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*How Infants Categorize and Individuate Faces*

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## Acknowledgements

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# 1        Framing the Issues: Perceptual Categorization of Visual Stimuli

From the moment we open our eyes for the very first time, we are surrounded by a highly complex visual environment that needs to be parsed into meaningful units. Different shapes and colors move across our visual field, fall on different areas of our retina, and take different neural pathways in our brain. The position of our eyes changes constantly, while visual entities in our environment move around, challenging us to parse entities and perceive objects in a coherent way. If our visual system failed at this process, we would be flooded by sensory inputs. A powerful function to parse the environment into meaningful units is sorting sensory inputs into categories. As adults, we are very apt at this process of visual categorization (Mack & Palmeri, 2015; Peykarjou, Hoehl, Rossion, & Pauen, 2015; Thorpe, Fize, & Marlot, 1996). The goal of the current thesis is to take a closer look at how these functions develop during infancy, focusing on the recognition and categorization of human faces.

**What is visual categorization?** Basically, any visual category is defined by a collection of different visual inputs that share a common set of features (e.g., the visual category of "human faces" consists of oval shapes in skin colors with facial features aligned from top to bottom as eyes, nose, and mouth). In some cases, certain features actually define the category (e.g., in the case of abstract forms like triangles or circles); but in most cases the category boundaries are more blurry or "fuzzy" because the features vary substantially between exemplars (e.g., in the case of the category "bird" or "monkey"). Rosch and colleagues (1976) argued that such categories have a prototype structure. The *prototype* results from taking the mean value from each feature dimension considered to be relevant for defining the category at hand. It is a hypothetical construct that best represents the given category.

Following Rosch and colleagues (1976), most natural categories are prototype categories organized within a hierarchical categorical system. This system ranges from very broad categories to increasingly specialized sub-categories (see Figure 1 for an illustration using the example of human faces). At the highest (i.e., the *global*) level, animate beings are discriminated from inanimate objects (e.g., Mandler, 1997). At the next lower (i.e., the *superordinate*) level, objects within one global domain are categorized into broad classes (e.g., mammals versus fish or birds). One level lower, Rosch and colleagues define the so-called *basic level* (e.g., humans versus apes or

dogs). On the lowest level, the *subordinate level*, different sub-types of exemplars of the same basic-level category can be discriminated (e.g., Caucasian faces versus Asian or African faces). Categorization can be understood as the process of showing a *generalizing response* to all items belonging to a given category on any level of abstraction (e.g., same response to all images of human faces) and a *discriminating response* to items from other categories (e.g., different responses to faces and toys; Rossion, Torfs, Jacques, & Liu-Shuang, 2015).

Though not generally included in the categorization hierarchy, in this thesis I will make the case that individuation should be regarded as a special instance of categorization. Individuation requires that a cognitive or neural representation is activated by all instances of a given entity, but not by instances from another entity (Tanaka, 2001; Yovel et al., 2012). For example, a representation of Marilyn Monroe will be activated by all different images showing Marilyn, but not by any image showing another blond Caucasian woman. Thus, the most specific categorization level is the *individual level*.

Inspired by the pioneering work of Rosch and colleagues (1976), the phenomenon of categorization has received much attention during the past 40 years, leading to more than 15000 papers (number generated by employing the term "visual categorization" as search criterion in PubMed in December 2016). One central finding of this research is that adults can categorize any given picture at the basic level (e.g., "face", "car", "dog"; Grill-Spector & Kanwisher, 2005; Mack & Palmeri, 2015; Rousselet, Mace, & Fabre-Thorpe, 2003) and at rather abstract levels (e.g., "living", "non-living"; Mack & Palmeri, 2015; Poncet & Fabre-Thorpe, 2014) after seeing it for a very short time only (i.e., even less than 50 ms). Moreover, categorization takes place very quickly (e.g., categorization as animal/no animal within 150 ms; Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001; Thorpe et al., 1996).

These findings suggest that perceptual categorization is one of the most important organizing principles of visual experience. Due to its high relevance for survival and environmental fitness, categorization is likely to be evolutionary ancient. Indeed, visual categorization on concrete levels has been observed in different species such as apes (Murai et al., 2005), monkeys (Kiani, Esteky, & Tanaka, 2005; Kriegeskorte et al., 2008), dogs (Range, Aust, Steurer, & Huber, 2008), rats (Brooks et al., 2013), and even fish (Schluessel, Fricke, & Bleckmann, 2012), and on broad

abstract levels in monkeys (Cauchoix, Crouzet, Fize, & Serre, 2016; Fize, Cauchoix, & Fabre-Thorpe, 2011; Kiani et al., 2005; Kriegeskorte et al., 2008). Categorization on highly abstract levels without prior training based on high-level representations has been observed in humans (de Heering & Rossion, 2015; Kriegeskorte et al., 2008; Mack & Palmeri, 2015; Rossion et al., 2015). Thus, natural and multi-level categorization seems to be characteristic of humans' efficient visual perception. This raises the question how visual categorization at different hierarchical levels develops ontogenetically.

**How does categorization develop?** Initially, the basic level (e.g., car, dog, house) was believed to emerge first during childhood (i.e., between 3 and 6 years of age; Rosch et al., 1976). In the meantime, looking-time measures have demonstrated categorization on different levels even in infancy (Arterberry & Bornstein, 2002; Quinn & Eimas, 1998; Younger & Fearing, 2000). As noted by Rakison (2000), the hierarchical taxonomy observed in adults may be matched only superficially in infants and toddlers. It has been suggested to refer to "basic-like" or "child basic" categories (Behl-Chadha, 1996; Rakison, 2000). This view is acknowledged, but for ease of reading, I will employ the terms developed to describe adult categorization. A large body of research has provided evidence that infants can categorize objects at the global (animate versus inanimate, e.g. Mandler, 1997), the superordinate (e.g., mammals versus other animals, Behl-Chadha, 1996), the basic (e.g., cats versus dogs, Arterberry & Bornstein, 2002; Quinn & Eimas, 1998), and subordinate levels (e.g., Saint Bernard versus beagles, Quinn & Tanaka, 2007). It has been suggested that categorization emerges from broader to more fine-grained levels (Pauen, 2002b; Quinn & Johnson, 2000; Younger & Fearing, 2000), enabling infants to identify animate beings from early on.

One question that is central for our understanding of infant categorization is how low-level cues, online category formation, the accumulation of data prior to the experiment and the development of semantic knowledge contribute to the development of categorization levels. The causes of categorization development are still hotly debated (Diesendruck, 2003; Pauen, 2002a; Quinn & Johnson, 1997; Westermann & Mareschal, 2012) and, despite recent attempts to address this problem via computational modeling (French, Mareschal, Mermillod, & Quinn, 2004; Westermann & Mareschal, 2012), we are currently lacking a common theory linking

the different factors driving categorization development. Though a crucial issue, accounting for the causes of categorization development is not the focus of this thesis.
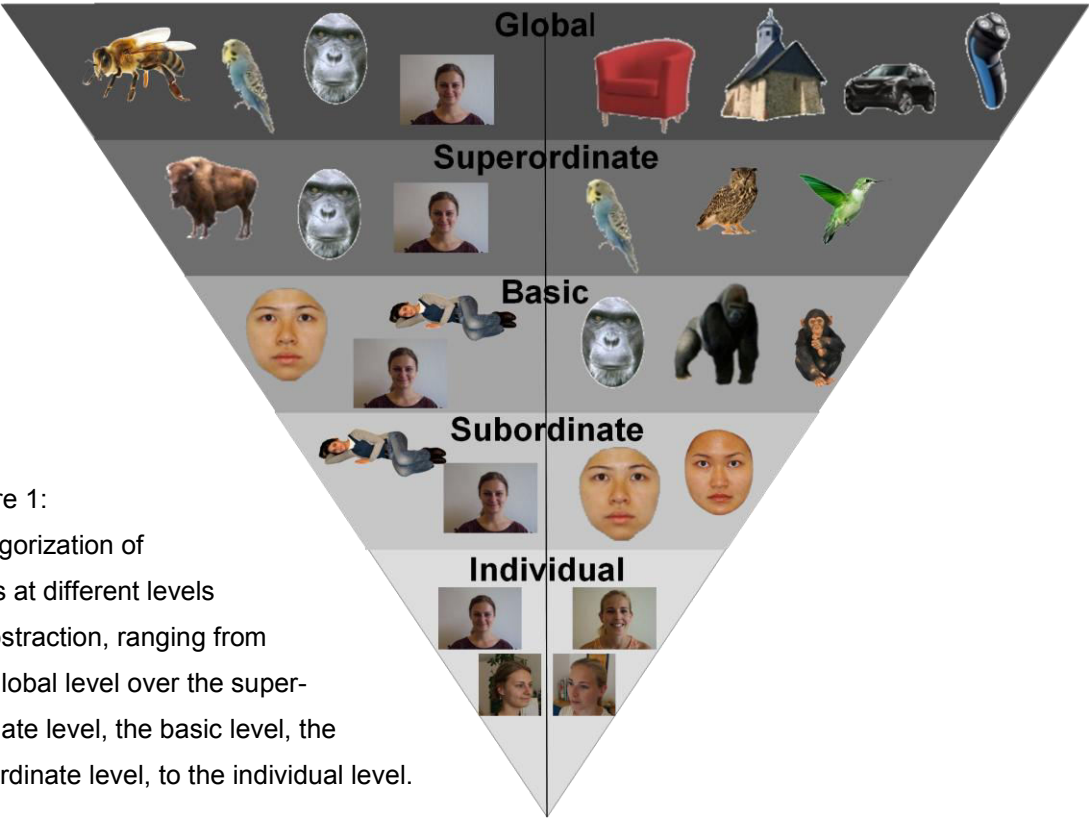


Figure 1: Categorization of faces at different levels of abstraction, ranging from the global level over the super-ordinate level, the basic level, the subordinate level, to the individual level.

