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Competition between Face and Nonface Domains of Expertise

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INTRODUCTION

We are confronted daily by the capacity-limited nature of human information processing. For example, talking on a cellular phone while driving makes it more difficult to pay attention to the road, suggesting that these tasks compete for overlapping limited processing resources. Measurements of interference between concurrently performed tasks can provide insight into the nature of the underlying neural substrates. For example, the reduction in the amount of visual information that can be kept in mind by a concurrent visual, but not verbal, task provides evidence for the independence of visual and verbal short-term memory systems (Baddeley & Hitch, 1974). Given the long-standing debate about whether the system supporting our expert face processing skills is modular, that is, dealing with faces only and independently from non-face object processes (e.g., Bodamer, 1947; Ellis & Young, 1989; Yin, 1969), an important question is whether face and nonface domains of expertise compete for common expert processes. If the cognitive system underlying face processing is domain specific so that it responds only to faces as suggested by some (e.g., Farah, Wilson, Drain, & Tanaka, 1995; Kanwisher, 2000; Nachson, 1995), then this competition should not occur. However, if this system is domain general, responding to other classes of visual stimuli with which we have substantial expertise, then acquiring expertise with a nonface category should increase interference or competition for this capacity across face and nonface domains of expertise.

There is already much evidence consistent with the proposal that face and nonface expert processing are supported by a domain-general system. Perceptual experts show similar visual short-term memory advantages, behavioral inversion effects, and holistic processing for nonface objects of expertise and faces (Curby & Gauthier, 2007; Curby, Glazek, & Gauthier, 2009; Diamond & Carey, 1986; Gauthier & Tarr, 1997, 2002). These holistic processes recruited for face and nonface objects of expertise render the features within an object inseparable from their context (Tanaka & Farah, 1993). For example, the features within a stimulus, such as the eyes, and their relations, such as the distance between the two eyes, are processed interactively. Nonface objects of expertise also appear to recruit brain areas responding preferentially to faces in the fusiform gyrus, providing a potential neural locus for this holistic processing (Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Xu, 2005). In addition, expertise effects for nonface objects are found in the first face-sensitive responses of the human brain as identified by event-related potential (ERP) studies (Busey & Vanderkolk, 2005; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002; Tanaka & Curran, 2001). The expertise account of these neural markers suggests that nonface objects (e.g., cars) can be processed by experts within the same system as faces because similar holistic processes are involved (Tarr & Gauthier, 2000). However, studies supporting this account only reveal similarity in processing and proximity of neural substrates: It remains possible that nonface objects of expertise are processed in a system that is similar and neighboring, but that does not interact with a face-specific system. Therefore, the domain specificity of face processes is still an open question.

The time course of processing is another important factor when considering whether the processing of face and nonface objects of expertise share resources. It is possible that face and object expertise recruits the same neural substrate, but at different stages of processing. For example, faces may recruit the "fusiform face area" (FFA) in a feed-forward manner, whereas activation in this area for nonface objects of expertise may come predominantly from feedback connections from higher-level processing areas. A spatial overlap without a temporal overlap would suggest important differences in the manner in which face and nonface objects of expertise are processed. This would also raise important questions about what constitutes a modular system or, more specifically, whether modular systems must be domain specific across time. For example, it is conceivable that a brain area such as the FFA might perform different functions at different stages of processing. Early responses in the FFA to feed-forward information may predominantly reflect perceptual processing of faces, whereas responses after re-entrant input has reached this area may reflect higher-level processing such as that triggered by the social or reward attributes of the stimulus (Schultz et al., 2003). Therefore, an overlap that occurs in both space and time would provide stronger evidence for a common processing system and mechanism for face and nonface objects of expertise. The temporal limitations of fMRI render such questions, namely whether the activation in response to face and nonface objects of expertise occur in the same time frame, almost impossible to examine through this method.

The greater temporal resolution of techniques such as event-related brain potentials (ERPs) or event-related magnetic fields (ERMFs) make these procedures ideally suited to address questions about the temporal overlap between face and nonface expert processing. However, these methods, ERPs in particular, are not without their own limitations. Visual potentials recorded on the human scalp, such as the N170/VPP complex, which is much larger to faces than any other object category (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Jeffreys, 1996; Joyce & Rossion, 2005) and whose amplitude is modulated by perceptual expertise (Busey & Vanderkolk, 2005; Rossion et al., 2002; Tanaka & Curran, 2001), are assumed to have a number of underlying sources. Thus, it is possible that the N170 evoked in response to objects of expertise may have a different set of sources than that in response to faces. Therefore, these effects of expertise found on the N170 in response to objects may arise not from face-related holistic processes, but instead from different processes occurring at approximately the same latency and with an overlapping scalp potential, as argued by some (McKone & Kanwisher, 2005; Robbins & McKone, 2006).

Recent reports of the capacity-limited nature of the system supporting face processing have provided a potential method for probing both the spatial and temporal nature of the overlap between face and nonface expert processing (Bindemann, Burton, & Jenkins, 2005; Jenkins, Lavie, & Driver, 2003; Palermo & Rhodes, 2002): If face and nonface objects of expertise recruit overlapping resources, the concurrent processing of these items should be more vulnerable to capacity limitations relative to the simultaneous processing of face and nonface objects of nonexpertise. Therefore, by pairing high–temporal resolution neuroimaging techniques such as ERPs with behavioral paradigms where the processing of faces and objects of expertise occur concurrently, cognitive neuroscientists can address the issue of the functional overlap of the systems supporting different-category expert processing.

In this chapter, we discuss a number of recent studies that use these paradigms to provide insight into the question of the domain specificity of face perception. To anticipate, these studies using interference paradigms suggest a functional overlap between face and nonface expert processing that occurs at the perceptual level. These findings lead to intriguing predictions about the potential for long-term interference between such processing. Evidence for such long-term interference effects between the development of expertise with face and nonface objects and their implications are also discussed.

CAPACITY LIMITATIONS OF THE FACE PROCESSING SYSTEM

Interference between face and nonface expert processing would be expected if holistic face processing is capacity limited, and this limitation is shared across face and nonface expert processing. This section outlines existing evidence suggesting that face processing is capacity limited, thus providing the foundation upon which interference studies between face and nonface expertise are based.

