

## Chapter 11

# Face Perception and Perceptual Expertise in Adult and Developmental Populations

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### Introduction

C11.S1

Both developmental and adult investigations of perception unequivocally suggest that experience shapes perceptual abilities beginning early in development and throughout the lifespan (e.g. Gauthier and Nelson, 2001; McKone et al., 2007; Bukach et al., 2006; Scott and Monesson, 2009; Scott et al., 2007). Investigators studying perceptual expertise typically consider how domain-general cognitive and neural mechanisms are recruited when individuals learn about and become experts at recognizing and distinguishing visual categories, including faces and objects (Bukach et al., 2006). The term perceptual expertise has been used in various ways, but generally refers to an increased ability to discriminate and recognize among exemplars within some categories of visual stimuli relative to others. Investigations of perceptual expertise are usually designed to uncover the underlying representational and neural changes accompanying the acquisition of expertise using a variety of methods (e.g. behavioral measures of accuracy and reaction time, functional magnetic resonance imaging (fMRI), event-related potentials (ERPs), magnetoencephalography (MEG), eye-tracking, and computational modeling) and with various study designs and populations (e.g. real-world experts, training studies, clinical populations, developmental populations, and non-human primates). This interdisciplinary and multimethod approach has significantly contributed to understanding how humans, animals, and computers solve complex visual problems. The present chapter will review how behavioral methods, ERPs, and fMRI have been used to understand the acquisition of perceptual expertise in both adult and developmental populations.

As will be discussed further, in the context of specific studies reviewed below, behavioral tasks designed to assess perceptual expertise in adults include: perceptual discrimination and matching, categorization and recognition memory tasks (e.g. Tanaka and Taylor, 1991; Gauthier et al., 1998; Scott et al., 2006a). In infants, visual preference tasks are used to measure their ability to discriminate stimuli (e.g. Pascalis et al., 2002, 2005; Kelly et al., 2007; Scott and Monesson, 2009). In both adults and infants, ERPs are used to assess neural responses before and after training or in experts. ERPs are recorded non-invasively from a net or cap of recording electrodes placed on the head and have very high temporal resolution. ERP amplitude and latency responses reflect the activity of simultaneously active populations of neurons in the cerebral cortex. This activity results in electrical signals that propagate up to the scalp and can be recorded in response to the presentation of images or sounds. Researchers typically examine two ERP components, the N170 and the N250, when adults view faces, trained objects, or objects of expertise (e.g. Tanaka and Curran 2001; Scott et al., 2006a, 2008; Tanaka and Pierce, 2009). Analogous infant components,

the N290 and P400, have also been identified in response to faces and objects. The advantage of using ERPs with developmental populations is that no verbal or motor response is required and, given the appropriate equipment, recording electrodes can be applied easily.

Unlike ERPs, which have excellent temporal resolution, fMRI has been used to examine the hemodynamic consequences of neural activity and allows for an examination of spatial resolution on the order of a few millimeters (Hu et al., 1997). Investigators using fMRI with adults have examined how regions of the occipital and temporal cortex respond to faces, trained objects, or objects of expertise (e.g. Gauthier et al., 1999; 2000a,b; Kanwisher et al., 1997, 2000).

Using these various methods and techniques, studies of perceptual expertise have proven useful to our understanding of specialization of perceptual skills and categorization abilities and have expanded our understanding of the function and plasticity of the visual system (Bukach et al., 2006). The purpose of the present review is to provide an overview of the research focused on these questions and understanding the role and nature of experience in both the acquisition of perceptual expertise and the development of expert face processing.

### C11.S2 **The acquisition of expertise in adults**

Training studies have been used to mimic the natural acquisition of face and non-face perceptual expertise. Although training in the laboratory cannot be equated to years of real-world expertise, training novices in the laboratory allows for careful control and manipulation of experience. The use of training designs to study perceptual expertise began with training participants with novel objects, called greebles (Gauthier and Tarr, 1997). Greebles are a class of non-face, novel, cartoon-like objects that can be classified at multiple levels (i.e. the individual level, the subordinate level, and the basic level). Greebles have four protruding parts originating from a central cylinder-like body. Based on the configuration and orientation of these parts each individual greeble belongs to one of two “genders” and one of five “families”. In a now classic investigation, Gauthier and Tarr (1997) trained adult participants to discriminate greebles and found that training led greebles to be treated similarly to faces. Relative to object processing, face processing requires attention to the relations between the parts within the face (i.e. configural relations; Diamond and Carey, 1986; Farah, 1990; Rhodes, 1988; Sergent, 1988). Gauthier and Tarr (1997) confirmed that laboratory-trained greeble experts, but not novices, were faster at identifying trained greeble configurations as compared to untrained greeble configurations suggesting that training increased configural processing of previously novel non-face objects. Subsequent greeble training studies also suggest that face-selective areas of the cortex are recruited after training (Gauthier and Tarr 2002; Gauthier et al., 1999) and that an electrophysiological index of face processing, the N170 ERP component, increases in response to greebles after training (Rossion et al., 2002).

Researchers use training designs to investigate the behavioral and neural correlates of the factors influencing the acquisition of expertise in both adult and developmental populations. These studies will be summarized below and special attention will be paid to understanding: (1) how the level of category specificity is related to increased perceptual expertise (i.e. whether a stimulus is identified at the individual, subordinate, basic, or exposure levels), (2) how perceptual expertise leads to transfer and generalization within and across domains of expertise (3) how stable expertise effects are over time, (4) how perceptual expertise in one domain interferes with learning or performance within another domain, and (5) how feedback during learning influences later perceptual expertise (Gillebert et al., 2009; Gauthier and Tarr 1997; Gauthier et al., 1998; Lebrecht et al., 2009; Rossion et al., 2002, 2004, 2007; Tanaka et al., 2005; Tanaka and Pierce 2009; Scott and Monesson 2009; Scott et al., 2006a, 2008).

