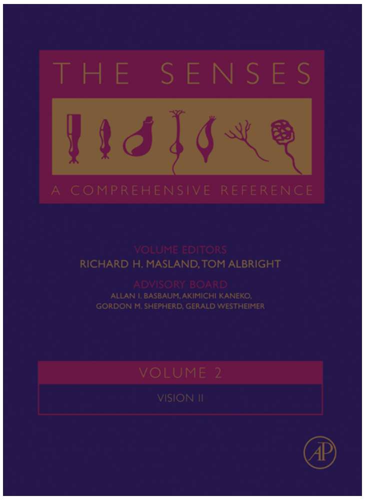

THE SENSES

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B Duchaine and G Yovel, Face Recognition. In: Allan I. Basbaum, Akimichi Kaneko, Gordon M. Shepherd and Gerald Westheimer, editors The Senses: A Comprehensive Reference, Vol 2, Vision II, Thomas D. Albright and Richard Masland. San Diego: Academic Press; 2008. p. 329-358.

2.21 Face Recognition

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The Senses: A Comprehensive Reference, vol. 2, pp. 329-357

Glossary

composite effect Behavioral effect seen when the top half of one face and the bottom half of another are combined. When these halves are aligned while upright, observers appear to fuse the two halves and so find it difficult to perceive the identity of either half. In contrast, performance with inverted composites shows little effect of alignment.

face inversion effects Perception and memory of faces is much more affected by stimulus inversion than other stimulus classes.

face-selective activation In functional magnetic resonance imaging studies, face-selective activations are areas that show a higher response to faces than other stimuli. They are usually defined by comparing the response to faces to the response to objects or places.

fusiform face area (FFA) A region in the fusiform gyrus defined by its greater response to faces than other visual stimuli. It is usually stronger in the right hemisphere than the left.

occipital face area (OFA) A region in the occipital cortex which shows face-selective activation.

other race effect The decrement in performance often seen when observers attempt to recognize faces from other races.

prosopagnosia A condition characterized by severe face recognition deficits. Acquired prosopagnosia occurs due to brain damage whereas developmental prosopagnosia is the result of a developmental failure.

superior temporal sulcus (STS) This sulcus in the temporal lobe contains areas which show face-selective activations.

2.21.1 Introduction

Face processing is one of the most important functions of the human visual system, and it is essential for normal social functioning. Gaze flits from face to face in social situations as we effortlessly assess identity, emotional state, attractiveness, and locus of attention. The use of faces in identification cards and police sketches attest to their primacy for identity recognition, and portraiture and busts are highly valued because viewers feel they gain insight into the personalities of the depicted individuals. Nonhuman animals also show great sensitivity to facial information (Sackett, G. P., 1966; Burghardt, G., 1990; Waitt, C. *et al.*, 2003), and natural selection has had eons to sculpt human face-processing abilities. When face processing is severely impaired due to brain damage or developmental problems, people experience great social difficulties (Duchaine, B. and Nakayama, K., 2006).

Consistent with its importance, face processing has been the focus of extensive research using a wide variety of methods. This work has led to the development of a number of models of face processing (Bruce, V. and Young, A. W., 1986; Burton, A. M. *et al.*, 1999; Haxby, J. V. *et al.*, 2000), with the Bruce and Young model (1986) providing the key cognitive framework for face-processing studies through the last 20 years (see Figure 1). In it, lower-level processes

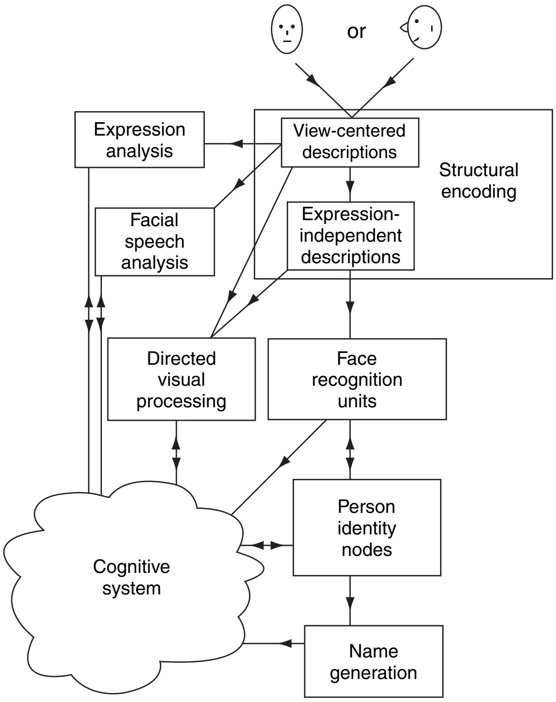

Figure 1 The Bruce and Young model of face processing. Reproduced with permission from the British Journal of Psychology © The British Psychological Society.

represent the facial image and later specialized modules carry out computations on different types of facial information such as identity, emotional expression, and mouth movements associated with speech. In this chapter, we review research investigating the processes involved in the recognition of facial identity, which is the best understood facet of face processing.

We first consider the nature of the perceptual/cognitive processes carrying out face recognition and discuss the special representation that is the basis of face recognition. Next, we review the neural basis of these computations, a research area which has seen an explosion of work in the last decade. We then discuss the neuropsychological impairments affecting these mechanisms and their implications for models of face recognition. We finish with a discussion of the development of face recognition mechanisms.

2.21.2 Cognitive Mechanisms

The idea that upright faces receive special processing has been supported by a number of cognitive experiments that reveal perceptual phenomena that are specific to faces. These studies suggest that faces are processed in a qualitatively different manner than objects or upside-down faces, and it is well accepted that they are represented holistically whereas nonfaces are processed in a more part-based manner. Although the term holistic has been defined differently in different papers (Maurer, D. *et al.*, 2002), it usually implies that faces are represented as one unit in which face parts are processed interactively rather than independently. Below we discuss several of the most robust cognitive effects indicative of holistic processing.

2.21.2.1 Inversion Effects

Aside from neuropsychological cases (see Section 2.21.4), cognitive studies provided the earliest and most convincing evidence that face processing engage specialized mechanisms. The first cognitive evidence came from a simple experimental procedure in which Yin R. (1969) asked subject to learn a set of faces and several sets of nonface objects (i.e., planes, houses, stick figures) to be recognize later. The stimuli were presented either upright or upside-down (inverted) during study and during test (see Figure 2). Although inversion of the stimuli resulted in lower recognition rates for all categories, the cost of inversion was much larger for faces. In fact, recognition rates for upright stimuli were best for faces whereas recognition rates for inverted stimuli were worst for faces. This robust phenomenon is typically referred to as the face inversion effect. It has been replicated numerous times since the original report and has been considered evidence that upright faces engage specialized mechanisms (e.g., Farah, M. J. *et al.*, 1998). Consequently, disproportionate inversion effects are sometimes used as a test to assess whether a given stimulus is processed by face-specific mechanisms or more general object mechanisms (Freire, A. *et al.*, 2000; Yovel, G. and Kanwisher, N., 2004; Duchaine, B. *et al.*, 2006).

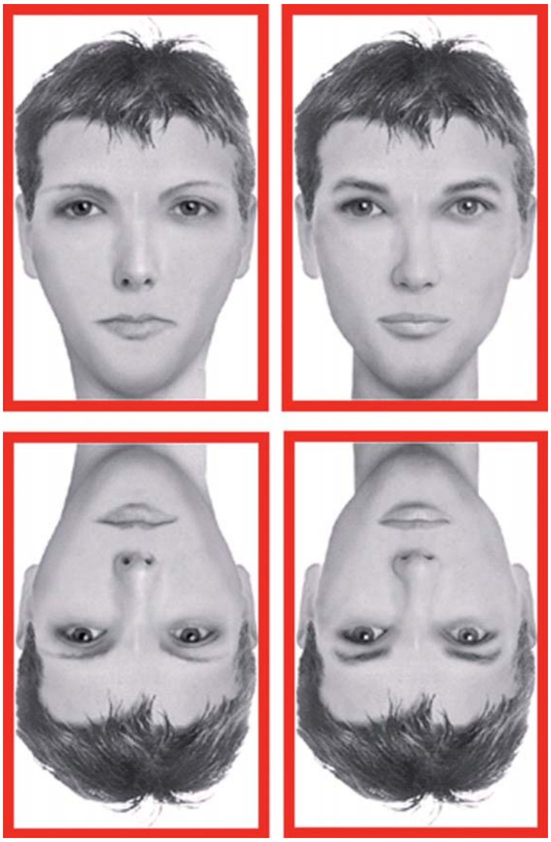

Figure 2 A pair of faces presented upright and inverted. Differences between the faces are much easier to perceive in the upright pair than the inverted pair.

2.21.2.2 Configural Processing

Later studies have tried to characterize the difference between upright and inverted face processing. Yin R. (1969) speculated that the difference involved a representation in which face configural information is better specified. Configural processing has referred to two main phenomena: (1) holistic processing, that is, interactive processing of face parts and (2) sensitivity to spacing information (second-order relations; Maurer, D. *et al.*, 2002).

2.21.2.2.1 Holistic effects

Several paradigms demonstrate that face parts are processed interactively rather than independently.

2.21.2.2.1.(i) Composite effects In a seminal study that revealed holistic processing of upright faces, Young A. W. *et al.* (1987) presented subjects with composite faces created by combining the upper half of one famous face and the lower half of another famous face. The two halves were either aligned to create a coherent facial image or misaligned (see Figure 3). Subjects were asked to name either the upper or the lower half-face and ignore the other part. Response times were much longer for recognition of the one half of the face when it was aligned with the inconsistent half than when the halves were misaligned. Importantly, this effect was found for upright faces only. For inverted faces, subjects showed no difference in recognition time for aligned and misaligned faces. These findings suggest that halves are processed interactively when upright but independently when inverted. The composite face effect has also been demonstrated in perceptual matching tasks with unfamiliar faces in which subjects were asked to match the upper or lower halves of two sequentially presented faces (Hole, G., 1994; Le Grand, R. *et al.*, 2004). Thus, the two halves of the face are processed holistically at early perceptual stages and not only when they are stored for later recognition.

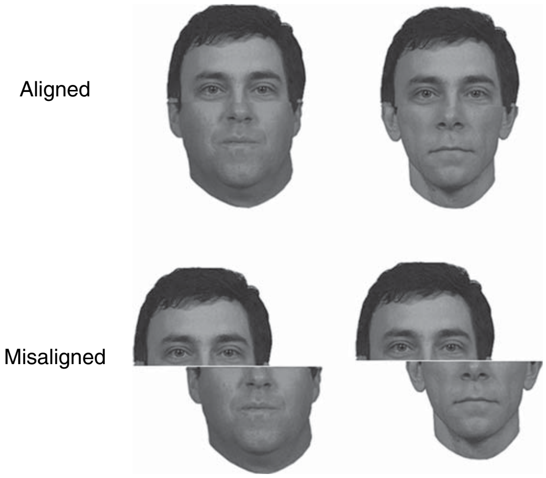

Figure 3 Composite faces created by combining the same top half with two different bottom halves. In tasks with composite faces, subjects find it much more difficult to determine whether the top halves are the same or different when they are aligned with the bottom halves than when they are misaligned. The difference between aligned and misaligned is much weaker or absent when the faces are inverted.

2.21.2.2.1.(ii) Part-whole effects Part-whole paradigms are another method that demonstrates that face parts are processed interactively for upright faces but not inverted faces. Tanaka J. W. and Farah M. J. (1993) presented subjects with a memory task in which subjects were asked to memorize a face and its name. During the test, a face part was presented to subjects either in isolation (part condition) or embedded in the original face (whole condition), and subjects decided whether the face part belonged to a given person (name). Performance was much better in the whole condition than the part condition (the part-whole effect). This effect was observed only for upright but not for inverted faces, upright houses, or inverted houses. In a follow-up study, Tanaka J. W. and Sengco J. A. (1997) showed that the precise location of the other face parts also interacts with recognition of individual parts. In particular, recognition of a face part was better when it was presented in the original face than in an original face in which the location of the other parts was altered. These findings suggest that face perception mechanisms encode both the shape of parts and their specific location (see also Section 2.21.2.2.2).