Evidence from Distractor Interference Paradigms

Most studies explore the capacity of face processing mechanisms indirectly. They operate under the assumption that a distractor stimulus or a secondary task will interfere with the processing of a central stimulus, providing that (1) it recruits overlapping capacities, and (2) the central task does not recruit the entire face processing capacity. A number of studies have measured the impact of the *congruency* between a distractor and target in order to estimate category-specific perceptual capacity limitations (Bindemann et al., 2005; Jenkins et al., 2003). For example, in a sex categorization task, if the target is a female face, a distractor taking the form of a male face would constitute an *incongruent* event, whereas the presentation of a female distractor face would be a *congruent* event. Using this general paradigm, a recent study provided evidence that our processing capacity for faces may be as little as one item. When making a sex or semantic judgment about a face, participants experienced distractor congruency effects when the distractor was a word but not when it was another face (Bindemann et al., 2005). Importantly, when the target was a word, distractor congruency effects were present regardless of whether the distractor was a face or a word (Bindemann et al., 2005). Based on the absence of interference from distractor face on a central face judgment, the authors of the study suggested that visual face processing is capacity limited, with no more than *one* face processed at a time.

In contrast, other studies have reported evidence that the capacity for face processing is greater than one. Jenkins and colleagues (2003) demonstrated that when subjects performed an occupation judgment about a centrally presented famous individual's name, the influence of a famous face distractor depended on whether it was congruent (i.e., a politician's face with a politician's name) or incongruent (i.e., politician's face with a pop star's name). As expected, performance was worse when the distractor was incongruent versus when it was congruent. Notably, however, the presence of a task-irrelevant additional unknown face diluted this distractor congruency effect, although the presence of other stimuli did not influence this effect. The dilution of the distractor effect by the presentation of an additional unknown face suggests that we can in fact process more than one face at a time. Although the Bindemann and Jenkins' studies lead to different conclusions about the precise capacity of face processing mechanisms, they both agree that not only do faces draw on a limited capacity resource, but that this resource is face specific.

Although a number of studies suggest that the presence of additional faces in one's visual field can interfere with the processing of a central face, it is unclear from these studies whether this interference occurs during perceptual encoding or at later processing stages. More specifically, it is unclear whether observers can actually encode multiple faces at once, which then compete with each other at later output stages leading to the observed interference effect. Alternatively, the distractor interference might instead reflect the sharing of limited resources insufficient to encode multiple faces at once, thus suggesting that the interference occurs at a perceptual level. This distinction is critical for interpretations with regard to the capacity-limited nature of face processing and its consequences for nonface expert processing.

Evidence from ERP studies suggests that this interference occurs at a perceptual level: The occipito-temporal N170 potential elicited in response to a laterally presented face is considerably reduced in amplitude when participants fixate on a centrally presented face as compared to the fixation of a nonface central stimulus (phase-scrambled face, Jacques & Rossion, 2004; see Figure 8.1). This reduction in the amplitude of the N170 holds even when the target stimulus is presented at the fovea and the distractor is presented laterally (Jacques & Rossion, 2006). Notably, this effect takes place on the earliest face-selective response in the brain, occurring only 130 ms after the face is presented (N170, 130–200 ms), suggesting that the interference occurs during the perceptual processing of the faces rather than at later stages. More specifically, the modulation of the N170 potential is consistent with a significant overlap and competition in the neural representations used for individual faces. Presumably, such overlap would lead to perceptual capacity limitations because neural resources required to encode face representations would become more scarce with increasing face load, as each face stimulus would compete for more and more of the same neurons.

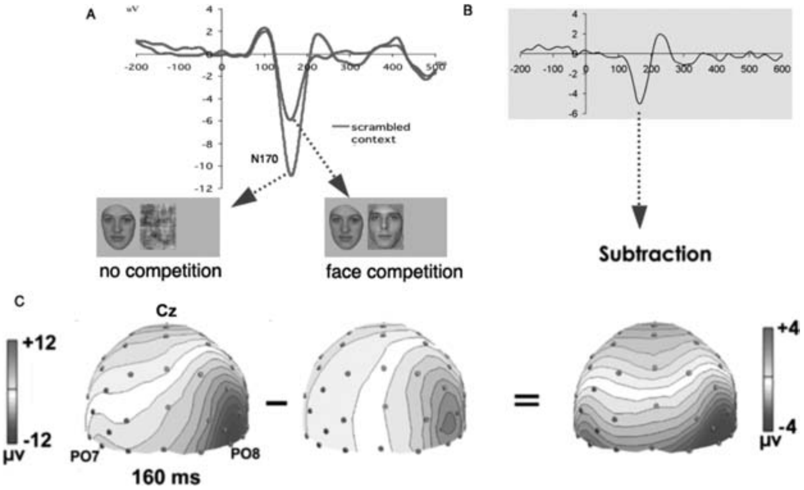

Figure 8.1 (A) ERP waveforms at right occipitotemporal sites (here PO8 electrode) following the onset of a face stimulus presented in the left visual field, either when subjects fixate another face stimulus (face competition) or a phase-scrambled stimulus of equal size and luminance. The N170 is substantially reduced in amplitude when subjects are fixating the face stimulus, illustrating the competition effect within the face domain. (B) Subtraction between the two waveforms, showing that the competition effect starts at about 130 ms following stimulus onset. (C) Topographical maps of the back of the head for the electrical potentials observed at 160 ms in the two conditions and the result of their subtraction. Note that the topography of the competition effect is highly similar to the original N170 scalp distribution (figure adapted with permission from Jacques & Rossion, 2004, "Concurrent processing reveals competition between visual representations of faces, *NeuroReport 15*(15), 2417–2421. © 2004 Lippincott Williams & Wilkins/Wolters-Kluwer Health) (See color Plate 6).

The observation of a reduction in the amplitude of the N170 potential for faces perceived in the context of a face distractor relates to several single-cell recording studies in the monkey brain: When two visual stimuli are present at the same time within a neuron's receptive field, the response of the neuron appears to be a weighted average of the responses to the individual stimuli when presented alone (Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999). That is, if a preferred visual stimulus for a cell is presented together with a poor visual stimulus, the cell's response is reduced compared to that elicited by the single good stimulus. This sensory suppressive interaction among multiple visual stimuli has been observed at the single-cell level in several visual areas in the ventral stream of the monkey brain (V2, V4, IT; Miller, Li, & Desimone, 1993; Moran & Desimone, 1985; Reynolds et al., 1999; Rolls & Tovee, 1995) and is generally interpreted as an expression of competition for neural representation (Desimone, 1998; Kastner & Ungerleider, 2001). In the inferotemporal cortex, it was described for neurons responding preferentially to faces (Miller et al., 1993; Rolls & Tovee, 1995). In the same vein, fMRI studies performed on human subjects reported a reduction of BOLD signal in several extrastriate visual areas of the ventral stream (V2, V4, TEO, TE) when presenting complex shapes simultaneously compared to sequential presentation (Kastner, De Weerd, Desimone, & Ungerleider, 1998; Kastner & Ungerleider, 2001). Thus, the results outlined in this section from studies using distractor interference paradigms are well grounded in the basic physiological properties of the visual system.