## Level of categorization and perceptual expertise

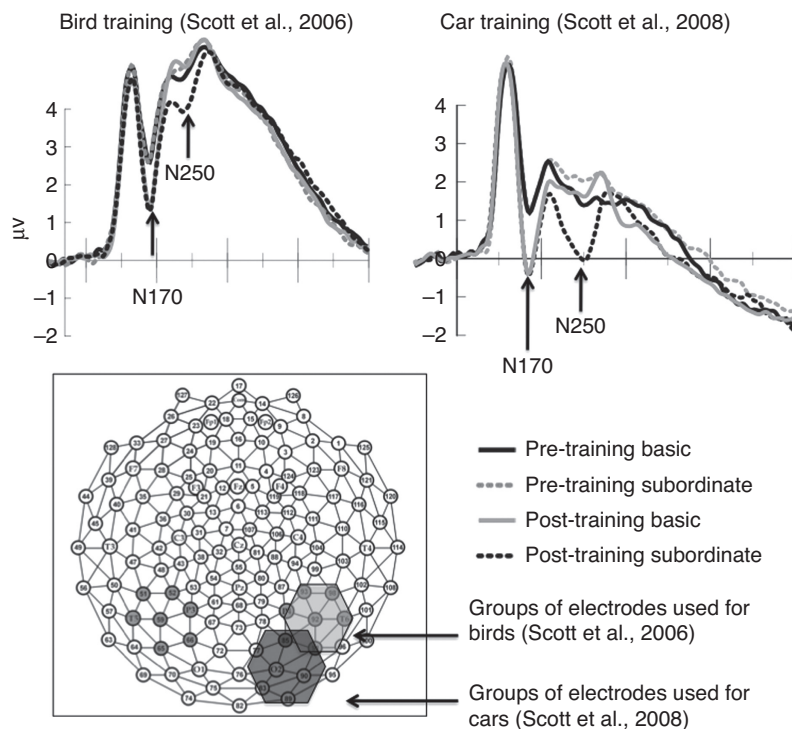
C11.S2.1

From the adult categorization literature we know that visual object and face categorization is unconstrained in the sense that a single object or face can be classified at multiple levels of abstraction. For example, Barack Obama can be categorized as a “human” at the superordinate level, a “man” at the basic level, an “African American man” at the general or subordinate level, and “Barack Obama” at the individual level. Consistent with this example, research has shown that when recognizing and discriminating familiar groups of faces, humans typically do so at the level of the individual (e.g. Johnny versus Billy; see Tanaka, 2001). In contrast, when recognizing and discriminating objects, such as the Eastern Screech Owl, people typically classify them at the basic level (i.e. bird; Jolicoeur et al., 1984; Murphy and Smith, 1982; Rosch et al., 1976). However, as expertise is acquired for a certain object category (such as expert bird watchers or car enthusiasts) individuals identify objects within this category at more subordinate levels (e.g. Barred Owl, BMW Z4) compared to non-experts (Tanaka and Taylor, 1991). Moreover, people who learn objects at more specific (“This is Mary’s mug”) compared to more general (“This is a mug”) levels extract different perceptual features during encoding, which subsequently improves performance on a change-detection task involving the trained objects (Archambault et al., 1999). Combined, these findings suggest that perceptual expertise can arise when discrimination and recognition demands require that exemplars within a category be differentiated from one another at more specific levels of abstraction (as is the case with faces).

Evidence for perceptual expertise arising when it becomes important to discriminate among category exemplars also comes from investigations which manipulated the level at which participants learn birds (Tanaka et al., 2005; Scott et al., 2006a), cars (Scott et al., 2008), other-race faces (Tanaka and Pierce 2009), four-circle blob stimuli (Nishimura and Maurer 2008), and artificial objects called “Ziggerins” (Wong et al., 2009). These investigations consistently find that subordinate- or individual-level learning leads to increased within-category discrimination abilities, greater configural processing, and more specialized neural responses. For example, in one study, adult participants were trained to categorize one family of birds (e.g. owls) at the subordinate level and another family of birds (e.g. wading birds) at the basic level across six training sessions over a two-week period (Scott et al., 2006a). Before and after training, participants completed a sequential species-level discrimination task while behavioral measures of accuracy and cortical ERPs were recorded. Results showed increased accuracy, as measured by  $d'$ , after species-level training (the subordinate-level) but not after family-level training (the basic level). This improvement generalized to untrained exemplars within the trained species as well as untrained species within the same family. These behavioral differences were also mirrored in the electrophysiological response. Typically, the N170 is recorded over occipitotemporal brain regions and is thought to be an index of face processing and perceptual expertise as it is consistently larger in response to faces relative to objects (Carmel and Bentin 2002; Bentin et al., 1996; Botzel et al., 1995; Eimer 2000; Rossion et al., 2000; see Eimer, Chapter 17, this volume) and in response to objects of expertise relative to other objects (Tanaka and Curran, 2001). The N250 component is also related to face processing and is evoked in response to repeated and familiar faces compared to novel or unfamiliar faces (Schweinberger et al., 2002, 2004; Tanaka et al., 2006). Expertise training with birds increased the amplitude of both the N170 and N250 ERP components (Scott et al., 2006a). However, the N170 increased equally for both subordinate-level, and basic-level training whereas the N250 only increased in response to subordinate-level training. These results suggest that N170 amplitude is likely influenced by general effects of category experience resulting in expert categories, such as faces or objects of expertise, eliciting greater amplitude N170s.

Both the behavioral and ERP results reported by Scott and colleagues (2006a) were replicated in a subsequent investigation with car stimuli (Scott et al., 2008). In this study an additional exposure-only condition was added and participants returned for post-test assessments immediately after training and 1 week after training ended. Training included antique cars, modern SUVs, and modern sedans and each participant was trained with exemplars from each of these three categories at either the subordinate, basic, and exposure-only level. Results revealed increased behavioral performance after subordinate-, but not basic-level or exposure training and an increased N170 in response to all three types of training. Similar to the behavioral results, the N250 increased only in response to subordinate-level training. The results from both of these investigations suggest that subordinate-level training leads to an increased ability to discriminate exemplars within a category, which is indexed by the N250 ERP component. Figure 11.1 shows both the N170 and N250 results in response to basic- and subordinate-level training.