**Are faces categorized in a special way?** Faces form a relatively homogeneous stimulus group, consisting of an oval shape with facial features aligned from top to bottom as eyes, nose, and mouth, and they elicit increased attention compared to other objects (Fletcher-Watson, Findlay, Leekam, & Benson, 2008). In adults, faces activate specialized neural networks along the ventral visual pathway (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997), and elicit specialized cognitive and neural processing (Farah, Wilson, Drain, & Tanaka, 1998; Rossion & Jacques, 2008; Yovel, 2016). The special status of faces for adults raises the question whether human faces are processed in a special way from early on. Regarding categorization, it is of particular interest whether face categorization develops according to a similar trajectory as categorization of other object categories (from global to more fine-grained levels), or whether specialized brain regions allow us to categorize *and* individuate faces from very early on.

Even during infancy, human faces are the most salient and most regularly perceived stimuli (Di Giorgio, Turati, Altoè, & Simion, 2012; Kwon, Setoodehnia, Baek, Luck, & Oakes, 2016; Sugden, Mohamed-Ali, & Moulson, 2014). Preferences for face-like stimuli have been demonstrated within a few hours after birth (Farroni et al., 2005; Johnson, Dziurawiec, Ellis, & Morton, 1991). Early face-preferences in newborns are likely driven by perceptual biases (Macchi Cassia, Turati, & Simion, 2004; Macchi Cassia, Valenza, Simion, & Leo, 2008) and may rely on subcortical processing (Morton & Johnson, 1991). Following rapid development early in life, cortical processes and face-specific biases (Chien, 2011; Morton & Johnson, 1991; Nakano & Nakatani, 2014) seem to drive infants' face preference from 2-3 months of age. However, the mere existence of a preference for human faces shortly after birth is not sufficient to indicate categorical representation as defined earlier, which requires generalizing and discriminating among exemplars. Evidence on the development of categorical representations for human faces is described in chapter 3.

As argued before, the identification of a specific face (or any specific exemplar from a given category) can be conceived as categorization because the same exemplar may appear differently across situations (e.g., from different angles and under different lightning conditions). Adults' ability to individuate familiar faces is striking (Burton, Wilson, Cowan, & Bruce, 1999), whereas errors are much more frequent with unfamiliar faces (10-30% error rate, Bruce et al., 1999; Bruce, Henderson, Newman, & Burton, 2001; Jenkins & Burton, 2011). Even newborn infants recognize their mother's face or the face of another familiarized female (Coulon, Guellai, & Streri, 2011; Sai, 2005). This skill seems critical for survival, and provides the basis for developing stable relationships and becoming attached to caregivers. However, little is known regarding the robustness to facial transformations and neural correlates of face recognition in infancy. Research characterizing infants' categorization of individual faces will be described in chapter 2.

**How are Faces Encoded?** Face encoding is often conceived as a process in which a given face is represented in terms of its deviations from an average (or prototype) face *template* (Mauro & Kubovy, 1992; Solso & McCarthy, 1981). Average face representations are formed by infants, even at three months of age (Damon et al.,

2017; de Haan, Johnson, Maurer, & Perrett, 2001). Detecting a categorical deviation from the face template should require less fine-grained processing than detecting individual deviations: Categorization requires matching the face stimulus to the general face template and detecting deviations beyond typical within-category variation (e.g., detecting that a monkey face deviates distinctly from the human face template in terms of color, spacing and shape of features). In contrast, individuation requires processing of individual features (such as eye and hair color, the relative distances of facial features, and surface information) that deviate from the face template in typical, expected degrees. The same holistic face template may thus serve to code face category (as match or mismatch with a given template) and face identity (as degrees of deviation from the average template within the category boundary). As strong, categorical deviations from the face template are easier to detect, a tentative hypothesis would be that, under many circumstances, infants may be able to categorize a face, but not to individuate that face. Likewise, it should be easier to detect severe deviations, e.g. spanning the animate-inanimate distinction, than finer deviations within a basic category.

Crucial for the ease with which faces will be encoded categorically and individually is accumulating experience with and incorporating a large number of faces into the face template(s), a variable that is likely to change dramatically throughout the life-span. We know that even newborn infants possess a rudimentary face template that is sensitive to face-like proportions (i.e., a symmetric top-heavy blob stimulus, Macchi Cassia et al., 2004; Macchi Cassia et al., 2008). Thus, we can assume that a face template is available when investigating face perception regardless of the age group. What is changing across development is likely the specificity of the template, the number of faces incorporated into the template, and the availability of several distinct face templates (e.g., differentiated templates for different face races). The same process of encoding by comparing the given exemplar to a general face template is applied on face stimuli by observers of different ages. Apart from domain-general development (Crookes & McKone, 2009; Crookes & Robbins, 2014; Hood et al., 1996) that may influence parameters such as the speed with which stimulus and template are compared, the content and form of the face template will exert crucial influence on face categorization and individuation across development.

Having raised some of the issues regarding infant face categorization, I will next discuss methods available for assessing these questions.

**What methods are used to study infant categorization?** In typical behavioral studies on categorization, infants are presented with items belonging to two different categories, employing either three-dimensional objects (object-exploration-task, OET; Mandler & McDonough, 1993; Mandler & McDonough, 1998) or images (visual familiarization-preference-for-novelty task, VFPN; Quinn & Eimas, 1998). In both tasks, infants are presented with several exemplars from one category until they are familiarized with it. Upon test, exemplars from the contrasting category are presented. Categorization is inferred from an increase in looking time (VFPN) or examining (OET) at test. Another looking time task that has been used in this context is the visual paired comparison (VPC) tasks, where only one visual item is presented during familiarization (Fagan, 1970). At test, the same item is presented again along with an item from a contrasting category, and discrimination is inferred from a looking preference toward the novel item. Figure 2 illustrates this paradigm. Though recognition is usually inferred from a preference for the novel item or category in all these paradigms, depending on infant age and task characteristics, a familiarity preference may be expected (Fantz, 1964; Houston-Price & Nakai, 2004; Roder, Bushnell, & Sasseville, 2000).

While familiarization or dishabituation tasks are suited to probe infant discrimination and to evaluate general categorization abilities (e.g., detecting out-of-category items), they are limited in several ways. First, looking behavior is influenced not only by the stimulus material, but also by factors such as mood or tiredness; accordingly, test-retest correlations range around zero (Ashmead & Davis, 1996; Ritz, Woodruff, & Fagen, 1984; but see Bornstein & Benasich, 1986, for a demonstration of low but significant test-retest reliability). Therefore, sensitivity of looking-time measures may be limited. Second, looking-time or examination measures cannot easily be applied on older populations (children and adults), creating a challenge of relating different measures to one another. Third, looking-time and examination measures require long stimulus presentation times and represent the result of various processing stages, making it impossible to disentangle sensory and higher cognitive contributions to categorization.

Electrophysiological measures with their high temporal resolution are much better suited to capture the different stages of the process resulting in visual categorization. Moreover, electroencephalographic (EEG) methods can reveal neural underpinnings of visual representations and may be applied in similar ways across age-groups, facilitating the detection of continuous and discontinuous pathways of categorization development. Unfortunately, most event-related potential (ERP) studies fail to report reliability, which may be an indication that reliability is not as high as desirable (for a review on strengths and challenges of EEG studies with developmental populations, see Hoehl & Wahl, 2012).

The current thesis employs two methodological approaches that might prove useful to clarify main points of debate on infant categorization, especially regarding the contribution of low-level cues to visual categorization: rapid repetition event-related potentials (rrERPs) and Fast Periodic Visual Stimulation (FPVS). In the rrERP paradigm (Jacques, d'Arripe, & Rossion, 2007; Vizioli, Rousselet, & Caldara, 2010), an adaptor stimulus (e.g., a face) is presented for a short time (typically 20 – 3,000 ms), followed by an inter-stimulus interval (ISI), and then by the target (e.g., the same face as the adaptor or another face) while recording EEG. Repetition effects in the form of repetition suppression or enhancement are assumed to indicate that a common neural representation has been activated by adaptor and target (Henson, 2003).

In the FPVS paradigm, EEG is recorded while images are presented at a fixed rate of 6 images per second, with categorical changes introduced periodically at every 5th cycle (de Heering & Rossion, 2015; Liu-Shuang, Norcia, & Rossion, 2014). This approach elicits strong responses to general visual stimulation, which can be isolated from the response to categorical change by means of its frequency tag. The common response to periodically presented images is captured in a small frequency band directly related to the stimulation frequency (i.e., when presenting 6 images per second, it is elicited at 6 Hz and harmonics), and likewise the categorization response is elicited in a specific frequency bin (i.e., 5/6 Hz = 1.2 Hz) and its harmonics (i.e., 2*5/6 Hz = 2.4 Hz, 3*5/6 Hz = 3.6 Hz, etc).

**Summary and Perspectives.** To sum up, this thesis will address face individuation and categorization during infancy. It discusses evidence for neural representations of

## Visual Paired Comparison (VPC) task

**Familiarization phase**



**Test phase**
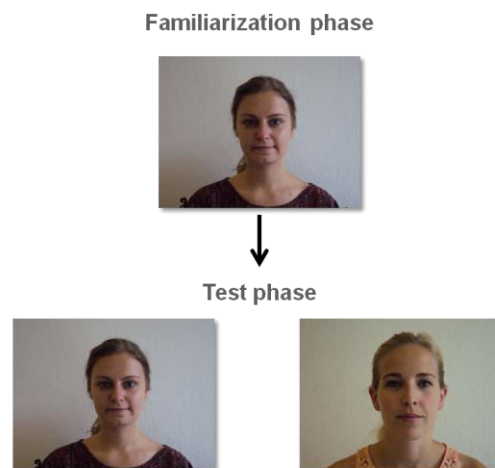


## Rapid repetition ERP (rrERP) paradigm



## Fast Periodic Visual Stimulation (FPVS) paradigm
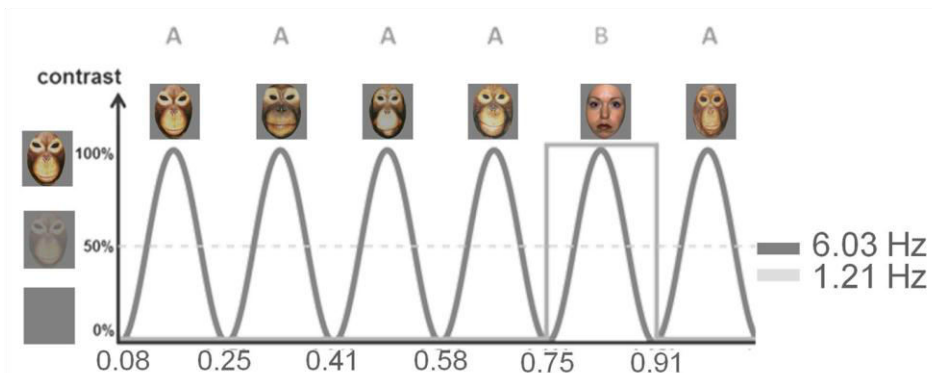


Figure 2. Illustration of main paradigms relevant for this thesis. **VPC:** During the familiarization phase, the image of one face is presented. During the test phase, the same face is presented alongside a novel face. Recognition is inferred when infants look longer at the novel face. **rrERP paradigm**: Following an adaptor stimulus (e.g., a face), the target (e.g., the same face) is presented while recording EEG. Repetition effects in the form of repetition suppression or enhancement indicate that a common neural representation has been activated by adaptor and target image. **FPVS paradigm:** EEG is recorded while images are presented at a fixed rate of 6 images per second, with categorical changes introduced periodically at every 5th cycle. The common response to periodically presented images is reflected in the respective frequency band at 6 Hz, and likewise the categorization response is reflected in a specific frequency band at 1.2 Hz (i.e., 5/6 Hz = 1.2 Hz) and its harmonics.

face categories and individual faces and aims at determining circumstances under which categorization or individuation will emerge.