Evidence from Other Interference Paradigms

Studies using other paradigms, such as visual search, have also provided evidence consistent with an early perceptual capacity limitation for face processing. However, such studies suggest a larger capacity limit than that suggested by those studies using distractor interference paradigms. One such study utilizing a visual search paradigm found evidence that 2–4 faces can be perceived during one 200 ms fixation (Nasanen & Ojanpaa, 2004). This finding suggests either that faces are processed *very* rapidly or that more than one face can be processed in parallel, and thus that the capacity for face processing mechanisms is indeed greater than one. Consistent with this latter interpretation, there is evidence that visual processing in the inferotemporal cortex can occur in parallel, but only during the very early stages of processing (Rousselet, Thorpe, & Fabre-Thorpe, 2004). The capacity of this parallel system is relatively unknown. Therefore, the larger capacity limit for faces found in this search task (compared to that reported in studies using distractor interference paradigms) may reflect this very early processing limit, while other studies demonstrating a smaller perceptual capacity may reflect later perceptual processing stages. Thus, the amount of sharing of this limited perceptual capacity across images may vary from little (Jenkins et al., 2003) to none (Bindemann et al., 2005) depending on the task.

Further evidence for the capacity-limited nature of the perceptual processing of faces is provided by the failure of a target face to "pop out" from an array of faces (Purcell, Stewart, & Skov, 1996). The phenomenon of "pop-out"—when the time to find a target among an array of distractors is independent of the number of items to be searched—is believed to reflect preattentive processing that is immune to attentional capacity limits (Treisman & Gelade, 1980; Wolfe, Cave, & Franzel, 1989). Notably, though, observers experience a pop-out effect when searching for a face among nonface objects (Hershler & Hochstein, 2005). Some suggest that this pop-out effect may be due to low-level properties of face stimuli (VanRullen, 2006). However, others interpret this finding as consistent with previous studies suggesting that face processing is supported by a domain-specific, but capacity-limited mechanism.

Dual-task paradigms have also been used to explore capacity limitations, specifically assessing the degree to which two tasks interfere. In such paradigms, as the name implies, participants are required to perform two tasks concurrently. One such paradigm was used to demonstrate that face processing is perceptually limited: Palermo and Rhodes (2002) showed that the holistic encoding of a central face was reduced when participants concurrently performed a matching task on two flanking faces. The degree of holistic processing of the central face was measured using a paradigm similar to that used by Tanaka and Farah (1993); holistic processing was operationalized as the advantage for matching a face part encoded in the context of a whole face compared to when it was encoded in isolation. Tanaka and Farah (1993) found that holistic processing of faces is limited to those in an upright orientation, and thus it is noteworthy that holistic processing of the central face in this task appeared to be unaffected when the flanking faces were presented upside-down (Palermo & Rhodes, 2002). The results of this study demonstrate that interference between concurrently processed faces is not only found when two face stimuli are simply detected or perceived, but also when they actively recruit certain perceptual processes in the context of a deliberate task.

PERCEPTUAL PROCESS SHARING BETWEEN FACE AND NONFACE EXPERT PROCESSING

Evidence from Distractor Interference Paradigms

As outlined in the previous section, there is much evidence to suggest that face processing is capacity limited. Therefore, if face and nonface objects of expertise recruit overlapping processing resources, then these same general paradigms used to explore the capacity-limited nature of face processing should also reveal interference between face and nonface expert processing. Participants who possess expertise with a nonface category should experience greater capacity limitations (interference) when processing face and nonface objects of expertise concurrently, relative to novice observers processing the same face and nonface objects concurrently.

This hypothesis can be tested, for example, using the ERP distractor interference paradigm described earlier (Jacques & Rossion, 2004, 2006). This is possible because the reduction in the amplitude of the N170 in response to a target face stimulus due to the ongoing processing of another face stimulus most likely arises from regions in the cortex where "face-specific" activity is found, or, more specifically, where faces and nonface objects are functionally segregated. Notably, the onset of the reported N170 amplitude difference between faces and other objects (e.g., Bentin et al., 1996; Rossion et al., 2000) has a similar latency as the onset of the competition effect between individual faces (Jacques & Rossion, 2004, 2006). Moreover, the competition effect has a very similar distribution on the scalp as a classical N170 response to faces, suggesting that the locus of the competition effect largely lies in the occipitotemporal regions that participate in generating the N170 (Figure 8.1). Finally, both the N170 amplitude advantage for faces over objects (e.g., Bentin et al., 1996; Rossion, Joyce, Cottrell, & Tarr, 2003) and the competition effect between concurrently presented faces are larger in the right hemisphere, in agreement with the prominent role of this hemisphere in face processing (e.g., Hillger & Koenig, 1991; Sergent & Signoret, 1992).

If expertise leads to an overlap in the processes recruited for face and nonface objects, interference between the concurrent processing of face and nonface objects of expertise (as detected using the distractor interference paradigm) should increase with the development of expertise with the nonface object category. To address this question, Rossion, Kung, & Tarr (2004) used an established lab-based expertise training protocol to train participants to become experts with a category of novel objects, namely Greebles (Gauthier & Tarr, 1997). The N170 elicited by laterally presented faces was measured while participants were fixating on nonface objects (either Greebles or control stimuli of equivalent complexity). All participants were tested before expertise training with the Greebles set, at the middle of training, and following their reaching of an expertise level defined by a criterion used in previous behavioral studies (Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998). Following expertise training with the nonface object category, there was a substantial reduction in this N170 amplitude (~20% of signal) at occipitotemporal sites where the response to faces was maximal (Figure 8.2). Thus, the N170 amplitude in response to faces was strongly modulated as a consequence of expertise training with novel nonface objects. The reduction was specific to the object category trained (Greebles) but was not tied to specific items: The N170 amplitude reduction in response to faces was equally large whether participants focused on novel or old individual Greebles. In addition, the effects of expertise were gradual: There was already a substantial face N170 reduction midway through training. Thus, the increase in the degree of interference between the processing of face and nonface objects with expertise training provides strong support for the role of learning in the functional reorganization of occipitotemporal cortices.

