·Review·

# The early development of face processing – What makes faces special?

Stefanie Hoehl, Stefanie Peykarjou

*Department of Psychology, University of Heidelberg, Hauptstr. 47-51 Heidelberg 69117, Germany*



**Abstract:** In the present article we review behavioral and neurophysiological studies on face processing in adults and in early development. From the existing empirical and theoretical literature we derive three aspects that distinguish face processing from the processing of other visual object categories. Each of these aspects is discussed from a developmental perspective. First, faces are recognized and represented at the individual level rather than at the basic level. Second, humans typically acquire extensive expertise in individuating faces from early on in development. And third, more than other objects, faces are processed holistically. There is a quantitative difference in the amount of visual experience for faces and other object categories in that the amount of expertise typically acquired for faces is greater than that for other object categories. In addition, we discuss possible qualitative differences in experience for faces and objects. For instance, there is evidence for a sensitive period in infancy for building up a holistic face representation and for perceptual narrowing for faces of one's own species and race. We conclude our literature review with questions for future research, for instance, regarding the exact relationship between behavioral and neuronal markers of face processing across development.

**Keywords:** face processing; development; infants; visual expertise; holistic processing; event-related potential

## 1 Introduction

When a newborn infant opens her eyes, one of the first stimuli she encounters is likely to be the face of another human being. Less than one hour after birth, infants prefer to follow a slowly-moving face-like configuration with their eyes compared to other similarly complex visual stimuli that do not resemble a face[1]. A few hours after birth, infants are able to recognize their mother's face[2,3]. Do the remarkable abilities to detect faces and to recognize a particular face shortly after birth imply that human infants are born with a specified face-processing module in the brain?

Corresponding author: Stefanie Hoehl
Tel: +49-6221-547373; Fax: +49-6221-547326
E-mail: stefanie.hoehl@psychologie.uni-heidelberg.de
Article ID: 1673-7067(2012)06-0765-24
Received date: 2012-03-03; Accepted date: 2012-05-16

In adults the "fusiform face area" in the inferior temporal cortex is more activated in response to displays of faces than other objects[4]. Consequently, it has been argued that the processing of facial identity is a domain-specific mechanism involving activation of parts of the fusiform gyrus[5]. However, face-selective areas of the fusiform gyrus can also be recruited by non-face objects for which a person has acquired expertise, albeit to a lesser extent[6]. This observation has led to the suggestion that face processing may only appear to be a specific mechanism, since all humans typically acquire expertise in face recognition[7]. In this view, the fusiform face area is not face-selective but selective for all categories of stimuli for which a person has acquired a certain amount of visual expertise. However, this view has been criticized and it is still debated whether there is a sensitive period for acquiring face expertise in infancy[5]. Looking at early development may thus yield important information on how the face processing networks develop and how special faces really are as a visual object category.

In this review, we discuss three important aspects that distinguish faces from other visual object categories: (1) faces are represented and recognized as individuals[8,9], whereas most objects are first recognized at a "basic level" of categorization[10]; (2) humans typically acquire extensive expertise in distinguishing individual faces from early on in development[11]; and (3) more than other types of visual stimuli, faces are processed and represented holistically[12,13].

When encoding and recognizing faces, we use both "featural" information regarding the shapes and pigmentation of facial features and "configural" information regarding the spatial relations between features. According to Maurer and colleagues, three types of configural face processing can be distinguished[12]. On a very basic level, configural processing entails the detection of first-order relations between facial features, i.e. the presence of two eyes above a nose and mouth. Holistic processing, the second type of configural process according to Maurer *et al.*, refers to integrating facial features together into a coherent Gestalt, making it difficult to isolate parts from the whole when processing a face. In the present article, we refer to the third kind of configural processing described by Maurer and colleagues as second-order relational processing, i.e. processing of the spacing among individual features in a face. Besides the shapes of individual features, second-order relations between features are a critical cue for face identification.

What is the relationship between these three aspects of face processing? Theoretically, it is plausible that extensive expertise in distinguishing individual faces from each other, together with semantic and episodic knowledge associated with familiar faces, leads to the formation of individual-level representations of faces that are easier to access than basic-level representations, such as "human face". However, expertise in distinguishing individuals may not even be necessary for individual-level representation, since there is evidence that personally familiar objects are also recognized at the individual level[9]. Further, it has been suggested that expertise in individuating faces may lead to holistic face processing, since faces are exemplars of a relatively homogenous visual category, and relational information between features may be particularly diagnostic for face recognition leading to enhanced processing of faces as a whole[14]. As we discuss later, we are uncertain regarding the relationship between the characteristic aspects of face processing. In our opinion, there is only limited evidence that expertise in individuating exemplars of a category leads to holistic processing. Furthermore, the exact relationship between second-order relational processing and holistic processing still needs to be clarified.

We start our review with an overview of the characteristics of face processing at the behavioral level in adults. We then describe developmental studies looking at behavioral indices of face processing in infancy before reviewing neurophysiological studies in adults and infants. Based on this empirical background we outline how and why faces are processed differently from other object categories. We conclude with suggestions for further research.

## 2 What's special about face processing in adults?

In this section, we provide a brief overview of face-specific processing at the behavioral level in adults. The most important behavioral findings regarding the central characteristics of face processing are summarized in Table 1. More extensive reviews on this topic can be found elsewhere[12,13,15,16]. In the introduction, we claimed that the processing of faces differs from the processing of other object categories in at least three particular ways.

First, faces are recognized at the individual level, whereas most objects are first recognized at the basic level. Face identification is fastest on the individual level ("Bill Clinton"), compared to the superordinate level ("living"), or the basic level ("human face";[9]). In contrast, objects are generally represented and recognized at the basic level (e.g. "dog";[10]). Object expertise induces a shift from the basic level to a more subordinate level, e.g. "German shepherd dog", for real-world objects[17], and similarly for artificial

**Table 1. Summary of studies yielding evidence for the proposed specifics distinguishing the visual processing of faces from other objects**

| | Adults | Infants |
|---|---|---|
| Individual-level recognition | Faster face identification on the individual level than on the superordinate or basic level[9] | Perceptual narrowing for recognizing human faces between 6 and 9 months of age[41], and for recognizing faces of one's own ethnicity between 3 and 9 months of age[43] |
| | Increase of discrimination ability for faces of other ethnicities through individuation training[46,47] | Preservation of discrimination ability for monkey faces through individuation training[18] |
| Experience in distinguishing individuals | | Looking preference for the mother's face in newborns[2,3] |
| | | Recognition of individual faces in 1-month-old infants after short familiarization[49] |
| Holistic processing | Inversion effect. Reduced accuracy and increase in reaction time for the recognition of inverted compared to upright faces[19-21] | Discrimination of thatcherized faces when stimuli are presented upright but not inverted in newborns[53] |
| | Part-whole effect. Higher accuracy for the identification of face-parts in intact faces than in isolation[29] | Sensitivity to a switch of facial features between two faces in habituation tasks in 10-month-old infants[54] |
| | Composite effect. Reduced accuracy for the recognition of a face top half when it is presented with the bottom half of another face unless face-halves are misaligned[30] | Perceptual narrowing. Holistic processing of own- and other-race faces in a switch-face task in 4-month-olds, but only for own-race faces in 8-month-olds[64] |

objects[14], although in both cases the original basic level seems to retain a special status.

Identification of exemplars on a subordinate level and especially on the individual level requires detailed visual processing and, in the case of faces, the detection of sometimes very subtle featural and second-order relational information. Besides visual expertise, however, another important factor that contributes to processing exemplars of a certain category on the individual level is individual familiarity and the availability of detailed semantic information. Even without extensive visual expertise, participants categorize towers (e.g. Leaning Tower of Pisa) that are familiar to them faster on the individual level than on the basic level[9]. Thus, besides acquiring extensive visual expertise for faces from early on, another factor that sets faces apart from other objects is that we gain semantic (and episodic) knowledge for a large number of individuals throughout life.

The second way in which faces differ from other object categories is that we acquire extensive expertise in distinguishing individual faces from early on in development[11,18]. We review the empirical evidence for this claim in the following section on behavioral studies on face processing in early development.

Third, more than objects from other categories, faces are processed holistically. This characteristic of face processing is reflected in several phenomena that have been widely studied and replicated. Figure 1 shows some typical face stimuli used in these studies. One classic finding is the face-specific *inversion effect*[19]. A substantial decrement in precision and an increase in reaction times are typically found for the recognition of upside-down *versus* upright faces[19-21]. Although recognition is somewhat impaired for other kinds of objects that are presented upside down, this effect is especially large and robust when faces are used. Some authors have found that discrimination and recognition of upside-down faces is particularly hard when faces differ mainly in terms of spacing between features, while the inversion effect is diminished for faces that mainly differ in the shape of individual features[20]. The inversion ef-