The increased accuracy and differential ERP responses after subordinate-level training were recently replicated using face stimuli (Tanaka and Pierce, 2009). In this study, Caucasian adults were trained with African or Hispanic faces at either the individual (each face was assigned a different label) or category (all faces were labeled the same) levels. Post-training recognition accuracy increased after subordinate-level but not category-level individuation training regardless of race. In addition, the N250 ERP response also increased after subordinate-level individuation



C11.F1 **Fig. 11.1** Event-related potentials (ERPs) before and after basic-, and subordinate-level expertise training in two recent adult investigations (Scott et al., 2006a, 2008). Groups of electrodes (shaded regions), recorded over occipital and temporal brain regions, were averaged for both the N170 and N250 components.

training, further suggesting that the N250 is an index of increased subordinate-level discriminatory abilities for faces and objects. In another investigation, individual-level training with other-race faces also decreased implicit racial biases, suggesting a link between the perceptual and social face biases (Lebrecht et al., 2009).

Holistic and configural visual processing are hallmarks of both face processing and real-world perceptual expertise (see Tanaka and Gordon, Chapter 10, this volume; Busey and Vanderkolk, 2005; Diamond and Carey, 1986) and previous studies reported increases in holistic and configural processing after perceptual training (Gauthier and Tarr, 1997; Gauthier et al., 1998; Wong et al., 2009). Although definitions of holistic and configural processing vary, three types of configural processing have been examined in relation to face processing (for review see Maurer et al., 2002). First-order configural processing occurs during the general detection of a face (two eyes above a nose, above a mouth). Second-order configural processing involves detecting spatial relations among face features. Finally, holistic processing involves integrating information across the face.

To examine second-order configural processing of non-face objects, one investigation trained participants with stimuli comprised of four circular blobs (Nishimura and Maurer, 2008). Two groups of participants learned these stimuli at either the individual (Bobo 1, Bobo 2, Bobo 3) or the basic (all stimuli named Bobo) level and were tested before and after training using a same/different discrimination task. Results revealed increased sensitivity to second-order configural stimulus changes after adults were trained at the individual level relative to the basic level. Recently, two groups of adults were trained with artificial objects called “Ziggerins” (Wong et al., 2009). In this study individuation, but not categorization, training led to increased holistic processing as measured by a composite task in which the top and bottom halves of the stimuli were manipulated.

In sum, the results from studies using perceptual training suggest that subordinate- or individual-level learning leads to increased perceptual expertise as indexed by both behavioral and electrophysiological indices. Behaviorally, adults trained at more specific levels of abstraction show increased performance on a change-detection task with objects (Archambault et al., 1999), increased ability to discriminate exemplars within trained categories of faces and objects (Scott et al., 2006a, 2008; Tanaka et al., 2004; Tanaka and Pierce, 2009), decreased implicit racial biases (Lebrecht et al., 2009), and increased configural processing (Nishimura and Maurer, 2008; Wong et al., 2009). In addition, training at the subordinate level increased the amplitude of both the N170 and the N250 ERP components (Scott et al., 2006a; 2008; Tanaka and Pierce, 2009). However, the N170 also increased after basic-level category training as well as exposure training (Scott et al., 2008) suggesting that it may index increased exposure to object categories whereas the N250 is an index of subordinate or individual level learning.

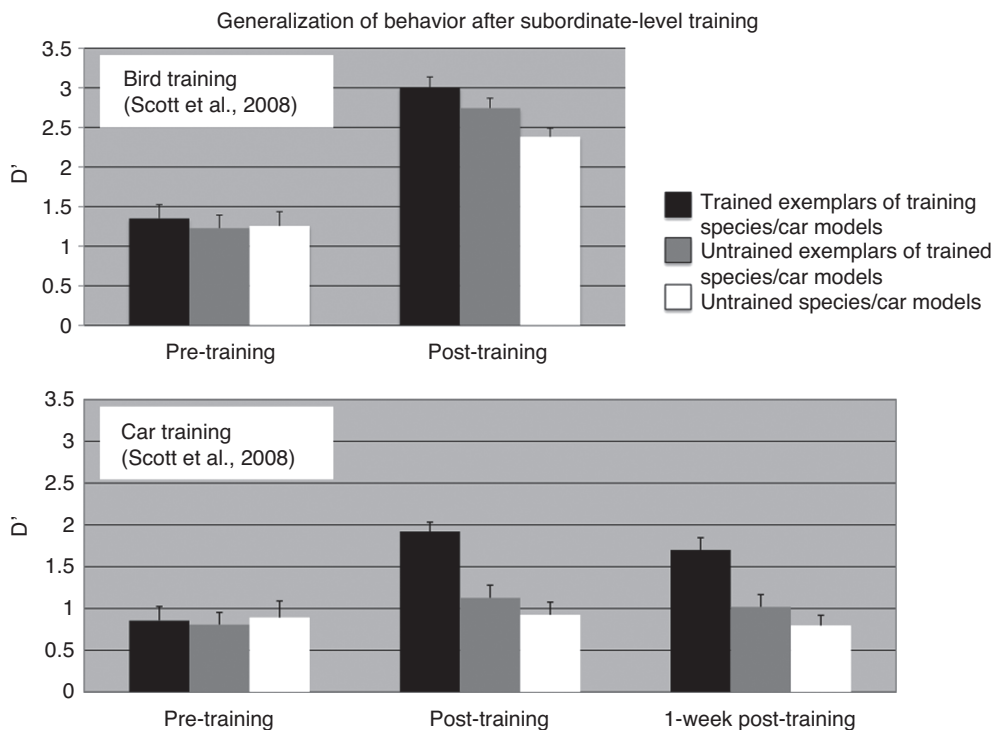
## Generalization of perceptual expertise