2.21.2.2.1.(iii) A whole face is more than the sum of its parts The composite face effect and the whole-part effect have examined recognition of face parts (e.g., a half-face, a face part) to determine how they are processed with relation to the rest of the face. Using a different paradigm, Yovel G. *et al.* (2005) estimated the extent to which face parts (i.e., right and left halves) are processed interactively or independently when subjects discriminate complete faces. In a face-matching task, facial stimuli were presented as either right half-faces, left half-faces, or complete faces. If the two halves are processed independently, the sum of accuracies for the right and left half-faces $[p(L)+p(R)-p(L)p(R)]$ will be comparable to the accuracy for complete faces. In contrast, if the two halves are processed interactively, performance with the complete faces will be better than the sum of the performance with the half-faces. Compared to this independence estimation, performance was higher for complete faces, which suggests interactive processing of the two half-faces. Like the composite and the part-whole results, interactive processing of face parts was significantly reduced or absent for inverted faces.

2.21.2.2.2 Spacing effects

The experiments discussed above conceptualized configural processing as interactive processing of different parts or areas of the face. Configural processing has also been regarded as the sensitivity to the exact location of face parts or the spacing among the parts. Recent studies have tried to characterize what type of information is extracted by specialized face mechanisms. Studies of object recognition suggest that object processing is primarily part-based (Biederman, I., 1987; Braustein, M. L. *et al.*, 1989). In contrast, studies with faces have shown that we are very sensitive to minor dislocation of face parts (Haig, N. D., 1984) for upright but not inverted faces (Kemp, R., *et al* 1990). Thus, several studies have postulated that specialized face-processing mechanisms primarily extract information about the spacing among parts but not about the shape of the parts.

To assess this prediction directly, Freire A. *et al.* (2001) conducted a sequential same–different task with upright and inverted faces in which faces differed in one of two ways. On spacing pairs, faces differed only in the spacing among parts but the parts themselves were identical. Conversely, the part pairs consisted of faces in which the parts were different but the spacing of the parts remained the same (see Figure 4). The inversion effect was much larger for faces that differed only in spacing than for faces that differed only in parts. Based on the assumption that the size of the inversion effect reflects the extent to which information is extracted by specialized face-processing mechanisms, the authors concluded that these specialized mechanisms primarily extract information about the spacing but not the shape of parts (see also Leder, H. and Bruce, V., 2000; Le Grand, R. *et al.*, 2001; Mondloch, C. J. *et al.*, 2002).

However, the spacing and part tasks used by Freire A. *et al.* (2001) and Le Grand R. *et al.* (2001) were not matched for performance level (Yovel, G. and Kanwisher, N., 2004; Yovel, G., and Duchaine, B., 2006). In addition, the part manipulation was not limited to changes in the shape of parts, but these parts also differed in contrast and brightness. Thus, the absence of the inversion effect may reflect the operation of low-level visual mechanisms, which are

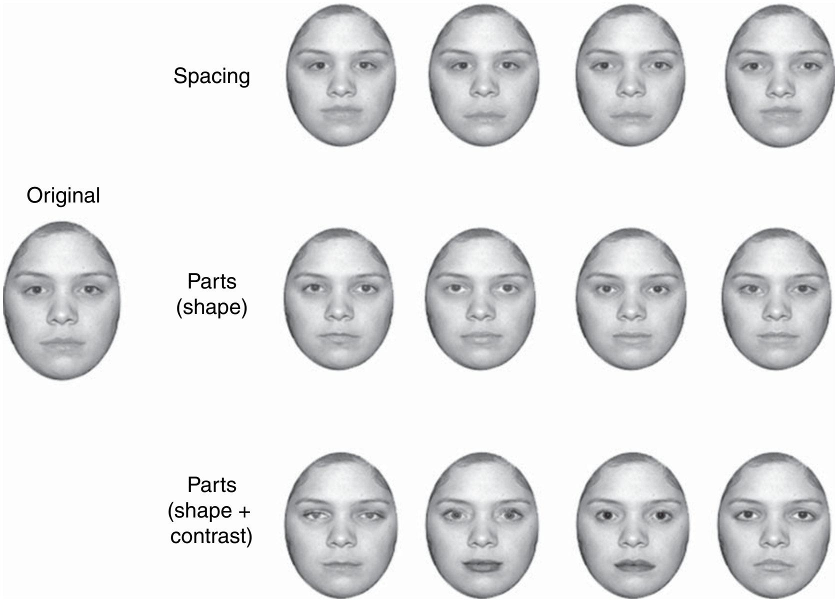

Figure 4 Faces from a same–different discrimination with three types of changes. The faces in the rows were created by modifying the original face on the left. In the spacing faces, the face parts are identical but the location of the eyes and mouth are varied. For the part (shape) faces, the locations of the features are identical but the face parts are different. The part (shape and contrast) faces also hold location constant but face parts differ in both shape and contrast. Rotate the figure to experience the inversion effect for the stimuli, differences are much more difficult to detect in the spacing and part (shape) variants than the part (shape and contrast) variants. Reproduced from Yovel, G., and Duchaine, B. 2006. Specialized face perception mechanisms extract both part and spacing information: evidence from developmental prosopagnosia. J. Cogn. Neurosci. 18, 580–593, with permission.

able to discriminate between the faces regardless of orientation based on color/contrast information. Indeed, several studies which matched performance for the spacing and part discriminations and which varied part shape but not contrast information found similar sized inversion effects for part and spacing discriminations (Riesenhuber, M. *et al.*, 2004; Yovel, G. and Kanwisher, N., 2004; Malcolm, G. *et al.*, 2005; Yovel, G. and Duchaine, B., 2006). Similar stimuli were presented in a fMRI study which examined the response of the face-selective fusiform regions during part and spacing discriminations with upright and inverted faces (Yovel, G. and Kanwisher, N., 2004). Face-selective regions showed a similar response to upright faces regardless of whether the discrimination involved parts or spacing and also showed a weaker response to inverted faces. Other evidence that face-specific mechanisms process parts and spacing comes from developmental prosopagnosia (Yovel, G., and Duchaine, B., 2006). These individuals have severe difficulties with both parts and spacing discriminations in faces despite normal performance on the same discriminations in houses. Furthermore, when face parts differ in contrast information, prosopagnosics were able to discriminate them as well as controls and control subjects showed no inversion effect for such face stimuli (Yovel, G. and Duchaine, B., 2006).

Finally, more direct evidence that spacing and parts are processed by shared rather than independent mechanisms was revealed in a study that employed an individual differences approach, in which the correlation across subjects between performance level for matching faces and house stimuli that differed in spacing or parts (Yovel, G. and Kanwisher, N., 2007). A significant positive correlation between performance for spacing and part discrimination was found only for upright faces. For inverted faces or houses, performance between the two tasks was not correlated. This suggests that face-processing mechanisms are special in that they represent information about spacing and parts, whereas general-object mechanisms processed the two types of information independently.

2.21.2.3 Are Faces Processed by Face-Specific or General-Purpose Configural Processing Mechanisms?

Whereas most researchers agree that faces are processed by holistic/configural mechanisms, the domain of these mechanisms is still debated. This mechanism could operate only on faces (Duchaine, B. *et al.*, 2006, Yovel, G. and Duchaine, B., 2006) or could process a wide variety of object classes (Levine, D. N. and Calvanio, R., 1989; Behrmann, M. *et al.*, 2005). Next we will review three nonface tasks that have been recently used to address this question.

2.21.2.3.1 *The face-house spacing-part task*

As mentioned above, several studies have shown that humans are very sensitive to the exact location of face parts and to the spacing among them (Freire A. *et al.*, 2000; Le Grand, R. *et al.*, 2001). These findings led researchers to suggest that face-processing mechanisms primarily extract spacing but not part based information. As we discussed above, recent studies have shown that both the spacing and the shape of parts are extracted by face-processing mechanisms, however, it is still not clear whether the ability to extract spacing information is limited to faces or is found also for nonface images. To answer this question Yovel G. and Kanwisher N. (2004) created house stimuli that, like the face stimuli, differed in the spacing among windows and doors or the shape of the windows and doors (part-task). These faces and houses were presented in a sequential matching task either upright or inverted. If configural-processing mechanisms are specific to faces, we should observe inversion effect for only faces but not houses. If, however, the mechanisms used with faces are also engaged in the processing of spacing information of non-faces, we should see an inversion effect in the house-spacing task. The results supported the face-specific hypothesis. Whereas faces yielded significant and equal sized inversion effects for both the spacing and the part task, there was no inversion effect for the house stimuli on either discrimination. These findings suggest that the specialized face-processing mechanism are specific to upright faces are not engaged by the processing of spacing information of non-faces.

2.21.2.3.2 *Facelike processing of body stimuli*

As mentioned above, the disproportionately large face inversion effect has been considered the hallmark of face-specific mechanisms. No other objects have produced a face-sized inversion effects until recently. Reed C. L. *et al.* (2003) have reported that human bodies yielded an inversion effect as large as they found with faces. In a perceptual matching task, subjects were presented with upright or inverted pairs of faces and houses that differed in identity and whole bodies that differed in posture. Findings showed similar sized inversion effects for body posture and facial identity discriminations but no inversion effect for houses, though it is important to note that these effects (bodies = 5%; faces = 7%) were smaller than most face inversion effects (see Yovel, G. and Tambini, A., 2007 for a larger face than body inversion effect). In a more recent study, Reed C. L. *et al.* (2006) have examined whether the body inversion effect is specific for whole bodies or is also found for body parts. In one experiment, subjects matched whole bodies and houses or parts of bodies (leg, hand) and houses (window, door). Stimuli were presented either upright or inverted. Findings showed a larger inversion effect for whole bodies than whole houses and no inversion effect for body or house parts. In a second experiment, a comparison between whole bodies and faces to half bodies and half-faces revealed a similar significant inversion effect for all four conditions. These findings imply that, like upright faces, upright bodies are processed with special procedures.

Importantly, however, Reed's findings do not suggest that faces and bodies are mediated by the same configural mechanism. In fact, other studies suggest that they are mediated by distinct mechanisms. Yovel G. and Tambini A. (2007) found a larger inversion effect for faces and bodies and no correlation between performance on a face and body perception tasks (Yovel, G., and Tambini, A., 2007). Furthermore, recent functional magnetic resonance imaging (fMRI) findings revealed no overlap between face-selective and body-selective regions in the fusiform gyrus (Schwarzlose, R. F. *et al.*, 2005). Finally, developmental studies showed very early preference for the processing of upright than inverted faces (as early as the first day of life; Cassia, V. M., *et al.*, 2004), whereas the ability to discriminate between intact and jumbled body stimuli develops only during the second year of life (Slaughter, V. *et al.*, 2002). Thus, even if bodies are processed configurally, it appears likely that they are processed by configural mechanisms that are distinct from face configural mechanisms.

2.21.2.3.3 General expertise

A long-running debate in studies of face recognition concerns whether the putative face-specific effects are actually the hallmarks of expert processing (Diamond, R. and Carey, S., 1986; Tarr, M. J. and Gauthier, I., 2000; McKone, E., *et al.*, 2007). According to the expertise view, faces are processed in a qualitatively distinct manner but so are other object classes with which humans have substantial experience. Expert classes are claimed to be processed configurally, (Diamond, R. and Carey, S., 1986), and this predicts that experts will show the same effects that are seen for faces.

