features, and 1 where all three features differed). There were 112 trials in total with 56 "same"

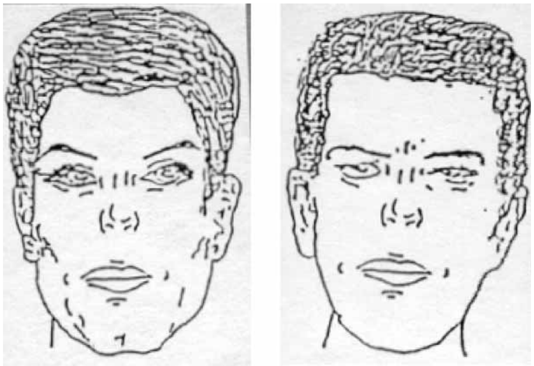

Figure 2. *Stimuli from tests of configural perceptual processing for faces. In this example, the faces differ by all three features.*

trials and 56 "different" trials. Two faces were presented simultaneously on a card, and performance was timed by a stop watch. F.B. was uncomfortable performing this task with computer presentations.

Results

The percentages and number of correct responses and the mean RTs on different trials are given in Figure 3. The mean RTs on same trials were 5.08 and 1.96 s ($SD = 0.62$) for F.B. and the controls, respectively. F.B. performed with a high degree of accuracy making only one error overall (in the single-feature chin change condition). The controls also made few errors (3.2% overall). F.B.'s RT data were analysed by treating each RT as a separate subject (De Haan et al., 1987). There was no advantage for faces differing by three or two features relative to performance when the faces differed by the fastest single feature, $F(2, 29) = 2.34$, $p = .115$ (for a comparison between one-, two-, and three-feature different trials involving the feature hair, treating each RT as a separate subject). There were no differences between the fastest single feature (hair) and comparisons involving the same feature when there were differences in two features: hair versus hair and eyes, $t(14) = 1.58$, $p > .05$; hair versus hair and chin, $t(14) = 0.11$, $p > .05$. There were no differences between the fastest two-feature condition involving the fastest feature (eyes and hair) and the three-feature conditions ($t < 1.0$). For the controls, a comparison was made between performance in the fastest condition with a single-feature difference and the fastest condition where there were two features different (where one of the features involved the fastest single feature). RTs were faster when there were two features different than in the fastest single-feature condition, $t(7) = 3.30$, $p < .025$. Controls were also reliably faster in making "different" judgements when the faces differed in all three features than when faces differed in two features: comparing RTs for the fastest two-feature change faces with RTs when all three features changed, $t(7) = 2.36$, $p < .05$.

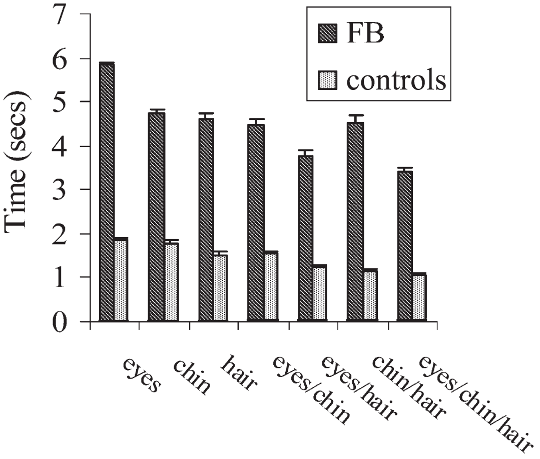

Figure 3. *The mean reaction time (RT) to respond to different faces for F.B. and the controls. The error bars indicate 1* SE *for F.B. and the mean of the 1* SE *values calculated within each participant, for the controls.*

Discussion

The data from Experiment 1 converge with the results from F.B.'s face-matching performance (where she was impaired at matching across views). There were no reliable benefits for F.B. in judging that faces were different when they differed by more features. If F.B. was using configural processing, such a benefit would be expected. Similarly to the control data reported by Takane and Sergent (1983), our controls were faster at responding to faces differing in two features than they were at responding to faces differing by the most salient single feature, and they were faster at discriminating faces differing in three features than faces differing by the most discriminable two features.