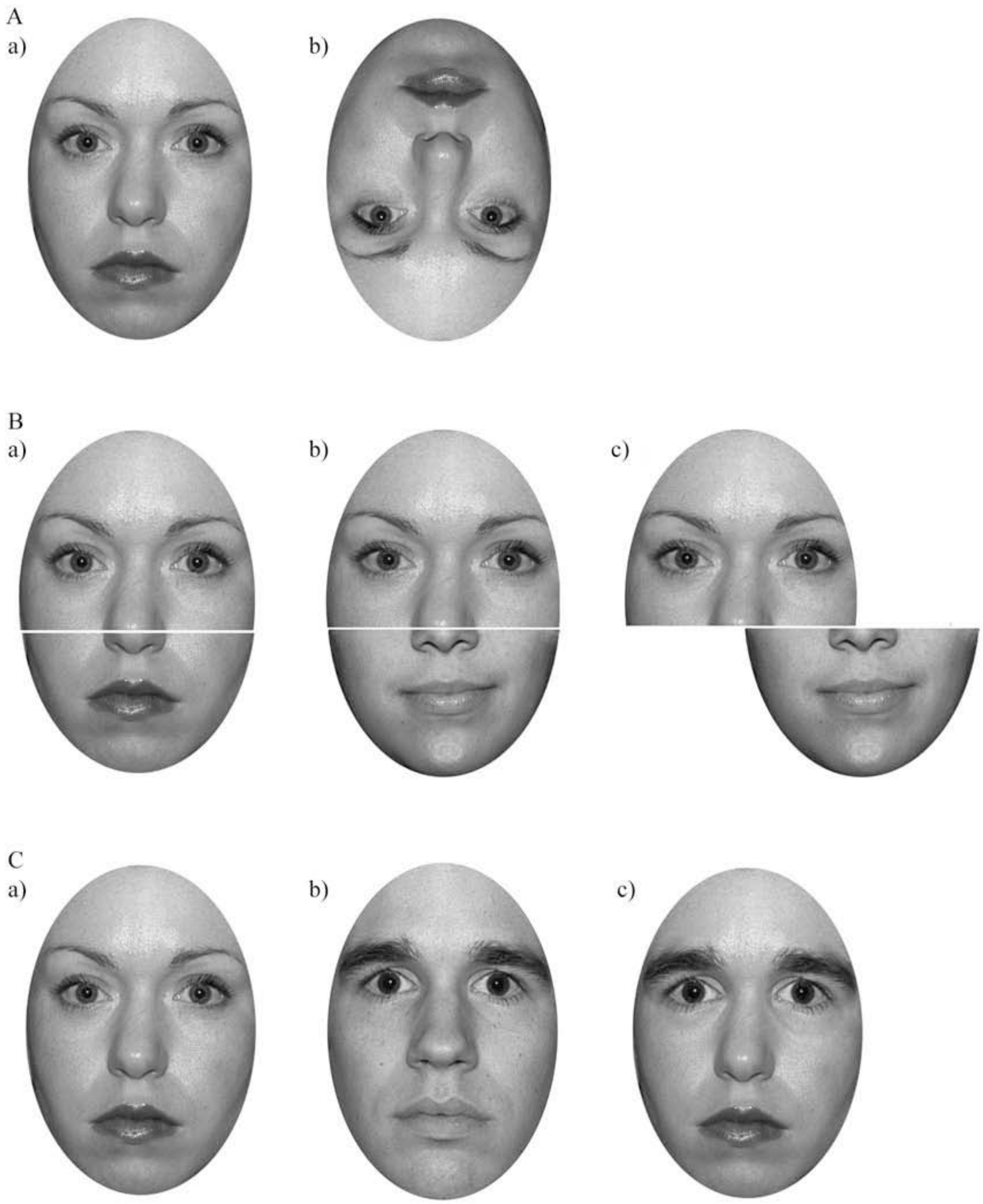


**Fig. 1. Exemplary stimuli used in face processing tasks. A: Inversion effect. a, upright face; b, inverted face. B: Composite effect. a, original face; b, composite face, aligned; c, composite face, misaligned. C: Switch-face task. a, female face; b, male face; c, switch face, eyes switched. Original faces were taken from the MacBrain Face Stimulus Set[145].**

fect has therefore been attributed to a disruption of second-order relational processing of faces[20] and face-parts[22]. In accordance with this view, it is difficult to notice whether the eyes and mouth of a smiling face are rotated 180° ("thatcherized", see Fig. 2) in an inverted face, while the same manipulation is quickly detected and perceived as a bizarre deformation in an upright face[23]. It has to be noted, though, that other researchers have found inversion effects for the detection of feature shape changes within the context of a face as well (not for isolated features, though), leading to the suggestion that inversion generally disrupts holistic face processing which entails both second-order relational information and feature shape information[24]. In fact, it may be very difficult to isolate both kinds of information from each other because feature shape changes may also affect spacing between features and *vice versa*[25,26]. While the inversion effect has been established for faces, there is conflicting evidence as to whether a similar inversion effect can be found for other objects of expertise[21,27,28].

Further support for the claim that faces, more than other object types, are processed holistically comes from studies on the *part-whole effect* and the *composite effect*. The term part-whole effect refers to the finding that it is easier to identify face-parts in the context of an intact face than in isolation[29]. This is not the case for other object types and much less the case for objects of expertise[5,29]. The composite effect refers to the phenomenon that it is difficult to recognize the top half of one face when it is presented with the bottom half of another face unless the face-halves are offset laterally (misaligned) or inverted[30]. These effects are interpreted as evidence that faces are processed holistically, i.e. processed as a whole rather than feature-based. Both the part-whole effect and the composite effect are diminished for inverted faces[29-31], suggesting that inversion interferes with processing a face holistically[12]. It has been debated, though, whether the perception of second-order spatial relations between features is more dependent on holistic processing than the perception of other cues to face identification like the shapes of local features[25], or whether holistic face processing is better understood as entailing both relational and feature-shape information without a special role for either kind of information in the inversion effect[24,32].

Recently, the validity of the composite effect in standard paradigms has been put into question. It has been argued that, in studies in which the irrelevant face halves are always different from each other, subjects may be biased to judge two identical relevant face halves as being different because the information derived from the upper and lower face half is incongruent, i.e. leads to different answers[33,34].

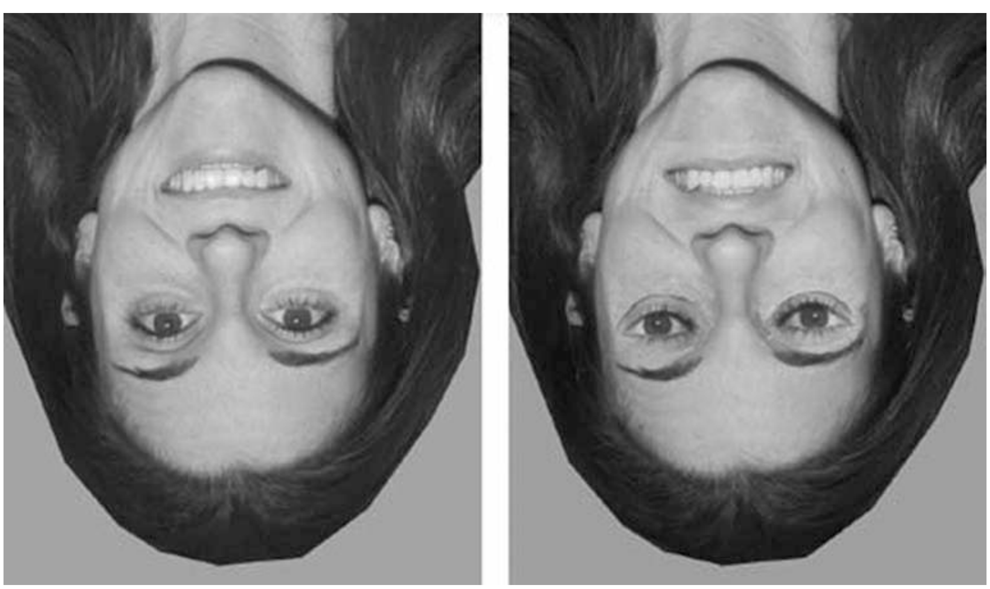

**Fig. 2. Example of an inverted face (left) and an inverted "thatcherized" face (right) as used in the study by Leo and Simion[53]. Reprinted with permission.**

Therefore, it was suggested to add conditions to the composite task in which irrelevant face parts are identical in order to avoid confounding effects of in/congruency. In response to this criticism, McKone and Robbins[35] point out that it is not clear why such a response bias should produce differences between aligned and misaligned trials, which is typically taken as evidence for holistic processing of faces, or why such a response bias should be specific to upright faces and not to other objects.

To sum up, faces differ from other object categories in that they are represented and recognized as individuals. In addition, more than other object categories, faces are processed holistically in tasks such as the part-whole task and the composite task. It has been suggested that holistic face processing derives from a holistic face representation in the brain that develops based on extensive expertise with upright faces[25]. There is conflicting evidence, however, whether objects of expertise, e.g. dogs for dog experts, are also processed holistically and/or relationally[21,27]. In contrast to other object categories, humans typically acquire extensive expertise for faces from the day they are born. We therefore continue with a review of face processing in early development before turning to the neuronal correlates of face processing.

## 3 Face processing in development – behavioral evidence

All three characteristics of face processing, namely individual representation, extensive expertise, and holistic processing (although measured with different tasks than in adults) already play a role in the first year of infancy. In this section, we outline the specialization of infants' initially broadly-tuned face detection and face discrimination abilities for human faces in the first year. Based on the existing data it will become evident that humans acquire extensive expertise in discriminating and identifying individual faces from early on in development. We conclude this section with a review of studies on the development of holistic face processing in infancy.

Shortly after birth, infants demonstrate visual preferences for faces and schematic face-like stimuli[1,36]. Although the neuronal basis of these preferences remains uncertain, it is unlikely that face-selective cortical regions are mature and already specialized for faces in newborns. It has been suggested that a subcortical pathway, including the amygdala, may be involved in the detection of face configurations in newborns[37]. Early visual preferences for faces may ensure that infants acquire extensive visual experience with faces from early on, given that they grow up in a typical rearing environment and encounter faces regularly[37].

Newborns are sensitive to both images of human faces and schematic face-like configurations, suggesting that their face-processing system is initially broadly-tuned and flexible. This notion is supported by the recent finding that newborn infants do not discriminate between a human face and a monkey face, but that they prefer to look at an upright monkey face rather than an inverted monkey face, as they do when seeing photographed or schematic human faces[38]. Although development in face recognition can be observed until 5 to 7 years of age[39,40], specialization for specific types of faces occurs first between six and nine months[41]. Pascalis and colleagues presented human faces and monkey faces to 6- and 9-month-old infants and to adults in a familiarization-preference-for-novelty paradigm. Participants were first familiarized with a human face or monkey face and were then presented with a novel human face or monkey face next to the one they were already familiar with. In all age groups, participants looked longer toward the novel human face than the familiar human face. This novelty-preference indicates that the novel face can be discriminated from the familiar face. When monkey faces were presented, however, only the 6-month-old infants showed this novelty-preference for a novel *versus* a familiar monkey face. This suggests that 6-month-olds, but not 9-month-olds and adults are able to discriminate individual monkey faces in this task.

Why could that be? Between 6 and 9 months, the human face-processing system narrows down to perceiving differences between individual faces of our own species, whereas the ability to discriminate between faces of other species declines. This process is an example of perceptual narrowing. Perceptual narrowing was first observed in the auditory domain, where, for instance, infants' ability to distinguish between certain speech sounds that are not common in their first language declines in the second half of the first year[42]. Perceptual narrowing allows us to focus on the discrimination of stimuli that are directly relevant to us. While we are born with the ability to learn any language and to distinguish any kind of face stimuli, in the second half of the first year we specialize on the language we are exposed to and the kind of faces we are surrounded by. Flexibility is exchanged for focus and (at least in the language domain) increased precision.

Specialization for human faces between 6 and 9 months of age seems to rely on two factors: exposure and individuation. In the first year after birth, infants specialize in distinguishing the kind of faces they encounter the most. These are usually human faces. And in many cases, infants are predominantly exposed to faces of a certain race or ethnicity. In fact, between 3 and 9 months of age, infants not only lose the ability to discriminate between faces of other species but also between faces of other racial groups[43,44]. Kelly and colleagues found that 3-month-old English infants were able to discriminate just as well between Caucasian faces as between African, Middle Eastern and Chinese faces. This ability started to decline around 6 months of age, and at 9 months infants were only able to discriminate reliably between faces of their own racial group[43]. In adults, the phenomenon that faces of other ethnicities are harder to recognize and to discriminate from each other than faces of one's own ethnicity has been termed the *other-race-effect*[45].

However, exposure to certain kinds of faces seems not to be enough to preserve the ability to discriminate between individual faces. In addition, faces have to be represented as *individuals*. In a recent study, infants were exposed regularly to a set of monkey face pictures between 6 and 9 months of age[18]. In the exposure-training group the infants' parents were asked to show the pictures to the infants without using labels. In the category-training group all monkeys were labeled as monkeys. In the individual-training group, each monkey received an individual name (e.g. Carlos) that parents were asked to use when showing the monkey pictures to their infant according to a specific schedule. After 3 months of training, only infants in the individual-training group preserved the ability to discriminate between novel monkey faces, whereas infants in the other training groups showed the typical perceptual narrowing effect and were no longer able to discriminate between monkey faces at 9 months of age[18]. This finding is particularly interesting as infants in all training groups received the same amount of exposure to the monkey faces, but only the individual naming of monkeys led to preserved individuation of monkey faces in 9-month-olds. Similarly, training adults in individuating faces of another race diminishes the other-race effect whereas training in categorizing faces as, for instance, African American does not[46,47]. This suggests that the representation of exemplars of a particular category as individuals is critical for maintaining the ability to discriminate individual faces beyond the first few months of infancy. Visual exposure alone is not sufficient. Unfortunately, there is no specification of whether and what labels were used in the methods section of another successful training study with 6- to 9-month-old Caucasian infants who were trained with Chinese faces[48].