The seminal finding for the expertise view comes from Diamond and Carey's study of dog show judges (Diamond, R. and Carey, S., 1986). These dog experts, but not dog novices, showed face-sized inversion effects for the breed that they specialized in. To study the development of expertise in the laboratory, Gauthier and colleagues created the Greebles, a set of computer-generated objects designed to place similar demands on recognition mechanisms as faces. In training sessions, subjects learn individual Greeble names, their sex, or their family membership and are then tested on their recognition. A typical training regimen consists of eight sessions. Gauthier and colleagues have argued that Greeble training leads to behavioral results revealing configural/holistic effects (Gauthier, I. and Tarr, M. J., 1997; Gauthier, I. *et al.*, 1998; Gauthier, I. and Tarr, M. J., 2002) as well as neural effects similar to those seen in response to faces (Gauthier, I. *et al.*, 2000; Tarr, M. J. and Gauthier, I., 2000; Rossion, B. *et al.*, 2002).

New studies and close scrutiny of the evidence however reveals that the support for the expertise view of face recognition is weak (McKone, E. and Kanwisher, N., 2005; McKone, E., *et al.*, 2007). First, no findings with real world experts similar to the Diamond R. and Carey A. (1986) have been made in the intervening 20 years, and a recent study found that dog expertise did not show a larger inversion effect, part-whole effect, or composite effect than dog novices (Robbins, R. and McKone, E., 2007; for discussion, see McKone, E. and Robbins, R., 2007 and Gauthier, I. and Bukach, C., 2007). Despite many claims about Greeble effects, facelike effects do not emerge after Greeble training (Gauthier, I. and Tarr, M. J., 1997; Gauthier, I. *et al.*, 1998; Gauthier, I. and Tarr, M. J., 2002) and there has not even been a clear demonstration that Greeble training improves recognition of new Greebles (Gauthier, I. and Tarr, M. J., 1997). Recent fMRI work has found that expertise with objects increases responses in object-selective areas, not face-selective areas (Moore, C. D. *et al.*, 2006; Op de Beeck, H. *et al.*, 2006; Yue, X., *et al.*, 2006).

2.21.2.4 The Other Race Effect

The other race effect is a well-established, robust phenomenon in which individuals show better recognition for faces of their own race than faces of other races (e.g., Caucasian individuals recognize Caucasian faces better than Asian or black faces). As expected, it is not the race of the individual per se that determines the level of recognition of own and other race faces, but the type of faces that an individual has been exposed to throughout his life. For example, it has been shown that Caucasian individuals who frequently watch basketball games, which are dominated by black players, show good recognition of black faces (Li, J. C., *et al.*, unpublished). Interestingly, a study by MacLin O. H. and Malpass R. S. (2003) has shown that a racially ambiguous face will show another race effect when combined with other race hair but not when it is combined with own-race hair style. These findings suggest that when a face is categorized as another race face (based on non-facial features like hair), its facial features are not represented as well as when it is categorized as an own-race face. However, as discussed below, categorization is not the only factor that determines the way other race faces are represented.

Several studies have examined whether the poor recognition of other race faces may be associated with an absence of holistic processing for such faces. Earlier studies that examined the inversion effect for other-race relative to own-race faces have reported mixed results. Whereas some reported smaller inversion effect to other than own-race faces (Rhodes, G. *et al.*, 1989), other studies did not reveal similar findings (Valentine, T. and Bruce, V., 1986). One problem with studies that reported smaller inversion effect for other race faces is that they did not match performance level for the upright condition so the smaller inversion effect to other race faces may reflect scaling effect.

Studies that employed more direct measures of holistic processing, such as the abovementioned part-whole effect (Tanaka, J. W. *et al.*, 2004) or the composite face effect (Michel, C. *et al.*, 2006) revealed larger holistic effects for own than other race faces. Thus, the extensive exposure to own-race faces appears to be important for generating a holistic representation. It remains to be determined whether it is elevated holistic processing that allows better recognition of own-race faces or whether holistic representation and recognition abilities are two independent outcomes of extensive exposure.

The other race effect is typically attributed to perceptual mechanisms tuned to better represent same race faces than other race faces due to differential exposure. However, increased contact with other race faces has often failed to lessen the other race effect (reviewed in Levin, D., 2000). Levin D. (2000) suggests that other race effects are caused by selection of different facial features in same and other race faces. He proposes that individuating information is selected in same race faces whereas race specifying information is emphasized in representations of other race faces at the expense of individuating information. Consistent with this hypothesis and inconsistent with a simple perceptual tuning account, Levin D. (2000) found that subjects who showed the other race effect were better able to discriminate face race (e.g., which face is blacker?) than subjects who did not show the other race effect. Hence, for this task subjects with another race deficit better represented faces from other races than subjects who did not show an other face deficit. Levin argues that the differential selection is determined by higher-level cognitions such as whether an individual is concerned with the identity of a person or their race. This account is supported by recent findings showing that the other race deficit is eliminated by a positive mood induction (Johnson, K. J. and Fredrickson, B. L., 2005) and the effect of hair on faces with ambiguous race (MacLin, O. H. and Malpass, R. S., 2003).

2.21.3 Neural Basis of Face Recognition

Neurophysiological studies have reported ample evidence for specialized neural mechanism for faces. A robust face-selective response (a much higher response to faces than non-faces) has been reported with all relevant neurophysiological methods, including single-cell recordings, event-related potential (ERP), magnetencephalography (MEG), positron emission tomography (PET), and fMRI. Thus, the neural networks for face processing have been investigated with both high temporal resolution, which reveal face-selective neural response about 170–200 ms after stimulus onset, and with high-spatial resolution, which reveal face-selective regions in the occipitotemporal regions.

2.21.3.1 Single-Cell Recording

Single-cell recordings by Gross and colleagues and later in other laboratories during the 1970s and 1980s revealed cells in the superior temporal sulcus (STS) and inferior temporal cortex that showed highly specific responses to faces (Gross, C. G., *et al.*, 1972; for review see Gross, C. G., 2005). Examination of the response properties of these face cells has revealed a variety of response properties. The response of some cells was invariant to the size and position of the face image (Perrett, D. I. *et al.*, 1982). Others were view-selective with different cells responding to different views (e.g., Perrett, D. I. *et al.*, 1985; 1992), whereas others responded to all views (Desimone, R. *et al.*, 1984). Manipulations of the intactness of the face image, such as covering or scrambling face parts weakened the response of some of the cells, which responded vigorously only to intact faces (Perrett, D. I. *et al.*, 1982; Desimone, R. *et al.*, 1984). Head rotation and face inversion resulted in increased latencies of some of the cells (Perrett, D. I. *et al.*, 1998). Recent fMRI studies with monkeys, which will be discussed later, revealed activations that are consistent with this early single-cell recording work. Furthermore, studies with humans have also reported neural responses that are highly selective to faces as detailed below.

2.21.3.2 Event-Related Potentials

During the mid- and late 1990s, electrophysiological studies with humans revealed a robust and reliable selective response to faces. In particular, ERP studies measure a scalp electrical response that is time-locked to a given stimulus. ERP studies that presented subjects with various images such as faces, objects, or animals revealed a negative bilateral component that peaked 170 ms after stimulus onset (N170) at occipital-temporal electrodes that was much larger to faces than non-face images and larger over the right than the left temporal electrodes (Eimer, M., 1998; Bentin, S. *et al.*, 1996; see Figure 5). Further studies have shown that the N170 is influenced by variations in the intactness of the face image. Scrambling, contrast reversal, and orientation inversion elicit an N170 of slightly larger amplitude and a small but significant delay (George, N. *et al.*, 1996). Furthermore, the N170 shows a much larger response to presentation of eyes only (Bentin, S. *et al.*, 1996), which led some researchers to suggest that it is generated by the STS, which is sensitive to social aspects of facial information such as gaze (Hoffman, E. A. and Haxby, J. V., 2000; Hooker, C. I. *et al.*, 2003).

The question of whether the N170 encodes only the structure of the face image or also face identity information is still debated. Earlier studies found no difference between the response to familiar and unfamiliar faces and concluded that the N170 is not sensitive to face identity (Bentin, S. and Deouell, L. Y., 2000). However, studies that examined repetition effects (i.e., different response to second presentation of the same stimulus) to repeated presentation of unfamiliar faces reported mixed results. Whereas some studies found lower amplitude for repeated

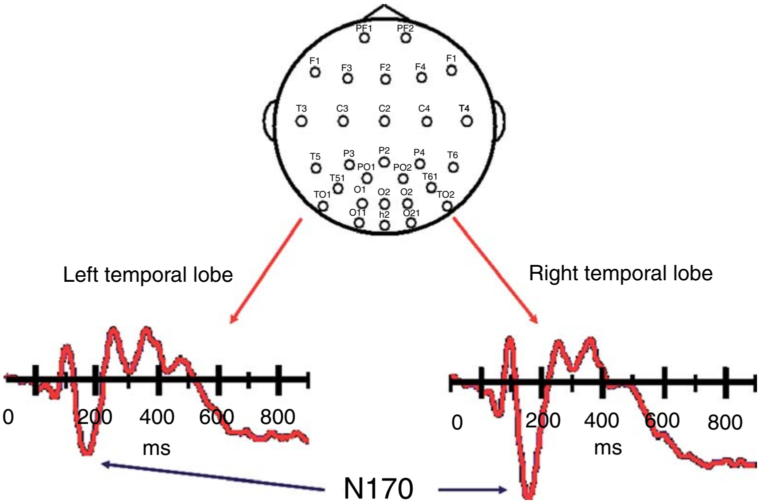

Figure 5 Schematic showing the sensors producing the largest N170 in event-related potential studies. The N170 to faces is much larger than that seen in response to other categories, and as in the figure, it is right lateralized.

presentation of the same individual face (Campanella, S. *et al.*, 2000; Itier, R. J., and Taylor, M. J., 2004a; Jacques, C., and Rossion, B., 2004), others reported no modulation by repetition (e.g., Yovel, G. *et al.*, 2003). The discrepancy between findings may be due to differences in the lag between repetitions and the number of repeated presentation. Thus, these studies suggest that, at least under some conditions (familiarization (Campanella, S. *et al.*, 2000), several repetitions (Itier, R. J., and Taylor, M. J., 2004a), or short delays (Jacques, C., and Rossion, B., 2004)), the N170 is sensitive to face identity information.

Another face-selective ERP component, the vertex positive potential (VPP), is observed at the same latency as the N170 but is maximal at a central electrode (Jeffreys, D. A., and Tukmachi, E. S., 1992). Like the N170, the VPP is delayed by face inversion or contrast inversion but it is not affected by familiarity and some studies have tried to assess the extent to which the VPP reflects the same neural source as the N170. In a recent systematic investigation, Joyce C. and Rossion B. (2005) have examined the effect of the location of the reference electrode and experimental manipulations on the VPP and N170 and found that the manipulated factors had similar effects on both components. Taking together with results of source localization, they concluded that the VPP and N170 are generated by the same source.

2.21.3.3 Magnetoencephalography Studies

MEG studies, which measure the magnetic fields produced by electrical activity in the brain, have revealed a similar face-selective negative component that also appears 170 ms after stimulus onset at lateral posterior electrodes. In addition, Liu J. *et al.* (2002) reported an earlier face-selective component that appeared 100 ms after stimulus onset (M100). Similar to the N170, the M100 and the M170 are delayed for orientation-inverted faces (Liu, J. *et al.*, 2000) and contrast-inverted faces (Itier, R. J. *et al.*, 2006); however, in contrast to the N170 these have no effect on amplitude. Another difference between the ERP and the MEG face-selective components is that the amplitude of the M170 is similar over the two hemispheres, whereas the N170 is larger over the right hemisphere (Bentin, S. *et al.*, 1996; Henson, R. N. *et al.*, 2002; Yovel, G. *et al.*, 2003).