EXPERIMENT 2

Here we contrasted the effects of simultaneous matching of "thatcherized" and normal upright and inverted faces. As noted in the Introduction, face recognition is highly sensitive to inversion (Yin, 1969). In normal observers, the face inversion effect has been attributed to impaired configural processing when faces are shown upside down. This may particularly reflect processes that are sensitive to the spatial relations between facial features. Leder, Candrian, Huber, and Bruce (2001) had participants make judgements about interocular distance. They found a strong advantage for upright over inverted faces when the whole face was inverted. However, when the local features were held constant (so the eyes remained upright in the inverted condition) then the advantage for upright faces disappeared. This loss of sensitivity to the relations between local inverted features can be strikingly illustrated by the use of the Thatcher illusion, so called because it was originally demonstrated with Margaret Thatcher's face (Thompson, 1980). The illusion is created by inverting features (the eyes and the mouth) in an upright face. The resulting face is grotesque; however, if the whole face is inverted, the grotesqueness disappears. The disappearance of the bizarre aspects of Margaret Thatcher's face is consistent with the configural distortion between the local feature being reduced when the features are inverted. Boutsen and Humphreys (2003) formally tested this hypothesis by using same/different matching tasks with normal and thatcherized faces that were presented in either upright or inverted orientations. They argued that if normal relational information in faces is disrupted by thatcherizing the features, then the normal advantage for upright relative to inverted faces should disappear for thatcherized faces. Their procedure was as follows: On "same" trials a normal face was paired with itself or a thatcherized face was paired with itself so that the images were identical. On "different" trials, a normal face was paired with a thatcherized face (both in either an upright or an inverted orientation). The results showed that responses to upright faces were faster than those to inverted faces (by nearly 100 ms) and that responses to normal faces were faster than those to thatcherized faces (by nearly 150 ms). Importantly, there was an interaction between face orientation and face type with normal faces showing an inversion effect of nearly 200 ms while there was no reliable effect of inversion for thatcherized faces. Boutsen and Humphreys argued that the failure to demonstrate an inversion effect with the thatcherized faces suggests that the processing of these faces is similar regardless of whether the face is presented in an upright or an inverted orientation, because the presence of the thatcherized features interferes with configural processing in the upright faces. Boutsen and Humphreys also contrasted same/different matching performance with whole faces with performance on a similar task where the face parts appeared in isolation (Boutsen & Humphreys, 2003, Exp. 1). Participants were again slower to make same/different judgements for the thatcherized than for the normal face features. Interestingly, the inversion effect for face parts was no different from the effect with whole faces, consistent with the argument that configural information is determined by feature relations alone and not the global context. Consistent with this, there were minimal differences in overall RTs between whole-face stimuli and face parts.

Boutsen and Humphreys performed the same experiments with a patient with both visual agnosia and prosopagnosia (H.J.A.; Boutsen & Humphreys, 2002). H.J.A. was severely impaired at matching whole faces (he was at chance, scoring 120/240 correct). Performance with face parts was markedly better (209/240 correct). Boutsen and Humphreys (2002) argued that this pattern of performance suggested an inhibitory influence of face context on H.J.A.'s processing of local parts and a relatively intact ability to process part-based information from a face (when there was no interfering effects of context). It is also noteworthy that H.J.A. showed no effects of inversion. In some prosopagnosic patients the processing of inverted faces can even be better than the processing of upright faces (e.g., De Gelder & Rouw, 2000b; Farah, Tanaka, & Drain, 1995), suggesting the possibility that there is a face-specific processor that is maladaptive in prosopagnosia, but which continues to dominate face processing, resulting in poor performance with upright faces. With inverted faces more general visual pattern perception mechanisms can operate.

We assessed F.B. using Boutsen and Humphreys's (2003) stimuli (see Figure 4). Since we have failed to demonstrate configural processing of faces with F.B. (see Experiment 1), we expected that she would not show an inversion

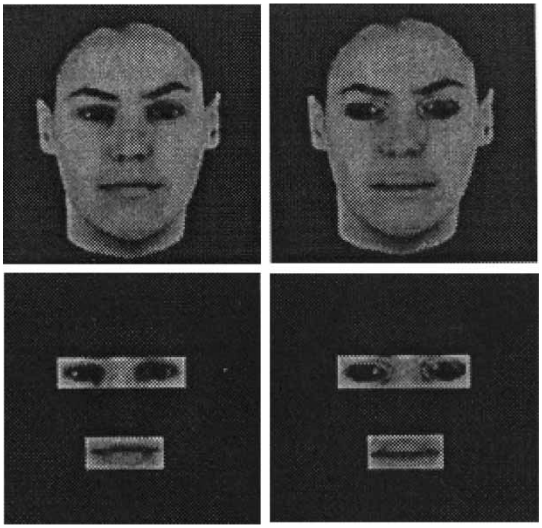

Figure 4. *Example whole and part faces shown in the study requiring discrimination of "thatcherized" faces.*

inferiority effect with normal faces but that she would perform in a similar way to normal subjects with the thatcherized faces.