It is hard to argue against the claim that human faces are the kind of visual stimuli we are exposed to the most from early on in infancy. Above and beyond being exposed to faces a lot, however, newborn infants start to individuate faces from the day they are born. Hours after birth, infants prefer to look at their mother's face compared to an unfamiliar female face[2,3]. One-month-old infants recognize individual faces after only eighty seconds of exposure to a static photograph[49]. From an evolutionary perspective, it makes sense that infants quickly learn to recognize the faces of people in their environment and discriminate individual faces from early on, since infants are very vulnerable and dependent on their caretakers and the members of the social group into which they are born[11]. Thus, two of the three characteristics of face processing we outlined in the introduction already play a crucial role in early infancy: individual representation of faces and experience in discriminating individual faces. What about the third characteristic: holistic processing?

There is empirical evidence that infants are sensitive to configural visual information from birth[50]. When viewing faces, newborn infants prefer to look at a face with canonical first-order relations between features, i.e. the alignment of two eyes above a nose and a mouth compared to an inverted or scrambled configuration, although they do not seem to detect 90° rotations and lateral shifts of facial features within their respective areas of the face[36,51]. Thus, there is evidence that newborns are to some degree sensitive to first-order relations of facial features. Whether these visual preferences are due to some innate representation of an unspecific face template, general attention biases to certain kinds of (top-heavy) patterns[51,52], or quick learning within the first minutes after birth, remains an unresolved question. To some degree, newborn infants are also sensitive to the second-order relations of facial features. Newborns discriminate a thatcherized face (with eyes and mouth rotated 180°, see Fig. 2) from an unaltered face when realistic photographs instead of schematic faces are used and when faces are presented in an upright instead of an upside-down orientation[53]. The finding that newborns do not discriminate a thatcherized face from an unaltered face when stimuli are presented upside-down suggests that in newborns second-order relational processing is impaired by face inversion, even before infants are able to acquire extensive visual expertise for faces. This suggests that an unspecific holistic face representation, including first- and second-order relational information, exists even shortly after birth. However, further evidence for holistic and second-order relational face processing in newborns should be collected before a firm conclusion on this matter can be drawn.

Despite evidence for configural and second-order relational face processing in newborns, 4-month-olds do not seem to notice when facial features (mouths and eyes) are switched between two faces, suggesting that 4-month-olds apply more analytic or feature-based face processing than holistic processing[54] (Fig. 1). Ten-month-olds, in contrast, notice switched eyes and mouths, suggesting that they process faces holistically[54]. Thus, there seems to be a transition from primarily analytic to more holistic processing in infancy when habituation switch-face tasks are used, although even newborns show some sensitivity to first-order and second-order relations between facial features.

The finding that there seems to be a shift from more analytic to more holistic face processing in infancy seems to be at odds with the suggestion that infant face processing is initially mediated by a subcortical pathway feeding primarily on low spatial frequencies that provide information on the coarse configuration of a stimulus rather than the finer details[37]. Furthermore, like adults, 4- to 9-month-old infants show a right-hemisphere advantage for face-recognition when tested with divided visual field presentations[55], which has been attributed to the right hemisphere's proclivity to process visual information in a global or holistic manner based on low spatial frequency information[56].

However, despite young infants' limited visual acuity[57,58], the parvocellular pathway that is sensitive to higher spatial frequencies and color seems to mature earlier than the magnocellular pathway that is sensitive to low spatial frequencies and motion[59-61]. In fact, young infants' attention to facial features is in line with a general shift from more feature-focused to broader and more holistic visual scanning patterns in infancy[62,63]. Nevertheless, even newborns show evidence of configural processing in that they distinguish between visual patterns that consist of the same features arranged in different configurations, countering the claim that the magnocellular system may not function at all at birth[50,53]. Rather, there is evidence that both the parvocellular and the magnocellular pathways are functional from early on in development[60] and that young infants' more focused and restricted scanning patterns may favor more analytic visual processing of complex patterns, including faces, very early in development.

Expertise and perceptual narrowing seem to play a role in the development of holistic and featural face processing. In a recent study, 4-month-olds showed evidence of holistic processing in a habituation switch-face task for both same-race and other-race faces, whereas 8-month-olds only showed evidence of processing own-race faces holistically[64]. However, the study leaves open whether 8-month-olds process other-race faces based on features, because infants discriminated neither between the familiar face and the switch-face nor a completely novel face (note that there is somewhat mixed evidence as to whether other-race faces are processed less holistically than own-race faces in adults, and that experience with other-race faces seems to play an important role[65-69]). Furthermore, there is evidence that visual deprivation during infancy impairs holistic face processing as measured by the composite task even in adulthood, suggesting that there may be a sensitive period for developing holistic face processing in infancy[70].

To conclude, all of the three characteristics of face processing we noted in the introduction have their roots in early infancy. In fact, all the properties of adult face recognition that have been tested in infants and young children seem to exist from early on in development[40]. This has led to the suggestion that there are no major qualitative changes in face recognition beyond early childhood, whereas quantitative changes need to be better distinguished from general domain improvements (e.g. attention span, memory) in future research before firm conclusions on quantitative improvements in face recognition beyond early childhood can be drawn[40].

Infants gain experience in discriminating individual faces from the day they are born[3]. The representation of faces as individuals seems to be crucial for maintaining (and regaining) the ability to discriminate between faces of a certain race and species beyond 6 months of age[18,46,47]. Although configural and relational processing can be observed to some degree from birth[53], there seems to be a shift from more analytic to more holistic processing as measured by habituation switch-face tasks between 4 and 10 months of age[54]. Expertise with certain kinds of faces seems to favor holistic processing by 8 months of age[64], whereas a lack of visual input in infancy leads to long-lasting impairments in holistic face processing as evidenced by a lack of the composite effect for faces in adulthood[70]. Possibly, this is because a holistic neuronal representation of a face is built up within the first year of infancy, based on experience with different faces of a certain kind. Later in development, this representation or template is activated when upright faces are perceived leading to holistic processing[25,32]. It remains unclear whether an unspecified face template is already present at birth, immediately allowing for the detection of faces, or whether it is built from scratch after birth. In the following two sections we review neurophysiological studies on face processing in adults and in infants that have complemented behavioral work and that have added further insight but also raised further questions about face processing across development.

## 4 The neurophysiology of face processing

Electrophysiological studies on the neuronal processing of faces in adults have identified one particular component of the event-related potential (ERP) that plays an important role in processing structural information from faces and eyes. The N170 on lateral posterior channels is reliably larger and faster in response to faces than to other object categories[71] (see Table 2 for a summary of the response properties of the N170 and N250 in face processing studies). N170 amplitude is also larger in response to Mooney faces (high-contrast two-tone pictures of faces only depicting shadow *versus* light information, see Fig. 3) that are consciously perceived as faces *versus* Mooney faces that are not perceived as faces, suggesting that the identification of a stimulus as a face is related to the N170 response[72], though there is also evidence that the N170 can be elicited in response to unconsciously perceived faces in patients with neglect[73].

Cortical sources of the N170 have been identified in the fusiform gyrus[74] and in the superior temporal gyrus[75]. Both cortical regions also show activation in response to faces in fMRI studies[4,76].

Several studies using priming or habituation paradigms have shown reduced N170 amplitude (or M170 amplitude in MEG studies) in response to faces that were preceded by faces compared to non-face stimuli[74,77-81]. These repetition suppression or adaptation effects are typically taken as evidence that the preceding stimulus and following stimulus activate a common neuronal representation at

**Table 2. Response properties of the N170 and N250**

| | N170 | N250/N250r |
|---|---|---|
| Inversion | Enhanced amplitude and/or delayed latency[87,99-101] | Reduced amplitude[98] |
| | | Delayed repetition effects[95] |
| Contrast-reversal | Enhanced amplitude[99] | Repetition effects spread over longer time-window[95] |
| Eye removal | Similar amplitude for complete faces and faces with eyes removed[86] | - |
| | No effects of inversion or contrast-reversal for faces with eyes removed[103] | - |
| Isolated eyes | Similar or enhanced amplitude compared to intact faces[87] | - |
| Holistic processing | Shorter latency for repeated face halves in aligned faces[110] | Longer latency for aligned compared to misaligned face halves[110] |
| | Less repetition suppression to aligned face stimuli for half-identical or completely new faces compared to identical faces[111] | - |
| Second-order relational processing | Conflicting evidence on the effects of thatcherization on processing of upright and inverted faces[114-116] | - |
| | Larger amplitude for configurally than featurally altered faces over the right hemisphere[117] | |
| Stimulus repetition | Repetition suppression. Reduced amplitude for repetition of different[74,77, 80,81] or same faces[94] | Repetition enhancement. Enhanced amplitude for repetition of same faces[88,91,92] |

**Fig. 3. Example of an upright (left) and an inverted (right) Mooney face as used in the study by George and colleagues[72]. Reprinted with permission.**

the processing level of the affected ERP component. For instance, the finding that the N170 amplitude for eyes is similarly suppressed in the context of frontal-view faces and profile-view faces has been taken as evidence that a view-invariant representation of faces is accessed in both cases[82].

The degree to which adaptation/habituation effects on the N170 are specific to faces and facial features still remains unclear, however. One study found similar repetition suppression effects on the N170 in response to hands primed by hands *versus* faces as for faces primed by faces *versus* hands[77], suggesting that shape-selective mechanisms but not necessarily face-selective mechanisms may be involved. When using long lags between identical prime and target stimuli, the N170 is reduced for repeated familiar faces as well as for repeated line drawings of objects[83]. In another study, however, category-level habituation of the N170 was found for faces but not for words presented sequentially in blocks compared to alternating faces and words[84,85]. This suggests that habituation effects may indeed be specific for certain categories of visual stimuli. Whereas habituation and adaptation effects on the N170 have been found consistently for faces, category-level habituation for different words that are perceived in sequence would make reading a continuous text quite difficult[84]. However, the evidence to date does not suggest that adaptation effects on the N170 are completely face-specific since similar effects have been observed for hands, drawings of objects, and cars[77,83, 85].

Whereas the N170 is thought to reflect the structural encoding of faces[86,87], access to representations of individual faces may be reflected by the subsequent N250[88]. The N250 has a more anterior and inferior distribution than the N170[89] and its neuronal generators have been localized in regions corresponding to the fusiform gyrus[88]. The N250 is consistently elicited for familiar faces, especially one's own face[90], but it is reduced in response to unfamiliar faces[89]. N250 amplitude is also increased for personally familiar cars and dogs compared to novel stimuli, suggesting that it reflects processing of individuated stimuli regardless of category[90]. In addition, N250 responses to birds are enhanced by subordinate-level training compared to basic-level training[91].