In an elegant study, Liu J. *et al.* (2002) examined the role of the M100 and M170 in face categorization (discrimination between a face and a house) and face identification (discrimination between two faces). In a behavioral study, the authors determined the level of noise that allows categorization and the level that allows recognition for each subject. These at-threshold stimuli were presented to the subjects during MEG recordings and the evoked responses were classified based on subjects' success or failure in a face/house categorization and in their ability to recognize particular faces and houses. Results clearly showed that the M100 was sensitive to success in face categorization but not face identification. The M170 was sensitive to success in face categorization and identification. These components were not sensitive to performance for house stimuli or for stimuli for which subjects had expertise (Xu, Y. *et al.*, 2005). Finally, a recent study that examined category repetition effects for faces and houses (i.e., reduced amplitude for a second presentation of the same category) revealed that the M170 shows repetition effects (lower response for repetition of face–face than face–house) only when the delay between the first and second presentation is shorter than 400 ms (Harris, A. and Nakayama, K., 2007). These findings suggest that the M170 is generated by very early stages of face processing in which the facial image is not maintained for long durations.

In summary, although the N170 and M170 share some similar features in their response to faces, differences exist. It is unclear whether these reflect differences between electrical and magnetic responses from the same source or different sources (Itier, R. J. *et al.*, 2006).

2.21.3.4 Intracranial Recording of Neural Responses

Studies with epileptic patients enable intracranial recording of electrophysiological responses in humans. Such recording, which provides both high temporal and spatial resolution of the neural response, has been applied with face stimuli both with macroelectrodes which allow recording of evoked responses over the cortex and microelectrodes which allow recording of single cells. In an extensive investigation of intracranial ERPs of 98 epileptic patients, McCarthy G. *et al.* (1999) found a face-selective negative ERP component that appeared 200 ms after stimulus onset (N200). The face-selective component was maximal over certain patches in the ventral occipitotemporal cortex. Consistent with the N170 laterality, such patches were larger over the right than left hemisphere.

Investigation of the properties of this component showed invariance to size, color, and blurring. The response was largest for full faces and weaker for isolated face parts (eyes, nose, mouth), which evoked strong responses in other nearby locations. Similar to single-cell recordings, face rotation altered the amplitude of the N200, which was lowest for profile views (McCarthy, G. *et al.*, 1999). Like the N170, the N200 was not sensitive to face familiarity or to semantic priming and was therefore considered a neural correlates of initial structural encoding of face information prior to extraction of identity information (Puce, A. *et al.*, 1999).

In another study, single-cell recordings in epileptic patients conducted in the medial temporal lobe revealed neurons that responded selectively to images of faces, scenes, or objects (Kreiman, G. *et al.*, 2000). Further investigation of these cells (Quigora *et al.*, 2005) revealed that some of these cells respond selectively to certain individual familiar faces (e.g., Jennifer Aniston, Halle Barry) or familiar locations (Sydney Opera House). Furthermore, these cells are remarkably invariant to radical image variations (e.g., rotation, lighting, coloring) and in some cases were activated by letter strings of the name of the individual face/place. These findings suggest that some of these cells, which are anterior to the location of the N200 or the N170, are not purely visual but represent some abstract concept of individuals.

2.21.3.5 Functional Magnetic Resonance Imaging Studies of Face Recognition

2.21.3.5.1 *Face-selective functional magnetic resonance imaging regions*

Selective activation to faces in temporal occipital regions was first reported in PET studies. Sergent J. (1991) reported right lateralized fusiform activation to faces relative to scrambled faces. However, the first systematic investigations of brain regions that selectively respond to faces were fMRI studies by Kanwisher N. *et al.* (1997) and McCarthy G. *et al.* (1997). These studies revealed regions that elicited a much higher fMRI response to faces than non-face stimuli in the fusiform gyrus (see Figure 6). Kanwisher N. and colleagues (1997) referred to these face-selective regions as the fusiform face area (FFA). The FFA was larger over the right than the left hemisphere and showed a very selective response to any stimulus that contained facial information, including upright Mooney faces, animal faces, cartoon faces, and inverted faces (Tong, F. *et al.*, 2000), but not to any objects or other body parts such as hands and feet (see also Schwarzlose, R. F. *et al.*, 2005). The FFA also showed selective response to imagery of faces (O'Craven and Kanwisher., 2000; Cox, D., *et al.*, 2004) and during periods when subjects perceive a face rather than a non-face when binocular rivalry is created by presenting different stimuli to each eye (Tong, F. *et al.*, 1998).

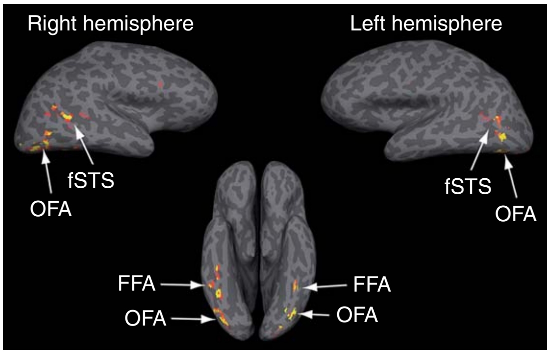

Figure 6 Inflated brain showing three face-selective areas: fusiform face area (FFA), occipital face area (OFA), and the face selective area in the posterior part of the superior temporal sulcus (fSTS).

2.21.3.5.2 *The nature of the face representation in face-selective regions*

Several studies suggest that the FFA contributes to face identification. Grill-Spector K. *et al.* (2004) reported that the FFA response is modulated by successful recognition of familiar faces. Yovel G. and Kanwisher N. (2005) employed an event-related fMR-adaptation design in which the response to different stimuli is compared to the response of identical stimuli. A higher response to different than same pairs suggests that a given region is sensitive to the difference between the stimuli (for review see Grill-Spector, K. *et al.*, 2006). Findings show fMR-adaptation effect for unfamiliar upright faces in the FFA, but importantly non-face-selective regions, such as the object general lateral occipital complex (LOC), showed no fMR-adaptation for faces (see Figure 7).

As reviewed in Section 1, cognitive studies have demonstrated that faces are processed holistically. Do face-selective regions generate this holistic representation? Several early studies compared the response to upright and inverted faces in FFA and found a similar response to both. More recent studies however that measured fMR adaptation revealed that the

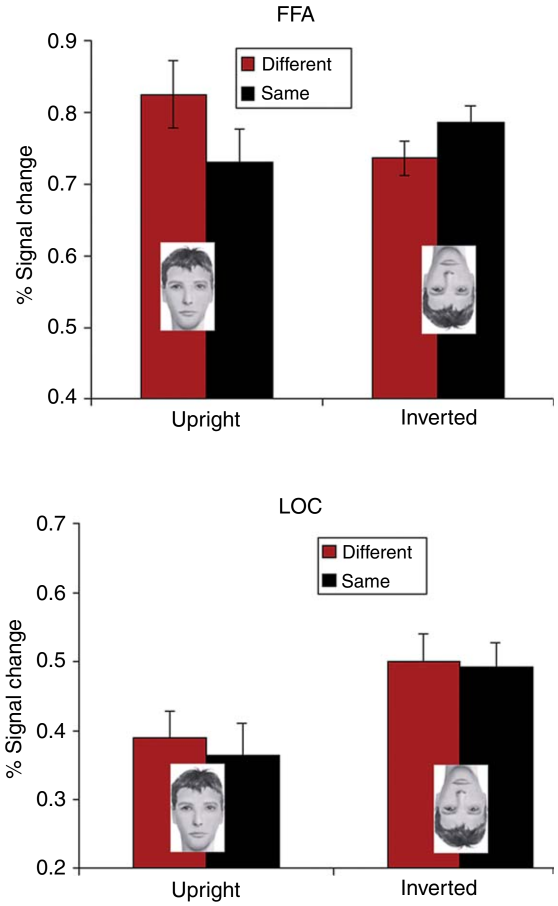

Figure 7 fMRI adaptation to same and different pairs of faces in the fusiform face area (FFA) and lateral occipital complex (LOC). FFA shows greater activation in response to different upright face pairs than same pairs. This adaptation is specific to upright faces in FFA in that LOC does not show adaptation to upright faces and neither FFA nor LOC show adaptation to inverted faces.

FFA showed a larger adaptation effect to upright than inverted faces (Yovel, G. and Kanwisher, N., 2005; Mazzard *et al.*, 2006; Schiltz, C. and Rossion, B., 2006), which is consistent with the behavioral phenomenon of better discrimination of upright than inverted faces. Interestingly, the general object region (LOC) showed an opposite effect of larger response to inverted than upright faces and no fMR adaptation to identity of upright or inverted faces (see Figure 7). These findings highlight the specialized representation for faces in face-selective mechanisms.

However, as mentioned above, the magnitude of the face inversion effect is not a direct measure of holistic processing. To directly assess the extent to which faces are represented holistically, paradigms such as the composite face task (Young, A. W. *et al.*, 1987) have been employed during fMRI experiments. Schiltz C. and Rossion B. (2006) found larger adaptation effect for aligned than misaligned faces, which is consistent with the behavioral composite effect in which identical half-faces are perceived as different faces when they are aligned to different faces than when they are misaligned.

2.21.3.5.3 Two other face-selective regions: occipital face area and superior temporal sulcus

In addition to the FFA, two other face-selective regions are commonly found in most fMRI studies: a region in the posterior STS and a lateral occipital region known as the occipital face area (OFA; see Figure 5). Several studies have shown clear dissociations between the role of the STS and FFA in face processing. The first study reporting such a dissociation revealed greater FFA activation when subjects attend to identity information than to gaze information and the opposite effect in the STS (Hoffman, E. A. and Haxby, J. V., 2000). These and other studies have led to the suggestion that the STS extracts dynamic aspects of face information such as emotion or gaze direction whereas the FFA represents nondynamic face information such as identity and sex (Haxby, J. V. *et al.*, 2000). Consistent with this finding, Grill-Spector K. *et al.* (2004) did not find modulation by successful face recognition in the STS, and Yovel G. and Kanwisher N. (2005) revealed similar response to same and different pairs of faces in the STS (no fMR adaptation). Furthermore, although both the FFA and the STS show lower response to inverted than upright faces, only the FFA inversion effect is correlated across subjects with the behavioral inversion effect as measured in a face identity discrimination task (Yovel, G. and Kanwisher, N., 2005).

The role of the OFA in face processing is less clear. For example, Rotshtein P., *et al.* (2005) presented subjects with pairs of different morphed famous faces that were either perceived as the same identity or were perceived as different identities. The FFA showed fMR adaptation for different morphs that were perceived as the same identity but not to different morphed faces that were perceived as different identities, which is consistent with its sensitivity to identity information. In contrast, the OFA appeared to be sensitive to physical differences, because it showed no adaptation to different morphed stimuli regardless of whether they were perceived as the same identity or different identities. Yovel G. and Kanwisher N. (2005) also found dissociation between the OFA and FFA in a study that examined the role of face-selective regions in the behavioral face inversion effect. Whereas the FFA showed a higher response to upright than inverted faces and a correlation with the behavioral face inversion effect, the OFA showed a similar response to upright and inverted faces and no correlation with the behavioral inversion effect. These findings suggest that the OFA is primarily sensitive to physical information in the face image rather than its specific identity. In summary, the three face-selective regions seem to play different roles in the processing of the complex, rich information in the facial image.