I will commence by describing research on face individuation. Study 1 approaches some open questions on face individuation by testing infants' in an rrERP paradigm. Then I will describe infant face categorization at higher levels, raising questions regarding the locus of categorization which will be evaluated in study 2. The question arising from these demonstrations of flexible activations of face representations is under which circumstances infants will individuate or categorize human faces. This question will be evaluated empirically in study 3.

The following questions will be discussed and evaluated during the course of this thesis: *1. Is there evidence for representations of individual unfamiliar faces in infancy? 2. Do infants perceptually categorize unfamiliar faces, and if yes, according to which dimensions? 3. Given the opportunity to categorize and individuate human faces, which factors will determine the level(s) on which representations are activated?*

## 2 The Development of Face Individuation

Arguably, the simplest case of categorizing is identifying two visual inputs as representing the exact same entity. Though sounding simple at first, individuation is not a trivial challenge: Such a representation needs to be robust against transformations within and across situations (e.g., size, orientation, and lightning conditions, but also time, location and scene). At the same time, it should be specific enough not to be activated by similar-looking but non-identical entities.

The way individuation has been tested in most experiments is, in contrast, relatively simple. In VPC tasks, one image of a specific face is presented for a relatively long time (in different studies between 20 and 175 seconds, e.g., Kelly, Quinn, et al., 2007; Pascalis, de Haan, & Nelson, 2002). At test, the same face is presented again along with a contrasting face to probe infants' looking preferences (Kelly, Quinn, et al., 2007; Pascalis et al., 2002; Pascalis, de Haan, Nelson, & de Schonen, 1998). In experiments with newborns, participants first watch a movie of the target face talking and are subsequently presented with a frame from that movie and another face (Coulon et al., 2011). The similarity between the familiarization and the test stimulus is usually high, with many studies presenting identical images (Kelly,

Quinn, et al., 2007; Pascalis et al., 1998; similar limitations apply to many adult studies, e.g. Herzmann & Sommer, 2007; Schweinberger, Pfütze, & Sommer, 1995).

From such looking-time experiments, we have learned that newborns show a preference for their mother or an unfamiliar female when she has previously talked to them (Coulon et al., 2011; Sai, 2005). At one month, infants can recognize four different faces and at three months they can form an average representation of these four faces (de Haan et al., 2001). By six months, they can recognize and form an average of up to eight faces (Rubenstein, Kalakanis, & Langlois, 1999). At the same age, electrophysiological responses discriminate the mother's from a stranger female's face (de Haan & Nelson, 1997; Mash, Bornstein, & Arterberry, 2013). At six to nine months, the emerging ability to categorize faces (described in Chapter 4) influences infants' ability to individuate faces: In VPC tasks, infants show a preference only for novel same-race faces, but not for novel other-race faces (Kelly et al., 2009; Kelly, Quinn, et al., 2007). At earlier ages, novel other-race faces also elicit increased attention. However, in an ERP study, 9-month-old infants showed increased N290 amplitude for familiarized faces regardless of species (human or monkey, Scott, Shannon, & Nelson, 2006). Thus, it seems that a gain in categorization skills comes along with a loss in individuation ability, but how exactly both abilities are linked has yet to be determined.

Behavioral studies as the ones described so far are limited because they (a) often use only a few different exemplars as stimuli, (b) present each image for a relatively long time, and (c) rarely control for perceptual variability between the familiarization and the test stimuli, thus rendering it likely that low-level confounds contribute to or even explain recognition effects. To overcome some of these limits, it may thus be of interest to adapt methods that have been applied successfully on adults.

Adult face individuation has been successful investigated using the rrERP paradigm (Jacques et al., 2007; Vizioli et al., 2010). Repetition effects following categorical and/or individual adaptation have been reported for multiple visual ERP components (Caharel, Collet, & Rossion, 2015; Schweinberger, Huddy, & Burton, 2004). Which of those face-related components shows adaptation effects may rely on task properties such as presentation time of adaptor and target images and the duration of the ISI (Feuerriegel, Churches, & Keage, 2015). Though many studies

looking at face individuation employed the same image as adaptor and target (e.g., Amihai, Deouell, & Bentin, 2011; Schweinberger et al., 2004), several studies also demonstrated that the representation of an unfamiliar face is repressed when the image is not identical, for instance when the perspective changes (Caharel et al., 2015). In a study employing a 1-back repetition paradigm with infants, novel compared to repeated female faces elicited increased N290 amplitude, whereas no repetition effect was observed for male faces (Righi, Westerlund, Congdon, Troller-Renfree, & Nelson, 2014). The face-sensitive N290 is considered to be the infant precursor of the N170 component in adults (de Haan, Johnson, & Halit, 2003; Hoehl & Peykarjou, 2012).

Adaptation is well compatible with a neural model of repetition in which repeated processing of a stimulus requires less neural activation. However, several studies have reported repetition enhancement for repeated faces (Eimer, Kiss, & Nicholas, 2010; Nemrodov & Itier, 2012). Following Henson (2003), repetition enhancement may be elicited when additional processing is needed for the target relative to the adaptor, for instance when a neural representation is still being built up. Another factor that may influence the direction of effects is the ISI. When the ISI is not jittered, components may superimpose and results may be contorted. Overall, relating ERP polarities to increased or decreased neural activation is challenging, and the direction of effects should therefore always be interpreted with great caution.

To sum up, behavioral and ERP studies have provided evidence for face individuation during infancy, even though they have largely been limited to cases involving long presentation times, and recognition without change between familiarization and target stimuli. The rrERP paradigm has been successfully employed to study face recognition in adults, using tasks of varying complexity. This method will be applied to study 9-month-old infants' face individuation (see study 1, Chapter 6). In the next chapter, I will describe the development of face categorization during infancy.

## 3    The Development of Face Categorization

Compared to the conceptually simple case of mapping two instances of the same image onto another, categorization is more complex because it requires detecting similarities between all kinds of different stimuli. How much these stimuli differ in

perceptual terms depends on the level of the categorical contrast considered. For example, two young Caucasian girls may look rather similar to each other, whereas many differences exist between each girl and a beetle. And yet humans and the beetle may be categorized together as "animate beings" by adults (Kriegeskorte et al., 2008; Peykarjou et al., 2015).

Despite the apparent computational challenge of categorization at increasingly abstract levels, broad categorization (i.e. discriminating objects at the global or superordinate level) is very important to enable adequate visual perception. Indeed, to move about and behave appropriately in this world, it is more important to identify cars in the street and people on the walkway than spotting a good friend among those people. And though individuating and recognizing significant others is a crucial prerequisite for developing a social bond with caregivers (Schaeffer & Emerson, 1964), in the first instance it may be more important for the newborn infant to detect human faces in the environment and identify potential social partners.

Is there any evidence suggesting that young infants have the capacity to form a category of human beings, and that they also sort humans into subgroups based on their potential supportive capacity? Indeed, ERP studies suggest that 7-month-old infants categorize human beings, displayed with head and body information, from furniture items (Peykarjou, Wissner, & Pauen, 2016) and from other animals (Marinovic, Hoehl, & Pauen, 2014). Regarding human faces, infants process faces differently than cars at three months of age (Peykarjou & Hoehl, 2013) and show a face-specific inversion effect on the N290 ERP component. The inversion effect, increased ERP amplitude for stimuli presented upside-down (and longer reaction time for recognition of inverted faces), is regarded as an indicator for holistic processing and a proxy for processing expertise (Robbins & McKone, 2007; Wong, Palmeri, & Gauthier, 2009; Yin, 1969). Holistic processing refers to the process of "glueing together […] features into a Gestalt" (Maurer, Grand, & Mondloch, 2002, p. 255) and is applied on faces in particular. Given the far distance of faces and cars in the categorization hierarchy that spans the animate-inanimate distinction, low-level cues like the curvature and angularity of shape may contribute to this early categorization (Torralba & Oliva, 2003). However, in a recent study four- to six month old infants categorized human faces from all sorts of other visual stimuli (including, but not restricted to, animals, landscapes and man-made objects; de Heering &

Rossion, 2015). By using very diverse stimuli as control items, the contribution of shape and surface features to this categorization response was minimized, and a control experiment demonstrated that indeed low-level cues did not contribute to categorization. But in this study, human faces were the single most frequent category and might therefore have stood out. Together, these studies indicate that infants form a category of human faces in the first half year of life, but they leave open the question whether human faces are also discriminated from well-matched animate categories when they appear with equal frequency as faces.

A different line of work (de Haan et al., 2003; de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003) addresses this question. The authors compared neural processing of human and ape faces, a control category with a coherent shape, distinct color scale and a facial configuration that is similar to human faces. Moreover, ape faces are evolutionary likely to be relevant for us, more so than other animal face or inanimate categories. Throughout the first year of life, human and ape faces elicit different neural responses (de Haan et al., 2003), but a human-specific face inversion effect has not been observed in infants younger than 12 months of age (Halit et al., 2003). A full evaluation of infants' categorization of faces according to species has, however, not been presented so far. Such an evaluation would need to be based on a paradigm that requires the infant to generalize across faces of one species and discriminate those faces from faces of another species, a requirement that was met by study 2 (chapter 7).