Method

The method followed that described by Boutsen and Humphreys (2003; Exps. 1 and 3). There were three factors in each experiment: face type (normal/thatcherized), orientation (upright/inverted), and response (same/different). In Experiment 2a whole faces were presented. In Experiment 2b only the critical face parts (eyes and mouth) were visible. Three male and three female faces were shown in each of four conditions: upright normal, upright thatcherized, inverted normal, and inverted thatcherized. Inverted faces were rotated 180° from the upright. Examples of the stimuli are shown in Figure 4. The six faces were used to create a set of 48 face pairs, 24 for each response type (same/different). Each pair was presented five times resulting in a total of 240 trials. The pairs of faces were presented side by side, centred on the screen, and subtended $4.92 \times 10.76^\circ$ on the screen. All pairs were same-person pairs in that faces in a pair (on both same and different trials) depicted the same person. On same trials, a normal face was paired with itself, and a thatcherized face was paired with itself (i.e., the stimuli in same pairings were identical). On different trials, a normal face was paired with a thatcherized face (of the same person) with both faces appearing in the same global orientation. The left–right position of each face was counterbalanced. Half the pairs were the same, and half were different; half depicted upright faces, while the other half were inverted; half were normal, and half were thatcherized. The experiment was run on an IBM-compatible computer. Stimuli were presented on a 15-inch monitor in 800 × 600 graphics mode. Responses were collected by two keys mounted on a box and connected to the parallel port.

Results

F.B.'s RTs for same responses for whole and part faces are shown in Figures 5a and 5b. "Same" responses occurred when faces were both normal or both thatcherized. The pattern on "different" (one face normal, one thatcherized) was similar. RTs for whole upright and inverted faces were 1,888 and 2,193 ms; RTs for part upright and inverted faces were 1,721 and 1,752 ms, respectively. An analysis of variance (ANOVA) on the data for same responses revealed a significant advantage for part over whole faces, $F(1, 225) = 72.1$, $p < .001$. No other effects were reliable. For different trials there were again reliable advantages for part over whole faces, but also now an advantage for upright over inverted stimuli, $F(1, 209) = 40.2$, $p < .001$; $F(1, 209) = 19.7$, $p < .001$. There was an error rate of 10% (see Figures 5c and 5d for the RT data for whole and part faces, respectively). There was an overall advantage in accuracy for part over whole faces, $\chi^2(1) = 18.52$, $p < .001$. No other differences were reliable.

Further analyses were performed to contrast F.B.'s performance with that of the controls for whole and part stimuli. To take any differences in accuracy into account, these analyses used a combined measure of "processing efficiency" (RT/proportion correct; see Townsend &

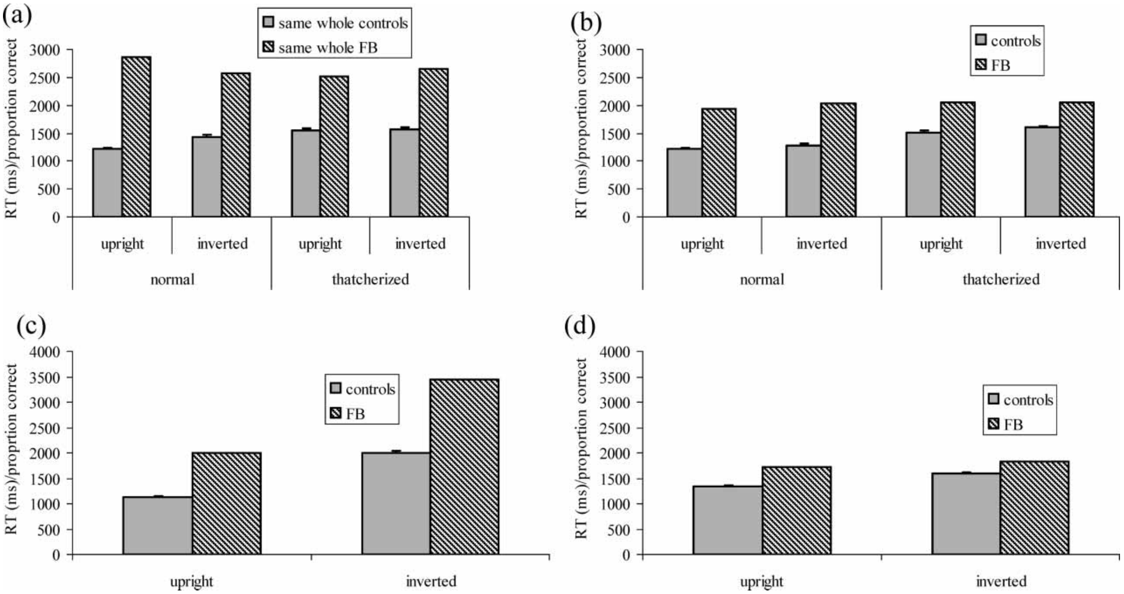

Figure 5. *Performance for F.B. and the controls with normal and thatcherized face wholes and parts (presented upright or inverted). The data are presented as a function of reaction time (RT) divided by proportion correct. Standard error bars for the controls are given. (a) Data for same responses for whole faces. (b) Data for same responses for part faces. (c) Data for different responses for whole faces. (d) Data for different responses for part faces.*