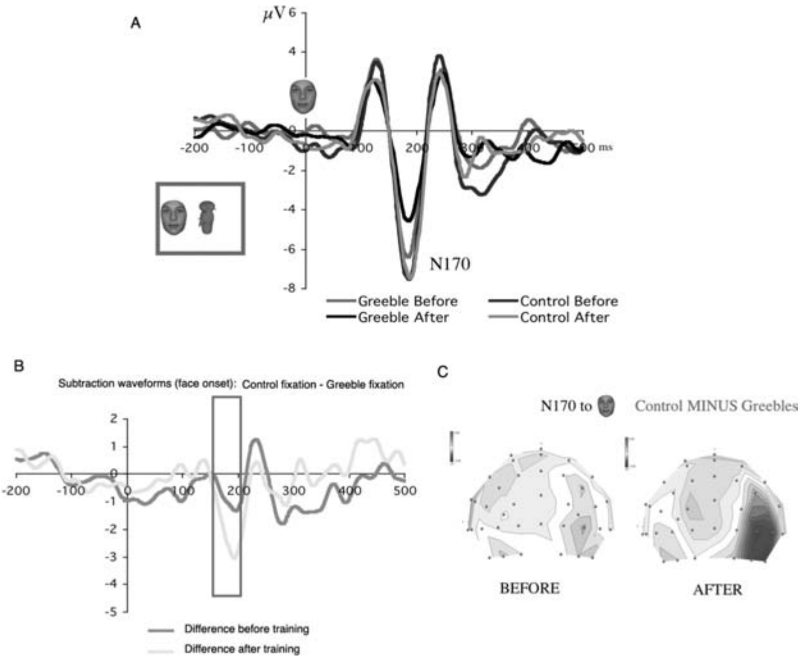

Figure 8.2 A. competition effect between Greebles and faces. The waveforms (average of four right occipitotemporal channels) follow the presentation of a lateralized face stimulus while participants fixate either a central Greeble or a control object. Following expertise training with the Greebles, there was a substantial and specific reduction of amplitude of the N170 in response to faces when participants fixate a stimulus from the Greeble category (novel or old, see Rossion, Kung, & Tarr, 2004). (B) Subtraction waveforms, showing the competition effect, that is, the reduction of the N170 for faces while fixating Greebles as compared to control objects (yellow waveform is the result of the subtraction between green and black traces displayed above). The red rectangle represents the time window used to display topographical maps of the back of the head on C. All waveforms are recorded in response to faces and thus show a strong modulation of the N170 amplitude to this category following training with nonface objects (adapted with permission from Rossion, Kung, & Tarr, 2004, “Visual expertise with nonface objects leads to competition with the early perceptual processing of faces in the human occipitotemporal cortex,” PNAS 101(40), pp. 14521–14526, ©2004 National Academy of Sciences (See color Plate 7).

More recently, Rossion, Collins, Goffaux, & Curran (2007) utilized a similar distractor interference paradigm to explore the question of interference between face and nonface domains of expertise in real-world experts, specifically participants with expertise at visually recognizing cars. Consistent with the findings from the study using lab-trained experts, the reduction in the amplitude of the N170 elicited by laterally presented faces while participants were fixating on pictures of cars relative to control stimuli (fixation cross and scrambled cars) was larger among car experts than car novices (Figure 8.3). This observation indicates that naturally developed long-term visual expertise with nonface objects can interfere with face processes at the perceptual level. Thus, perceptual expertise appears to lead to a functional overlap in the neural networks supporting the processing of face and nonface objects of expertise.

Notably, in both of these studies that report interference between the processing of face and nonface expert categories, the effect was much larger in the right hemisphere, reinforcing the idea of an overlap with the right dominant face processes, and in line with the localization of

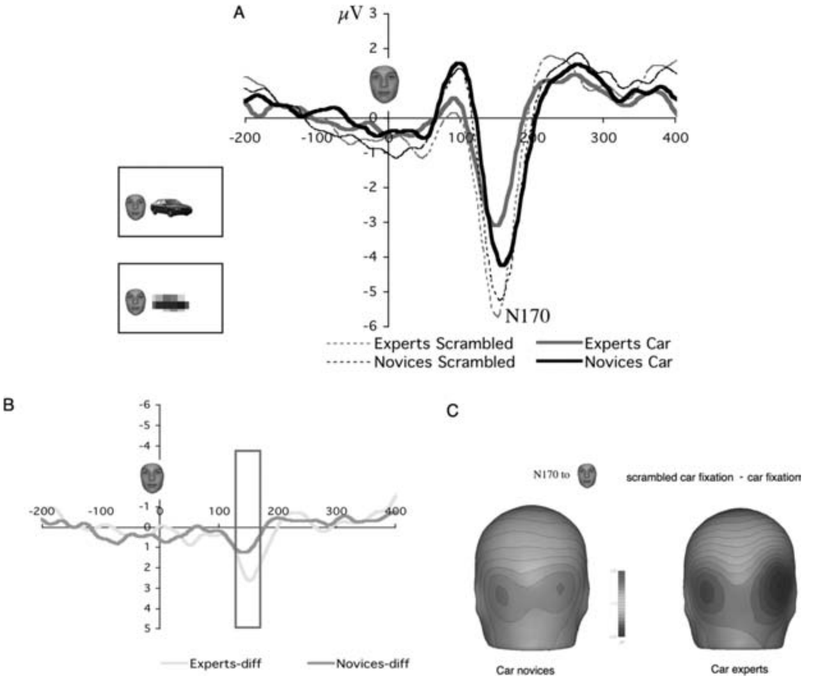

Figure 8.3 Competition effect between cars and faces. (A) The waveforms (T6 – right occipitotemporal channel) follow the presentation of a lateralized face stimulus while participants fixate either the picture of a car or a scrambled car (stimuli on the left). Relative to novices, car experts show a substantial and specific reduction of amplitude of the N170 in response to faces when they fixate novel cars (see Rossion, Collins, Goffaux, & Curran, 2007). (B) Subtraction waveforms, showing the competition effect, that is, the reduction of the N170 for faces while fixating cars as compared to scrambled cars for car experts and novices. The red rectangle represents the time window used to display topographical maps of the back of the head on C. All waveforms are recorded in response to faces and thus show a strong modulation of the N170 amplitude to this category following training with nonface objects (adapted with permission from Rossion et al., 2007, "Long-term expertise with artificial objects increases visual competition with early face categorization processes," *Journal of Cognitive Neuroscience,* 19(3), 543–555, Copyright 2007 MIT Press) (See color Plate 8).

previous effects of visual expertise in neuroimaging studies (e.g., Gauthier et al., 2000; Gauthier, Curby, Skudlarski, & Epstein, 2005; Gauthier & Tarr, 2002; Xu, 2005). The reduction of the N170 amplitude for faces was substantial in the two studies, contradicting the claim that facelike effects of visual expertise are generally small and/or nonreplicable (McKone & Kanwisher, 2005; McKone, Kanwisher, & Duchaine, 2007). Moreover, the link between visual expertise and the face N170 effect was reinforced by complementary analyses showing a highly significant correlation between the amount of visual expertise with cars, as measured in an independent behavioral task, and the N170 reduction for faces during the interference paradigm (Rossion et al., 2007). This indicates that visual expertise with nonface objects, and thus interference with face processes, is not all-or-none, but rather a matter of degree.