In repetition paradigms, the N250r can be observed if the same face is presented successively[88,92,93]. In contrast, evidence on identity repetition effects for the N170 is mixed[88,94-96]. The N250r seems to reflect person recognition rather than just picture recognition as it is enhanced in amplitude to targets both when the same picture is presented twice[89,92] and when two different pictures of the same individual face are presented in succession[88,94,96,97]. Repetition paradigms have also yielded evidence that the N250r differentiates faces and objects. Whereas a diminished N250r has been observed for repeated familiar words[93] and ape faces[98], no N250r has been observed in response to repeated cars[98].

Are there other indicators that the N170 or the N250 is face-specific? The N250r is reduced by face inversion[98], which may result from impeded access to the representation of an individual face. It can be speculated that this effect reflects the disruption of individual face recognition through inversion, which is also observed in behavioral tasks[20-22], but direct evidence on this relationship has not been presented.

The N170 is delayed and/or enhanced by face inversion, but it is less affected by object inversion[87,99-101] (Fig. 4). This finding has been taken as evidence that the N170 reflects structural encoding of faces[86,87]. The inversion effect on N170 amplitude and/or latency has often been interpreted as an indirect index of disrupted holistic processing when faces are perceived upside-down[102,103]. Apparently, this makes sense given that the inversion effect on N170 amplitude seems to be face-specific and is not found for objects[99,100], except for objects of expertise after extensive training[28,104]. However, it is not entirely clear why face inversion results in an increase of N170 amplitude. It has been suggested that smaller inter-stimulus perceptual variance for faces *versus* contrasted object categories may account for N170 differences[105], but this argument has been criticized on the theoretical and empirical levels[71]. Based on fMRI studies, some authors have suggested that the increased N170 amplitude for

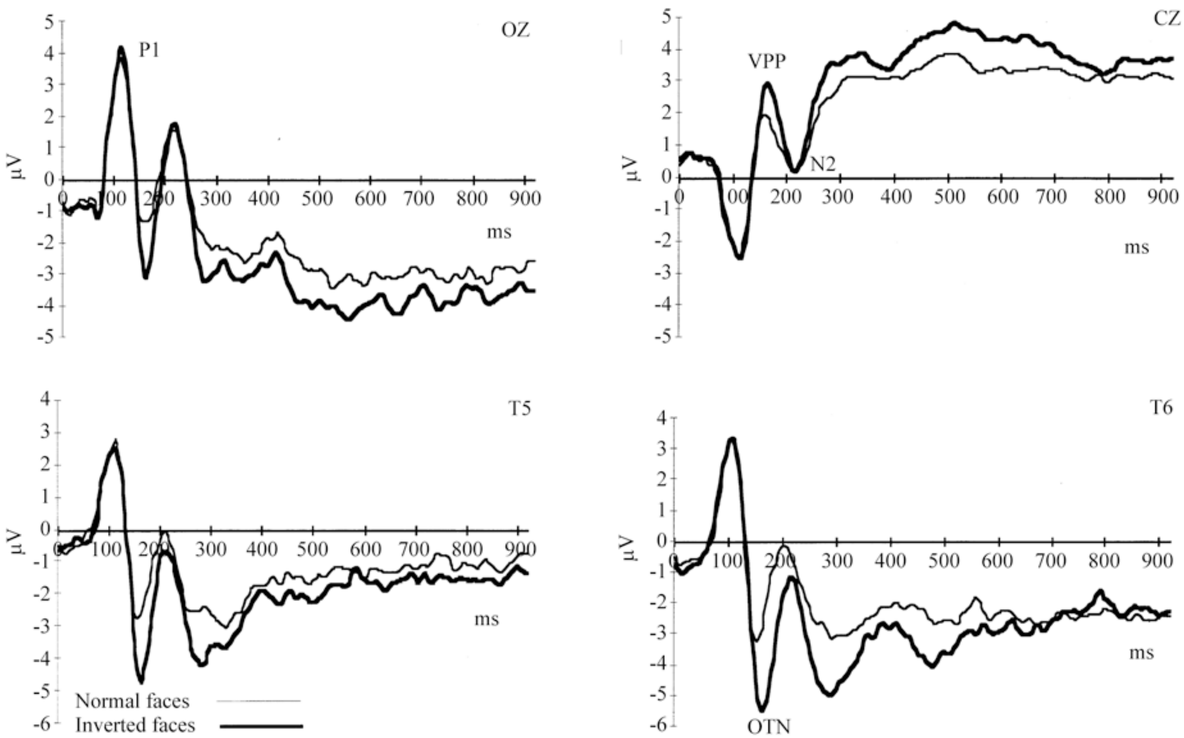


**Fig. 4. Typical N170 inversion effect for faces as reported by Rossion and colleagues[101]. N170 amplitude on occipital and temporal channels is larger for inverted faces than for upright faces. OTN, occipito-temporal negativity, equivalent to N170; VPP, vertex positive potential. Reprinted with permission.**

inverted faces may reflect additional recruitment of object-sensitive neurons[106,107]. If this is the case, the disruption of first-order relations of facial features in inverted faces may result in activation of object-selective neurons, but this does not necessarily imply that impaired holistic or second-order relational processing is reflected in the N170 inversion effect.

Another more recent interpretation of the increased N170 amplitude for inverted faces is that the N170 may reflect activation of neurons sensitive to facial configuration and neurons sensitive to the presence of eyes[99,103]. It is well-established that the eyes play an important role in face processing and presumably are the most informative and most attended feature in the human face[108]. It seems to be the information presented in the eye region that determines whether a stimulus is processed as a face. No face inversion effect is found on the N170 for schematic faces with line drawings of objects substituting the eyes, but it is found for schematic faces with little faces (including eyes) at the position of the eyes[109]. The amplitude of the N170 in response to isolated eyes is equal to or even larger than the N170 amplitude to complete faces, which initially led to the suggestion that the N170 might reflect the operation of an eye processor[87]. However, the amplitude of the N170 does not differ in response to intact faces *versus* faces with the eye region removed[86]. Itier and colleagues[103] suggest that the N170 for intact upright faces and for faces without eyes reflects the activation of face-selective neurons, whereas eye-selective neurons do not respond to these stimuli. When isolated eyes are presented, however, both face-selective and eye-selective neurons respond, similarly as for inverted and contrast-reversed faces with eyes. Therefore, N170 amplitude is increased for inverted and contrast-reversed faces and isolated eyes compared to complete upright faces[99]. This interpretation is supported by the finding that the effects of inversion and contrast-reversal on N170 amplitude are absent if faces without eyes are presented[103]. Thus, the N170 does not merely reflect the activity of neurons sensitive to the presence of eyes, but may rather be induced by neurons sensitive to faces with or without the contribution of neurons sensitive to eyes, depending on the context[99,103,108].

According to Itier and colleagues, inversion and contrast-reversal of faces seem to isolate the eyes from the face context and result in neuronal responses similar to those to isolated eyes, but how this is accomplished remains unclear. Regarding face inversion, this effect may follow from disrupted holistic and relational processing. To test this possibility more directly, it would be very interesting to examine the effects of eye removal on the behavioral indices of holistic face processing. The co-occurrence of impaired relational and holistic processing at the behavioral level and increased N170 amplitude at the neuronal level for inverted faces does not provide direct evidence that these phenomena are related.

To our knowledge, only two studies have directly tested N170 involvement in holistic face processing by using a sequential composite face task[110,111]. In the first study, subjects were slower and less accurate in judging whether two sequential faces had the same top- or bottom-half in intact *versus* misaligned faces, but N170 amplitude in the left hemisphere was the shortest for repeated (i.e. identical) face-halves in intact faces[110]. Thus, the behavioral composite effect that is taken to reflect holistic face processing was not reflected in the response properties of the N170. Interestingly, the N250 peaked later in intact face trials than in misaligned trials, thus mirroring task difficulty better than the N170, which speaks to the relationship between the N250 and the representation of individual faces or face parts. The N170 was larger for faces with misaligned face-halves *versus* intact faces, thus confirming the role of the N170 in processing or detecting first-order relations of facial features. Another study with no explicit composite task but similar stimuli found that this latter effect is larger when both parts of the stimulus consist of face halves instead of only one part depicting a face half and one part consisting of visual noise[112]. Moreover, the effect disappears when faces are presented upside-down, suggesting that it is not generally elicited in response to misaligned patterns ([112], see also[113] for similar results).

In the second ERP study using a composite task, an adaptation paradigm was applied and subjects were asked to fixate and attend to the top halves of the faces[111]. Again, a behavioral composite effect and larger N170 amplitude for misaligned than aligned faces was found. In addition, both faces that differed in top and bottom half from the adapting stimulus and faces that only differed in the bottom part elicited a larger N170 amplitude (i.e. less adaptation) in the right hemisphere compared to faces identical to the adapting stimulus. Thus, half-identical faces elicited similar responses to completely different faces. Interestingly, this effect was only found in the aligned condition where subjects had difficulty recognizing that top halves were identical in the trials with only different bottom halves. However, no adaptation effects were observed in the misaligned condition, thus it is not clear whether the sequential presentation of stimuli that are identical only in one half is enough to elicit adaptation effects in the N170 even when no holistic processing is involved. Therefore, we conclude that there is not sufficient evidence available to argue for a direct relationship between the N170 and holistic processing as measured in the composite task.

Regarding N170 involvement in second-order relational processing, some studies have recorded ERP responses to upright and inverted thatcherized faces in which eyes and mouth are rotated 180°[114-116]. These studies have provided conflicting results as to whether the thatcherization of faces increases or decreases N170 amplitude and whether these effects are restricted to upright *versus* inverted faces.

In another study, participants were familiarized with a face, i.e. they were presented a picture of a face and were asked to press a button when they felt confident to be able to recognize it in subsequent trials[117]. Then participants were shown the original face, a face with altered spatial relations between features (configural change condition) or with altered features (feature change condition) and a novel face in an ERP paradigm. The N170 did not differ significantly in amplitude between stimuli in either condition. However, the difference in N170 amplitude between original and altered faces in the left hemisphere was larger for the feature change condition and in the right hemisphere for the configural change condition. Thus, there is some evidence that the N170 is sensitive to both featural and second-order relational changes in a face.

To test whether the N170 is involved in second-order relational processing, it would also be possible to compare ERP adaptation/priming effects of identical faces *versus* faces with altered second-order relations *versus* faces with altered feature shapes as primes on the N170 for target faces. If the N170 is involved in processing of second-order relations we might expect different priming effects of faces with altered second-order relations *versus* altered features on the N170 for upright faces but less so when prime and target faces are inverted. Based on the findings by Scott and Nelson, hemispheric differences for feature changes *versus* second-order relational changes may be expected[117].

To sum up, the adult N170 seems to reflect the activity of neurons sensitive to eyes as well as neurons sensitive to facial configuration whose activation relies on a view-invariant neural representation of human faces that can also be accessed if eyes are not visible in the face and if isolated eyes are presented[80,82,86,99]. Even though often stated in the literature, it is not entirely clear to what extent the N170 reflects holistic and second-order relational processing of faces and more studies on this topic are clearly needed. The N250r seems to reflect the representation of individual faces[88,89], but its relationship to experience and holistic processing requires further research. In the next section we review neurophysiological studies on how the face processing system develops in infancy.