C11.S2.2

One question that permeates the study of perceptual learning as well as the study of perceptual expertise is whether or not training effects generalize to novel exemplars of trained categories. Investigations of low-level perceptual learning (e.g. Ahissar et al., 1998; Fiorentini and Berardi, 1980; Poggio et al., 1992) often find little if any generalization of learning after training. Failure to generalize learning has also been found in more complex forms of perceptual learning including domains of expertise. For example, although radiologists are experts at finding and detecting radiological anomalies they do not show a general advantage in visual search tasks such as “Where’s Waldo” or the “NINA” drawings from *The New York Times* (Nodine and Krupinski, 1998). In another investigation, parents of monozygotic twins were faster at discriminating their own twins’ faces, but this increased discrimination did not generalize to unfamiliar twin pairs (Saether and Laeng, 2008). However, other investigations have found at least partial generalization

after expertise training. For example, after greeble training, learning generalizes to structurally similar, but not structurally dissimilar, exemplars of greebles (Gauthier et al., 1998).

Generalization of learning was also found after training with birds (Scott et al., 2006a) and cars (Scott et al., 2008). Training with birds led to an increased ability to discriminate untrained exemplars of trained species and untrained species of birds within the trained family (i.e. owls or wading birds; see Figure 11.2). Car training, on the other-hand, led to a small increase in ability to discriminate untrained exemplars of trained models but this increase did not generalize to untrained models within the trained car family (i.e. SUVs or Sedans). This generalization discrepancy after bird and car training suggests that stimulus features within the trained category may influence generalization. There are several differences between birds and cars that might lead to more or less generalization. For example, features like color, texture and contrast are helpful diagnostic cues for subordinate-level bird learning, but not subordinate-level car learning. In addition, participants in the car training study likely had more previous experience categorizing and labeling cars than those in the bird training study had with birds, which might interfere with their ability to learn new subordinate-level labels. Finally, the generalization differences may also reflect differences between natural kinds and artifacts (or living versus non-living things). These hypotheses can be tested using computer-generated categories of objects that are previously unfamiliar to participants and can be made to be more car- or bird-like.



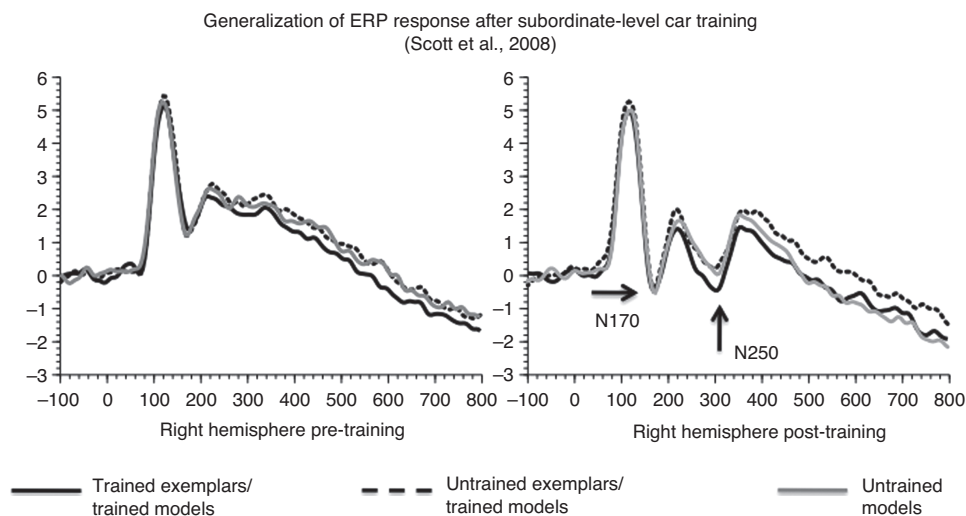
**Fig. 11.2**  $D'$  before and after and subordinate-level expertise training in two recent adult investigations (Scott et al., 2006a, 2008). Generalization of training was tested in two conditions (untrained exemplars of trained species/car models and untrained exemplars of untrained species/car models). The top panel pictures results after bird training and the bottom panel pictures results after car training.

Despite the less than perfect behavioral generalization for birds and cars after training, both the N170 and the N250 responses generalized perfectly for untrained exemplars of trained species/models of birds/cars and untrained species/models of birds/cars (see Figure 11.3 for an example from Scott et al., 2008). Thus, the electrophysiological increases are not limited to the specific episodic experiences because they generalize to untrained exemplars. It is currently unclear why this disconnect between behavioral and electrophysiological generalization exists. However, given that the electrophysiological responses reported by Scott and colleagues (2006, 2008) index early visual processing, it would not be surprising if additional later occurring perceptual and cognitive processes contributed to the observed behavioral responses resulting in this discrepancy.

### Stability of perceptual expertise

C11.S2.3

Training studies are also useful for understanding how people maintain perceptual expertise over time. Scott and colleagues (2008) used a pre- and post-test design that included an immediate post-test and a 1-week post-test. After training at the subordinate, basic and exposure levels with three different classes of cars, ERPs and behavioral discriminability were measured at both post-tests. Neither basic-level nor exposure training led to increased discrimination after training. However, subordinate-level training led to increased discrimination immediately and one week after the end of training. An increased N170 response was found at the immediate post-test for all three types of training. However, this increase did not carry over to the 1-week post-test. This lack of stability suggests that continued category exposure over time is necessary to maintain amplitude increases seen for the N170. It is possible that previous reports of increased N170 amplitudes to faces are due to the consistent exposure humans have with faces. The N250 only increased in



**Fig. 11.3** Event-related potentials (ERPs) before and after subordinate-level expertise training in a recent adult investigation (Scott et al., 2008). Pictured are the N170 and N250 components, recorded from averaged electrodes over occipital and temporal brain regions. Generalization of training was tested in two conditions (untrained exemplars of trained species/car models and untrained exemplars of untrained species/car models). N170 and N250 ERP increases generalized across all conditions.