Assuming that categorical representations of human and ape faces are indeed formed around 12 months of age, then facial categories which are more closely related (human and ape faces, Halit et al., 2003) would also be discriminated later in development than those that are less similar (humans and objects or animals, Marinovic et al., 2014; Peykarjou et al., 2016). Does this logic apply to subcategories of human faces as well, that is, are male and female or same-race and other-race faces discriminated even later in development than faces from different species? Evidence indicates that face subcategories are categorized during the second half of the first year of life: In a familiarization-preference-for-novelty paradigm, 9-month-olds (but not 6-month-olds) discriminated faces according to race (Anzures, Quinn, Pascalis, Slater, & Lee, 2010). Likewise, categorization of faces according to gender has been observed from 9-10 months of age in habituation-dishabituation studies

(Leinbach & Fagot, 1993; Younger & Fearing, 1999). At younger ages, preferences for familiar face race and face gender categories have been observed (Bar-Haim, Ziv, Lamy, & Hodes, 2006; Kelly, Liu, et al., 2007; Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002), but these results do not necessarily imply that distinct categorical representations are formed (c.f., Ramsey, Langlois, & Marti, 2005). Therefore, it seems that face subcategories are discriminated later than faces and other objects, but further evidence is required to characterize the sequence in which infants develop face categorization levels.

In sum, prior studies have provided evidence that infants can categorize faces during the first year of life. The contribution of different factors such as prior experience or low-level image characteristics to categorization has not been fully evaluated yet. In the following chapter, evidence for infant face categorization and individuation will be related and integrated.

## 4 Advances toward Predicting Infant Face Categorization and Individuation

In the preceding chapters on face individuation (chapter 2) and face categorization (chapter 3), and particularly in studies 1 (chapter 6) and 2 (chapter 7), I have provided evidence that young infants are able to form categories of faces on different levels of abstraction and similarity, and that they are also able to individuate large numbers of unfamiliar human faces. Categorization abilities can likely be attributed to high-level visual processing, as recent studies have taken great care to control low-level contributions to categorization and individuation and employ similar methods for evaluating infant and adult abilities (study 2; de Heering & Rossion, 2015).

**Which Questions Regarding Infant Face Individuation and Categorization Remain?** Several questions regarding infant face categorization and individuation remain open, however. Individuation of faces during development has mostly been tested using only one image of the face, that is, the response to a face image that is shown repeatedly has been compared to the response to a different face. To solve this task, the participant only needs to discriminate novel faces from the familiar face image, but does not need to generalize knowledge of the familiar face across instances. In order to attribute to the infant a representation of face identity, similar to categorization research, a task is needed that requires both discrimination of the single face from others *and* generalization across different images of one face.

Whether such a categorical representation of single faces can be observed early in life is crucial for our understanding of the face categorization hierarchy. If face individuation was just a very specific case of categorization with narrow categorical bounds, the general trend of broader to more fine-grained categorization during development (Pauen, 2002b; Quinn & Johnson, 2000; Younger & Fearing, 2000) would be expected to extend to individuation, and categorical individual perception should be subsequent to the development of global and basic level categories. But, touching upon one of the core questions of social neuroscience, it might also be that the face categorization hierarchy is "special" (that is, different from other non-face stimuli) because of the high social relevance of faces. Therefore, developmental trajectories of categorization will need to be compared for social and non-social stimuli using the exact same methods.

Testing the developmental trajectory of categorical representations of faces on each level of abstraction is beyond the scope of this thesis. However, studies 1 and 2 demonstrate that at nine months of age, infants can categorize human faces on individual, basic, and superordinate levels. One may wonder what determines infants' level of perception in a given situation. Imagine an infant at the end of the first year of life in her stroller on the street. People pass her by, peek into the stroller, and she glimpses different faces, each only for a short moment. Figure 3 illustrates the situation. Given the large variety of potential categorization levels, how will she perceive the face?

To approach this question, it is helpful to consider the perception of less and more advanced processors. A newborn infant has not yet developed different levels of abstract categorization and likely lacks cognitive and attentional resources to process a large number of different faces. Thus, the newborn may be attracted by faces, but is not likely to categorize them. In contrast, an adult briefly encountering many different faces is principally able to categorize them on all levels of categorization, and may adapt his perception to the circumstances: For example, at a small conference, he may try to keep track of the identity of all unfamiliar people, whereas on holiday in a big city, he may disregard identity and rather focus on identifying cultural groups. At 9 months of age, the infant is somewhere between those two extremes; she can perceive faces on different levels of abstraction, but she

Figure 3. The perceptual challenge young infants face when encountering an unfamiliar person.

likely has not yet developed mature mechanisms to guide her attention towards specific levels of perception. The remainder of this thesis and study 3 will be devoted to developing a framework that allows one to predict whether infants will categorize or individuate faces, and to providing an initial examination of selected factors.

**Which factors may modulate the level on which infants encode faces?** As described in the section on face individuation, infants recognize their mother particularly early in development (de Haan & Nelson, 1997; Sai, 2005). Thus, (1) *familiarity* may be one factor that modulates infant face categorization. When given the opportunity to acquire sufficient familiarity with a previously unfamiliar face (e.g., 20-175 seconds in familiarization studies, Kelly, Quinn, et al., 2007; Pascalis et al., 1998), infants will recognize that face. How much time exactly is required for infants to develop familiarity with a given face, and how this changes with development, remains an open question. Given the evidence that even newborn infants can

recognize their mother (Bushnell, Sai, & Mullin, 1989; Sai, 2005), this factor likely influences perception from birth on.

In general, the (2) *speed of presentation* needs to be considered. If several different faces are presented in short succession, it seems likely that the infant will try to group the faces into meaningful categories, but when given sufficient time, infants may be able to recognize many (even unfamiliar) faces on an individual level (e.g., Fair, Flom, Jones, & Martin, 2012). We have some evidence indirectly suggesting that indeed young infants need more than a second to encode individual novel exemplars: The Positive Slow Wave (PSW) ERP component is elicited around 1000-2000 ms at fronto-central leads and has been related to updating of representations (Nelson, 1994; Snyder, Garza, Zolot, & Kresse, 2010). Obviously, timing depends on the particular method, including both presentation form (e.g., static image vs. video clip) and dependent measure (EEG, looking time or behavioral measure). Study 1 demonstrates that a relatively short presentation time of 1.5 seconds may be sufficient for the infant to individuate a face using EEG methods. The minimum amount of time necessary for behavioral face recognition has not been systematically evaluated, but prior studies have presented the familiarization face for at least 15 seconds (Otsuka et al., 2013; Pascalis et al., 2002; Righi et al., 2014). In addition, processing time is known to change as a function of age, with a U-shaped development from the newborn period to later infancy (Hood et al., 1996; Shaddy & Colombo, 2004). Thus, a systematic investigation of the relations of these elements is necessary before the role that speed of presentation plays in categorization and individuation can be specified.

Moreover, (3) *familiarity with the face category* may influence categorization: As demonstrated by research on the same-race effect, older infants who have developed face race categories are less likely to recognize faces from unfamiliar race categories, and more likely to categorize those faces (Kelly, Liu, et al., 2007; Kelly et al., 2009). Face categories emerge around nine months of age (species: study 2; face race: Anzures et al., 2010; gender: Leinbach & Fagot, 1993). Thus, a particularly strong influence of familiarity with face categories on infant perception can be expected from that age onward.

Another factor that might modulate categorization is the (4) *amount and complexity of information* available, particularly during the learning or encoding

phase. Evidence has been presented which suggests that face recognition is influenced by many stimulus characteristics. It is facilitated by (a) motion and transformation of the face (e.g., in form of a videoclip of a moving face, Bulf & Turati, 2010; Otsuka et al., 2009), (b) multimodal information (e.g., a talking face, Coulon et al., 2011), (c) emotional information (e.g., a smiling face, Gross & Schwarzer, 2010; Turati, Montirosso, Brenna, Ferrara, & Borgatti, 2011), (d) direct gaze (Farroni, Massaccesi, Menon, & Johnson, 2007; Yamashita, Kanazawa, & Yamaguchi, 2012), (e) outer facial contours (Turati, Macchi Cassia, Simion, & Leo, 2006), and (f) similarity of learning and test images (e.g., 3/4 compared to profile view of face, Rose, Jankowski, & Feldman, 2002; Turati, Bulf, & Simion, 2008). On the other hand, highly complex information such as repetitive actions performed by actors may impair face recognition, as the action attracts attention away from the face (e.g., brushing hair, blowing bubbles; Bahrick, Gogate, & Ruiz, 2002; Bahrick & Newell, 2008). Likewise, reduced complexity of information may hinder recognition (e.g., reducing spatial frequency content; de Heering et al., 2008). Thus, a medium level of complexity seems to be conducive for face individuation. What a medium level of complexity is for the observer likely changes with age, but studies comparing the influence of stimulus characteristics on face perception have rarely compared different age groups.

Finally, the (5) *availability of categories and exemplars* must be taken into account. If the deviations between images are relatively subtle, for instance when all individuals belong to one face subgroup such as young Caucasian females, it seems more likely that infants will attend to those subtle differences related to identity. If different basic or broad natural categories are presented, infants will likely be induced to attend to differences between categories and neglect variations within these categories. When an infant is being walked down the street and perceives novel houses, trees, humans, and cars, she may be driven towards the differences between those categories; when she is at home and sees her parents' friends at a party, she may be driven towards the differences between those people. Though experimental evidence for this factor is scarce, it seems likely that it plays a role from early on in development and should receive attention in future studies.

Figure 4 illustrates the proposed framework. If faces are familiar, or when sufficient processing time is given, it is very likely that infants will individuate faces

(left panel). If exemplars from different categories are also available, it may be that faces are also categorized. Only if the level of information complexity is either too high or too low will infants fail to recognize the faces. If faces are neither familiar, nor is processing time long, it is likely that infants will categorize faces (right panel): If exemplars from different categories are presented together with faces, the face category is unfamiliar, or the level of information complexity is too high/too low, categorization but no individuation is expected. But if exemplars from the same category are available, the face category is familiar, and the information available is of medium complexity, faces may be individuated (and categorized eventually).