Ashby, 1983). Note that, rather than being interested in absolute differences in performance here, we assess the relative effects of the part–whole variable. We assessed the contrast between processing efficiency with whole and part faces separately using Hulleman and Humphreys's (2007) modified F test for comparing a single case against a group of participants. This test adjusts the confidence levels to take account of differences in variance and to minimize the likelihood of Type I error. F.B. showed a larger difference between her performance with whole and part stimuli for normal faces, both when upright, $F(1, 11) = 5.49$, $p = .037$, and when inverted, $F(1, 11) = 5.08$, (adjusted) $p = .046$, both two-tailed. The contrast between whole and part performance for F.B. relative to the controls did not differ for thatcherized faces ($F < 1.0$ for both upright and inverted stimuli). Compared with the controls, F.B. was worse with wholes than with parts for normal faces. The lack of a reliable difference with thatcherized faces may reflect increased variance with these items, plus a requirement to process them as parts under all conditions.

Discussion

The normal participants described by Boutsen and Humphreys (2003) were as fast to process whole faces as parts, and there was an inversion effect with normal faces (participants were slower to respond to inverted than to upright faces). In contrast to this, F.B. showed a clear impairment when matching whole faces compared to face parts, and she also tended to be slower to respond to upright whole faces than to inverted whole faces. This pattern of performance, with responses to face parts being better than those to whole faces, matches the pattern of data reported by Boutsen and Humphreys (2002) with H.J.A., a patient for whom there are clear grounds for proposing a perceptual locus for his deficit. Given that matching was required here, and the task did not depend on access to stored knowledge about individual faces, the results provide strong evidence for F.B. having a perceptual deficit in face processing, with the extra information provided by whole faces disrupting her performance (cf. De Gelder & Rouw, 2001).

EXPERIMENT 3

Duchaine et al. (Duchaine, Dingle, Butterworth, & Nakayama, 2004; Duchaine & Nakayama, 2006; Duchaine et al., 2006) report the case of a developmental prosopagnosic who performed normally when trained to learn the identities of different "greeble" exemplars (exemplars based on different spatial arrangements of different part elements). However, they did not contrast performance with novel stimuli to that with faces; similar improvements in performance may have been achieved with faces under similar test conditions.

Behrmann, Marotta, Gautier, Tarr, and McKeeff (2005) also successfully trained an acquired prosopagnosic to identify greebles and compared performance with these stimuli with performance on untrained greebles, faces, and objects. As we have indicated earlier, the patient was able to learn greebles, was able to generalize to new exemplars, and showed improvement in identifying common objects. However, the training had a detrimental effect on face recognition. Behrmann et al. (2005) discuss two further cases of acquired prosopagnosia (as yet unpublished, though one case is discussed in Bukach et al., 2006, and the other was originally discussed by Rossion et al., 2003). The two cases showed different effects of training; one failed (despite extensive training) to identify greebles, the other was able to identify the trained greebles, but generalization performance was poor.

In a final experiment we contrasted F.B.'s ability to learn the names to novel multipart stimuli that had similar parts and part relations across the set of items presented. Each stimulus was given an English girl's name. A similar learning task was then run using grey-level images of unfamiliar female faces using the same names as those given to the novel stimuli. We also examined for generalization of learning by manipulating both novel stimuli and face stimuli in a number of different ways.