2.21.3.6 Combined Functional Magnetic Resonance Imaging and Electrophysiological Studies of Faces

How face selective are regions showing a face-selective response in fMRI? This question has been impressively investigated by a recent study that combined fMRI and single-cell recording in monkeys (Tsao, D. Y. and Freiwald, W. A. 2006). Three face-selective patches are present in monkeys, and recordings from single cells were carried out in the middle face patch while the monkeys viewed face and various non-face stimuli. Of the nearly 200 visually responsive cells sampled, 97% showed a much higher response to faces than objects and the response to most objects was not significantly different from baseline. Of the non-face objects to which the cells responded, most had shapes similar to faces. These findings suggest that the face-selective response in face-selective areas human reflect the response of areas committed to face processing. The properties of the cells in the middle face patch were similar to the properties of face cells that were reported 20–30 years earlier without the guidance of fMRI (see Section 2.21.3.1 above). These unguided recordings usually found that about 20% of visually responsive cells were face selective, which suggested a seemingly sparse face-selective response. The new results demonstrate that face-selective cells are densely packed and reveal the great promise of studies combining fMRI with single-cell recording.

The relationship between the fMRI and electrophysiological responses to faces has also been assessed in humans in the few studies that collected data with both electroencephalography (EEG) and fMRI in different sessions under similar experimental procedures. Henson R. N. *et al.* (2002) examined the effect of familiarity and repetition with ERP and fMRI. The ERP and fMRI studies were conducted in different sessions on different groups of subjects. By examining the modulation of the N170 and fMRI measures to repetition and familiarity, the Henson R. N. and colleagues attempted to assess whether the N170 originates in the fusiform or the STS face regions. Because the N170 and the STS showed similar right hemisphere laterality and no effect of face familiarity and face repetition, the authors concluded that the N170 is associated with the face activity in the posterior STS. However, Horovitz S. G. *et al.* (2004) examined the effect of different levels of noise in a face on the pattern of response of the N170 and fMRI response to faces. Their results show a similar pattern of modulation of the stimulus on the N170 and the FFA. Recently, Iidaka T. *et al.* (2006) recorded ERP and fMRI using the same paradigm in separate sessions but revealed very weak correlations between the ERP and the fMRI response to faces. So far there have been no studies that recorded ERP and fMRI simultaneously. Hopefully such future studies will shed light on the relationship between temporal (ERP) and spatial (fMRI) aspects of the neural and response to faces.

2.21.4 Neuropsychological Deficits of Face Recognition

Deficits involving face recognition are some of the most dramatic conditions in neuropsychology and have provided powerful evidence that face recognition involves face-specific mechanisms. A variety of face recognition deficits have been documented, but we will focus our review on prosopagnosia, the most thoroughly researched and commonly reported deficit of face recognition.

Prosopagnosia is characterized by severe face recognition deficits which are not due to problems with lower-level visual problems or higher-level semantic problems. Prosopagnosics are usually able to perceive that they are viewing a face and the features that make them up, but they have great difficulties identifying individual faces (Blanc-Garin, J., 1984; Humphreys, G. W. and Riddoch, M. J., 1987; Ellis, H. D. and Florence, M., 1990). The description of one of Bodamer's patients nicely illustrates the experience of many prosopagnosics:

> S is told to look at his own face in a mirror. At first he mistakes it for a picture but corrects himself. He stared for a long time as if a totally strange object is before him, then reports that he sees a face and describes its individual features. He knows it is his own face but does not recognize it as his own. It could be that of another person, even a woman. (Ellis, H. D. and Florence, M., 1990, p. 86).

This patient not only had deficits with facial identity recognition, but was also unable to discriminate gender from the face and other observations demonstrated that he was unable to recognize facial expressions of emotion (Ellis, H. D. and Florence, M., 1990). General deficits with face processing including expression, gender and identity are not uncommon in prosopagnosia (Bornstein, B., 1963; Ellis, H. D. and Florence, M., 1990; Duchaine, B. *et al.*, 2006), but dissociations between the processing of facial identity and other face-processing abilities have been reported (Duchaine, B. *et al.*, 2003) and suggest that different types of face processing involve separable components (Bruce, V. and Young, A. W., 1986; Haxby, J. V. *et al.*, 2000; Duchaine, B. *et al.*, 2006; but see Calder, A. J. and Young, A. W., 2005).

Prosopagnosia often leads to serious social difficulties. Prosopagnosics' failure to recognize acquaintances, friends, or family members can be perceived as an intentional snub and create offense when none is intended. Prosopagnosics who have contacted our laboratory have sadly described lost romantic opportunities, workplace disasters, and strained family relations due to failures of face recognition. Person recognition in neurologically typical individuals relies on a range of information including voice, gait, hair, body shape, and context, and prosopagnosics rely on these cues to identity (Bornstein, B., 1963; Duchaine, B. and Nakayama, K., 2006). They also often make use of distinctive facial features such as especially prominent features, moles, or scars (Ellis, H. D. and Florence, M., 1990; Duchaine, B., 2000). However, none of these means is as reliable or efficient as normal recognition of the face. Prosopagnosics not only fail to recognize people, but many also sometimes falsely recognize strangers as familiar (Duchaine, B. and Nakayama, K., 2006).

Until recently, the great majority of studies of prosopagnosia were restricted to patients who lost their face recognition ability due to brain damage. These acquired prosopagnosics were usually well aware of their face deficits, because they recalled how effortless face recognition was prior to their brain damage. In recent years, however, it has become clear that many individuals who have not experienced brain damage have severe deficit with face recognition (Kress, T. and Daum, I., 2003a; Behrmann, M. and Avidan, G., 2005; Duchaine, B. and Nakayama, K., 2006). These individuals are referred to as developmental or congenital prosopagnosics, and this condition appears to be much more common than acquired prosopagnosia.

2.21.4.1 Acquired Prosopagnosia

Given the difficulties that face recognition impairments present to patients, it is not surprising that prosopagnosia following brain damage was documented early on. In the first report in the neurological literature, Wigan A. L. (1844) described a man who could not recognize faces yet reported no other visual problems and could recognize people from their voices. There were a number of other reports of prosopagnosia in the late nineteenth century and early twentieth century (Charcot, J. M., 1883; Jackson, J. H., 1876; Quaglino, A. *et al.*, 2003; see Grusser, O. J. and Landis, T. 1991 for a review), but Hoff H. and Pöltz O. (1937) were the first to suggest that deficits with face recognition was a different disorder than object agnosia. Their patient was unable to identity familiar faces, including his own, but recovered his ability to read and retained some object recognition abilities.

A decade later, Bodamer in 1947 (Ellis, H. D. and Florence, M., 1990) described three patients who showed selective deficits of face perception or recognition subsequent to brain damage suffered in World War II. In his seminal paper, he extended the argument of Hoff H. and Pöltz O. (1937) and coined the term prosopagnosia by combining *prosopon*, the Greek word for face, with *agnosia*. One of Bodamer's patients was able to recognize faces normally but he experienced distortions restricted to faces. This metamorphopsia caused him to perceive faces as stretched or squished and features were sometimes displaced. In contrast, his perception of other objects was normal. The other two patients showed a number of characteristics typical of prosopagnosia. Both had suffered occipital lesions. They were impaired not only with face recognition, but had severe face perception deficits. Patient 1 described faces as "strangely flat, white with emphatic dark eyes, as if made from a flat surface, like white, oval plates, all alike." Both patients also experienced deficits which sometimes co-occur with prosopagnosia such as object agnosia, cerebral achromatopsia, and difficulties with facial expression. Despite their severe difficulties with face recognition, their deficits were not readily apparent because both men compensated well by relying on non-facial information.

Since Bodamer's landmark paper, well over 100 cases of acquired prosopagnosia have been documented in the literature (see Farah, M. J., 1990; Grusser, O. J. and Landis, T., 1991 for reviews). These cases have contributed to debates about the neural areas involved in face recognition (Landis, T. *et al*., 1986; Barton, J. J. *et al*., 2002; Bouvier, S. E. and Engel, S. A., 2006), the nature of the mechanisms carrying out face recognition and face processing more generally (Damasio, A. *et al*., 1982; Bruce, V. and Young, A. W., 1986; Farah, M. J., 1990; Farah, M. J. *et al*., 1995), and even consciousness (Bauer, R. M., 1984; de Haan, E. *et al*., 1987). However, despite the considerable research investigating acquired prosopagnosia, our understanding of this fascinating condition remains limited.

2.21.4.1.1 Frequency of acquired prosopagnosia

A number of studies have attempted to estimate the frequency of prosopagnosia in patients who have suffered brain damage. Such estimates are, of course, dependent on the criteria used for classification, the method by which patients are obtained, and the time since the event causing the brain damage. In the earliest studies addressing this issue, Hecaen H. and Angelergues R. (1962) found that only 6% of 382 patients who had suffered unilateral or bilateral posterior lesions experienced prosopagnosia. This low estimate was followed by a report from Gloning I. *et al*. (1967) that only one out of 241 patients with lesions to occipital or nearby areas experienced pure prosopagnosia. Similarly, Zihl J. and von Cramon D. (1986) reported that none of their 258 posterior lesioned patients had isolated prosopagnosia.

As we discuss below, prosopagnosia is often accompanied by a number of other deficits so strict criteria regarding purity are likely to make it appear extremely rare. Valentine T. *et al*. (2006) tested 91 brain-damaged subjects with a battery of cognitive and perceptual tests. These patients were a minimum of 6 months removed from their brain damage. Patients and their caregivers were asked to report on the patient's everyday face recognition abilities. Fifty per cent of patients and caregivers reported that patients would be able to recognize close acquaintances but would have difficulty recognizing people only seen a few times. Test results also indicated that many of the patients had trouble with face recognition, especially unfamiliar face recognition. On Warrington's Recognition Memory for Faces test, 77% scored more than two standard deviations below the mean. On less demanding tests of unfamiliar face memory, 20% were more than two standard deviations below. Many also had difficulties with famous face tests. Although the face recognition impairments many of these patients showed are likely to reflect higher level cognitive problems such as general memory deficits rather than problems with face-specific processes, the high proportion of impaired patients nonetheless indicate that problems with face recognition are more common than past studies suggested.

2.21.4.1.2 Conditions associated with acquired prosopagnosia

Acquired prosopagnosia often results from extensive bilateral lesions and is usually accompanied by a number of other visual impairments. Visual field defects are one of the most common co-occurring impairments. This was discussed by neurologists early on (Faust, C., 1955; Meadows, J. C., 1974), and a recent review found that only 12% of 69 prosopagnosic patients had no field defects (Bouvier, S. E. and Engel, S. A., 2006). Especially likely are defects in the left superior quadrant which result from lesions to the right inferior bank of the calcarine sulcus. This association fits nicely with neuroimaging (Sergent, J. *et al*., 1992; Bentin, S. *et al*., 1996; Kanwisher, N. *et al*., 1997) and behavioral evidence (Levy, J. *et al*., 1972; Gilbert, C. and Bakan, P., 1973; Christman, S. D. and Hackworth, M. D., 1993) indicating left visual field/right hemisphere dominance for face processing. Among the 41 patients in the review mentioned above who had visual field defects that could be assigned to a quadrant(s) or central vision (Bouvier, S. E. and Engel, S. A., 2006), 34 had defects in the upper left quadrant and 13 of these patients had defects restricted to this quadrant. In contrast, 22 had defects in the upper right field but only one patient had defects limited to it. Similarly, 15 had lower left defects and no patients had defects restricted to it.

Difficulties with face processing tasks other than identity computations are also common in acquired prosopagnosics. The quote about Bodamer's patient 1 revealed his problems with nonidentity face computations and similar difficulties have been repeatedly noted (Bornstein, B., 1963; Bowers, D. *et al*., 1985;

Davidoff, J. B. and Landis, T., 1990; Ellis, H. D. and Florence, M., 1990; Humphreys, G. W., *et al.*, 1993; McNeil, J. and Warrington, E., 1993; de Renzi, E. and di Pellegrino, G., 1998; Humphreys, K. *et al.*, 2007). Some individuals with face recognition impairments have shown normal emotion recognition (Bruyer, R. *et al.*, 1983; Tranel, D. *et al.*, 1988), but Calder A. J. and Young A. W. (2005) have argued that limitations in these papers raise the question of whether identity and emotion can dissociate when tested under comparable conditions.