## 5 Neurophysiology of face processing in development

In electrophysiological studies, the infant N290 and P400 have been identified as potential precursors of the adult N170 component. The N290 has been observed in response to static faces in infants from 3 months of age and it is comparable to the adult N170 with respect to its topography and polarity, though it is a little delayed, more medially distributed and smaller in amplitude[118]. Figure 5 shows typical ERP responses to faces in two infant age groups and in adults. Among the cortical sources of the N290 are the fusiform gyrus, lateral occipital area, and superior temporal sulcus[119], which are similar to the cortical sources that have been reported for the N170 in adults[74,75].

The only ERP study using repetition suppression to investigate the infant N290 showed that in 3- to 4-month-olds the response to isolated eyes is reduced in the context of frontal view faces *versus* houses but not in the context of profile view faces with closed eyes *versus* cars[82]. The authors concluded that frontal view faces activate to some extent the same neurons as isolated eyes at the processing stage of the N290, whereas profile view faces with closed eyes and objects do not. Thus, in contrast to adults, a view-invariant representation of human heads that is independent of the presence of visible eyes has not been developed at this age.

N290 amplitude is increased for faces relative to matched visual noise in 3-month-olds[120]. In 3-, 6-, and 12-month-olds, the N290 amplitude was found to be greater for human faces than monkey faces[121,122]. Furthermore, N290 amplitude is increased for inverted human faces *versus* upright human faces at 12 months, but not at 6 and 3 months of age[121,122]. This adult-like inversion effect was absent for monkey faces in all tested age groups. At 3 months, the N290 does not consistently differ between faces with scrambled inner features and canonical faces[123-125], suggesting that in young infants the N290 does not seem to be sensitive to distortions of the face configuration, although 3-month-olds discriminate between canonical and scrambled faces on the behavioral level[123,126]. In 6-month-olds the P400 was found to be of larger amplitude for upright *versus* inverted faces, but this effect was found both for human faces and monkey faces[121]. In addition, the P400 in 6-month-olds is of shorter latency for faces compared to objects when upright stimuli are used[127].

Nine-month-old infants who received visual experience with monkey faces in combination with individual

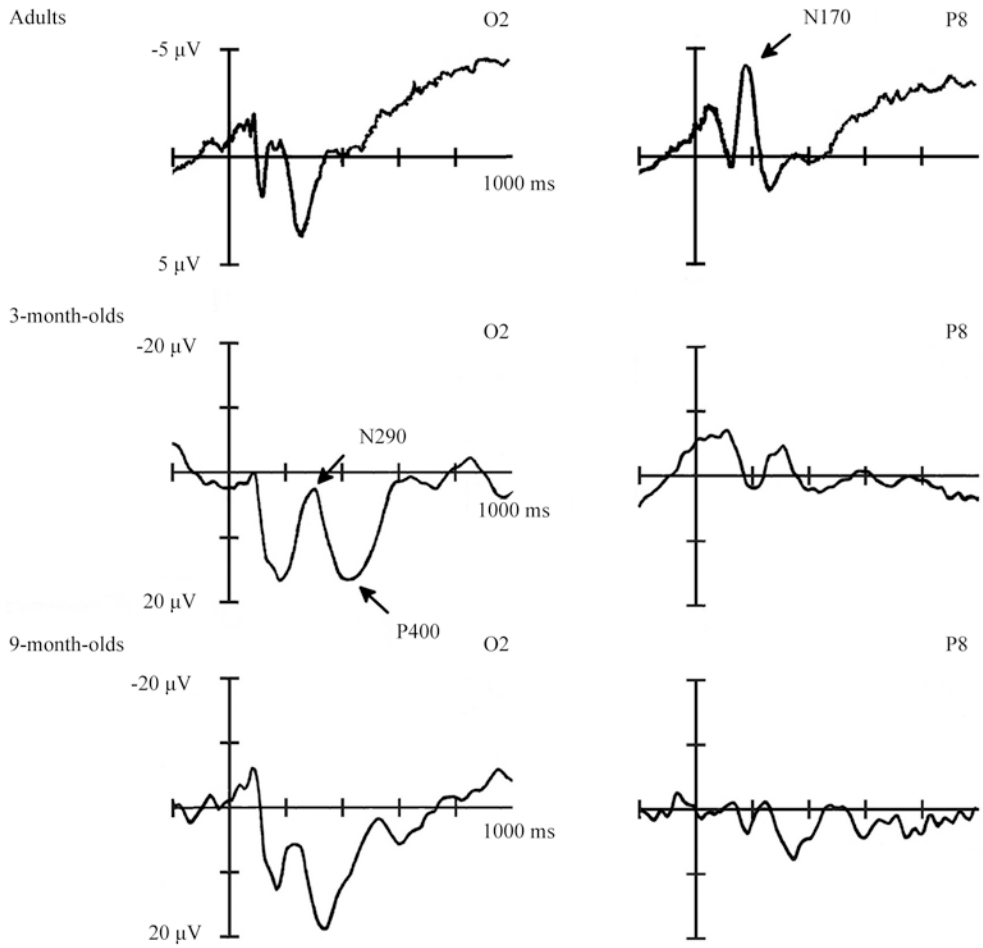


**Fig. 5. ERP responses to upright human faces in adults, 3-month-olds, and 9-month-olds. Whereas in adults the N170 is more laterally distributed (P8), the N290 and P400 are more medially distributed (O2) in infants.**

labels between 6 and 9 months of age responded with increased P400 amplitude for inverted monkey faces *versus* upright monkey faces[102]. This effect was not found following exposure without labels or with basic category labels (i.e. "monkey"). This finding suggests that visual experience in combination with individual representations of monkey faces not only promotes the discrimination of monkey faces at 9 months on a behavioral level[18], but also affects the neurophysiological inversion effect. However, it remains unclear why inversion of a human face leads to an increased N290 amplitude in 12-month-olds[122], whereas inversion of monkey faces leads to an increased P400 amplitude (and a slightly decreased N290 amplitude) in trained 9-month-olds[102].

All of the above studies suggest that the infant N290 and P400 possess some functional commonalities with the adult N170, which has led to the suggestion that both components become integrated into the mature N170 across development[121]. The exact mechanisms that are reflected by the N290 and P400 across development remain unclear, however. If the mature N170 indeed reflects the activation of face-selective and eye-selective neurons[103], this may also be the case for the infant N290/P400. As we have argued elsewhere[128], it is also possible that the relative contribution of eye-selective *versus* face-selective neurons to the N290 is greater in infants and in children than in adults. In children, the amplitude of the N170 in response to isolated eyes is much larger than the N170 in response to faces[129]. The N170 in response to isolated eyes also matures earlier than the N170 in response to complete faces[129]. Furthermore, the infant N290 seems to be less sensitive to disruption of facial feature configuration than the adult N170[123,130]. There is currently a lack of studies on the N290 in response to isolated eyes and faces without eyes in infancy. However, our own preliminary work suggests that N290 amplitude in 4-month-olds is as large in response to isolated eyes as it is in response to complete faces (in preparation). This finding suggests that the N290 responds to the presence of eyes in both cases, without the contribution of face-selective cells that are thought to decrease the activation of eye-selective neurons in response to upright faces in children and adults and that add to the N170 response to isolated eyes in children and adults. Furthermore, we have found a significantly reduced N290 amplitude in the right hemisphere for faces without eyes compared to complete faces (in preparation). In adults, in contrast, the N170 is not reduced in amplitude for faces without eyes[86]. Thus, although requiring replication, our data suggest that the N290 in 4-month-olds may indeed primarily reflect the activation of eye-selective neurons. The relative contribution of face-selective neurons may become greater as a more stable and more specified face representation is built up in early development.

Infants' neurophysiological response to the rapid repetition of individual faces has, to our knowledge, not been investigated so far. Therefore, it is unclear whether any response comparable to the adult N250r can be observed during infancy. Exploration of the adapting properties of the N290 and P400 and potential further repetition components to familiar and unfamiliar faces may further our understanding of the representation of individual faces in early childhood. In young children, reports of N170 double-peaks[131,132] may cautiously be interpreted as relating to the N170-N250 complex. The small amplitude of the N250 compared to the N170 and the lack of repetition studies in infants and young children may have aggravated the distinction of the two components in early development.

More research is clearly required to obtain a more consistent and more comprehensive understanding of face-selective brain responses in early development. There is reason to assume that the N290 and P400 are precursors to the N170 in older children and adults, whereas precursors of the N250r have not been examined so far. The functional relevance of the observed components and the meaning of the face inversion effect on these components are still unresolved issues. So far, there is only limited evidence that the inversion effect on the N170/N290/P400 does reflect a disruption of relational or holistic face processing as is often stated in the literature[102,103]. This issue should be further addressed in future studies on face processing across development. In addition, the role of eye-selective *versus* face-selective neurons as contributors to the N290/P400 throughout development warrants further research.

## 6 Under what conditions does face-like processing of exemplars of a visual category occur?

We have reviewed a large number of studies investigating face-specific processing on the behavioral level and on the neurophysiological level in adults and in infants. Most of these studies were concerned with the question of how face processing is different from the processing of other object categories. In this section we choose the opposite approach and ask under what conditions does face-like visual processing occur?

First, it has to be ensured that exemplars of the given category are represented as individuals. As we have reviewed above, faces are individuated by human infants starting from the day they are born[3]. Individuation and individual representation seem to have an important influence on how faces are processed throughout development. Discrimination between faces of other species and races can only be successfully trained in infants and in adults if exemplars are individually labeled[46,47,102]. Individuation of large numbers of exemplars from early on in development is surely one of the characteristics of face processing that can hardly be mimicked experimentally with other categories. Expertise in individuating exemplars of other categories induces a shift from access to primarily basic level representations to more subordinate representations, but, in contrast to faces, the basic level seems to keep a privileged status for objects of expertise[14,17]. However, access to semantic knowledge about individual objects seems to favor individual-level processing for familiar objects[9]. Thus, although individual-level processing is a characteristic of face processing, representations of individually-known exemplars of other categories may also be accessed on the individual level rather than at the basic level.

Extensive visual expertise with faces from early on in development is the second important characteristic that distinguishes faces from other visual categories. As mentioned above, more than mere exposure, expertise in discriminating and individuating faces may distinguish faces from other categories. The degree to which face expertise is qualitatively or quantitatively different from other kinds of object expertise has been a matter of lively debate, however[5,7].