Method

Novel multipart stimuli

On each trial F.B. and 6 age- and education-matched control participants (3 male) were shown 12 grey-level images of novel multipart stimuli (see Figure 6a). Stimuli were obtained from Michael Tarr's website (http://alpha.cog.brown.edu:8200/stimuli/novel-objects). Each novel stimulus was composed of the same four parts around a common base shape, and the 12 novel stimuli were chosen from a larger family created by changing the relative locations of the local parts, while keeping the part identities constant. There were six members of the set derived by interchanging the locations of two parts from the original "parent" object; four members were derived by interchanging the positions of two of the parts in the parent object, and one member was created by shifting the spatial position of one part (from low on the "body" to a higher location; see Figure 6). Each novel stimulus was 3 × 4 cm. The stimuli were presented one at a time on a table top (they were thus viewed from 30 cm), while an English girl's name was read aloud by the experimenter. Once the experimenter had been through the set, the images were randomized, and each participant was presented with one image at a time and had to name it. This procedure was

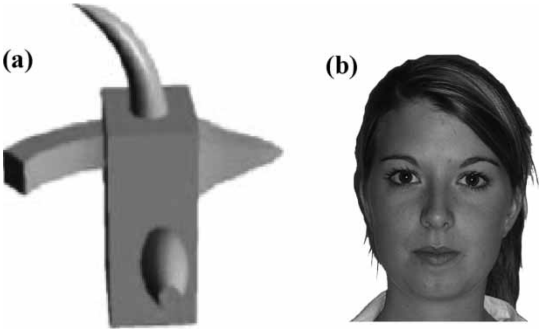

Figure 6. *Examples of a novel stimulus (a) and a face stimulus (b) used in Experiment 3.*

repeated until all the names were correctly assigned to each of the novel stimuli. Learning was then continued for three trials postasymptote for each participant. The novel stimuli were then presented simultaneously on a table. The names of the stimuli were also presented, each written on a separate card. Participants had to place the card with the correct name on the appropriate novel stimulus as quickly as possible (timed by stopwatch).

Face stimuli

A similar procedure to that used for the novel multipart stimuli was followed here but now 12 grey-level images of girls' faces were used (see Figure 6b). The girls were randomly chosen and had different hair colours and styles. Each face was viewed from the front.

Manipulations to novel multipart stimuli

Participants were given sets of the novel stimuli in which exemplars changed their size, depth rotation, or contrast to background, had visual noise or an occluder added, or were inverted (see Figure 7). Image sizes were increased by 150%. Stimuli were rotated around 60° in depth. Contrast was reduced by 50%, and 50% contrast masking noise was added. The occluder was a single solid black bar, positioned so that critical features remained visible.

Manipulations to face stimuli

The manipulations described for the novel multipart stimuli were again performed but now using 12 grey-level images of girls' faces (Figure 8).

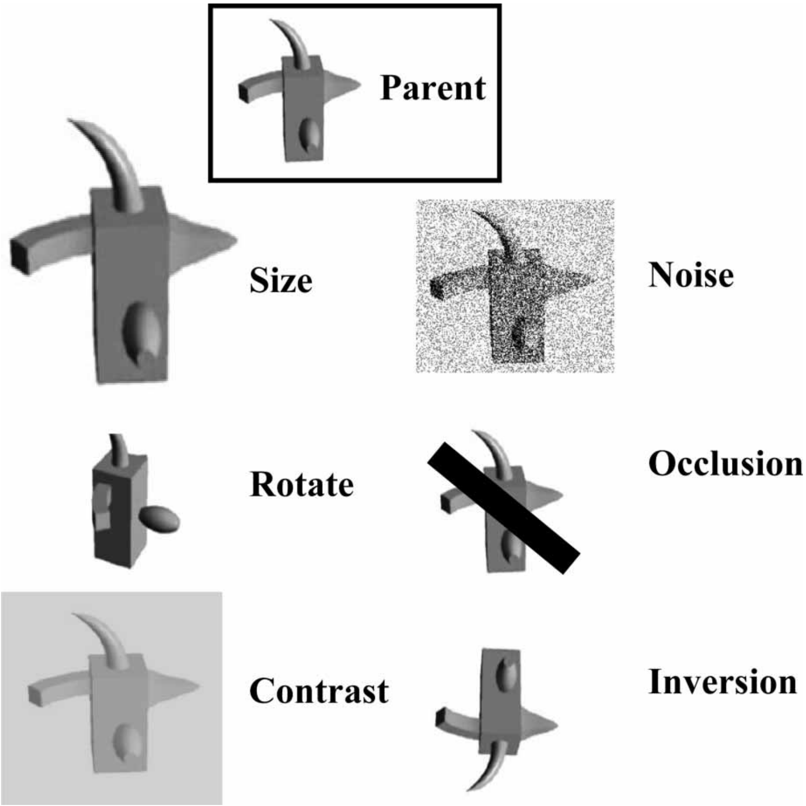

Figure 7. *Examples of the different manipulations of the novel stimuli.*

Results

F.B. was able to perform the task with the novel multipart stimuli without difficulty and achieved asymptotic learning within 5 trials. This was better than the average of the controls, the best of whom only achieved asymptotic learning after 5 trials, and 1 did not achieve asymptote after 10 trials (Figure 9a). In the postlearning test of recognition speed, F.B.'s mean response time per novel stimulus was 750 ms; the mean of the controls was 823 ms (*SD* = 98).