C11.F3

response to subordinate-level training and this increase remained stable at the immediate-and 1-week post-test. These results further support the notion that more specific levels of training lead to enhanced perceptual expertise, as indexed by increased discrimination, which is reflected in increases in the N250 ERP component.

#### C11.S2.4 **Interference across domains of perceptual expertise**

Evidence from real-world and from laboratory-trained experts suggests that perceptual expertise with non-face objects leads to neural competition with faces within occipitotemporal regions of the cortex (Gauthier et al., 2003; Jacques and Rossion 2004; Rossion et al., 2004). In one study, holistic processing of cars in car experts reduced holistic processing of faces and the N170 amplitude difference between cars and faces was reduced with increased car expertise (Gauthier et al., 2003). In addition, after greeble training, the amplitude of the N170 is significantly decreased in response to faces when they are viewed concurrently with greebles compared to other (non-expert) objects (Rossion et al., 2004). Interference across expertise domains suggests that non-face perceptual expertise and face processing may rely on shared neural resources (Gauthier and Curby 2005).

#### C11.S2.5 **Feedback during the acquisition of perceptual expertise**

Results reported by Scott et al. (2008) suggest that mere exposure is not sufficient for improved perceptual expertise, but that subordinate- or individual-level learning is required for the acquisition of perceptual expertise for categories of objects and faces. Thus, increases in perceptual expertise may require category exposure coupled with learning at more specific levels of abstraction. These results are consistent with a neurocomputational model of basic- and subordinate-level learning that relies on both unsupervised and supervised mechanisms to simulate expert perceptual discrimination (Nguyen and Cottrell, 2005). In this computational model and in human training studies, feedback during learning appears to play a critical role. When learning to categorize or discriminate visual stimuli both explicit and implicit rules are formed via feedback-dependent mechanisms (Ashby and O'Brien, 2005; Ashby et al., 1998). Several brain regions, including the inferior temporal cortex, the basal ganglia, the anterior cingulate cortex, and the frontal cortex, mediate these feedback-dependent processes.

To understand the role of feedback in the acquisition of expertise Krigolson and colleagues (2009) trained adult participants with several exemplars of two different categories of computer generated blob stimuli, which were labeled "A" or "B" and then recorded ERPs while they completed a category-verification task and were given positive and negative feedback. The category verification task included exemplars from the A and the B category as well as a morphed category (50% A and 50% B). Participants were required to indicate whether or not images of blobs matched or did not match the provided label. Feedback for the morph category had a 50% probability of being positive or negative. Behaviorally, two groups emerged, including: (1) low learners and (2) high learners (greater than 70% performance). The high-learner, but not low-learner group, exhibited a greater amplitude N250 and ERN (error related negativity) response during the category verification task. The ERN is an ERP component that occurs in response to internal error detection (response ERN) or external error detection (feedback ERN) and is thought to be mediated by the anterior cingulate cortex (Holroyd et al., 2004). Krigolson and colleagues (2009) found increased amplitude for both types of ERNs in the high, but not low, learners. These findings support a link between the reinforcement learning system in medial-frontal regions of the brain (as indexed by the ERN) and the perceptual category learning systems in the occipital and temporal regions of the brain (as indexed by the N250) during the acquisition of perceptual expertise.

## Summary of perceptual expertise in adults

C11.S2.6

Investigations using training designs with adults have provided us with invaluable information about the neural and behavioral mechanisms whereby people acquire perceptual expertise. From these studies it is clear that subordinate- and/or individual-level learning, mediated by feedback, is important for the acquisition of expertise. Moreover, increased perceptual expertise is associated with increased configural processing, increased neural competition when concurrently processing faces and objects of expertise, and increased generalization to similar non-expert domains for some stimuli. However, increased perceptual expertise with faces may also lead to perceptual biases such as the other-race effect, the other-age effect, and the other-species effect (see Pascalis and Wirth, Chapter 37; Lee et al., Chapter 39, this volume). These naturally occurring biases likely originate early in development and are a result of greater individual-level experience with familiar groups of faces (Scott and Monesson, 2009).

## The acquisition of perceptual expertise during development

C11.S3

Recently, the acquisition of perceptual expertise in adulthood has been hypothesized as a model for understanding the development of face processing abilities in infancy and childhood (Scott and Monesson, 2009; Quinn, in press). However, the study of development has also helped inform our understanding of adult perceptual expertise (Gauthier and Nelson 2001). Researchers studying perceptual expertise and face processing in development typically use both behavioral and ERP methods. Preferential looking paradigms, which measure infant looking duration and direction of visual fixations, have been used to examine infant preferences and discrimination. One such paradigm is the visual-paired comparison (VPC) method. This method capitalizes on infants' preference for novelty after either a familiarization or habituation period (for review see Synder et al., 2007). Studies using ERPs have helped elucidate the neural mechanisms involved in the development of face and object processing during the first year of life (e.g. de Haan and Nelson, 1999; de Haan et al., 2002; Halit et al., 2003; Scott and Nelson, 2006; Scott et al., 2006b).