Are faces just objects for which we have acquired a lot of expertise? Can expertise help to explain the third important characteristic of face processing: holistic processing? As mentioned above, evidence for the holistic processing of objects of expertise in the composite task is mixed[5,14,21,27,28]. While some studies have found evidence for face-like holistic processing of objects of expertise[27], others have not[21]. In some cases (e.g. Chinese characters) expertise may even lead to less holistic processing in experts than in novices[133]. Chinese characters are an interesting visual category, since individual graphemes signify individual words and experts have acquired experience in individuating characters since childhood. Like for faces, the entry level for recognizing Chinese characters in experts seems to be the individual level[134]. However, whereas features (strokes) and first-order relations between strokes are important for recognizing characters, second-order spatial relations are not[133]. Thus, in the case of Chinese characters, expertise may entail paying closer attention to features or components of the characters making it easier to isolate components from the whole in a composite task and leading to less holistic processing with increasing expertise (see[135] for an account why interference from irrelevant stimulus parts may have been found for novices in this study, and[136] for a study of holistic processing of English written words).

It has been suggested that expertise in individuating exemplars of a certain category in which, in contrast to Chinese characters, second-order spatial relations are important for individuation, may lead to more holistic processing for these objects similar to holistic face processing[137]. However, the only study testing this claim directly using trained stimuli in a composite task did not show an advantage for processing misaligned *versus* aligned objects of expertise which is typically taken to reflect holistic processing for faces[14]. In infants, visual expertise with individually-labeled strollers between 6 and 9 months led to enhanced visual discrimination after training, whereas category-level training did not[138]. Interestingly, before training, infants in all groups were not able to discriminate between strollers, suggesting that perceptual narrowing is not involved in this kind of object processing and may indeed be specific for faces. On the neuronal level, an increased N290 amplitude was found for upright *versus* inverted strollers after individual label training only[138]. The waveforms in this study resemble those found for inverted *versus* upright monkey faces after similar training[102], although the difference between upright and inverted strollers starts earlier than for monkey faces and does not extend to the P400. It is unclear why upright trained strollers and monkey faces elicit a larger N290 than inverted stimuli, whereas a larger N290 has been observed for inverted *versus* upright human faces in slightly older infants[122]. As mentioned above, further research is needed to determine to what extent holistic processing is reflected in the N170/N290/P400 response.

Thus, to date there is no convincing evidence that individual-level training leads to more holistic processing of objects other than faces in the composite task. This may be due to the fact that the amount of expertise in training studies cannot possibly match the amount of expertise with faces acquired in development. However, it cannot be ruled out that both the quantity and quality of expertise differ between categories in expertise or training studies and faces[5]. For instance, there may be a sensitive period for acquiring holistic face processing in infancy, although direct evidence for this possibility is rare in humans and mostly comes from case studies[70]. Sugita[139] conducted a visual deprivation study with macaque monkeys. Even though monkeys were completely prevented from seeing faces of any species from birth, they showed a visual preference for pictures of human and monkey faces over objects, similar to the visual preference observed in human newborns[38]. Furthermore, during deprivation, monkeys were able to discriminate both between individual human faces and between individual monkey faces. They were able to use both featural information and second-order relational information for discrimination. After one month of exposure to either monkey or human faces they showed evidence for perceptual narrowing and were only able to discriminate faces of the species they were exposed to first[139]. The particular duration of deprivation or the age of first exposure to faces did not play a major role, suggesting that there is no preset sensitive period in which a specialized face representation can be built, but that this process can be suspended until at least two years of age in monkeys. It would be interesting to examine in further studies whether these monkeys show evidence of holistic face processing (e.g. by using a switch-face task as in human infants). Possibly, specialization for certain kinds of species can be caught up on in case of early deprivation (at least in monkeys), whereas holistic face processing in the composite task relies on visual input within a sensitive period in infancy[70].

To conclude, exemplars of an object category have to be represented at the individual level and be processed holistically in order to elicit face-like processing. In addition, extensive experience with individuating exemplars has to be acquired that can hardly be simulated experimentally. Therefore, it is possible that differences between face and object processing are mainly due to quantitative differences in expertise. However, as we have reviewed above, developmental research provides evidence for some qualitative differences in visual experience for faces and objects. First, there seems to be a sensitive period in infancy for developing holistic face processing as measured by the composite task[70]. Second, perceptual narrowing for faces of one's own race and species takes place in infancy, a process that may be unparalleled in other domains of visual object processing[18,43,138]. Finally, individual-level learning and representation of faces *versus* predominantly basic-level learning and representation of other objects may be seen as a qualitative difference in experience that can nonetheless also occur for other kinds of objects that are individually familiar[9,138].

## 7 Conclusions and future directions

In the present article we have reviewed studies on the central characteristics of face processing including individual representation, extensive expertise in distinguishing individuals, and holistic processing. In addition to behavioral studies with adults, developmental research and neurophysiological investigations have offered important insights, but we have also highlighted some unresolved questions (see Table 3 for open questions and suggestions for future studies).

For instance, it is unclear whether an unspecific face template exists at birth or is developed shortly afterwards. Visual preferences for faces in visually-deprived monkeys suggest that learning is not required to develop these preferences in monkeys[139]. Thus, it is possible that an unspecific mechanism that responds to first-order face configurations and resembling stimuli[37,52] quickly determines whether a visual stimulus is a face and thus will be preferentially attended to in primates. Computational models that have been applied successfully to investigate face processing[26,140-142] may help solve the question whether such a mechanism is necessary to (re-)produce the characteristics of face processing.

Future studies should try to determine to what extent behavioral characteristics of face processing, e.g. holistic processing, are reflected in neurophysiological responses to faces. As we have argued above, to date, there is only limited evidence that the N170 ERP component reflects the holistic processing of faces and only one study has pro-

**Table 3. Summary of open questions and future directions**

| | |
|---|---|
| Relationships between the characteristics of face processing | How are configural and featural processing related to holistic processing? |
| | Is expertise in face-processing quantitatively and/ or qualitatively different from object processing? |
| | Does expertise in distinguishing individuals lead to enhanced holistic processing? |
| | What is the contribution of individual-level processing and access to semantic information to face-specific processing? |
| ERP studies | To what degree are ERP repetition effects face-specific or related to expertise? |
| | What influence does eye removal or eye isolation exert upon the N250? |
| Relation of behavioral and ERP studies | Do N170 and N250 inversion and eye removal effects relate to behavioral indices of disrupted holistic face processing? |
| | How do N170 and N250 relate to configural and featural processing? |
| | How do the response properties of eye- and face-selective neurons relate to concepts of holistic processing? |
| Development of face-specific processing | Do newborns enter the world with an unspecified face template or is the template built past birth? |
| | How do N290 and P400 relate to the N170? |
| | How is face identification as indexed by the N250 in adults reflected in the infant ERP? |
| | What is the relative contribution of face- and eye-selective neurons to the N290 and P400? |

vided evidence that the N170 is involved in both featural and second-order relational processing of faces[117].

It will also be important to investigate more closely the relationship between holistic and second-order relational processing. Both are sometimes referred to in the literature as configural processing, but, in fact, holistic processing as measured in the composite task, and second-order relational processing, may not be completely mutually dependent. Many researchers seem to agree that holistic face processing is based on a face representation for upright human faces that is holistic[25,26,32]. This representation is accessed when an upright face is perceived. Both featural cues and second-order relational cues are part of this holistic representation and both kinds of information are used to discriminate and identify faces. Second-order relational cues may be more dependent on holistic processing than featural cues, i.e. the use of this kind of information may be more impaired by disrupted holistic processing as in inverted faces[25]. However, contrast-reversed faces seem to be processed holistically in the composite task[143], but processing of second-order relations between facial features is impaired in these stimuli[144]. Similarly, there is evidence that other-race faces can be processed holistically in the composite task and part-whole task, whereas both featural and second-order relational processing are impaired for other-race faces[65]. This suggests that while second-order relational processing of faces may rely on access to a holistic face representation, sophisticated second-order relational processing is not, in turn, mandatory for holistic processing.

To conclude, we infer from the existing literature that faces differ from other object categories in that they are recognized and represented on the individual level. In addition, faces are processed more holistically than other visual object categories. Extensive expertise in distinguishing individual faces based on feature shapes and second-order spatial relations between features is probably crucial to develop a specialized (in terms of species and ethnicity) and holistic face representation in early development. Since it is not possible to provide comparable expertise for other categories experimentally, differences in the processing of faces and other visual object categories might be due to quantitative differences in the amount of visual experience. Nevertheless, developmental research also provides evidence for qualitative differences in experience with faces *versus* other object categories, such as a sensitive period for holistic processing[70] and a period of perceptual narrowing[18,43].

## References:


[1] Johnson MH, Dziurawiec S, Ellis H, Morton J. Newborns' preferential tracking of face-like stimuli and its subsequent decline. Cognition 1991, 40: 1–19.

[2] Sai FZ. The role of the mother's voice in developing mother's face preference: Evidence for intermodal perception at birth. Infant Child Dev 2005, 14: 29–50.

[3] Bushnell IWR, Sai F, Mullin JT. Neonatal recognition of the mother’s face. Br J Dev Psychol 1989, 7: 3–15.

[4] Kanwisher N, McDermott J, Chun MM. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 1997, 17: 4302–4311.

[5] McKone E, Kanwisher N, Duchaine BC. Can generic expertise explain special processing for faces? Trends Cogn Sci 2007, 11: 8–15.

[6] Gauthier I, Tarr MJ, Anderson AW, Skudlarski P, Gore JC. Activation of the middle fusiform ‚face area‘ increases with expertise in recognizing novel objects. Nat Neurosci 1999, 2: 568–573.

[7] Gauthier I, Nelson CA. The development of face expertise. Curr Opin Neurobiol 2001, 11: 219–224.

[8] Tanaka JW. The entry point of face recognition: evidence for face expertise. J Exp Psychol Gen 2001, 130: 534–543.

[9] Anaki D, Bentin S. Familiarity effects on categorization levels of faces and objects. Cognition 2009, 111: 144–149.

[10] Rosch E, Mervis CB, Gray WD, Johnson DM, Boyes-Braem P. Basic objects in natural categories. Cogn Psychol 1976, 8: 382–439.

[11] Pascalis O, de Vivies XD, Anzures G, Quinn PC, Slater AM, Tanaka JW, *et al.* Development of Face Processing. Wiley Interdiscip Rev Cogn Sci 2011, 2: 666–675.

[12] Maurer D, Grand RL, Mondloch CJ. The many faces of configural processing. Trends Cogn Sci 2002, 6: 255–260.

[13] Farah MJ, Wilson KD, Drain M, Tanaka JN. What is “special” about face perception? Psychol Rev 1998, 105: 482–498.

[14] Wong AC, Palmeri TJ, Gauthier I. Conditions for facelike expertise with objects: becoming a Ziggerin expert—but which type? Psychol Sci 2009, 20: 1108–1117.

[15] Bruce V, Young AW. Understanding face recognition. Br J Psychol 1986, 77: 305–327.

[16] Sinha P, Balas B, Ostrovsky YM, Russell R. Face recognition by humans: Nineteen results all computer vision researchers should know about. Proc IEEE 2006, 94: 1948–1962.

[17] Johnson KE, Mervis CB. Effects of varying levels of expertise on the basic level of categorization. J Exp Psychol Gen 1997, 126: 248–277.

[18] Scott LS, Monesson A. The origin of biases in face perception. Psychol Sci 2009, 20: 676–680.

[19] Yin RK. Looking at upside-down faces. J Exp Psychol 1969, 81: 141–145.