F.B. was slower to reach asymptote in her learning with the faces than were the controls, all of whom attained maximum scores after four learning cycles, whereas F.B. took seven (Figure 9b). Note that the controls were faster to learn the faces than the multipart stimuli ($p < .001$), whereas F.B. was slower. F.B.'s mean response time to place the names on the faces was 1,124 ms, which was more than 3 standard deviations from the mean of the controls ($M = 801$ ms, $SD = 64$).

The results for F.B. and the controls for the manipulations of multipart stimuli and faces are presented in Tables 5a and b (the data are presented as percentage correct, with the standard deviations of the controls included in parentheses). With multipart stimuli, F.B. was as good as the controls at generalizing her responses, suggesting that learning was not based on some local image property. In contrast, with faces, F.B.'s identification levels were more than 3 standard deviations from the controls for all image changes aside from size.

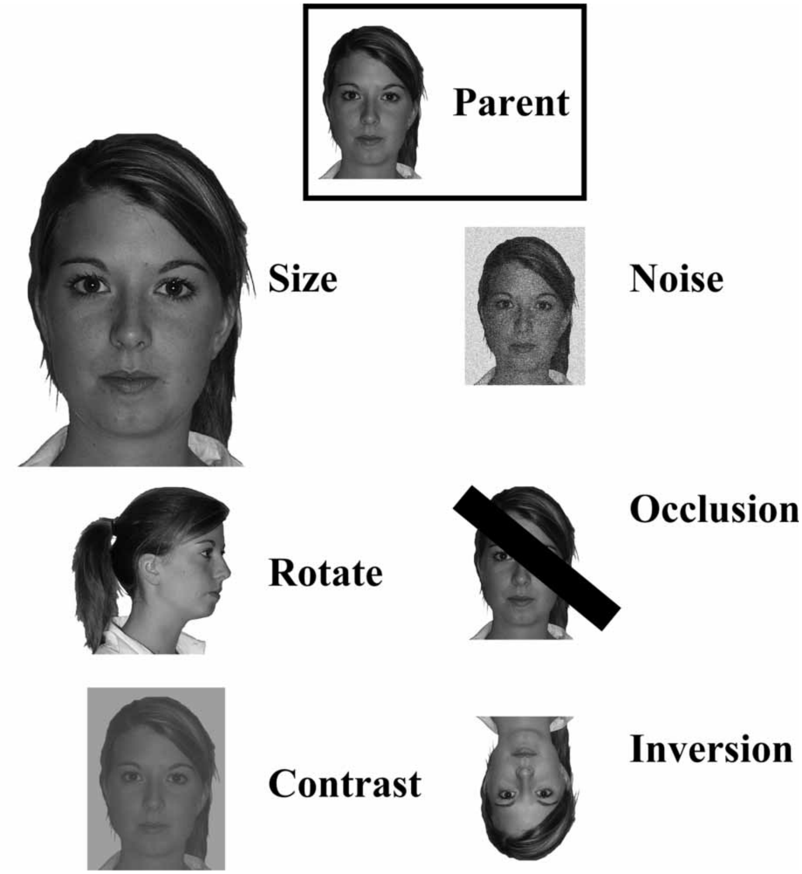

Figure 8. *Examples of the different manipulations of the face stimuli.*

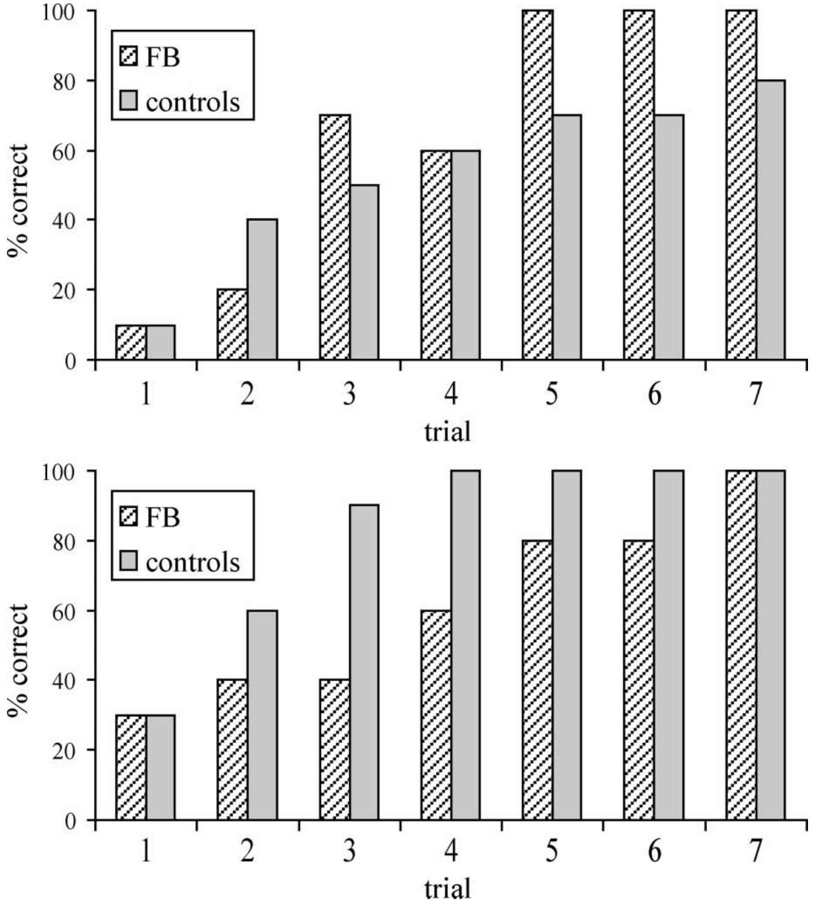

Figure 9. *(a) The percentage of names correctly reported per trial in the novel stimuli learning task. (b) The percentage of names correctly reported in the face learning task.*

Table 5. *F.B.'s and control performance with multipart (5a) and face (5b) stimuli*

		Size	*Rotation*	*Contrast*	*Noise*	*Occlusion*	*Inversion*
(a)	F.B.	100	60	100	100	100	90
	Controls	100 (0)	59 (8)	92 (6)	100 (0)	92 (6)	92 (9)
(b)	F.B.	100	40	60	50	50	40
	Controls	100 (0)	92 (8)	100 (0)	98 (4)	94 (8)	82 (10)

Note: Standard deviations in parentheses.

Discussion

The results were clear. F.B. was able to learn the names for the novel stimuli normally and generalized learning across several image changes. This was despite the fact that the same parts were used across the set of stimuli, with the stimuli differing only in the arrangement of the parts. F.B. continued to perform well with novel objects even when the stimuli were altered by depth rotation, presented with lower contrast, and had either noise or an occluder added. The data contrast with her performance with faces. F.B. tended to be slower to learn the face–name associations than were the control participants, even though these associations could be based on particular image properties. The controls also found it easier to learn face–name associations than to learn associations between names and the multipart objects, whereas the opposite held for F.B. This demonstrates that F.B. was not simply differentially