**How Can We Evaluate the Proposed Framework?** Investigations are needed in which all factors are controlled, and in which processing on different levels of abstraction is possible, to assess the validity of this framework. Whereas most prior studies (including, but not limited to, study 1; study 2; de Haan et al., 2001; de Heering & Rossion, 2015; Kelly, Quinn, et al., 2007) tested infants' face processing abilities in paradigms that allowed participants to either individuate or to categorize faces, study 3 (chapter 8) provides a first step toward testing categorization on different levels of abstraction within-subjects. In this study, processing of target images was compared following same category and different category adaptors. Infants' categorization of human faces on the individual, the basic, and the superordinate levels was evaluated within-subjects. ERP responses revealed that infants categorized faces on the superordinate and basic level, but did not individuate them. This results pattern is compatible with the proposed framework (unfamiliar faces, short processing time, exemplars from different categories available, familiar face category, medium complexity of information).

One reason we were interested in superordinate categorization of human and ape faces into a common category of "faces" was to determine whether humans represent a special category in the categorization hierarchy that might not be included in a general "animate" category. This possibility has, to my knowledge, not been fully investigated. Whereas prior research indicates that different animal categories can be categorized together as belonging to the animate category (Jeschonek, Marinovic, Hoehl, Elsner, & Pauen, 2010; Pauen, 2002b), no such evidence has been provided for humans. Prior studies have focused on infants'

If

Familiar Face
AND/OR
Long Processing Time

**+**

**+**

Other Exemplars from Same and/or Different Categories Available
AND
Familiar and/or Unfamiliar Face Category
AND
Medium Complexity of Information Available

Other Exemplars from Different Categories Available
AND
Familiar and/or Unfamiliar Face Category
AND
Medium or Very Low/Very High Complexity of Information Available

If

Unfamiliar Face
AND
Short Processing Time

**+**

**+**

Other Exemplars from Same Category Available
AND
Familiar Face Category
AND
Medium Complexity of Information Available

Other Exemplars from Different Categories Available
OR
Unfamiliar Face Category
OR
Very Low/Very High Complexity of Information Available
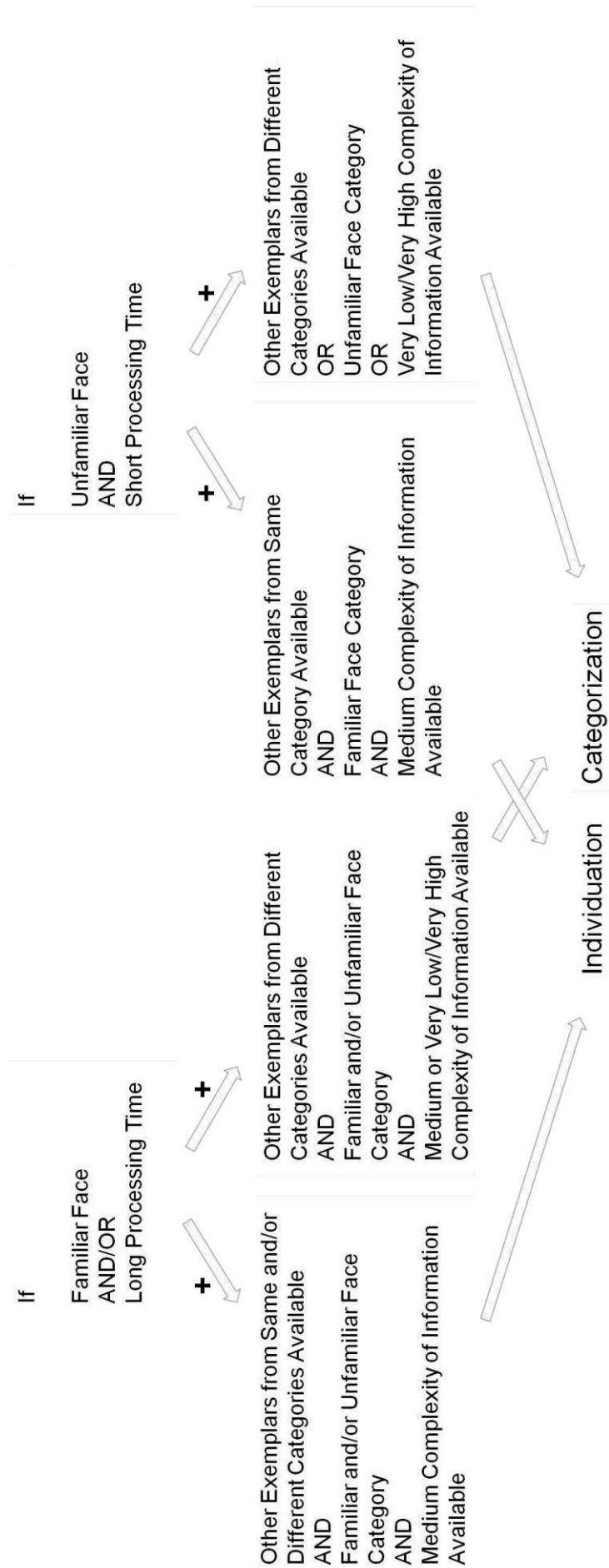
Individuation

Categorization

Figure 4. Framework relating factors that may determine whether infants categorize and/or individuate faces.

discrimination ability and demonstrated that 7-month-olds can discriminate humans from other animals (e.g., Marinovic et al., 2014).Therefore, future work should address whether humans are fully integrated into the animate category during development (see, for example, Kriegeskorte et al., 2008 for such an inclusive animate category in adults). In study 3, 9-month-old infants formed a common category of human and ape faces (in addition to forming separate basic level categories), providing first tentative evidence for the hypothesis that human faces may be integrated into general animate category.

Although this thesis is concerned with face categorization and individuation in infancy, a similar approach might help predict face categorization across the life-span. Several rrERP studies have provided evidence for individuation of unfamiliar faces (Caharel et al., 2015; Caharel, Jacques, d'Arripe, Ramon, & Rossion, 2011; Vizioli et al., 2010) even under demanding situations in young adults (e.g., changes in viewpoint), and there also is sufficient evidence for rapid categorization of unfamiliar faces (Eimer et al., 2010; Kovacs et al., 2006; Rossion et al., 2015). Studies in which participants have the opportunity to categorize faces (on various dimensions from individual to global levels) are scarce, however (but see Amihai et al., 2011; Feuerriegel et al., 2015). Therefore, we have relatively little information about how factors interact which determine the level(s) of perception in adults. A recent study employed the paradigm of study 3 and found that adults processed faces similarly to infants (Peykarjou, Pauen, & Hoehl, in prep.): Participants categorized faces according to superordinate and basic levels, but did not individuate them. In order to improve our understanding of the development of face perception, future studies might control the proposed factors, and test face processing using the same methods across development.

## 5    Conclusions

In the present thesis, I have asked whether young infants can categorize and individuate faces and which process(es) will be elicited under which circumstances. The data presented demonstrate that 9-month-old infants are able to recognize face identity of unfamiliar faces (study 1). They also categorize unfamiliar faces according to face species (studies 2, 3). Thus, infants can activate categorical neural representations of human faces and specific representations of individual faces. I

have described factors that, with further specifications requiring empirical testing, might serve to predict categorization based on situational factors (e.g., task framing and type/amount of information available regarding the faces). In a first evaluation of these factors, I have provided evidence that under relatively difficult processing circumstances, infants will categorize but not individuate faces (study 3). By further specifying the suggested parameters, it might be possible to predict the precise level(s) of categorization on which a stimulus will be perceived and how categorization changes with age. By carefully evaluating infant face categorization abilities using, among others, the methods presented in this thesis, we can approach the question how factors such as online category formation and prior knowledge interact to drive the development of categorization.

It is essential for all animals to organize our visual impressions in a way that enables us to determine *what* and *whom* we perceive. By carefully evaluating the development of these abilities ontogenetically, we have begun to gain major insights into what is peculiar in human perception, and to discover characteristics of the development of high-level visual perception.

## 6 Study 1: Nine-Month Old Infants Recognize Individual Unfamiliar Faces in a Rapid Repetition ERP Paradigm

Study 1 was developed to adapt the rrERP paradigm to infant participants and test recognition of a large number (80) of different unfamiliar faces within a short amount of time (1,500 ms per image) while controlling for potentially confounding factors such as brightness, size, shape, and gender. We investigated neural indicators of unfamiliar face recognition by comparing processing of human faces preceded by the same face (identical image) and another face. We found that N290 latency was reduced for repeated compared to unrepeated faces. The N290 is often considered the precursor of the N170 component in adults and is related to face processing (de Haan et al., 2003; Hoehl & Peykarjou, 2012). A similar effect on N170 latency was observed when testing adults using the exact same paradigm (Peykarjou, Pauen, & Hoehl, unpublished data). This is important because different studies with varying presentation time-courses have observed different forms of repetition effects on different visual ERP components in adults (Caharel et al., 2015; Schweinberger et

al., 2004). Together, these data imply that the current presentation course elicits a similar repetition effect on the N170 in adults and its precursor N290 in infants.

Thus, infants can encode and activate neural representations of unfamiliar faces within a short amount of time. Variations of this paradigm (e.g., presentation duration of adaptor image, duration of ISI, or similarity between adaptor and target faces) might be used with infant participants to characterize the development of face individuation more comprehensively.

## 7    Study 2: At a Glance – Rapid Categorization of Ape vs. Human Faces in 9-Month-Old Infants

Studies demonstrating face categorization according to species, race, and gender have not systematically investigated how low-level perceptual cues contribute to categorization responses. This leaves open the possibility that the emergence of face categories around nine months of age reflects increased sensitivity to image characteristics like color or spatial frequency content. In study 2, we assessed 9-month-old infants' categorization of human and ape faces using an FPVS paradigm (de Heering & Rossion, 2015; Liu-Shuang et al., 2014). In this paradigm, EEG is recorded while images are presented at a fixed rate of 6 images per second, with categorical changes introduced periodically at every 5th cycle. The visual system's precise temporal synchronization to periodic visual inputs is reflected by a brain response at the same frequency as the visual input. The common response to periodically presented images is captured in a small frequency band directly related to the stimulation frequency (i.e., when presenting 6 images per second, it is elicited at 6 Hz), and the categorization response is elicited at the specific frequency bin (i.e., 5/6 Hz = 1.2 Hz) and its harmonics (i.e., 2*5/6 Hz = 2.4 Hz, 3*5/6 Hz = 3.6 Hz, etc).