Beyond these observations of sensory suppressive interactions between visual stimuli at the single-cell level or in fMRI, the interest of these competition effects observed in ERP studies is two-fold. First and most interestingly, they show that competition between different object shapes (i.e., a car and a face stimulus) can be dramatically increased with visual expertise and thus is not entirely dependent on the visual structure of the stimuli. Second, by virtue of the excellent temporal resolution offered by ERP recordings and the spatial sampling of the whole system, they demonstrate that visual competition between faces and objects of expertise takes place as early as 130 ms after the onset of the stimuli, during a limited time window, and in occipitotemporal areas. Overall, these observations indicate that the neurofunctional processes involved in processing objects of visual expertise directly compete with those recruited to process faces at the perceptual level.

Evidence from Dual-Task Paradigms of Shared Holistic Processes

In these ERP studies, the subject's task is simple: to detect laterally presented faces while nonface objects of expertise (or control stimuli) are attended to. This simple orthogonal task is used to maintain attention, while ensuring that general attentional factors do not play a role in the effects observed (for further arguments against spatial or selective attention accounts of these effects, see discussion sections in Rossion, Kung, & Tarr, 2004; Rossion et al., 2007; as well as empirical evidence by Jacques & Rossion, 2007). However, the visual expertise hypothesis suggests that the modulation of the N170 in response to faces by a distractor object of expertise does not only occur because of an overlap in the way that face and nonface objects of expertise are merely seen or detected, but because of shared specific *processes*. What kind of early perceptual process would be recruited selectively for both faces and objects of expertise? It has long been suggested by many authors that one fundamental characteristic of our face processing system is that it treats faces holistically (Galton, 1879). There have been many definitions of holistic (and configural) face processing in the literature, but a simple and widely accepted definition is that facial features are integrated rather than being processed and represented independently (Sergent, 1984; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). Perhaps the best evidence for holistic processing of faces comes from the so-called face composite effect first described by Young and colleagues (1987). This effect was reported as the slowing down at naming the top half of a familiar face (cut below the eyes) when it is aligned with the bottom part of another face, as compared with the naming when the same top and bottom parts are offset laterally (i.e., misaligned) (Young et al., 1987). Over the years, it has been used with unfamiliar faces in individual discrimination tasks (Endo, Masame, & Maruyama, 1989; Goffaux & Rossion, 2006; Hole, 1994; Hole, George, & Dunsmore, 1999; Le Grand, Mondloch, Maurer, & Brent, 2004; Michel, Rossion, Han, Chung, & Caldara, 2006; Robbins & McKone, 2006), to demonstrate that facial features (here the two halves of the face) cannot be perceived in isolation, that is, they interact with each other during face processing. A functional locus of the effect is thought to be at early perceptual encoding stages for faces, being larger for low-spatial frequency faces (Goffaux & Rossion, 2006), and taking place primarily in the FFA with a right hemisphere advantage (Schiltz & Rossion, 2006).

There is evidence that faces are processed more holistically than other nonface objects in novices (Farah, Wilson, Drain, & Tanaka, 1998; Tanaka & Farah, 1993; Tanaka & Gauthier, 1997). However, visual expertise with nonface objects such as Greebles leads to enhanced holistic processing of these stimuli (Gauthier & Tarr, 1997, 2002; but see Robbins & McKone, 2006), raising the question as to whether these processes enter in competition for faces and nonface objects of expertise.

A dual task paradigm was developed to specifically test whether interference between the concurrent processing of face and nonface objects of expertise occurs at least in part due to competition for limited-capacity holistic processes (Curby & Gauthier, 2001; Gauthier, Curran, Curby, & Collins, 2003). In this interleaved two-back visual short-term memory task, car experts and car novices were required to process a face and a car in an overlapping manner (Figure 8.4); participants had to keep a face in mind while they processed the interleaved car and vice versa. All the images used in this task were composite images made by aligning the tops and bottoms of different cars or faces. Participants made same/different matching judgments about *only* the bottom halves of the images; the task-irrelevant (top) parts were either congruent (e.g., the two tops were different, and the correct response for the bottom judgment was "different") or incongruent (e.g., the two tops were different, and the correct response for the bottom judgment was "same"). Notably, the degree to which the congruency of the task-irrelevant part impacted performance on the task provided a means for measuring the degree of holistic processing of the faces in the car context. In order to specifically test for a trade-off between the *holistic* processing of faces and cars that is related to participants' expertise with cars, the degree of holistic processing of the cars was manipulated in two conditions: The