The ontogeny of face processing abilities is still a matter of active debate. Some have argued that expertise with faces stems from an innate neural module (e.g. Farah et al., 2000; de Schonen and Mathivet, 1989; Morton and Johnson 1991) and others argue that face processing abilities and the underlying neural specialization are acquired through experience (e.g. Gauthier and Nelson 2001; Le Grand et al., 2001, 2003). A close examination of the literature related to this debate reveals several important theoretical subtleties. For example, early work suggests that newborns prefer to look at face-like stimuli relative to inverted and scrambled control stimuli (Goren et al., 1975; Johnson et al., 1991). Although this early preference for faces is not debated, the mechanisms responsible for this preference are debated. One view is that the newborn preference for faces stems from an innate subcortical mechanism (CONSPEC) (Morton and Johnson 1991). CONSPEC leads infants to prefer face-like stimuli (two blobs over another blob). After the second month of life, CONSPEC is replaced by CONLERN, an experientially based mechanism that involves a diffuse network of cortical areas and allows for continued cortical specialization and tuning (Johnson 2000; Morton and Johnson 1991). An alternate account of the newborn face preference suggests that general, as opposed to specific, biases within the visual system lead newborns to prefer face-like stimuli (Simion et al., 2001, 2002). For example, newborns prefer stimuli with more elements in the upper relative to the lower half of a stimulus (i.e. "T"-like stimuli) (Simion et al., 2001, 2002). These researchers posit that the newborn face preference is not face-specific, but can be found to any stimulus whose inner and outer parts are congruent and top-heavy. Although important for understanding the origins of face processing, it has proven very difficult for

researchers to determine whether newborns prefer faces and stimuli with more elements in the upper half because they are face-like or because they have more elements in the upper half.

This debate notwithstanding, several studies have focused on understanding how early perceptual experience influences the behavioral and neural specificity of face processing during the first year of life. Research in this area has revealed several perceptual biases arising within the first year of life, including the other-race (Hayden et al., 2007, 2009; Kelly et al., 2005, 2007) and the other-species effects (Pascalis et al., 2002, 2005; Scott and Monesson, 2009), as well as a specific preference for female relative to male faces in infants whose primary caregiver is female (Quinn et al., 2002). The development of these perceptual biases is not surprising given a recent report suggesting that the majority of infants' time is spent interacting with same-race females (Rennels and Davis, 2008).

### C11.S3.1 Perceptual narrowing

Nelson (2001) proposed a model of the development of face perception, which suggests that infants tune their face processing system to better recognize and differentiate commonly experienced face groups. Thus, during development, infants' perceptual abilities are tuned to the demands of their environment, a process Nelson called *perceptual narrowing*. Perceptual narrowing is a form of developmental tuning that is present across several domains of perceptual development (for review see Scott et al., 2007). Results from investigations with infants are consistent with this model in that there appears to be a decline, from 6 to 9 months of age, in the ability to differentiate between two faces within a rarely experienced face category (e.g. other-species faces: Pascalis et al., 2002, 2005; Scott and Monesson, 2009, or other-race faces: Kelly et al., 2007; for review see Pascalis and Wirth, Chapter 37, this volume). For example, after familiarization to a single monkey face 6-month-old infants look longer at a novel monkey face when paired with the recently familiarized face, indicating discrimination of these two faces (Pascalis et al., 2002, 2005; Scott and Monesson, 2009). However, neither 9-month-olds nor adults show discrimination of a recently familiarized monkey face from a novel monkey face, unless they have had prior experience with monkey faces (Pascalis et al., 2002; Scott and Monesson, 2009).

In a recent non-human primate training study, infant monkeys were reared without exposure to faces for a period of between 6 and 24 months (Sugita, 2008). After this deprivation period monkeys did not show a preference for human or monkey faces, whereas control, non-deprived, monkeys preferred to look at monkey faces. After deprivation, one group of monkeys was exposed to human faces and another group of monkeys was exposed to monkey faces for one month. Using the VPC task, control monkeys discriminated familiar and novel monkey, but not human, faces. Deprived monkeys exposed to human faces preferred to look at human faces, looked equally at monkey faces and non-face objects, and could discriminate human but not monkey faces. Deprived monkeys with monkey face experience preferred to look at monkey faces and exhibited discrimination for monkey, but not human, faces. Finally, monkeys deprived of monkey face experience continued to showed deficits discriminating monkey faces 1 year after being placed in a typical environment with other monkeys. These results are consistent with reports of perceptual narrowing in human infants and support the existence of a sensitive period for the development of face expertise. However, the timing of this sensitive period is not well understood and may not be limited to the first year of life.

Initially, our understanding of perceptual narrowing was limited in that several investigations (Kelly et al., 2007; Pascalis et al., 2002, 2005) found a decline from 6 to 9 months of age, but none examined the early experiences that contribute to this decline. Pascalis and colleagues (2005) designed an infant training study to determine whether three months of experience with monkey

faces (six individually named monkey faces presented in a picture book) resulted in maintenance of the ability to distinguish these faces after training. Results revealed that 9-month-old infants with book training not only discriminated trained monkey from novel monkey faces, but also maintained the ability to discriminate a newly familiarized monkey face from a novel monkey face. This evidence of generalization is important for our understanding of category learning and the development of expertise with faces. However, following the pattern reported by Pascalis et al., (2002), 9-month-olds without training did not show evidence of discrimination. These results suggest that during the first 9 months of life, infants may be drawn to make perceptual distinctions among faces within commonly experienced, relative to uncommonly experienced, face groups. Furthermore, this increased sensitivity to familiar groups of faces may function to shape later perceptual abilities.