To illustrate the approach further, imagine an infant watching a fast stream of images showing human and ape faces. Between images of different ape faces, she detects human faces. Only if her brain discriminates the humans from the apes, and also generalizes from each human face to the next, is it able to detect the periodicity of categorical changes. If her brain either fails to discriminate humans from apes, or else fails to generalize across human faces, her brain will only respond to the periodic stimulation of 6 images per second.

In this study, human and ape faces were presented as frequent and rare stimuli in upright and inverted conditions while EEG was measured. In two independent samples, infants categorized upright human and ape faces, but the response to rarely presented ape faces was increased compared to rare human faces. Categorization was robust when controlling for low-level confounds (color, luminance, contrast). Moreover, responses were much reduced when faces were presented upside-down. Inverted presentation of faces disrupts holistic processing while preserving all low-level characteristics of the stimulus, providing a compelling control for the contribution of low-level factors to image processing. This indicates that distinct and high-level neural representations of human and ape faces were activated within ~170 milliseconds. The stronger categorization response for deviant ape faces likely reflects novelty detection and maybe reduced individuation of ape compared to human faces.

## 8      Study 3: How do 9-Month-Old Infants Categorize Human and Ape Faces? A Rapid Repetition ERP Study

Study 3 presents a first investigation of perception on different levels within one study, employing the rrERP method in 9-month-old infants. Prior categorization studies have tested infants' abilities to either discriminate human faces from basic-level object categories (such as ape faces, de Haan et al., 2002, or cars, Peykarjou & Hoehl, 2013) or, very broadly, from all other stimuli (de Heering & Rossion, 2015). The paradigm of study 3 allowed us to test whether infants may be able to detect categorical deviations from the face template and form categories at *different* levels of abstraction within a given situation. In this study, we tested whether human and ape faces were discriminated from each other (forming distinct basic-level categories), whether they were categorized together (as "faces"), and whether they were also recognized individually.

Study 3 provided participants with a large number (80 different exemplars each) of static images of unfamiliar human faces, ape faces, and house fronts, presented for a relatively short amount of time (one second). Among the human faces, 50% male and female faces were presented, and 10% represented faces from other races than Caucasian, the predominant face-race among our participants.

Thus, infants were unfamiliar with individual faces, but relatively familiar with the face category, had static visual information regarding three different basic-level categories (medium complexity information) and a short amount of time for processing. Thus, based on the factors proposed in chapter 4, infants could be expected to categorize but not to individuate the human faces.

Human and ape face targets were preceded by same-species faces (either identical to or different from the target, individuation condition), other-species faces (basic categorization condition), and houses (superordinate categorization condition). Early superordinate categorization was observed on the P1 ERP component. This repetition effect might be related to low-level factors like power-spectra which differ between animate and inanimate categories (Torralba & Oliva, 2003). Subsequently, at the level of the N290, basic level category membership was encoded. No repetition effect for face identity was observed in this study. Thus, as predicted based on the framework in Chapter 4, the complexity of this study's design elicited categorization, but no individuation of human faces in 9-month-old infants.

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**List of figures**

# Declaration in accordance to § 8 (1) b) and § 8 (1) c) of the doctoral degree regulation of Heidelberg University, Faculty of Behavioural and Cultural Studies

**Promotionsausschuss der Fakultät für Verhaltens- und Empirische Kulturwissenschaften
der Ruprecht-Karls-Universität Heidelberg**
**Doctoral Committee of the Faculty of Behavioural and Cultural Studies, of Heidelberg University**

**Erklärung gemäß § 8 Abs. 1 Buchst. b) der Promotionsordnung der Universität Heidelberg
für die Fakultät für Verhaltens- und Empirische Kulturwissenschaften**
**Declaration in accordance to § 8 (1) b) and § 8 (1) c) of the doctoral degree regulation of Heidelberg University, Faculty of Behavioural and Cultural Studies**

Ich erkläre, dass ich die vorgelegte Dissertation selbstständig angefertigt, nur die angegebenen Hilfsmittel benutzt und die Zitate gekennzeichnet habe.
I declare that I have made the submitted dissertation independently, using only the specified tools and have correctly marked all quotations.

**Erklärung gemäß § 8 Abs. 1 Buchst. c) der Promotionsordnung
der Universität Heidelberg für die Fakultät für Verhaltens- und Empirische Kulturwissenschaften**

Ich erkläre, dass ich die vorgelegte Dissertation in dieser oder einer anderen Form nicht anderweitig als Prüfungsarbeit verwendet oder einer anderen Fakultät als Dissertation vorgelegt habe.
I declare that I did not use the submitted dissertation in this or any other form as an examination paper until now and that I did not submit it in another faculty.

Vorname Nachname
First name Family name        Stefanie Peykarjou

Datum, Unterschrift
Date, Signature        24.03.2017,

# 9-Month-Old Infants Recognize Individual Unfamiliar Faces in a Rapid Repetition ERP Paradigm

## Stefanie Peykarjou, Sabina Pauen, and Stefanie Hoehl
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To investigate whether infants show neural signatures of recognizing unfamiliar human faces, we tested 9-month-olds ($N = 31$) in a rapid repetition ERP paradigm. Pictures of unfamiliar male and female faces (targets) were preceded either by a central attractor (Unprimed) or by a face (Primed). In the latter case, the prime faces were either identical to the target (Repeated) or not (Unrepeated). We compared processing of primed versus unprimed faces as well as processing of repeated versus unrepeated faces. Primed stimuli elicited decreased P1 amplitude, P1 latency and N290 amplitude, indicating categorical repetition effects very early during the stream of processing. For repeated relative to unrepeated faces, N290 latency was reduced. In addition, we observed an enhanced late positivity at occipital channels for unrepeated compared to repeated male faces, but no difference for female faces. Taken together, these results suggest that 9-month-olds categorize faces before discriminating them individually. Furthermore, infants' ability to recognize face identity seems to depend on familiarity with the given face category, as indicated by differences in brain responses to male and female faces.

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When sitting in their stroller or being carried around, infants see many different people passing by. Are they capable of discriminating between all these different faces, even if they see them only for a short amount of time?

A large body of studies has provided evidence that newborns and infants can recognize individual faces. A few hours after birth, infants are able to recognize not only their mother's (Sai, 2005), but also a stranger's face (Coulon, Guellai, & Streri, 2011). At 1 and 3 months, they can recognize four individual faces and even form an average representation (de Haan, Johnson, Maurer, & Perrett, 2001). At 6 months, event-related potential (ERP) responses discriminate between the infant's mother and a similar-looking as well as a dissimilar-looking stranger (de Haan & Nelson, 1997). At 6 and 9 months, infants readily recognize unfamiliar faces in visual-paired-comparison (VPC) paradigms (Kelly et al., 2007; Pascalis, de Haan, Nelson, & de Schonen, 1998). In these studies, infants are first familiarized with one face, and see the same and a novel face presented simultaneously at test. Increased looking times toward the novel face during the test phase are taken to indicate that infants recognize the previously seen face.

These and other studies clearly show that infants are capable of recognizing single faces, both familiar and unfamiliar ones. There are three major shortcomings associated with existing work, however: (1) In many cases, stimuli have not been controlled for perceptual similarity. For example, in VPC tasks, the familiar and the new face contrasted at test often show differences in global features (e.g., facial contour or hairstyle) as well as differences in low-level stimulus characteristics (e.g., luminance). Hence, infants may have recognized specific perceptual attributes rather than individual faces. (2) It is currently unclear whether infants are able to recognize faces they have seen only very briefly. In VPC tasks, familiarization time typically extends between 20 and 175 sec (Kelly et al., 2007; Pascalis, de Haan, & Nelson, 2002; Pascalis et al., 1998), in stark contrast to the 20–3,000 ms employed in adult ERP studies on repetition effects for individual faces (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Wiese & Schweinberger, 2011). Thus, it is well possible that infants need to accumulate more visual experience to build up a representation of an individual face. (3) Whereas infants often see multiple unfamiliar faces in everyday situations (e.g., while being taken for a walk in their stroller), classical VPC tasks only present two different faces at a time. Infants' visual working memory may be limited with regard to the number of items that can be encoded and stored in a short period of time; therefore, results obtained from VPC studies may only reveal how well infants recognize a

limited number of faces that have been presented repeatedly. Studies that present many exemplars are still rare.

Taken together, we conclude that more evidence is needed on infants' ability to recognize unfamiliar faces when (1) perceptual similarity between faces is controlled for, (2) presentation times are rather short, but long enough to allow for complete encoding, and (3) multiple exemplars are presented. ERP paradigms seem very useful in this context, because many different pictures can be presented within a short amount of time. Furthermore, the time course of ERPs can reveal important new insights regarding the processing sequence for faces in the infant brain.

This advantage has often been used in ERP studies with adults following repetition paradigms (Caharel et al., 2009; Eimer, Gosling, Nicholas, & Kiss, 2011; Schweinberger, Huddy, & Burton, 2004). In such paradigms, a face stimulus is typically preceded by another stimulus (face or nonface), and brain responses to the target are recorded. The adult brain differentiates basic-level categories such as houses, shoes, or faces around 170 ms after stimulus onset at the level of the N170 ERP component (Rossion & Jacques, 2011). Repetition effects for individual faces have also been reported on the N170 (Caharel et al., 2009) and on the N250 (Schweinberger et al., 2004). Task properties seem to be associated with individual repetition effects on these two components. Critically, however, the N250 is specifically elicited when face identity is highlighted by the paradigm, for example, by repetition or by presenting famous faces. When identity is task-irrelevant, it is absent or reduced (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion & Caharel, 2011). This turns the double-peaked negativity in the time-range of 150–300 ms, that is, the N170–N250 complex, into a particularly valuable phenomenon to investigate individual-level representations.