Object agnosia is also commonly associated with prosopagnosia. Below in our discussion about the specificity of prosopagnosia, we review cases that indicate that object and face recognition are dissociable, but the long-running debate revolving around this question (Damasio, A. *et al.*, 1982; Farah, M. J., 1990; McNeil, J. and Warrington, E., 1993; Moscovitch, M. *et al.*, 1997; Gauthier, I. *et al.*, 1999; Duchaine, B. and Nakayama, K., 2005) makes it clear that such dissociations are uncommon. Particularly rare are dissociations between recognition of individual objects (this car, this bird) and recognition of individual faces.

Meadows J. C. (1974) reviewed the many cases manifesting prosopagnosia and cerebral achromatopsia, and in their recent review, Bouvier S. E. and Engel S. A. (2006) found that the two conditions commonly co-occur. Of 73 cases of prosopagnosia they reviewed, 38 (52%) were also achromatopsic, and out of 38 achromatopics, 17 were prosopagnosic (Bouvier, S. E. and Engel, S. A., 2006).

Deficits impairing navigational abilities (topographagnosia) are also regularly seen. In some cases, representation of large-scale spatial information is impaired (Bornstein, B., 1963) while others are unable to recognize places (Bornstein, B., 1963). In the early analysis of Hecaen H. and Angelergues R. (1962) of the co-occurrence of prosopagnosia and topographagnosia in a large group of patients with unilateral lesions, they found that 38% of prosopagnosics also suffered from topographagnosia and that 77% of patients with topographagnosia were prosopagnosic. Landis T. *et al.* (1986a) examined their co-occurrence in 16 patients with topographic deficits and confirmed prosopagnosia in seven of these individuals.

2.21.4.1.3 Lesion location in acquired prosopagnosia

Neuroimaging and neurophysiology have demonstrated that occipitotemporal areas show a selective response to faces, particularly areas in the right hemisphere (Gross, C. G. *et al.*, 1972; Kanwisher, N. *et al.*, 1997; McCarthy, G. *et al.*, 1997). The consistent association of left field defects with prosopagnosia also argues for a right occipitotemporal locus for face recognition processing (Bouvier, S. E. and Engel, S. A., 2006), and studies of individuals born with cataracts demonstrate that the development of face recognition is more dependent on the right than the left hemisphere (Le Grand, R. *et al.*, 2003). In line with these findings, lesions in this region are crucial for acquired prosopagnosia. In fact, the debate about which areas were responsible for prosopagnosia centered not on whether right hemisphere lesions were necessary but whether they were sufficient (Hecaen, H. and Angelergues, R., 1962; Meadows, J. C., 1974; Landis, T. *et al.*, 1986b; de Renzi, E. *et al.*, 1994; Barton, J. J. *et al.*, 2002; Mayer, E. and Rossion, B., 2006). Most cases of prosopagnosia occur in individuals with bilateral lesions, so the decisive test cases were the few patients with unilateral lesions. With the advent of neuroimaging, this question has become much easier to address as it was no longer necessary to rely on autopsy findings. In recent years, structural imaging has demonstrated that lesions restricted to the right hemisphere are sufficient to cause prosopagnosia (Landis, T. *et al.*, 1988; Sergent, J. and Villemure, J. G., 1989; Sergent, J. and Signoret, J. L., 1992; Marotta, J. J. *et al.*, 2001; Barton, J. J. *et al.*, 2002; Uttner, L. *et al.*, 2002; Wada, Y. and Yamamoto, T., 2001). A few prosopagnosic cases have also been reported following lesions or atrophy not affecting posterior areas but more anterior temporal areas (Evans, J. J. *et al.*, 1995; Bukach, C. M. *et al.*, 2006).

Recent papers have attempted to more precisely assess lesion locations and their effects. Rossion and his colleagues carried out detailed structural and functional investigation of P.S., a prosopagnosic with especially face-selective deficits (Rossion, B. *et al.*, 2003; Schiltz, C., *et al.*, 2007; Sorger, B. *et al.*, 2007). These analyses showed that P.S. had lesions where the OFA is normally seen, activation in FFA though no adaptation, and an intact lateral occipital complex (an area selectively activated in object processing). A similar approach with other patients hold much promise. In the review of Bouvier S. E. and Engel S. A. (2006), lesion overlap in prosopagnosia was analyzed. Figure 8 shows the results of this, and as expected, high overlap was seen in right occipitotemporal areas with several peaks. Especially interesting to note is the lesion overlap results in comparison to face-selective activations seen in

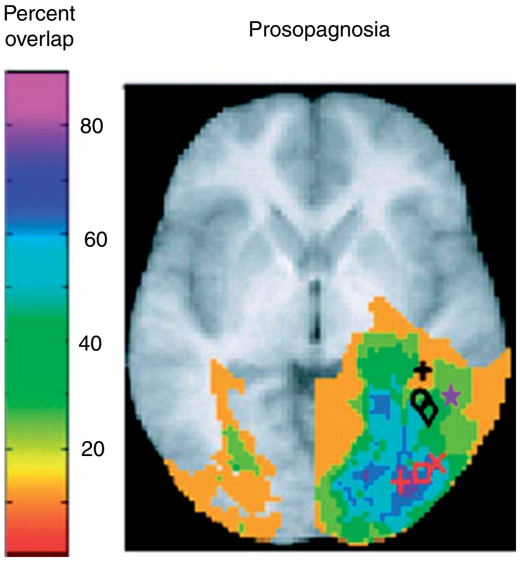

Figure 8 Lesion overlap results compared to face-selective activations in previous experiments with normal subjects. Three areas of peak overlap are shown in blue. Occipital face area activations are shown in red, fusiform face area in black, and superior temporal sulcus in purple. Bouvier, S. and Engel, S., Behavioral Deficits and Cortical Damage Loci in Cerebral Achromatopsia, Cerebral Cortex, 2006, 16, 2, 183–191, by permission of Oxford University Press.

fMRI experiments. The coordinates of OFA fall within the largest area of peak overlap whereas FFA and STS are anterior to this region and lateral to another peak. This suggests that lesions to OFA may be key to prosopagnosia, but given the apparent importance of FFA in face recognition (Grill-Spector, K. *et al.*, 2004; Yovel, G. and Kanwisher, N., 2005), it is surprising that FFA did not overlap with a peak. Bouvier S. E. and Engel S. A. (2006) point out that sampling bias may have contributed to this finding as images with medial lesions are more likely to be included in papers because of the availability of landmarks. In discussing this finding, Mayer E. and Rossion B. (2006) also noted that isolated lesions to middle fusiform are rare because it receives blood from both posterior and middle cerebral arteries.

2.21.4.2 Developmental Prosopagnosia

Although Bornstein B. (1963) appears to have noted the existence of developmental prosopagnosia, McConachie H. (1976) provided the first case study of an individual with face recognition deficits in the absence of any identifiable brain damage. A.B. was a highly intelligent 12-year-old girl who reported that she had never been able to recognize faces, except for those with which she was very familiar. She had great difficulty recognizing her uniformed classmates at school. When tested with familiar faces, she hesitantly but correctly identified her friends, and she appeared to score normally on a test of unfamiliar face recognition. She showed normal visual fields, read well, and performed normally on tests of spatial ability and basic level object recognition. Lending support to a developmental etiology, her mother also reported problems with face recognition. Although this case hinted that developmental problems can give rise to prosopagnosia, A.B.'s deficits were not firmly established. In a follow-up study done 15 years later, de Haan E. H. and Campbell R. (1991) clearly demonstrated that A.B. did have face recognition problems as well as facial expression and object recognition problems. Intriguingly, her deficits with tasks other than identity recognition and anecdotal reports that she has navigational problems suggested that developmental prosopagnosia co-occurs with the same conditions as acquired prosopagnosia.

After A.B.'s case was reported, only one new case of developmental prosopagnosia (unaccompanied by autism spectrum disorder) was documented in the 1980s and early 1990s (Temple, C., 1992) so developmental prosopagnosia appeared to be extremely rare. Since that time though, more than 24 papers have reported on developmental prosopagnosics (for reviews, see Galaburda, A. M. and Duchaine, B., 2003; Kress, T. and Daum, I., 2003a; Behrmann, M. and Avidan, G., 2005; Duchaine, B. and Nakayama, K., 2006). The surge of papers is likely the result of the internet allowing researchers and developmental prosopagnosics to make contact and the increased attention to prosopagnosia in the media. Many of these individuals feel great relief upon learning about developmental prosopagnosia, because they finally have an explanation for the great difficulties they have with person recognition.

Like many acquired prosopagnosics (Grusser, O. J. and Landis, T., 1991), developmental prosopagnosics are sometimes able to recognize faces, but they experience severe, recurring problems and many fail to recognize family and close friends (McConachie, H., 1976; Duchaine, B. and Nakayama, K., 2006). Substantial variability in the severity of their face recognition deficit exists among developmental prosopagnosics. Some are able to recognize faces if seen often enough. One man told us that he could recognize Bill Clinton after a few years of his presidency. Others recognize very few faces. One intelligent Englishman tested in our laboratory watches the news regularly yet failed to recognize Tony Blair, George Bush, Princess Diana, and Prince Charles. They tend to rely on nonfacial information to a much greater extent than people with normal face recognition. Movies and television programs are often difficult to follow because they cannot identify characters. Like acquired cases, many developmental prosopagnosics find ways to maneuver socially by faking recognition until verbal information clarifies identity and by preparing for or avoiding situations in which recognition will be challenging.

Although the prevalence of developmental prosopagnosia has not been firmly determined, it is clear that it is not as rare as once thought. From early 2002 until late 2006, approximately 1900 self-identified prosopagnosics contacted the website of the Harvard/UCL Prosopagnosia Research Center, and more than 1200 of these contacts came in 2006 due to media coverage. Of this sample, the great majority report no history of brain damage and years of difficulty with face recognition. When tested in the laboratory, we find that approximately 80% show severely impaired scores on our tests of face recognition. A German team recently estimated the prevalence of developmental prosopagnosia at 2% of the general population (Kennerknecht, I. *et al.*, 2006). While any estimate of prevalence is strongly dependent on the criteria used for diagnosis, this estimate suggests that there are millions of prosopagnosics in the world. Jane Goodall (Goodall, 1999) reports that she is prosopagnosic, and it appears that Robert Cecil, a late nineteenth century UK Prime Minister, was as well (Cecil, D., 1973). It is interesting to consider that individuals in modern societies are bombarded by faces whereas in ancestral environments the demands of face recognition were much less. In the small bands in which humans evolved (Foley, R. A., 1995), people with face recognition deficits may have been able to navigate the social world much more successfully than they can today.

It appears that a variety of causes can lead to developmental prosopagnosia. The first case study hinted at a genetic cause and other documented developmental prosopagnosics have mentioned that relatives share their difficulties (Duchaine, B., 2000; Behrmann, M. *et al.*, 2005; Duchaine, B. and Nakayama, K., 2005). de Haan E. (1999) found that three members of a family performed poorly on a famous face test. Approximately 30% of the developmental prosopagnosics who contact our website report genetic relatives with face recognition problems, and we have tested a number of families including one with ten affected members (Duchaine, B. *et al.*, 2007). A recent study using self-report data found that the inheritance patterns in seven families were consistent with dominant autosomal transmission (Kennerknecht, I. *et al.*, 2006). We also find that a substantial proportion (approximately 20%) of our contacts report severe early vision problems such as amblyopia, strabismus, and uncorrected myopia. This high proportion is consistent with developmental evidence indicating that visual input in the first months of life is crucial for the development of face processing (Le Grand, R. *et al.*, 2001; 2003). In many cases, there are no hints as to what may have led to prosopagnosia (Duchaine, B., *et al.*, 2003).