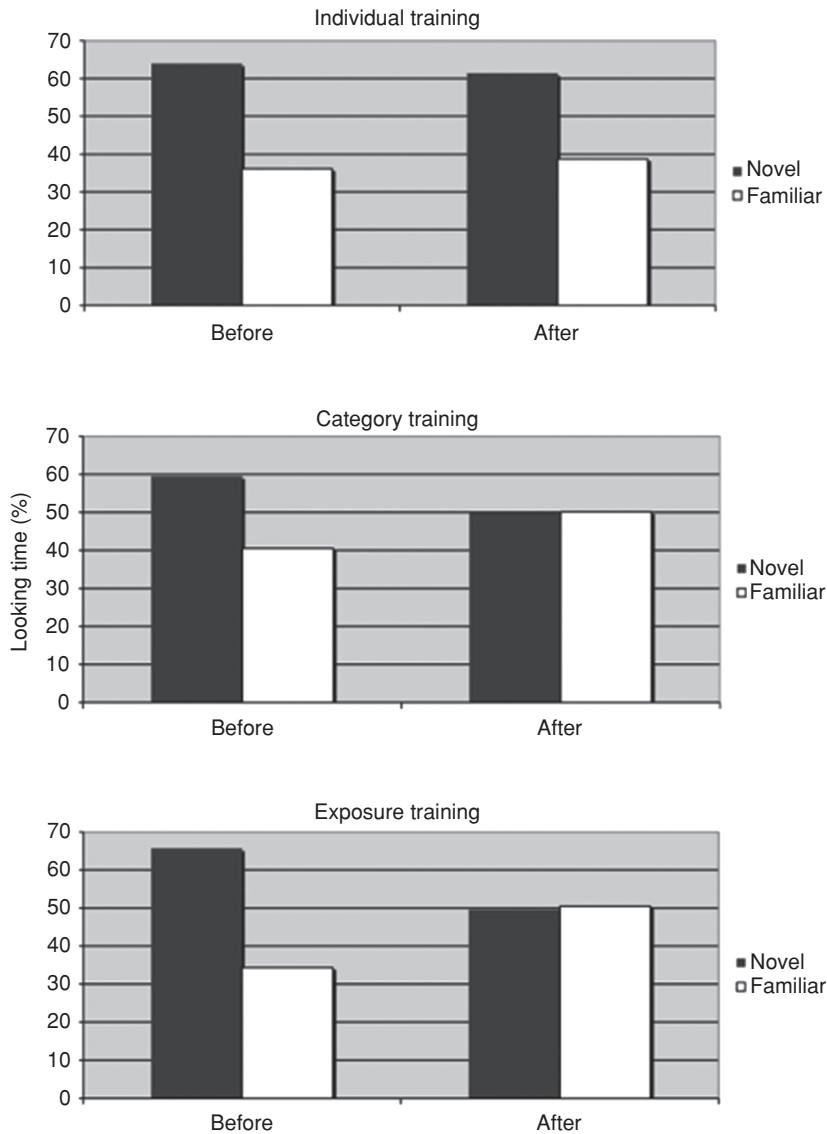
### Level of categorization and perceptual expertise

C11.S3.2

Scott and Monesson (2009) hypothesized that the manner in which perceptual expertise is acquired in adults (e.g. Scott et al., 2006a, 2008; Tanaka and Pierce 2009) is similar to the manner in which face expertise is acquired through experience in the course of normal development. Six-month-old infants were trained to recognize six monkey faces at the individual level (i.e. each face is individually labeled during training) over a 3-month period and, similar to previous findings, they maintained the ability to discriminate monkey faces. However, infants trained with these same six faces categorically (i.e. all faces are labeled “monkey”) or who were simply exposed (i.e. no label control group) to these faces, showed a decline in the ability to discriminate monkey faces (Scott and Monesson, 2009; see Figure 11.4). These results suggest that during the first year of life, the decline in infants’ ability to distinguish between two faces within an unfamiliar category (i.e. two other-species faces) is critically dependent on the lack of experience individuating these unfamiliar types of faces. These results are noteworthy because they suggest that face biases originate in infancy and are dependent on the relative lack of experience individuating unfamiliar groups of faces. Moreover, it appears that learning multiple exemplars at more specific levels may lead to greater expertise for familiar face groups.

In adults, the N170 component differentiates faces and objects (e.g. Carmel and Bentin, 2002) and is delayed (e.g. Bentin et al., 1996) and enhanced (e.g. Rossion et al., 1999) to inverted relative to upright faces (but not inverted relative to upright objects). However, in adults, inverting monkey faces, similar to objects, has no effect on the N170 (deHaan et al., 2002) (see Eimer, Chapter 17, this volume for further discussion of the adult N170). In infants, the N170 response is distributed across two components, a negative N290 component and a positive P400 component (de Haan et al., 2002; Halit et al., 2003; Scott and Nelson, 2006; Scott et al., 2006b). In 6-month old infants, the P400 is greater for upright versus inverted faces (de Haan et al., 2002) and delayed for objects compared to faces (de Haan and Nelson, 1999). Future work is needed to more clearly determine the relation between the adult N170 and N250 components and the infant N290 and P400 components.

In contrast to previous behavioral findings (Pascalis et al, 2002), the 9-month-old ERP response discriminates pictures of newly familiarized and unfamiliar monkey and human faces, as evidenced by clear amplitude (N290 and P400) differences (Scott et al., 2006b). However, infants’ amplitude response distinguished frontal and profile views of individual human faces better than frontal and profile views of individual monkey faces. These results support the hypothesis that by 9 months of age the face processing system is tuned to human faces. However, even in the absence of behavioral discrimination, the brain may continue to differentiate unfamiliar types faces, albeit less efficiently. The results from Scott et al. (2006b) suggest that perceptual narrowing should be characterized as a decline and not a loss of ability.