With respect to infants, reduced N290 amplitude for repeated faces has been observed in a 1-back task, but only for female faces (Righi, Westerlund, Congdon, Troller-Renfree, & Nelson, 2014). In this study, 7-month-olds saw the same face twice with one intermitting face (e.g., ABABCDCD). Infants showed increased N290 amplitude for female as compared to male faces; a repetition effect occurred only for repeated female faces. No double-peaked negativity like the N170–N250 was reported in this study, possibly due to the 1-back task. To enhance comparability with work in adults, and to investigate recognition processes more directly, a paradigm with immediate repetition seems preferable.

Another recent study following a similar approach as the present one investigated infants' representation of faces from different species on different levels of abstraction (Peykarjou, Pauen, & Hoehl, 2014). In that study, human and ape face targets were preceded by the same face,

another face, a face from a different species (human or ape), or a house. Evidence for a broad face–nonface distinction was found at the level of the P1, which was elicited with reduced latency and enhanced amplitude for faces preceded by faces relative to houses. Basic-level categorization (as human or ape face) was observed at the level of the N290, reinforcing the idea that the N290 is a precursor to the adult N170. Importantly, there was no evidence for individual-level repetition effects in infants.

Why did infants not exhibit brain signals of recognizing individual faces in that study? We suggest that at least three arguments are relevant in this context: First and foremost, the use of three different categories may have served as a cue for infants to extract categorical rather than individual information from faces. Second, a small amount of stimuli (i.e., 25% of faces) depicted other-race faces. Following a process of perceptual narrowing, 9-month-old infants' ability to individuate other-race faces is decreased (e.g., Pascalis et al., 2002). Third, stimuli were presented for 1,000 ms only, which may simply be too short for infants to develop a comprehensive representation of an individual face. As already mentioned, we still do not know exactly how much time infants need to build up a neural representation of a visual stimulus. In familiarization paradigms, infants typically have at least 20 sec to explore a given stimulus. However, as such long presentation times would likely induce motion artifacts, classical familiarization experiments with long presentation times of each individual stimulus are not well suited for infant ERP research.

As illustrated by this short summary of existing ERP work, research with adults has identified specific components of brain responses which seem characteristic of perceptual face recognition, but we still do not know whether infants less than 1 year of age are already capable of recognizing unfamiliar faces when being exposed to a large number of stimuli presented in fast succession, as this is often the case when infants are in public places. Hence, more studies are needed that overcome the limitations of existing work. This study was designed to meet this aim.

## GENERAL AIM AND HYPOTHESES

We focused on 9-month-olds' ability to perceptually encode and recognize individual faces when presented in sequence with many others, using a rapid repetition paradigm, and ERPs as dependent measure. We tested 9-month-old infants because they have already developed expertise in processing faces of their own species and race (Anzures, Quinn, Pascalis, Slater, & Lee, 2013; Scott, Pascalis, & Nelson, 2007), and can thus be

regarded as experts in individuating exemplars from familiar face categories. ERPs provide detailed information on the time course of brain responses to face stimuli and allow for a qualitative comparison of performance between infants and adults.

Differing from Righi et al. (2014), prime-target pairs of faces were presented in direct succession (i.e., without intermitting stimuli) to reduce interference effects. Similar to Peykarjou et al. (2014), infants were presented with a target face, primed either by the same (identical) face or by a different face, matched for gender, shape, size, and luminance. In contrast to that study, the only category was human faces, thus preventing infants from focusing on differences between global stimulus categories. All 120 faces were Caucasian (i.e., own-race faces for our participants), including 60 males and females each. This allowed us to explore whether infants show any systematic difference in priming effects between male and female faces, as observed by Righi et al. (2014). To support infants in forming individual face representations, we presented each stimulus for 1,500 ms, whereas in prior studies, stimuli were presented for only 500 ms (Righi et al., 2014) or 1,000 ms (Peykarjou et al., 2014). Taking into account the duration of the positive slow wave (PSW) which indicates stimulus or representational updating in infants (Nelson, 1994; Snyder, 2010), we reasoned that 1,500 ms should be sufficient to develop a more comprehensive visual representation of individual faces.

As follows from this description, we reduced task demands in comparison with previous infant ERP studies by prolonging the presentation of each stimulus, by including only (Caucasian) faces as stimuli, by presenting prime and target in direct succession, and controlling for perceptual similarity between pairs of faces.

Regarding identity repetition, adaptation (i.e., reduced amplitude) on the N170 and/or the N250 has been observed in adults (Caharel et al., 2009; Schweinberger et al., 2004). Adaptation is well compatible with a neural model of repetition in which repeated processing of a stimulus requires less neural activation. However, several studies have reported repetition enhancement as well (Eimer, Kiss, & Nicholas, 2010; Nemrodov & Itier, 2012). According to the model by Henson (2003), repetition enhancement is elicited when additional processing is needed for the target relative to the prime, for instance, when a neural representation is still being built up.

For faces that are preceded by faces, irrespective of face identity, we predict repetition adaptation on the P1, reflecting the identification of a given stimulus as a face early in the stream of visual processing (see also Peykarjou et al., 2014). For repeated presentations of the same face, we predict repetition effects on subsequent components, particularly the N290

as potential precursor to the adult N170. These effects might take the form of repetition enhancement or reduction, depending on whether infants were able to form comprehensive representations of the prime stimuli within the short presentation duration. Based on the study by Righi et al. (2014), we expected reduced N290 amplitude. In addition to the N290, we also examined repetition effects on the P400. This component is often discussed as another precursor of the N170 (de Haan, Johnson, & Halit, 2003). By comparing repetition effects on the N290 and the P400, we can provide clarifying information on the relation of these components to adult face-related components. We were also interested in the shape of the waveform elicited by primed faces, specifically whether a double-peaked negativity can be observed which relates to the N170–N250 complex in adults. This would provide additional information on how infant and adult face-sensitive ERP components are related.

## MATERIAL AND METHODS

### Participants

The sample consisted of 31 infants with an average age of 9 months and 13 days (age range 9 months, 1 day–9 months, 31 days, $SD$ = 8 days). Eighteen participants were male, 13 female. For a subgroup of $N = 17$ infants who provided sufficient numbers of trials, additional analyses were carried out separately for male and female faces. All infants were born full-term (>37 weeks of gestation) without a known record of neurological problems. All participants had at least one Caucasian caregiver, and 90% were reared by parents who both were Caucasians.

To be included in the sample, a minimum of 10 trials per condition had to be contributed for the analyses across gender, and a minimum of eight trials in the analyses for male–female faces separately (to decrease dropout rates, the criterion was lowered in the male–female contrast). For the overall analyses, an additional six infants were tested but not included in the final analyses because they failed to reach the minimum number of trials required for adequate ERP averaging (five participants) or due to insufficient data quality (one participant). This exclusion rate is particularly low compared to other visual ERP studies in infancy (Stets, Stahl, & Reid, 2012) and probably follows from the use of only three conditions (Unprimed, Repeated, and Unrepeated) in an engaging paradigm.

For the male–female contrast, another 14 infants had to be excluded because they provided insufficient numbers of artifact-free trials. Given the extraordinary requirement to reach the minimum number of trials in six

conditions (Unprimed, Repeated, and Unrepeated for female and male faces each), this exclusion rate of 62% seems acceptable.

## Stimuli/Presentation

Infants watched a presentation consisting of 120 trials in which human face targets were preceded by the same or a different face as primes. A sequential presentation of multiple exemplars of faces might have multiplied repetition effects. For example, the prime face following a trial in which the same face was presented as prime and target may be perceived as more novel than a prime face following a trial in which two different faces served as prime and target. Thus, to equalize processing at the beginning of each trial, and to chunk visual flow for our participants into clearly separated trials, every trial started with a colorful fixation triangle displayed for 500 ms, which attracted infants' attention to the screen and served as a deprime, followed by a 400- to 600-ms interstimulus interval (ISI) and the first face of a pair, displayed for 1,500 ms. This face served as target in the Unprimed condition and as prime for the subsequently presented face. Following another ISI of 500–700 ms, the target face was presented for 1,500 ms. This target stimulus could display either the same face as the prime (Repeated) or another face (Unrepeated). To examine general repetition effects for faces, a Primed condition was computed as average from Repeated and Unrepeated. Thus, processing could be compared for primed faces (preceded by a face) and unprimed faces (not preceded by a face), as well as for repeated (preceded by the same face) and unrepeated faces (preceded by another face). An exemplary trial sequence is displayed in Figure 1.

Trials were split into two blocks. Sixty different faces were presented two times as targets, once per block. Every target face appeared once in the Repeated and once in the Unrepeated condition. Repetition conditions were presented in semi-randomized order with the restriction that no condition was repeated more than three times successively and that both repe-



500ms   400-600ms   1500ms   500-700ms   1500ms   500-700ms   500ms   400-600ms   1500ms   500-700ms   1500ms

**Figure 1**   Exemplary trial sequence. Each trial commenced with a central attractor (500 ms), followed by a blank screen (400–600 ms). Then, the first face was presented for 1,500 ms, which served as Unprimed condition. After a blank screen (500–700 ms), the second face was presented for 1,500 ms. This face could be either the same face as the first one (Repeated) or a different one (Unrepeated). For analyses, Repeated and Unrepeated were averaged together to form the Primed condition.

tition conditions appeared with equal probability within the two presentation blocks.

Stimuli were 120 colorful images of Caucasian faces, consisting of 60 males and females, respectively. Stimuli were taken from standard face databases (i.e., MacBrain (Tottenham, 1998)[1] , RaFD (Langner et al., 2010)) and supplemented with pictures taken in the laboratory or found in the Internet. All pictures were taken in full-front view with a neutral expression and in high quality. All faces were cropped to the same oval shape and size to prevent simple contour repetition effects, extending $15.5 \times 22.5$ cm on the screen. Prime and target stimuli were matched for gender and mean luminance.