affected by task difficulty but rather showed a selective impairment for face learning. Furthermore, F.B.'s learning of faces did not generalize, with the sole exception of size change. The sensitivity of F.B.'s face–name learning to image change suggests that she was indeed making the associations based on rather superficial aspects of the images. Interestingly, the robustness of F.B.'s face–name learning to size change, and the lack of robustness to changes in view, may be related to changes in the invariant properties of cells in regions of visually responsive cortex. For example, studies using fMRI adaptation techniques have indicated that a region of the lateral occipital complex (LOa/pFs) shows invariant responses to size and position, but not to variations in illumination and viewpoint (Grill-Spector et al., 1999; see Grill-Spector, Kourtzi, & Kanwisher, 2001). Here F.B. was able to adapt her learning to new stimuli differing in size, but not under conditions of contrast or view change. It may be that her responses were based on spared regions of cortex, such as the LOa/pFs, which appeared to be structurally intact (Figure 1).

Our conclusions are that the processes, and neural substrates, used by F.B. to learn subordinate associations between names and multipart objects were not those used (and lesioned) for processing structural properties of faces linked to face identity. The items in our set had common parts, and so a simple strategy of learning an association between a part and a name would not suffice. In addition, the structural information supporting the learning gave rise to good generalization across image changes and so seems unlikely to have been image as well as single-part based. Though we cannot be certain about the information used in her learning, the data indicate that it did not give rise to efficient learning of faces, while the generalization of learning with faces was particularly poor.

It might also be argued that the tests of generalization here, which did not use RTs, were not sufficiently sensitive to demonstrate a deficit for F.B. with the novel stimuli. While this is possible, we noted no signs of F.B. performing differently from controls in terms of her response latencies when the generalization tests were done. We also note that the controls found learning more difficult for the novel stimuli than the face stimuli. If learning and generalization of the faces and the multipart stimuli were based on common processes, which were simply less efficient for F.B., then her learning and generalization should have been worse to the novel stimuli than to the faces. It was not.