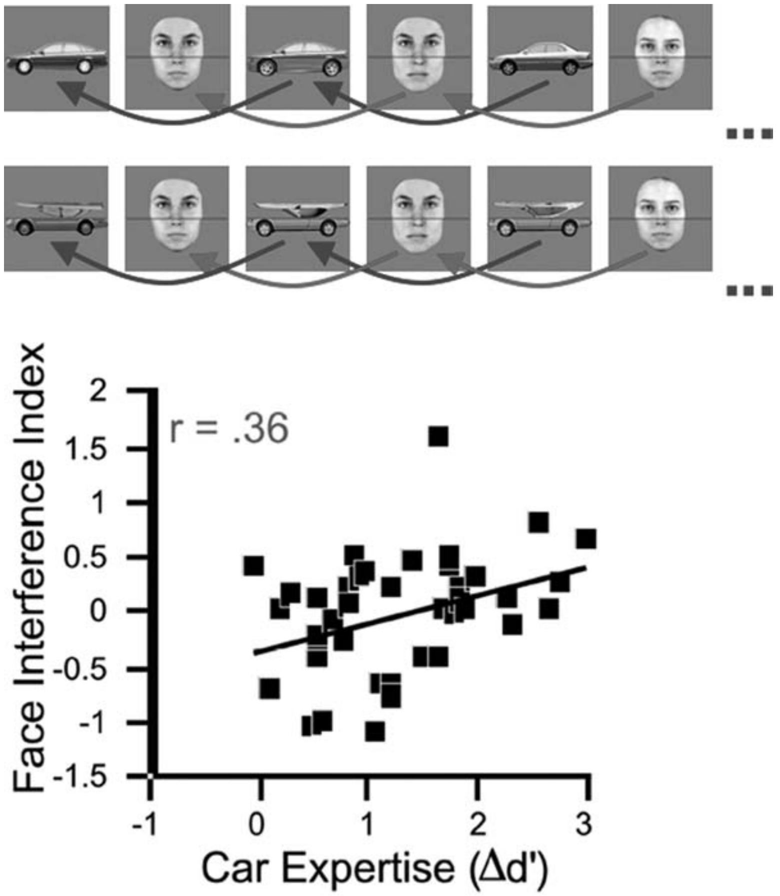

Figure 8.4 (A) diagram of the two-back task used to measure the interference effect of the cars on holistic face processing. Composites of faces and cars made of the top and bottom of different objects were alternately presented. Subjects were instructed to attend only to the bottom half of all the objects for the entire experiment and, for each one, to make a two-back judgment on whether the bottom part matched that of the last object from the same category. Normal faces (configurally intact) were interspersed with either normal cars (top row) or cars with a transformed configuration with the top half inverted (bottom row). (B) A scatter plot shows the correlation between the behavioral face interference index (i.e., holistic processing of faces in the context of normal cars minus holistic processing of faces in the context of configurally modified cars) and car expertise. The greater one's car expertise, the greater the reduction in holistic face processing in the normal car context relative to the configurally modified car context. (Figure adapted with permission from Gauthier et al., 2003, "Perceptual interference supports a non-modular account of face processing," *Nature Neuroscience*, 6(4), 428–432.) (See color Plate 9).

interleaved cars were either in a normal or modified configuration (i.e., their top halves were inverted) (Figure 8.4). Critically, disrupting the configuration of nonface objects of expertise (or faces) reduces the degree of holistic processing for these items (Gauthier et al., 2003; Gauthier & Tarr, 2002). Therefore, the interleaved cars in a modified configuration should compete less with the faces, relative to the interleaved cars in an intact configuration, for holistic processing resources.

The pattern of performance by experts and novices in this interleaved two-back task provided evidence for a functional overlap between holistic processes for face and nonface objects of expertise (Curby & Gauthier, 2001; Gauthier et al., 2003). Specifically, there was evidence of a trade-off between holistic processing of faces and cars that was related to expertise with cars; among experts, faces processed concurrently with cars in a normal configuration were processed less holistically than those processed in the context of cars in a modified configuration (tops inverted). Importantly, confirming the validity of the car manipulation, cars in the modified configuration were processed less holistically by experts and therefore presumably competed less for holistic processing resources. Notably, the degree to which the holistic processing of faces was impacted by the format of the cars was correlated with individuals' level of expertise with cars (Figure 8.4). Thus, the level of interference between the processing of these categories depended on the degree to which the car task recruited a holistic processing strategy; the level of interference depended both on one's visual expertise with cars and also whether the cars were intact (Curby & Gauthier, 2001). Therefore, the results of this study provide evidence of a functional overlap between the holistic processing of face and nonface objects of expertise.

This interference between holistic processes for faces and cars was also reflected in the N170 potential: the greater a participant's expertise with cars, the greater the N170 amplitude difference between faces presented among normal cars and faces presented among transformed cars (Figure 8.5; Gauthier et al., 2003). That is, the concurrent processing of intact cars, but not configurally modified cars, decreased the face N170 in car experts relative to that in car novices. Again, the expertise effect was located mainly on right occipitotemporal sites (Figure 8.5), as in the other studies showing more general competition effects between face and nonface objects of expertise (Rossion et al., 2004; 2007; Figure 8.2).

The demonstration of a functional overlap between face and nonface expert processing at perceptual stages (occipitotemporal N170) in the context of a dual-task paradigm is important as it provides further evidence that the interference between face and nonface expert processing measured using distractor interference paradigms is unlikely to arise through attentional confounds. Most notably, though, not only does it suggest that there is a behavioral consequence of this interference, but it also ties the source of such interference to the overlap in the early holistic processes recruited for face and nonface domains of expertise.

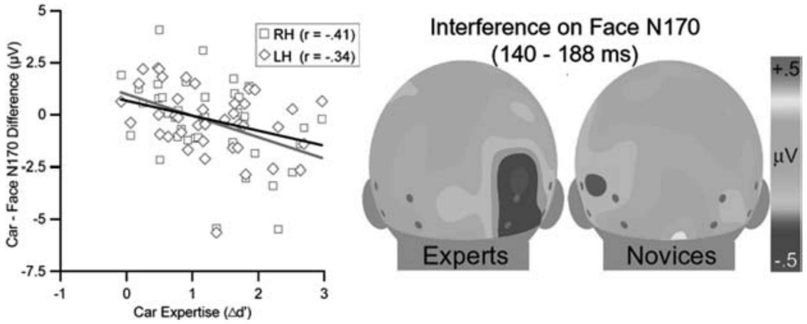

Figure 8.5 (A) A scatter plot shows the correlation between the electrophysiological face interference index (i.e., N170 amplitude for faces processed in the context of normal cars minus N170 amplitude for faces processed in the context of configurally modified cars) and car expertise. The greater one's car expertise, the greater the reduction in the N170 to faces processed in the normal car context relative to those processed in the configurally modified car context. (B) Electrophysiological map of the interference effect between face and cars illustrating the right hemisphere dominance of this effect. (Figure adapted with permission from Gauthier et al., 2003.) (See color Plate 10).

EVIDENCE FOR LONG-TERM INTERFERENCE BETWEEN FACE AND NONFACE EXPERT PROCESSING

The demonstration of interference between the processing of face and nonface objects of expertise leads to some intriguing questions regarding the long-term effects of dual expertise. Does such interference only occur when face and nonface objects of expertise are processed concurrently or are there long-term consequences of this resource overlap? More specifically, does the development of perceptual expertise with a nonface category reduce the resources available for face processing on a larger timescale?