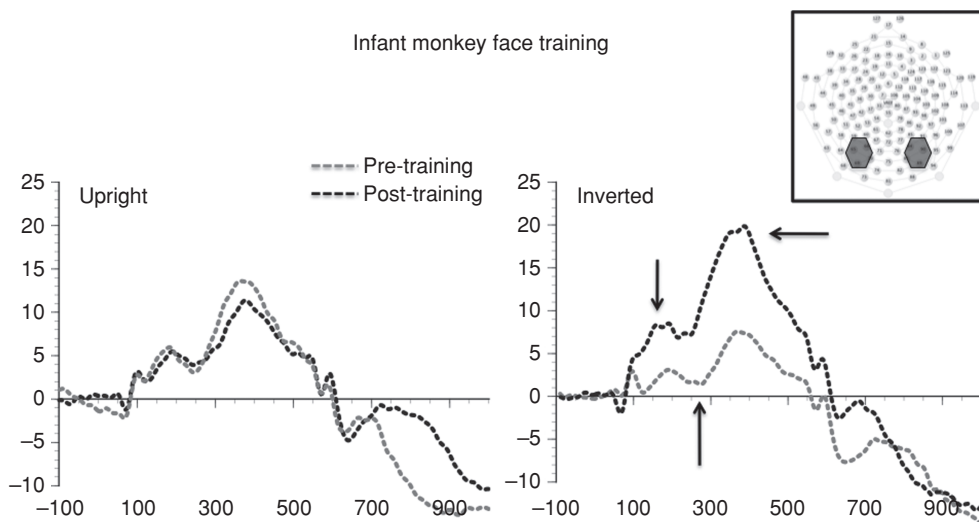


C11.F4 **Fig. 11.4** Mean percent looking time toward the novel and familiar monkey faces before and after 3 months of training at the individual (top), category (middle), and exposure (bottom) levels. Whereas individual training led to maintenance in ability to discriminate monkey faces, category and exposure training led to a decline. Reprinted with permission (Psychological Science).

It is possible that neural discrimination may allow for later behavioral discrimination if the environment demands change. In another investigation, ERPs were recorded before and after 3 months of monkey-face book training in order to better understand the neural bases of perceptual narrowing over time (Scott and Monesson, submitted). Infants viewed trained (or to-be-trained) and untrained monkey faces presented in the upright and inverted orientation. It was hypothesized that if individual-level training led to more face-like neural responses then infants

with individual-level, but not category-level, training should exhibit a differential ERP response to inverted monkey faces after training (similar to their response to human faces). Results confirmed that infants exhibited a differential neural response to inverted monkey faces at post-training relative to the pre-training (see Figure 11.5). This differential response was recorded over occipital and temporal electrode locations and began early and continued for the N290 and P400 components. These results suggest that experience individuating faces during the first year of life leads to adult-like face inversion effects. Moreover, combined with the behavioral results (Scott and Monesson, 2009) these data suggest that early labeling may be driving the development of perceptual representations for faces and objects. However, it is currently unclear whether verbal labels are necessary or simply sufficient for individuation learning to occur. It is possible that any correlated, individual-level cue, will lead to similar behavioral and neural specialization.

Face misperceptions and perceptual deficits are prevalent in a variety of developmental disorders, most notably in autism spectrum disorders (ASD) (for review see Webb et al., Chapter 43, this volume). For example, individuals with an ASD have difficulty remembering faces (Hauck et al., 1999) and have aberrant processing of emotional expressions (Ashwin et al., 2007). ASD individuals use feature-based, rather than holistic-based, face processing (Joseph and Tanaka, 2003; Senju et al., 2008) and spend less time directing their attention to the eye area of the face relative neurotypical children (Klin et al., 2002; Pelphrey et al., 2002). In addition, unlike typically developing individuals, individuals with an ASD do not show recognition deficits when faces are presented upside down (Hobson et al., 1998) and show aberrant electrophysiological responses to faces (Dawson et al., 2002). Recently, perceptual expertise training methods (Gauthier and Tarr, 1997) were adapted for autistic populations, to determine whether adolescents and young adults diagnosed with autism benefit from face training (Faja et al., 2008). Five individuals with autism were trained using explicit, rule-based instruction across several different training tasks. Training included learning to label faces at the individual level. Results revealed improvements in the



**Fig. 11.5** Infant ERP changes to upright and inverted monkey faces before and after 3 months of individual-level training. After training, the amplitude response to inverted, but not upright, faces increased significantly. C11.F5

ability to detect configuration changes and an increase in reaction time to inverted relative to upright faces (Faja et al., 2008). These inversion effects are consistent with previously reported adult (Tanaka and Pierce, 2009) and infant training studies (Scott and Monesson 2009; submitted) and further strengthen the argument that individual level learning plays an important role in the acquisition and development of perceptual expertise.

## C11.S4 Summary and conclusions

The acquisition of perceptual expertise and the development of face and object categorization have recently become mutually informative. This chapter provided an overview of studies, in both adult and developmental populations, examining visual perceptual learning over time using both behavioral and cognitive neuroscience methods.

The study of the acquisition of perceptual expertise in adults and in developing populations suggests that neural systems responsible for face and object processing are especially sensitive to the level of abstraction at which these categories are learned (Scott and Monesson submitted; Scott et al., 2006a, 2008). In adults, developing infants, and individuals with autism, learning to discriminate exemplars at more specific levels may lead to an increased emphasis on unique and individuating visual features whereas learning to categorize leads learners to focus on the visual features that stimuli within categories have in common. Labeling and feedback during perceptual learning with objects (in adults; Scott et al., 2006a, 2008) or with faces (in infants: Scott and Monesson, 2009; in adults: Tanaka and Pierce, 2009; in individuals with autism: Faja et al., 2008) enhances learning and leads to specialized behavioral and neural responses consistent with perceptual expertise. In adults, learning appears to generalize for some classes of stimuli (birds: Scott et al., 2006a) more than others (cars: Scott et al., 2008). In addition, learning in one domain may interfere with previously acquired perceptual expertise in another domain, leading to neural competition (Gauthier and Curby, 2005).

Here it is suggested that perceptual expertise arises similarly in adults and during development. Moreover, an effort to conduct experiments utilizing both adult and developmental populations may lead to a better understanding of how humans parse the world into categories of objects and people. In infants, we do not fully understand generalization and stability of learning, whether learning in one domain interferes with learning in another domain, or the role of labels and feedback during the acquisition of perceptual expertise. Future work in the area of development is needed to determine whether: (1) cortical regions, responsible for face and object processing, compete during development, (2) labeling objects at the individual level will lead to similar behavioral and neural response as has been found with faces, and (3) perceptual narrowing in human infants represents a sensitive period during development or whether the development of specialized face representations can develop at any time.

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