GENERAL DISCUSSION

F.B. is markedly impaired at recognizing familiar faces, while, at the same time, she has excellent identification of subordinate object exemplars. There were no signs of covert recognition, and face matching across different views was impaired. This last result suggests a problem in the perceptual processing of faces. This argument is supported by the data from Experiments 1 and 2. In Experiment 1 there was no benefit for faces differing in two or more features relative to faces differing in the most salient single feature (e.g., hair; see Figure 2). If configural processing was present, then we would have expected increasingly fast "different" responses as the number of different features increased—the pattern present in control participants. In Experiment 2, and in contrast to the normal data presented by Boutsen and Humphreys (2003), F.B. was much faster with face parts than with whole faces, whilst there were no effects of "thatcherization", and there were, if anything, beneficial effects of face inversion (Figure 5). The advantage for parts over faces matches with prior data on prosopagnosic patient H.J.A., for whom there is clear evidence of an underlying perceptual impairment (Boutsen & Humphreys, 2002; Riddoch, Humphreys, Gannon, Blott, & Jones, 1999), and suggest that F.B. has difficulty in dealing with all of the perceptual information present in faces, even when required simply to make a perceptual judgement to the stimuli (is the face thatcherized?).

Despite these problems on tasks requiring perceptual judgements to faces, F.B. was able to learn at a normal rate the identities of a set of novel stimuli (all containing the same parts and differing only in the relative locations of those parts). She also identified novel stimuli as fast as did controls, after learning, and she generalized her learning across transformations in image size, view, and quality. These last results suggest that her learning of novel stimuli was not based on some abnormal and time-consuming feature-based strategy. Note also that the novel stimuli had the same parts, which were positioned in different arrangements to create different items, so her learning and identification of these items was not due to labelling of particular parts. In marked contrast to this, F.B.'s learning of faces was poor; she was also slow to identify faces once learned, and face identification was vulnerable to effects of image change even after learning (with face identification decreasing abnormally when the faces were rotated or when noise was added). One prior case of developmental prosopagnosia has shown normal learning of greeble exemplars (Duchaine et al., 2004), though, as we have indicated, this was not contrasted with face learning, and the patient may have been able to learn associations between the name and an image of a face under similarly constrained learning conditions. Our patient, F.B., was an acquired case but she nevertheless learned names at a normal rate for novel stimuli drawn from a visually homogeneous set. Also, postlearning, F.B.'s identification of novel stimuli was faster than the mean of our controls, and she generalized her learning across several image changes.

These results demonstrate that acquired deficits in face processing can be very specific and can leave spared the ability to learn identification responses at a subordinate level with new visual exemplars. The data are consistent with face perception being dependent on cortical regions that operate in a domain-specific manner, tuned to optimize the identification of faces. This argument is supported further by the contrast between F.B.'s case and that of patient C.K., reported by Moscovitch, Winocur, and Behrmann (1997). C.K. was agnosic for visually presented objects and had an apparent perceptual locus to this deficit, being particularly poor when dealing with overlapping figures, for example. However, he showed no signs of prosopagnosia, and, with faces, he was able to perform similar tasks to those he failed on with objects (including discriminating between overlapping line drawings). Thus there is an apparent double dissociation between F.B., who had good object recognition including naming items from homogeneous categories at a subordinate level (birds, flowers) and poor face processing, and C.K., who had good face processing and impaired object recognition (even at a basic level). Also, since there was evidence for a perceptual locus to the deficits in each patient, there are grounds for distinct perceptual processes supporting face and object recognition In F.B. the perceptual processes specialized for faces are impaired, whilst leaving intact perceptual processes that discriminate between, and support the learning of, classes of objects with common parts in different spatial arrangements (birds, flowers, and even novel multipart stimuli).

Finally, we note that F.B. had sustained unilateral right hemisphere damage to regions including the fusiform gyrus, which have been strongly linked to processing in the neuroimaging literature (Kanwisher et al., 1997). It is possible that F.B.'s good object recognition was supported by the spared left hemisphere, perhaps reflecting the bilateral representation of perceptual processes supporting object identification. In contrast, the processes supporting the perception of facial identity seem more strongly lateralized. It is also of interest that F.B. demonstrated relatively spared judgements of facial age, gender, and emotion, despite damage to the right fusiform area. We have noted that F.B.'s judgements about facial emotions might have come about through attention to local detail (see Baudouin & Humphreys, 2006), and the same argument might also be applied to her age and gender judgements. This local processing strategy may compensate for the loss of normal age, gender, and emotion processes subserved by the right fusiform gyrus and associated regions damaged in F.B.

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