2.21.4.2.1 Conditions associated with developmental prosopagnosia

Like acquired prosopagnosia, developmental prosopagnosia shows considerable heterogeneity in the deficits commonly associated with it (Duchaine, B. and Nakayama, K., 2005; Harris, A., *et al.*, 2005; Le Grand, R. *et al.*, 2006). Many of the same deficits co-occur in both conditions, which suggests that developmental prosopagnosia sometimes results from a developmental failure which affects cortical areas near those areas involved with face recognition. Developmental cases sometimes have trouble recognizing facial expressions of emotion (Duchaine, B., 2000; Duchaine, B., *et al.*, 2006), classifying faces by sex (Duchaine, B. *et al.*, 2006), and judging facial attractiveness (Sadr, J. *et al.*, 2004). All documented developmental prosopagnosics perform normally with basic level object naming (car, dog), but many show deficits with tests of recognition of items from within a category (that car, that dog; Behrmann, M. *et al.*, 2005; Duchaine, B. and Nakayama, K., 2005). Also like acquired prosopagnosics, developmental prosopagnosics regularly report severe navigational problems. A.B.'s navigational difficulties were mentioned above, and among the prosopagnosics who have contacted the Prosopagnosia Research Center, approximately 15% report severe problems. In some especially severe cases, the navigations problems have a considerable impact. At present, almost no research has been carried out on developmental navigation deficits.

Although many associated conditions are seen in both forms of prosopagnosia, visual field defects and cerebral achromatopsia have not been reported in any developmental cases. Neuroimaging and neurophysiological work demonstrate that proximity explains their co-occurrence in acquired cases, so the absence in developmental cases is somewhat surprising. However, we expect that visual fields and color vision are often not assessed in developmental prosopagnosia. Lifelong defects such as these may be difficult to self-identify, especially defects limited to a small region of the visual field. Full-fledged achromatopsia would be apparent, but dyschromatopsia would be more difficult to detect.

2.21.4.2.2 Neural bases of developmental prosopagnosia

Given the cognitive heterogeneity in developmental prosopagnosia, it is likely that multiple neural abnormalities will be responsible for it. Studies that have investigated the neural bases in developmental cases have found some atypical neural responses but these atypicalities are not seen in all cases and no correspondence between response variability and cognitive variability has been identified.

Face-selective areas identified by fMRI were a natural first step in neural investigations of developmental prosopagnosia, but so far, few differences between controls and DPs have been found in these areas. Hassan U. *et al.* (2003) found that the magnitude of the FFA in Y.T. was normal, and normal FFA response was also found in a study involving four developmental prosopagnosics (Avidan, G. *et al.*, 2005). In addition, this study examined adaptation in FFA by comparing the response to 12 different faces to that of 12 repetitions of the same face. The developmental prosopagnosics showed adaptation comparable to the controls, which suggests that FFA is sensitive to identity information. However, adaptation in controls and the prosopagnosics was seen in a number of other visual areas, a finding consistent with an attentional account of the weakened response to repetition. Another recent single case study found weaker face activation in left FFA and bilaterally in the temporal poles (von Kriegstein, K. *et al.*, 2006).

The N170 and M170 have also been examined in developmental prosopagnosia. Bentin S. *et al.* (1999) found that the N170 in Y.T. was not as face-selective as controls, and Kress T. and Daum I. (2003b) found similar results in two other participants. In contrast, Harris A. *et al.* (2005) found mixed results when they examined the M170 in five developmental prosopagnosics. Two subjects showed a stronger response to faces than houses that was comparable to that for controls, while three failed to show a face-selective response. Analysis of the behavioral results for the two groups did not reveal any distinctions that mapped on to the M170 differences.

Behrmann M. *et al.* (in press) have reported structural abnormalities in developmental prosopagnosia. Morphometric and volumetric measurements were made in controls and six developmental prosopagnosics. Anterior fusiform gyrus was smaller in the developmental prosopagnosics than in controls, whereas middle temporal gyrus and posterior temporal gyrus were larger in the prosopagnosics than controls. Most impressively, the volume of the anterior fusiform gyrus was positively correlated with performance with famous faces in the developmental prosopagnosics.

2.21.4.3 Face-Specificity in Prosopagnosia

The cognitive and neural sections above described evidence indicating that faces are processed by face-specific mechanisms, and evidence from prosopagnosia has played a key role in the debate about specificity (Farah, M. J., 1990; Kanwisher, N., 2000; Tarr, M. J. and Gauthier, I., 2000). As mentioned above, many prosopagnosics experience both face and object recognition deficits. This association has led some researchers to argue that face recognition deficits are the most obvious manifestation of damage to more general purpose object recognition mechanisms (Damasio, A. *et al.*, 1982; Gauthier, I. *et al.*, 1999). Areas involved in face recognition, however, are adjacent to object recognition areas so an association is to be expected. The theoretically illuminating cases are those which show dissociations between face and object recognition, and such dissociations have been documented in both acquired and developmental prosopagnosia.

To demonstrate a dissociation between face and object recognition, it is crucial to test each at comparable levels of specificity. This has been done by comparing recognition of individual objects from within a category to recognition of individual faces (Davidoff, J., 1986; Moscovitch, M. *et al.*, 1997). A number of acquired cases have shown dissociations under such conditions. W.J. was a sheep farmer who experienced severe face-processing deficits following three vascular episodes (McNeil, J. and Warrington, E., 1993). In contrast, to his profound deficit with faces, W.J. was able to recognize many of the sheep in his flock of 36 and performed better than all controls (including two sheep experienced controls) on two sheep face recognition memory tests and a paired associates learning test with sheep faces. Similarly, R.M., a car enthusiast who suffered a lesion that left him with profound prosopagnosia, was better able to name the make, model, and year of a large set of cars than any controls (Sergent, J. and Signoret, J. L., 1992). Reports with other acquired cases have found similar results with other non-face categories (Farah, M. J., 1996; Henke, K. *et al.*, 1998; Rossion, B. *et al.*, 2003).

Face-selective deficits have also been demonstrated in developmental prosopagnosia (Nunn, J. A. *et al.*, 2001; Duchaine, B. and Nakayama, K., 2005). The clearest demonstration involved testing the predictions of each proposed account of prosopagnosia in a man named Edward (Duchaine, B. *et al.*, 2004; 2006). His normal performance on a wide range of tests including inverted face matching, within-class object discrimination, non-face configural processing, and expert processing (Greebles and human bodies) showed that his prosopagnosia could not be explained by any of the accounts except the face-specific explanation (Duchaine, B. *et al.*, 2006).

If faces are processed by mechanisms specialized for face processing, cases with object agnosia and normal or relatively spared face recognition should exist. A number of these cases have been documented in brain damaged patients (Bruyer, R. *et al.*, 1983; Assal, G. *et al.*, 1984; Feinberg, T. E. *et al.*, 1986; McMullen, P. A. *et al.*, 2000), and multiple papers have explored the profile of Mr. C.K., an object agnosia with wholly spared face recognition (Moscovitch, M. *et al.*, 1997; Moscovitch, M. and Moscovitch, D. A., 2000). Normal recognition of faces has also been seen in combination with severe place recognition deficits (Carlesimo, G. A. *et al.*, 2001). At present, no developmental cases showing normal face recognition and impaired object recognition have been reported.

Evidence for face specificity has also come from metamorphopsia, a disorder involving perceptual distortions. In his classic paper, Bodamer reported a double dissociation (Ellis, H. D. and Florence, M., 1990): patient 3 reported perceptual distortions restricted to faces whereas patient 1 reported that the edges of all objects in a scene, but not faces, appeared to flicker at times. Davidoff J. B. and Landis T. (1986) reported a woman who perceived all faces to be distorted on the left-side, yet she perceived objects normally. Following a stroke, a prosopagnosic woman experienced several visual preservations including one amazing episode involving a poodle face (Landis, T. *et al.*, 1986b). While sitting on a bus, she observed a poodle sitting on the lap of a person across from her. Upon looking up from the poodle to the people in the bus, she now saw the poodle face instead of a human face on each person (see Figure 9). Her quick exit from the bus did not end this bizarre state, but fortunately after 30 min, the perseveration ended. Her perseveration revealed the specificity of face processing, because the poodle was only pasted on to other faces and not on to any other objects in the visual scene.

2.21.5 Development of Face Recognition

Like the cognitive, neural, and neuropsychological aspects of face recognition, the development of face recognition has received extensive attention. The majority of this work has addressed cognitive development, but neural issues are receiving increasing attention. Developmental studies have revealed much about face processing at different ages but little about the changes that lead to mature face recognition abilities.

2.21.5.1 Face Processing in Newborns

Infants are born with visual systems which, though limited in acuity and color perception, allow them to perceive and respond to coarse aspects of the visual world. Considerable research carried out over the last 30 years has demonstrated that newborns attend to faces more than many other comparable stimuli (Goren, C. *et al.*, 1975; Johnson, M. H. and Morton, J., 1991). This revealing ability was first demonstrated by Goren C. *et al.* (1975) in a study with newborns with a mean age of nine minutes. Each infant was presented with four stimuli which included a schematic face, two scrambled faces, and a blank face. The stimuli traversed 180° arcs in front of the child while the infants' head and eye movements were recorded. The infants looked significantly longer at the schematic face than the other three stimuli. Other experiments have replicated these findings (Johnson, M. H. *et al.*, 1991) and extended them to show that newborns prefer faces with open eyes (Batki, A., *et al.*, 2000) and direct eye gaze (Farroni, T. *et al.*, 2002; see Figure 10).