A number of neurophysiological studies have demonstrated a clear effect of experience (or the absence thereof) on the organization of visual cortex. For example, Hubel, Wiesel, and LeVay (1977) demonstrated that preventing visual stimulation to one eye leads to a rewiring of monocular (eye-specific) columns in visual cortex in monkeys. Similarly, there are reports of an astounding degree of plasticity in somatosensory cortex in the brains of rodents, primates, and other animals (Buonomano & Merzenich, 1998; Feldman & Brecht, 2005; Kaas, Merzenich, & Killackey, 1983; Merzenich, Kaas, Wall, Nelson et al., 1983; Merzenich, Kaas, Wall, Sur et al., 1983). Elbert and colleagues (1995) have demonstrated that this plasticity is possible in the normal intact human brain even in the absence of the deprivation of experience. A group of string instrument musicians were found to have an increased representation for the little finger of the left hand, which correlated with the age at which the person started training (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995). Musicians, more generally, were also shown to have an increased representation for tones, pitch, and timbre in the auditory cortex (Pantev et al., 1995; Pantev, Engelien, Candia, & Elbert, 2001; Pantev et al., 1998). In addition to these functional differences, there have been reports of structural differences (white matter: Bengtsson et al., 2005; corpus callosum: Schlaug, Jancke, Huang, Staiger, & Steinmetz, 1995) that are believed to be a result of musicians' extensive experience and the resulting development of their specialized skills. Therefore, such demonstrations of experience-induced plasticity in the intact human brain suggests that the extensive experience required to develop perceptual expertise with an object domain could also potentially lead to a dynamic long-term reorganization of cortical areas. It is conceivable that such reorganization could lead to a trade-off between different expert categories that compete for the same limited processing capacity.

The first hints that a functional trade-off may occur between face and nonface expert processing were provided by Gauthier and colleagues (Gauthier et al., 1999). In their study, participants were scanned before, during, and after completing a lab-based expertise training paradigm with Greebles. In addition to the hypothesized finding of a training-related increase in upright Greeble-selective activation in the right middle fusiform area, there was an accompanying trend for a *decrease* in upright face-selective activation in this same region. More recent work, outlined below, suggests that this trend could reflect the early stages of experience-induced functional reorganization of this area.

A more recent training study with the patient SM who has visual agnosia with concomitant prosopagnosia provides support for the possibility of long-term interference between face and nonface object processing. Over the period of expertise training with Greebles, SM demonstrated a similar trade-off between face and nonface expert categories; SM's growing Greeble-selective activation in the fusiform region with training was accompanied by decreasing face selectivity in this same region (Behrmann, Marotta, Gauthier, Tarr, & McKeeff, 2005). However, presumably because SM's face system was already compromised through his acquired brain lesion in this region, this trade-off had severe consequences. SM's pattern of behavioral performance over the training period mimicked that of the fMRI results; SM's training-related performance increase in tasks with Greebles was coupled with decreasing performance in face perception tasks. SM's training with Greebles, however, did lead to some benefits; coupled with SM's improved ability to recognize novel Greebles was an improved ability to recognize common objects. Closer inspection of the fMRI data provided evidence consistent with a trade-off between the resources recruited for Greeble and face processing; areas of the brain that had once been face selective were no longer so after training and became more Greeble selective. These findings are consistent not only with the possibility of a dynamic reorganization of temporal cortex after extensive training, but also with the possibility that sharing and competition for resources between face and nonface processing can have long-term consequences.

Studies with real-world bird experts have also provided evidence consistent with the speculation put forth in this section. In a recent study, Kung

(2006) reported experiencing more difficulty locating a face-selective region in participants who were bird experts compared to those who were novices; using a standard method, an FFA could be localized in only four out of nine bird experts, whereas it was easily located in all nine novices. Kung (2006) proposed that the difficulty in defining a face-selective region among the expert group might be a result of a long-term dynamic reorganization of temporal cortex, resulting from these participants' extensive experience with birds. Consistent with this possibility, the degree of face-selective activation in or close to the FFAwas negatively related to performance in a behavioral measure of expertise with birds. This correlation was present across four different task comparisons (one- or two-back identity matching, one-back spatial location judgment, or passive viewing). Thus, supplementing studies reporting long-term interference between face and nonface objects of expertise in lab-trained participants, Kung's (2006) studies provided evidence of long-term interference in a group of real-world experts.

Notably, the possibility that there is long-term interference between face and nonface processing after the development of perceptual expertise with a nonface category is in conflict with a strong process map model of fusiform cortex. A strong process map model would only predict interference between face and nonface processing when the processing of the items from these two categories overlaps in time. Specifically, if brain regions in this area of cortex are defined in terms of processes rather than object categories and/or geometries, the development of expertise with a nonface category should not impact processing of faces as the same processes could presumably be used by both. Observations of long-term interference between face and nonface expert processing suggest that face and, for example, Greeble expertise, are coded by separate populations within the same area, and that visual expertise increases the representation for Greebles at the expense of the representation for faces. Interestingly, this would be akin to the competition between representations of different fingers in primary somatosenory cortex after a change in the relative stimulation of different fingers, such as in the case of string instrument musicians. Thus, the presence of long-term interference between face and nonface object domains of expertise would suggest that brain regions in the fusiform cortex are defined in terms of both processes and object category/geometry.

The studies reported in this section provide tantalizing hints suggesting the possibility of a long-term dynamic reorganization of temporal cortex after expertise training. This possibility would have profound consequences for our current understanding of the effects of learning in the brain. However, further work, with more rigorous pre- and posttraining comparisons and the use of high-resolution fMRI (Grill-Spector, Sayres, & Ress, 2006), is required to adequately test the validity of this hypothesis. In addition, studies utilizing single-cell neurophysiological recordings of pre- and posttraining activity could also provide much insight into the possibility of experience-induced long-term reorganization in the occipitotemporal cortex.

THE ROAD AHEAD: CLARIFYING THE NEUROFUNCTIONAL MECHANISMS UNDERLYING THE PERCEPTUAL COMPETITION BETWEEN FACE AND NONFACE OBJECTS OF EXPERTISE

In this chapter, we have outlined a number of studies that not only complement each other but also provide convincing evidence for a functional overlap between the processing of face and nonface objects of expertise. However, it is important to note that although there is evidence consistent with a functional overlap between face and nonface expert processing, two very important and related questions at the core of this overlap still remain unanswered: (1) *At what degree of resolution are the processes for faces and objects of expertise interfering*? and (2) *What are the neurofunctional mechanisms underlying this competition between face and expert processing*?

Spatial Resolution Issues and Neural Mechanisms of Interference Effects

The first question refers to the multiple levels of organization of the human brain (Churchland & Sejnowski, 1988), from synapses to networks of brain areas. In this chapter, we have reviewed recent evidence that there is competition between the processing of face and nonface objects of expertise at the systems level. These findings speak directly against a strong face modularist position that posits that the face processing system is functionally isolated or encapsulated. The data have been collected using behavioral and electrophysiological recordings in humans, with the results suggesting that the competition between face and expertise domains takes place at the perceptual level. A direct interpretation of these observations is that the development of expertise with nonface object categories (cars, Greebles) leads to an overlap of representations and processes for these nonface objects and faces. At what level of organization does this sharing take place? Are face-selective cells in the inferotemporal cortex (Gross, Roche-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982) becoming responsive to nonface object categories through expertise training? Or, alternatively, do these interference effects reflect the strengthening of inhibitory connections between anatomically distinct populations of neurons? Thus, the precise neural mechanisms underlying the interference between the processing of face and nonface objects of expertise are unclear.