[20] Freire A, Lee K, Symons LA. The face-inversion effect as a deficit in the encoding of configural information: direct evidence. Perception 2000, 29: 159–170.

[21] Robbins R, McKone E. No face-like processing for objects-of-expertise in three behavioural tasks. Cognition 2007, 103: 34–79.

[22] Leder H, Candrian G, Huber O, Bruce V. Configural features in the context of upright and inverted faces. Perception 2001, 30: 73–83.

[23] Thompson P. Margaret Thatcher: a new illusion. Perception 1980, 9: 483–484.

[24] McKone E, Yovel G. Why does picture-plane inversion sometimes dissociate perception of features and spacing in faces, and sometimes not? Toward a new theory of holistic processing. Psychon Bull Rev 2009, 16: 778–797.

[25] Rossion B. Distinguishing the cause and consequence of face inversion: The perceptual field hypothesis. Acta Psychol 2008, 132: 300–312.

[26] Schwaninger A, Wallraven C, Bülthoff HH. Computational modeling of face recognition based on psychophysical experiments. Swiss J Psychol 2004, 63: 207–215.

[27] Diamond R, Carey S. Why faces are and are not special: an effect of expertise. J Exp Psychol Gen 1986, 115: 107–117.

[28] Rossion B, Gauthier I, Goffaux V, Tarr MJ, Crommelinck M. Expertise training with novel objects leads to left-lateralized facelike electrophysiological responses. Psychol Sci 2002, 13: 250–257.

[29] Tanaka JW, Farah MJ. Parts and wholes in face recognition. Q J Exp Psychol A 1993, 46: 225–245.

[30] Young AW, Hellawell D, Hay DC. Configurational information in face perception. Perception 1987, 16: 747–759.

[31] Rossion B, Boremanse A. Nonlinear relationship between holistic processing of individual faces and picture–plane rotation: evidence from the face composite illusion. J Vis 2008, 8: 3 1–13.

[32] Riesenhuber M, Wolff BS. Task effects, performance levels, features, configurations, and holistic face processing: A reply to Rossion. Acta Psychol 2009, 132: 286–292.

[33] Richler JJ, Cheung OS, Gauthier I. Holistic processing predicts face recognition. Psychol Sci 2011, 22: 464–471.

[34] Gauthier I, Bukach C. Should we reject the expertise hypothesis? Cognition 2007, 103: 322–330.

[35] McKone E, Robbins R. The evidence rejects the expertise hypothesis: reply to Gauthier & Bukach. Cognition 2007, 103: 331–336.

[36] Farroni T, Johnson MH, Menon E, Zulian L, Faraguna D, Csibra G.

Newborns' preference for face-relevant stimuli: effects of contrast polarity. Proc Natl Acad Sci U S A 2005, 102: 17245–17250.

[37] Johnson MH. Subcortical face processing. Nat Rev Neurosci 2005, 6: 766–774.

[38] Di Giorgio E, Leo I, Pascalis O, Simion F. Is the face-perception system human-specific at birth? Dev Psychol 2012, 48(4): 1083–1090.

[39] Crookes K, McKone E. Early maturity of face recognition: no childhood development of holistic processing, novel face encoding, or face-space. Cognition 2009, 111: 219–247.

[40] McKone E, Crookes K, Kanwisher N. The cognitive and neural development of face recognition in humans. In: Gazzaniga MS (Ed.). The Cognitive Neurosciences. IV edition. Cambridge, MA: Bradford Books, 2009: 467–482.

[41] Pascalis O, de Haan M, Nelson CA. Is face processing species-specific during the first year of life? Science 2002, 296: 1321–1323.

[42] Kuhl PK, Tsao FM, Liu HM. Foreign-language experience in infancy: effects of short-term exposure and social interaction on phonetic learning. Proc Natl Acad Sci U S A 2003, 100: 9096–9101.

[43] Kelly DJ, Quinn PC, Slater AM, Lee K, Ge L, Pascalis O. The other-race effect develops during infancy: evidence of perceptual narrowing. Psychol Sci 2007, 18: 1084–1089.

[44] Anzures G, Quinn PC, Pascalis O, Slater AM, Lee K. Categorization, categorical perception, and asymmetry in infants' representation of face race. Dev Sci 2010, 13: 553–564.

[45] Meissner CA, Brigham JC. Thirty years of investigating the own-race bias memory for faces: A meta–analytic review. Psychol Public Policy Law 2001, 7: 3–35.

[46] Lebrecht S, Pierce LJ, Tarr MJ, Tanaka JW. Perceptual other-race training reduces implicit racial bias. PLoS One 2009, 4: e4215.

[47] McGugin RW, Tanaka JW, Lebrecht S, Tarr MJ, Gauthier I. Race-specific perceptual discrimination improvement following short individuation training with faces. Cogn Sci 2011, 35: 330–347.

[48] Heron-Delaney M, Anzures G, Herbert JS, Quinn PC, Slater AM, Tanaka JW, *et al.* Perceptual training prevents the emergence of the other race effect during infancy. PLoS One 2011, 6: e19858.

[49] de Haan M, Johnson MH, Maurer D, Perrett D. Recognition of individual faces and average face prototypes by 1- and 3-month-old infants. Cogn Dev 2001, 16: 659–678.

[50] Farroni T, Valenza E, Simion F, Umilta C. Configural processing at birth: evidence for perceptual organisation. Perception 2000, 29: 355–372.

[51] Macchi Cassia V, Turati C, Simion F. Can a nonspecific bias toward top-heavy patterns explain newborns' face preference? Psychol Sci 2004, 15: 379–383.

[52] Turati C, Simion F, Milani I, Umilta C. Newborns' preference for faces: what is crucial? Dev Psychol 2002, 38: 875–882.

[53] Leo I, Simion F. Face processing at birth: a Thatcher illusion study. Dev Sci 2009, 12: 492–498.

[54] Schwarzer G, Zauner N, Jovanovic B. Evidence of a shift from featural to configural face processing in infancy. Dev Sci 2007, 10: 452–463.

[55] de Schonen S, Mathivet E. Hemispheric asymmetry in a face discrimination task in infants. Child Dev1990, 61: 1192–1205.

[56] Deruelle C, de Schonen S. Hemispheric asymmetries in visual pattern processing in infancy. Brain Cogn 1991, 16: 151–179.

[57] Salomao SR, Ventura DF. Large sample population age norms for visual acuities obtained with Vistech-Teller Acuity Cards. Invest Ophthalmol Vis Sci 1995, 36: 657–670.

[58] Banks MS, Dannemiller JL. Infant visual psychophysics. In: Salapatek P, Cohen LB (Eds.). Handbook of Infant Perception. New York: Academic Press, 1987: 115–184.

[59] Hickey TL, Peduzzi JD. Structure and development of the visual system. In: Salapatek P, Cohen LB (Eds.). Handbook of Infant Perception. New York: Academic Press, 1987: 1–42.

[60] Atkinson J. Early visual development: differential functioning of parvocellular and magnocellular pathways. Eye (Lond) 1992, 6 ( Pt 2): 129–135.

[61] Hickey TL. Postnatal development of the human lateral geniculate nucleus: relationship to a critical period for the visual system. Science 1977, 198: 836–838.

[62] Salapatek P. Pattern perception in early infancy. In: Cohen LB, Salapatek P (Eds.). Infant Perception: From Sensation to Cognition. New York: Academic Press, 1975: 133–248.

[63] Bronson GW. Changes in infants' visual scanning across the 2- to 14-week age period. J Exp Child Psychol 1990, 49: 101–125.

[64] Ferguson KT, Kulkofsky S, Cashon CH, Casasola M. The development of specialized processing of own-race faces in infancy. Infancy 2009, 14: 263–284.

[65] Mondloch CJ, Elms N, Maurer D, Rhodes G, Hayward WG, Tanaka JW, *et al.* Processes underlying the cross-race effect: an investigation of holistic, featural, and relational processing of own-race versus other-race faces. Perception 2010, 39: 1065–1085.

[66] Bukach CM, Cottle J, Ubiwa J, Miller J. Individuation experience predicts other-race effects in holistic processing for both Caucasian and Black participants. Cognition 2012, 123: 319–324.

[67] Tanaka JW, Kiefer M, Bukach CM. A holistic account of the own-race effect in face recognition: evidence from a cross-cultural study. Cognition 2004, 93: B1–9.

[68] Michel C, Rossion B, Han J, Chung CS, Caldara R. Holistic processing is finely tuned for faces of one's own race. Psychol Sci 2006, 17: 608–615.

[69] McKone E, Brewer JL, MacPherson S, Rhodes G, Hayward WG. Familiar other-race faces show normal holistic processing and are robust to perceptual stress. Perception 2007, 36: 224–248.

[70] Le Grand R, Mondloch CJ, Maurer D, Brent HP. Impairment in holistic face processing following early visual deprivation. Psychol Sci 2004, 15: 762–768.

[71] Rossion B, Jacques C. Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. Neuroimage 2008, 39: 1959–1979.

[72] George N, Jemel B, Fiori N, Chaby L, Renault B. Electrophysiological correlates of facial decision: insights from upright and upside-down Mooney-face perception. Cogn Brain Res2005, 24: 663–673.

[73] Vuilleumier P, Sagiv N, Hazeltine E, Poldrack RA, Swick D, Rafal RD, *et al.* Neural fate of seen and unseen faces in visuospatial neglect: a combined event-related functional MRI and event-related potential study. Proc Natl Acad Sci U S A 2001, 98: 3495–3500.

[74] Itier RJ, Taylor MJ. Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. Neuroimage 2002, 15: 353–372.

[75] Itier RJ, Taylor MJ. Source analysis of the N170 to faces and objects. Neuroreport 2004, 15: 1261–1265.

[76] Hoffman EA, Haxby JV. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat Neurosci 2000, 3: 80–84.

[77] Kovacs G, Zimmer M, Banko E, Harza I, Antal A, Vidnyanszky Z. Electrophysiological correlates of visual adaptation to faces and body parts in humans. Cereb Cortex 2006, 16: 742–753.

[78] Harris A, Nakayama K. Rapid adaptation of the m170 response: importance of face parts. Cereb Cortex 2008, 18: 467–476.

[79] Harris A, Nakayama K. Rapid face-selective adaptation of an early extrastriate component in MEG. Cereb Cortex 2007, 17: 63–70.

[80] Eimer M, Kiss M, Nicholas S. Response profile of the face-sensitive N170 component: a rapid adaptation study. Cereb Cortex 2010, 20: 2442–2452.

[81] Eimer M, Gosling A, Nicholas S, Kiss M. The N170 component and its links to configural face processing: A rapid neural adaptation study. Brain Res 2011, 1376: 76–87.

[82] Gliga T, Dehaene-Lambertz G. Development of a view-invariant representation of the human head. Cognition 2007, 102: 261–288.

[83] Guillaume C, Guillery-Girard B, Chaby L, Lebreton K, Hugueville L, Eustache F*, et al*. The time course of repetition effects for familiar faces and objects: an ERP study. Brain Res 2009, 1248: 149–161.

[84] Maurer U, Rossion B, McCandliss BD. Category specificity in early perception: face and word n170 responses differ in both lateralization and habituation properties. Front Hum Neurosci 2008, 2: 18.