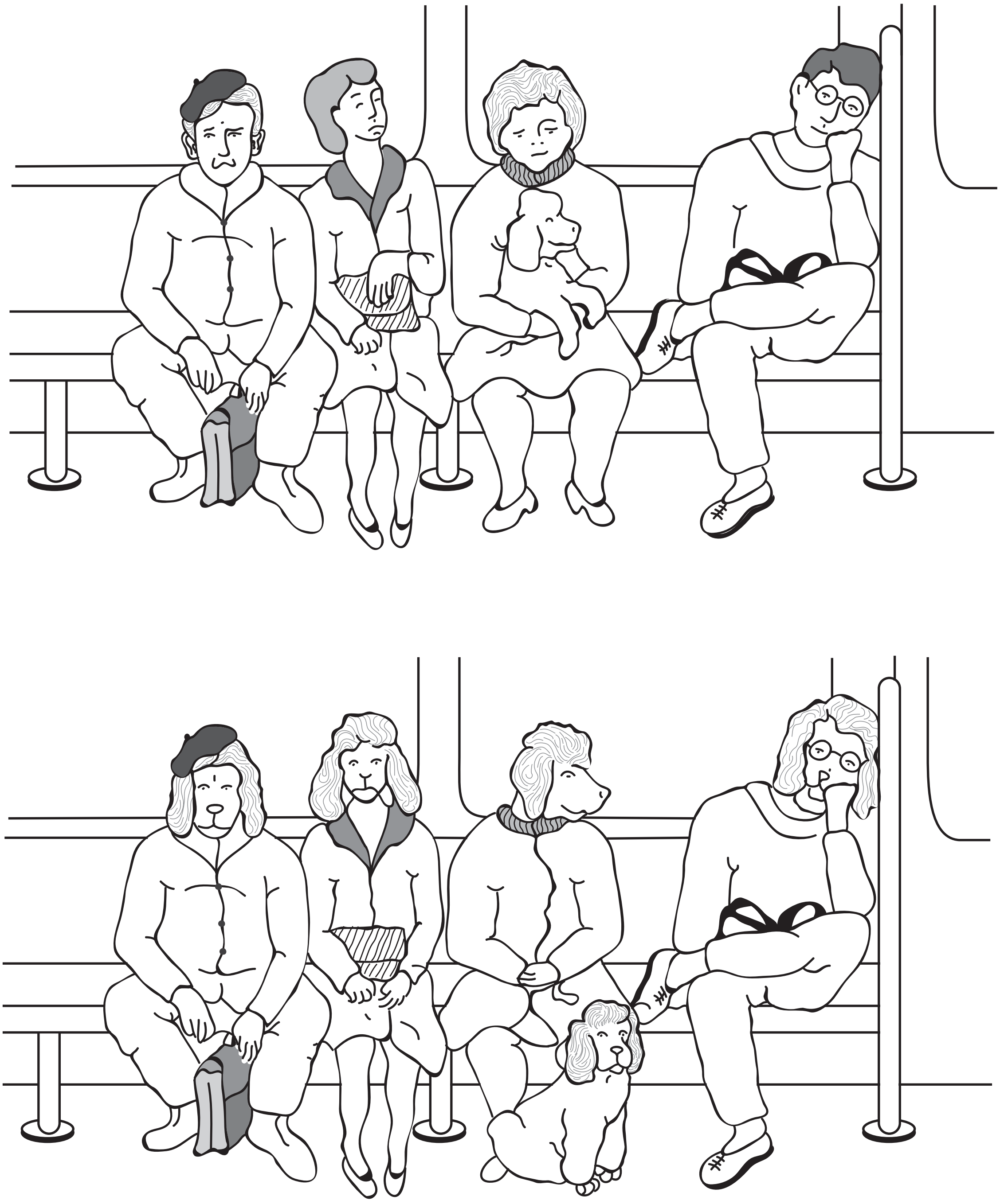

Figure 9 Drawing depicting the visual experiences of a woman experiencing metamorphopsia restricted to faces. Several weeks after suffering a stroke, she rode on a bus and viewed the scene in the top drawing. After looking at the face of the poodle, she looked back to the passengers. However, rather than seeing the faces of the passengers, she saw the poodle's face in place of all the other faces in the bus. This state lasted for approximately 30 min. Drawing by D. Starke.

Newborns also discriminate between different faces. Work examining newborn responsiveness to facial expressions and movements has demonstrated the existence of mechanisms sensitive to the face at birth. Field T. M. *et al.* (1982) found that neonates imitated facial expressions, and Meltzoff A. N. and Moore M. K. (1977) reported that neonates imitated facial gestures such as opening of the mouth and protrusion of the lips or tongue. Newborns also prefer attractive over unattractive faces (Slater, A., *et al.*,

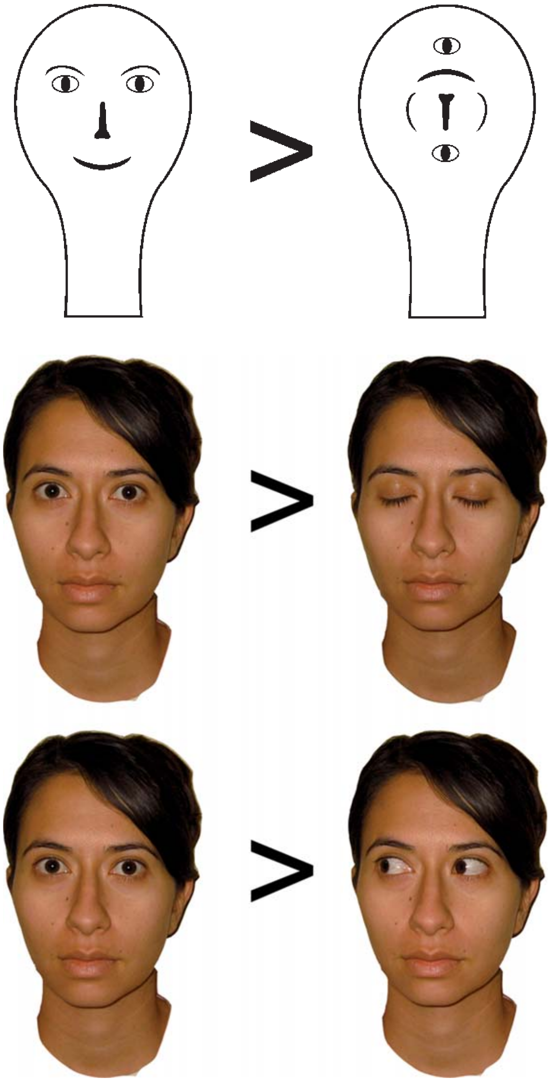

Figure 10 For each pair, newborns attend to the stimuli on the left longer than the stimuli on the right.

1998), and use the internal facial features to make this discrimination (Slater, A. *et al.*, 2000). While these experiments did not investigate face recognition, they clearly show that infants are born equipped to engage with faces.

2.21.5.2 Infant Face Recognition

In first days of life, infants look longer at their mother's face than a stranger's face (Field, T. M. *et al.*, 1984; Bushnell, I. W. *et al.*, 1989; Pascalis, O. *et al.*, 1995). It appears however that these discriminations are based on external features, particularly hair (Maurer, D. and Salapatek, P., 1976; Pascalis, O. *et al.*, 1995). Whether young infants are better able to recognize identity in upright faces than inverted faces is unknown.

The youngest evidence of the inversion effect is seen in infants at 4 or 5 months of age. Using a habituation paradigm, Turati C. *et al.* (2004) found that infants recognized facial identity better when faces were shown in different views in upright faces than inverted faces. Similarly, Bhatt R. S. *et al.* (2005) reported that 5-month-old infants were less sensitive to changes to the spacing of the eyes in inverted faces than upright faces. Neural measures have also demonstrated an early inversion effect. A differential ERP response to upright and inverted was seen in 6-month-old infants (de Haan, E. *et al.*, 2002), and near infrared spectroscopy, which noninvasively records hemodynamic changes, done with 5–8-month-old infants detected a stronger response to upright faces than inverted faces in right lateral areas (Otsuka, Y. *et al.*, 2007).

Recent work suggests that face recognition mechanisms in infants become tuned to the faces observed. Using preferential looking paradigms with infants and discrimination tests with adults, Pascalis O. *et al.* (2002) showed that 6-month-old infants, 9-month-old infants, and adults were able to discriminate between human faces but only 6-month-olds could discriminate between monkey faces. This phenomenon is similar to the loss of sensitivity to phonemes not used in the infant's native language (Werker, J. F. and Tees, R. C., 1984; Kuhl, P. K. *et al.*, 1992). As with phonemes, exposure to monkey faces during the period in which sensitivity is lost extends the period of sensitivity to monkey faces (Pascalis, O. *et al.*, 2005).

Differential processing of faces of different races follows a similar developmental course. Sangrigoli S. and de Schonen S. (2004) and Bar-Haim Y. *et al.* (2006) found that infants at 3 months discriminated between same race faces better than different race faces. This effect disappeared with pretest exposure to other race faces (Sangrigoli, S. and de Schonen, S., 2004). As expected, newborns show no preference for same race faces (Kelly, D. J. *et al.*, 2005).

2.21.5.3 Critical Period in the Early Months of Life

Some of the most revealing developmental studies have investigated face processing in individuals born with congenital cataracts (Le Grand, R. *et al.*, 2001; 2003). The lenses in these individuals were replaced in the first few months of life, and they had relatively normal visual experience after surgery. Participants ranged in age between 9 and 21 years of age when their face discrimination was tested. Despite years of experience with faces, these individuals showed clear deficits with the face discriminations (Le Grand, R. *et al.*, 2001).

Further research done with participants born with unilateral cataracts, which again were repaired in the first months of life, found eye-specific effects. Cataracts in the right eye had no effect on face discriminations while left eye cataracts led to deficits comparable to those seen in participants with bilateral cataracts (Le Grand, R. *et al.*, 2003). The eye-specific effects are possible, because retinas in infancy are primarily responsive to the temporal visual field (Lewis, T. L. and Maurer, D., 1992) and the immaturity of the corpus callosum appears to make it unable to allow functional integration of visual information (Liegeois, F., *et al.*, 2000). Hence, visual information from each eye is primarily in the contralateral hemisphere. The effect of left eye cataracts indicates that the development of normal face discrimination requires early input to the right hemisphere. Lens replacements were carried out between 2 and 6 months of age, and length of deprivation had no effect on performance (Le Grand, R. *et al.*, 2001; 2003).

2.21.5.4 Face Recognition in Childhood

By 4 years of age, children can be tested using paradigms similar to those used with adults, and results using these paradigms show that children experience many of the same effects considered evidence of face-specific processing in adults. Pellicano E. and Rhodes G. (2003) showed that children as young as 4 years show a part-whole effect, with better recognition of parts within the context of face than in isolation (Tanaka, J. W. and Farah, M. J., 1993). de Heering *et al.* (2006) found additional evidence for holistic processing by demonstrating that 4–6-year-olds showed strong composite effects (Young, A. W. *et al.*, 1987). Similarly, McKone E. and Boyer B. L. (2006) showed that 4-year-olds and adults find that spacing and feature changes have similar effects on distinctiveness judgments.

Although these investigations suggest that face-specific processing procedures operate in early childhood, recognition of unfamiliar faces in children is far from adult levels (Diamond, R. and Carey, S., 1977). What leads to this improvement? Early work suggested that changes in face-processing mechanisms were responsible for much of the change as early studies suggested that the inversion effect was not evident until 10 years of age (Diamond R. and Carey, S., 1977). More sensitive measures however show inversion effects in infancy (Turati, C. *et al.*, 2004; Bhatt, R. S. *et al.*, 2005), and a recent elegant study indicates that the effect of both inversion and contrast reversal are constant from age 8 years through to adulthood (Itier, R. J., and Taylor, M. J., 2004b). Participants had to detect repetitions of upright, inverted, or contrast-reversed faces shown with no lag or a one trial lag. Older participants performed better than younger participants, but the effect of inversion and contrast-reversal had comparable effects on accuracy and response times at all ages. These comparable effects suggest that the improvement seen as children grow older is caused primarily by changes to higher-level processes such as working memory rather than face-specific processes.

2.21.6 Conclusion

Converging evidence from studies that employed cognitive, neural, neuropsychological, and developmental approaches suggest that faces engage specialized processing mechanisms that represent information about faces in a qualitatively different way than inverted faces and non-face objects. In particular, upright faces are represented in a more holistic manner, with the features and the spacing of the features coded more precisely and interactively than other types of objects are. Early studies that employed cognitive methods to examine the nature of the representation of faces in normal and brain damaged patients that suffer from face recognition deficits anticipated the existence of a specific neural substrate for face processing. Indeed, electrophysiological studies and the explosion of neuroimaging work in the last ten years have revealed neural responses that are highly face-specific and seem to play a special role in face recognition processes. A variety of neuropsychological deficits affect face processing. The best studied is prosopagnosia, and it can result from brain damage or a failure to develop face recognition mechanisms. Studies of the development of face recognition revealed that newborns attend to faces more than comparable stimuli and many of the holistic and configural effects emerge early in childhood. Most excitingly, growing connections between these different levels of explanation are beginning to provide a more integrated theory of face recognition.

Although research into face recognition has led to an outline of what a detailed account of face recognition might look like, many fundamental questions remain unanswered. We still have little understanding of the stages of face processing, what sort of mix of face-specific and more general mechanisms contribute to face recognition, what operations different neural areas carry out, and how the system is modified by experience and maturation. Familial prosopagnosia reveals the existence of genes that are important for the development of face recognition, but little else is known about its genetic basis. Despite scores of neuropsychological studies, no effective treatments for face recognition deficits have been devised. However, the importance of face recognition in our daily life and the existence of specific neural, cognitive and possibly genetic mechanisms that are dedicated to face processing suggest that it will continue to be an area on the cutting edge that provides a model for research investigating other areas in cognitive neuroscience.

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http://www.faceblind.org – Harvard University/University College London Prosopagnosia Research Center. Faceblind