The first hypothesis is that the same populations of neurons responding selectively to faces in occipitotemporal areas start responding to nonface objects (i.e., cars) with the development of visual expertise. The face N170 potential is thought to originate from multiple brain areas located in the occipitotemporal cortex, including the fusiform gyrus, the superior temporal sulcus, and the middle and inferior temporal gyri (e.g., Henson et al., 2003; Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005) where cortical surface potentials in response to faces—N200s—have been observed at roughly the same latency (Allison, Puce, Spencer, & McCarthy, 1999). Single-cell recordings in the monkey inferotemporal cortex show that cells in these areas are organized into columns that may be highly selective to face stimuli (e.g. Desimone, 1991; Perrett, et al., 1982; Tanaka, 1996; Tsao, Freiwald, Tootell, & Livingstone, 2006). However, it is yet unclear whether these neurons are tuned to respond to faces only (i.e., are "domain-specific"), or if they may also fire in response to members of a nonface object category following extensive visual experience with this category. Responses of single neurons in the monkey IT can be tuned to novel, visually similar objects—bars or "amoeba" shapes—following expertise training (Baker, Behrmann, & Olson, 2002; Logothetis & Pauls, 1995), and these neurons appear to share a number of properties with face-selective neurons such as viewpoint selectivity (Logothetis, Pauls, Bülthoff, & Poggio, 1994; Logothetis, Pauls, & Poggio, 1995) and a strong sensitivity to the removal of parts of the stimulus (Logothetis & Pauls, 1995). However, recordings in these studies are made in more anterior and ventral areas of IT than in the regions where most face-selective cells have been reported, and the response of these cells to face stimuli is unknown.

Since different faces are represented by the same population of neurons in a distributed coding system (Rolls, 1992), the similarity between the N170 competition effects found within the face domain (Jacques & Rossion, 2004, 2006, 2007) and those found between faces and nonface objects of expertise (Rossion et al., 2004, 2007) supports this hypothesis of an overlap of representations at the cellular level. Moreover, instances of long-term interference effects described previously in the section "Evidence for Long-Term Interference between Face and Nonface Expert Processing" (Behrmann, Marotta, Gauthier, Tarr, & McKeeff, 2005; Gauthier et al., 1999; Kung, 2006), which suggest that face processes suffer from the development of visual expertise with nonface objects, also support this view: A substantial part of the face representations would no longer be tuned selectively to faces, leading to a decrease in performance and neural activation for faces even without the concurrent presentation of nonface objects.

A second hypothesis is that the competition between objects of expertise and faces may be due to competitive interactions from distinct but neighboring populations of cells through local lateral inhibitory connections (Allison, Puce, & McCarthy, 2002; Waltz & Stanfill, 1988). In the monkey brain, local inhibition contributes to generating the specificity of IT neurons to complex stimuli. Furthermore, blocking inhibition in IT neurons mostly reveals responses of a cell to new stimuli differing from a preferred stimulus in systematic ways along certain parameters (contrast, shape, etc.), suggesting that local competition between preferred stimuli at the single-cell level is not randomly organized, but depends on the object features (Waltz & Stanfill, 1988). This mechanism would be difficult to reconcile with findings suggestive of long-term interference between face and nonface expert processing described in the previous section but fits with the observation that the competition is larger when the two domains (faces and nonface objects of expertise) are presented concurrently rather than sequentially (Rossion et al., 2007).

In summary, the competition effects described in this chapter between faces and objects of expertise may result from the recruitment of face cells for nonface objects of expertise, or from an increase in local competition generated from distinct populations of cells coding for objects of expertise, following extensive visual expertise training. Given the evidence summarized here, our view would be that both mechanisms are possibly at work. In the novice brain, faces and nonface objects may be represented by separate populations of neurons organized in clusters of columns, at a spatial resolution level below that of a functional area such as the FFA (Allison, et al., 1999; Tsao et al., 2006; Wang, Tanaka, & Tanifuji, 1996). However, this functional organization of high-level visual areas would remain relatively plastic in the adult brain, such that visual expertise with certain classes of objects would both (1) increase the tuning of neuronal populations within the same area for these objects at the expense of the face representations and (2) increase the competition through inhibitory connections between representations for nonface objects of expertise and faces. Future studies coupling interference paradigms with high spatial resolution methods such as fMRI or optical imaging are needed to clarify this issue. As far as the face modularity debate is concerned, it does not matter much whether competition effects reflect the recruitment of an overlapping set of neurons or rather inhibitory mechanisms between neighbor populations of neurons. What matters is that these effects take place *within the same functional area*, indicating that they concern clusters of neurons that are degenerate, that is, that can potentially carry the same function (Leonardo, 2005; Tononi, Sporns, & Edelman, 1999), and thus these findings are inconsistent with the face modularist view.

Functional Mechanisms

Through what functional mechanisms does the development of visual expertise lead to increased competition between the processing of face and nonface objects? Even though this view is somewhat simplistic, holistic processing, in the sense of a stronger interdependence of features, is a main candidate. There is evidence not only that faces are processed more holistically than other nonface objects in general (Farah, et al., 1998; Tanaka & Farah, 1993; Tanaka & Gauthier, 1997), but also that visual expertise with nonface objects leads to a shift to a more holistic processing strategy (Diamond & Carey, 1986; Gauthier & Tarr, 1997). Most importantly, some studies reviewed here show that measures of holistic processing reflect interference between concurrently processed faces and nonface objects of expertise (Curby & Gauthier, 2001; Gauthier et al., 2003). However, much future work with more compelling evidence is required to confirm these observations (Robbins & McKone, 2006). In addition, before the potential of holistic processing to account for the functional overlap between face and nonface expertise can be properly assessed, a clear understanding of the mechanism responsible for face holistic processing effects is necessary (e.g., the composite effect forming the basis of the interference index used in the dual-task paradigm; Gauthier et al., 2003). Currently, the concept of holistic face processing is not only defined differently by different groups, but it all too often is described in terms of the end product rather than the actual mechanism underlying this phenomenon. For example, one of the most widely accepted definitions of holistic processing describes the inseparability of features from their context in holistic representations (Farah et al., 1998). This definition was responsible for inspiring over a decade of insightful work on face processing, but an important unanswered question is how this interdependence between features and their context arises. Such attempts to understand the mechanism rather than just the consequences of holistic processing are a worthy direction for future research and will provide much insight not only into the functional basis of the overlap between face and nonface expert processing, but also into perceptual expertise more generally.

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