[85] Mercure E, Cohen Kadosh K, Johnson MH. The n170 shows differential repetition effects for faces, objects, and orthographic stimuli. Front Hum Neurosci 2011, 5: 6.

[86] Eimer M. Does the face-specific N170 component reflect the activity of a specialized eye processor? Neuroreport 1998, 9: 2945–2948.

[87] Bentin S, Allison T, Puce A, Perez E, McCarthy G. Electrophysiological studies of face perception in humans. J Cogn Neurosci 1996, 8: 551–565.

[88] Schweinberger SR, Pickering EC, Jentzsch I, Burton AM, Kaufmann JM. Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. Cogn Brain Res 2002, 14: 398–409.

[89] Schweinberger SR, Pfütze EM, Sommer W. Repetition priming and associative priming of face recognition: Evidence from event-related potentials. J Exp Psychol Learn Mem Cogn 1995, 21: 722–736.

[90] Pierce LJ, Scott LS, Boddington S, Droucker D, Curran T, Tanaka JW. The n250 brain potential to personally familiar and newly learned faces and objects. Front Hum Neurosci 2011, 5: 111.

[91] Scott LS, Tanaka JW, Sheinberg DL, Curran T. A reevaluation of the electrophysiological correlates of expert object processing. J Cogn Neurosci 2006, 18: 1453–1465.

[92] Begleiter H, Porjesz B, Wang W. Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. Electroencephalogr Clin Neurophysiol 1995, 94: 41–49.

[93] Pfütze EM, Sommer W, Schweinberger SR. Age-related slowing in face and name recognition: evidence from event-related brain potentials. Psychol Aging 2002, 17: 140–160.

[94] Caharel S, d'Arripe O, Ramon M, Jacques C, Rossion B. Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: evidence from the N170 ERP component. Neuropsychologia 2009, 47: 639–643.

[95] Itier RJ, Taylor MJ. Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs. Neuroimage 2004, 21: 1518–1532.

[96] Kaufmann JM, Schweinberger SR. The faces you remember: caricaturing shape facilitates brain processes reflecting the acquisition of new face representations. Biol Psychol 2012, 89: 21–33.

[97] Bindemann M, Burton AM, Leuthold H, Schweinberger SR. Brain potential correlates of face recognition: geometric distortions and the N250r brain response to stimulus repetitions. Psychophysiology 2008, 45: 535–544.

[98] Schweinberger SR, Huddy V, Burton AM. N250r: a face-selective brain response to stimulus repetitions. Neuroreport 2004, 15: 1501–1505.

[99] Itier RJ, Latinus M, Taylor MJ. Face, eye and object early processing: what is the face specificity? Neuroimage 2006, 29: 667–676.

[100] Rossion B, Gauthier I, Tarr MJ, Despland P, Bruyer R, Linotte S,

*et al.* The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face–specific processes in the human brain. Neuroreport 2000, 11: 69–74.

[101] Rossion B, Delvenne JF, Debatisse D, Goffaux V, Bruyer R, Crommelinck M, *et al.* Spatio-temporal localization of the face inversion effect: an event–related potentials study. Biol Psychol 1999, 50: 173–189.

[102] Scott LS, Monesson A. Experience-dependent neural specialization during infancy. Neuropsychologia 2010, 48: 1857–1861.

[103] Itier RJ, Alain C, Sedore K, McIntosh AR. Early face processing specificity: it's in the eyes! J Cogn Neurosci 2007, 19: 1815–1826.

[104] Tanaka JW, Curran T. A neural basis for expert object recognition. Psychol Sci 2001, 12: 43–47.

[105] Thierry G, Martin CD, Downing P, Pegna AJ. Controlling for interstimulus perceptual variance abolishes N170 face selectivity. Nat Neurosci 2007, 10: 505–511.

[106] Aguirre GK, Singh R, D'Esposito M. Stimulus inversion and the responses of face and object-sensitive cortical areas. Neuroreport 1999, 10: 189–194.

[107] Haxby JV, Ungerleider LG, Clark VP, Schouten JL, Hoffman EA, Martin A. The effect of face inversion on activity in human neural systems for face and object perception. Neuron 1999, 22: 189–199.

[108] Itier RJ, Batty M. Neural bases of eye and gaze processing: the core of social cognition. Neurosci Biobehav Rev2009, 33: 843–863.

[109] Bentin S, Golland Y, Flevaris A, Robertson LC, Moscovitch M. Processing the trees and the forest during initial stages of face perception: Electrophysiological evidence. J Cogn Neurosci 2006, 18: 1406–1421.

[110] Letourneau SM, Mitchell TV. Behavioral and ERP measures of holistic face processing in a composite task. Brain Cogn 2008, 67: 234–245.

[111] Jacques C, Rossion B. The initial representation of individual faces in the right occipito-temporal cortex is holistic: electrophysiological evidence from the composite face illusion. J Vis 2009, 9: 8, 1–16.

[112] Jacques C, Rossion B. Misaligning face halves increases and delays the N170 specifically for upright faces: Implications for the nature of early face representations. Brain Res 2009, 1318: 96–109.

[113] Ishizu T, Ayabe T, Kojima S. Configurational factors in the perception of faces and non-facial objects: an ERP study. Int J Neurosci 2008, 118: 955–966.

[114] Boutsen L, Humphreys GW, Praamstra P, Warbrick T. Comparing neural correlates of configural processing in faces and objects: an ERP study of the Thatcher illusion. Neuroimage 2006, 32: 352–367.

[115] Milivojevic B, Clapp WC, Johnson BW, Corballis MC. Turn that frown upside down: ERP effects of thatcherization of misorientated faces. Psychophysiology 2003, 40: 967–978.

[116] Carbon CC, Schweinberger SR, Kaufmann JM, Leder H. The Thatcher illusion seen by the brain: an event-related brain potentials study. Cogn Brain Res 2005, 24: 544–555.

[117] Scott LS, Nelson CA. Featural and configural face processing in adults and infants: a behavioral and electrophysiological investigation. Perception 2006, 35: 1107–1128.

[118] de Haan M, Johnson MH, Halit H. Development of face-sensitive event-related potentials during infancy: a review. Int J Psychophysiol 2003, 51: 45–58.

[119] Johnson MH, Griffin R, Csibra G, Halit H, Farroni T, de Haan M, *et al.* The emergence of the social brain network: evidence from typical and atypical development. Dev Psychopathol 2005, 17: 599–619.

[120] Halit H, Csibra G, Volein A, Johnson MH. Face-sensitive cortical processing in early infancy. J Child Psychol Psychiatry 2004, 45: 1228–1234.

[121] de Haan M, Pascalis O, Johnson MH. Specialization of neural mechanisms underlying face recognition in human infants. J Cogn Neurosci 2002, 14: 199–209.

[122] Halit H, de Haan M, Johnson MH. Cortical specialisation for face processing: face-sensitive event-related potential components in 3- and 12-month-old infants. Neuroimage 2003, 19: 1180–1193.

[123] Macchi Cassia V, Kuefner D, Westerlund A, Nelson CA. A behavioural and ERP investigation of 3-month-olds' face preferences. Neuropsychologia 2006, 44: 2113–2125.

[124] Parise E, Handl A, Striano T. Processing faces in dyadic and triadic contexts. Neuropsychologia 2010, 48: 518–528.

[125] Gliga T, Dehaene-Lambertz G. Structural encoding of body and face in human infants and adults. J Cogn Neurosci 2005, 17: 1328–1340.

[126] Maurer D, Barrera M. Infants' perception of natural and distorted arrangements of a schematic face. Child Dev 1981, 52: 196–202.

[127] de Haan M, Nelson CA. Brain activity differentiates face and object processing in 6-month-old infants. Dev Psychol 1999, 35: 1113–1121.

[128] Hoehl S, Reid VM, Parise E, Handl A, Palumbo L, Striano T. Looking at eye gaze processing and its neural correlates in infancy - implications for social development and autism spectrum disorder. Child Dev2009, 80: 968–985.

[129] Taylor MJ, Edmonds GE, McCarthy G, Allison T. Eyes first! Eye processing develops before face processing in children. Neuroreport 2001, 12: 1671–1676.

[130] Macchi Cassia V, Kuefner D, Westerlund A, Nelson CA. Modulation of face-sensitive event-related potentials by canonical and distorted human faces: the role of vertical symmetry and up-down featural arrangement. J Cogn Neurosci 2006, 18: 1343–1358.

[131] Kuefner D, de Heering A, Jacques C, Palmero-Soler E, Rossion B. Early visually evoked electrophysiological responses over the hu-

man brain (P1, N170) show stable patterns of face-sensitivity from 4 years to adulthood. Front Hum Neurosci 2010, 3: 67.

[132] Taylor MJ, Batty M, Itier RJ. The faces of development: a review of early face processing over childhood. J Cogn Neurosci 2004, 16: 1426–1442.

[133] Hsiao JH, Cottrell GW. Not all visual expertise is holistic, but it may be leftist: the case of Chinese character recognition. Psychol Sci 2009, 20: 455–463.

[134] Wong AC, Gauthier I. An analysis of letter expertise in a levels-of-categorization framework. Vis Cogn 2006, 15: 854–879.

[135] Richler JJ, Wong YK, Gauthier I. Perceptual expertise as a shift from strategic interference to automatic holistic processing. Curr Dir Psychol Sci 2011, 20: 129–134.

[136] Wong AC, Bukach CM, Yuen C, Yang L, Leung S, Greenspon E. Holistic processing of words modulated by reading experience. PLoS One 2011, 6: e20753.

[137] Bukach CM, Gauthier I, Tarr MJ. Beyond faces and modularity: the power of an expertise framework. Trends Cogn Sci 2006, 10: 159–166.

[138] Scott LS. Mechanisms underlying the emergence of object representations during infancy. J Cogn Neurosci 2011, 23: 2935–2944.

[139] Sugita Y. Face perception in monkeys reared with no exposure to faces. Proc Natl Acad Sci U S A 2008, 105: 394–398.

[140] Jiang X, Rosen E, Zeffiro T, Vanmeter J, Blanz V, Riesenhuber M. Evaluation of a shape-based model of human face discrimination using fMRI and behavioral techniques. Neuron 2006, 50: 159–172.

[141] McCleery JP, Zhang L, Ge L, Wang Z, Christiansen EM, Lee K, *et al.* The roles of visual expertise and visual input in the face inversion effect: behavioral and neurocomputational evidence. Vis Res 2008, 48: 703–715.

[142] Stollhoff R, Kennerknecht I, Elze T, Jost J. A computational model of dysfunctional facial encoding in congenital prosopagnosia. Neural Netw 2011, 24: 652–664.

[143] Hole GJ, George PA, Dunsmore V. Evidence for holistic processing of faces viewed as photographic negatives. Perception 1999, 28: 341–359.

[144] Kemp R, McManus C, Pigott T. Sensitivity to the displacement of facial features in negative and inverted images. Perception 1990, 19: 531–543.

[145] Tottenham N, Tanaka JW, Leon AC, McCarry T, Nurse M, Hare TA, *et al.* The NimStim set of facial expressions: judgments from untrained research participants. Psychiatry Res 2009, 168: 242–249.