To ensure that gender of the faces was recognizable and that high-level attributes potentially influencing recognition were comparable across gender, 17 adult volunteers (students receiving course credit for participation, mean age = 24 years; six males) rated our stimuli with regard to masculinity, femininity, averageness, and attractiveness on a Likert scale from 1 (not at all) to 5 (very). Those ratings confirmed that male faces were perceived as more masculine (masculinity: $M = 4.1$, $SD = 0.3$; femininity: $M = 1.5$, $SD = 0.3$, difference significant, $t(59) = -33.342$, $p < .001$) and female faces as more feminine (masculinity: $M = 1.4$, $SD = 0.4$; femininity: $M = 4.0$, $SD = 0.5$, difference highly significant, $t(59) = 26.710$, $p < .001$). Averageness and attractiveness did not differ between both gender categories (averageness: male faces, $M = 2.9$, $SD = 0.5$; female faces, $M = 2.8$, $SD = 0.5$, $t(59) = 1.321$, $p = .19$; attractiveness: male faces, $M = 2.7$, $SD = 0.8$; female faces, $M = 3.0$, $SD = 0.9$), $t(59) = -1.343$, $p = .18$).

## Procedure

Infants were placed on their parent's lap in front of a 17″ TFT presentation screen with a distance of approximately 45 cm. This unit was surrounded by a dark blue folding screen to minimize distraction. Parents were asked not to interact with their infant during data collection. The stimuli were presented while the infants' looking behavior was monitored and recorded on video. When the infants started to fuss, they were offered a short break in which a black-and-white rotating spiral appeared on the screen accompanied by a short interesting sound to refocus attention. Ses-

[1]Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development (Tottenham et al., 2009).

sions were terminated when infants' attention could no longer be directed to the presentation.

## ERP recording and analyses

The EEG measures were obtained applying a BrainProducts actiCap (Gilching, Germany) with 32 active Ag-AgCl electrodes arranged according to the 10/10 system and a right mastoid reference. Sampling rate was set at 250 Hz, and the EEG signal was amplified via a BrainAmp amplifier. Impedances were considered acceptable if <20 kΩ. Offline, filters were applied at 0.3–30.0 Hz. To maximize the distinctness of the visual ERP components, data were re-referenced to an average reference, excluding horizontal and vertical ocular channels. Prior to averaging, up to four channels with data loss (if they were not channels of interest, see below) were interpolated by computing the mean of four surrounding channels. EEG was time-locked to target onset and segmented into epochs from 200 ms before stimulus onset to 1,500 ms past stimulus onset. A baseline correction was applied using the average voltage of the 200 ms prior to stimulus onset.

Infants' looking behavior was inspected offline to exclude trials in which the infant's eyes were not directed to the screen. In addition, electrical artifacts caused by sweat or body movements were rejected offline using BrainAnalyzer's automatic artifact detection methods (electrical artifacts: voltage change >200 $\mu$V within 100 ms on channels of interest: O1, O2, Oz). Blinks and horizontal eye movements were identified in the ocular channels and rejected by hand-coding.

Individual averages for each of the three conditions (Repeated, Unrepeated, and Unprimed) were computed. On average, infants contributed 94 artifact-free trials (Repeated $M = 24.3$, $SD = 10.5$; Unrepeated $M = 23.6$, $SD = 10.7$; Unprimed $M = 46.3$, $SD = 21.2$). For further analyses, a category Primed was computed by averaging trials from Repeated and Unrepeated ($M = 47.9$, $SD = 20.8$).

All typical infant visual ERP components, the P1, N290, and P400, were observed. Particularly for primed faces, we also observed a negative peak preceding the N290, which occurred at around 160 ms, roughly corresponding to the time-window of the adult N170. To avoid confounds with the adult N170, here we will refer to this component as "N160." Moreover, visual inspection suggested that a difference between conditions emerged in a late time-window, around 600–1,500 ms. Therefore, we also analyzed amplitude of this late positivity.

For a subsample of $N = 27$ infants who provided a sufficient number of artifact-free trials on fronto-central channels, we also explored repetition

effects on attention- and memory-related components. No repetition effects were observed on the Nc (300–700 ms) or PSW (800–1,500 ms), replicating findings of prior studies on repetition effects in infants (Peykarjou et al., 2014; Righi et al., 2014). Therefore, those analyses are not reported further.

Time windows for the components of interest were selected based on previous reports and visual inspection: P1, 80–120 ms; N160, 120–200 ms; N290, 200–300 ms; P400, 300–650 ms; late positivity, 600–1,500 ms (Balas et al., 2010; Scott, Shannon, & Nelson, 2006). Mean amplitude and latency to peak were extracted for P1, N160, N290, and P400. As there was no clear peak for the occipital late positivity, only mean amplitude was extracted for this component. Components were analyzed using BrainVision Analyzer over occipital cortices at three electrode sites: O1, O2, and Oz. These electrode sites correspond to electrode clusters in which the components of interest have been recorded in previous studies (Parise, Handl, & Striano, 2010; Peykarjou et al., 2014; Scott & Monesson, 2010). Compared to the N170, which is most prominent at P8/PO8 in adults, infant face-sensitive responses are more medially distributed (de Haan et al., 2003; Hoehl & Peykarjou, 2012).

First, we compared processing of Primed and Unprimed by running repeated-measurements analyses of variance (rmANOVAs) on the components of interest. In a second step, we examined repetition effects for individual faces by comparing Repeated and Unrepeated in rmANOVAs. In addition to analyses averaging across all trials, we also compared ERPs between male and female face pairs in the Primed condition. All statistical tests were performed on a .05 level of significance (two-tailed). Bonferroni and Greenhouse–Geisser corrections were performed if applicable. Preliminary analyses indicated that participant sex did not interact with any of the factors analyzed here. Therefore, participant sex is excluded from all reported analyses.

## RESULTS

### Primed versus unprimed

First, categorical repetition effects on face-related components were examined by comparing processing of faces that were preceded by faces (computed as average from Repeated and Unrepeated) and faces that were preceded by the central attractor. The effects on the amplitude and latency of the P1, N160, N290, and P400, and the amplitude of the late positivity were tested using 2 (repetition condition: Primed, Unprimed) × 3 (electrode: O1, O2, Oz) rmANOVAs. All means and

standard deviations (*SD*s) for the different repetition conditions are reported in Tables 1–5. Waveforms of the Primed–Unprimed contrast are displayed in Figure 2.

### Complete sample

P1 amplitude was reduced for Primed relative to Unprimed, $F(1,30) = 5.345$, $p < .05$, $\eta^2 = .22$ (Primed $M = -4.46$ $\mu V$, $SD = 6.3$; Unprimed $M = -1.59$ $\mu V$, $SD = 5.7$). P1 latency was also reduced for Primed ($M = 109.08$ ms, $SD = 7.3$) compared to Unprimed ($M = 111.74$ ms, $SD = 5.4$), $F(1, 30) = 5.415$, $p < .05$, $\eta^2 = .15$. Moreover, primed stimuli elicited smaller N290 amplitude than unprimed stimuli, $F(1,30) = 4.467$, $p < .05$, $\eta^2 = .13$ (Primed $M = 6.41$ $\mu V$, $SD = 12.7$; Unprimed $M = 2.16$ $\mu V$, $SD = 11.6$). No other comparisons yielded significant results. Thus, we observed repetition effects for primed stimuli at the level of P1 amplitude and latency and N290 amplitude.

### Male–female contrast

In the next step, we tested whether male and female faces were processed differently in the reduced sample that provided sufficient numbers of trials. Here, we ran 2 (face gender: male, female) × 2 (repetition condition: Primed, Unprimed) × 3 (electrode: O1, O2, Oz) rmANOVAs. For ease of comprehension, we only report those main effects and interactions that involve gender of the face. With regard to overall repetition effects,

TABLE 1
Means and Standard Deviations (*SD*s) of the P1 Grand Average Response

| Condition | P1 Amplitude mean | P1 Amplitude SD | P1 Latency mean | P1 Latency SD |
|---|---|---|---|---|
| Repeated | −3.72 | 7.59 | 109.25 | 7.7 |
| Male | −4.91 | 7.0 | 109.80 | 5.7 |
| Female | −2.82 | 8.1 | 109.57 | 7.0 |
| Unrepeated | −5.21 | 6.8 | 108.90 | 7.5 |
| Male | −4.75 | 7.1 | 108.94 | 9.4 |
| Female | −5.19 | 12.2 | 110.12 | 6.1 |
| Primed | −4.46 | 6.3 | 109.08 | 7.3 |
| Male | −4.83 | 5.5 | 109.37 | 7.1 |
| Female | −4.01 | 7.2 | 109.84 | 5.8 |
| Unprimed | −1.59 | 5.7 | 111.74 | 5.4 |
| Male | 1.73 | 4.3 | 110.75 | 5.0 |
| Female | −1.70 | 5.8 | 112.47 | 4.9 |

TABLE 2
Means and Standard Deviations (*SD*s) of the N160 Grand Average Response

| Condition | N160 Amplitude mean | N160 Amplitude SD | N160 Latency mean | N160 Latency SD |
|---|---|---|---|---|
| Repeated | 0.71 | 8.3 | 151.48 | 23.6 |
| Male | 0.14 | 8.8 | 152.78 | 23.4 |
| Female | 1.55 | 8.3 | 158.12 | 25.0 |
| Unrepeated | −0.23 | 6.9 | 145.16 | 19.2 |
| Male | 1.37 | 8.6 | 144.31 | 22.1 |
| Female | −0.51 | 10.6 | 154.04 | 24.4 |
| Primed | 0.24 | 6.8 | 148.32 | 18.8 |
| Male | 0.76 | 7.4 | 148.55 | 18.8 |
| Female | 0.52 | 7.0 | 156.08 | 19.0 |
| Unprimed | 0.66 | 8.3 | 163.10 | 25.9 |
| Male | 4.37 | 8.8 | 163.22 | 26.5 |
| Female | 1.08 | 7.0 | 173.49 | 21.1 |

TABLE 3
Means and Standard Deviations (*SD*s) of the N290 Grand Average Response

| Condition | N290 Amplitude Mean | N290 Amplitude SD | N290 Latency Mean | N290 Latency SD |
|---|---|---|---|---|
| Repeated | 6.77 | 15.0 | 227.74 | 29.8 |
| Male | 2.81 | 12.8 | 237.25 | 36.5 |
| Female | 2.98 | 11.8 | 235.14 | 35.5 |
| Unrepeated | 6.04 | 12.1 | 243.40 | 33.6 |
| Male | 5.50 | 12.8 | 238.98 | 31.6 |
| Female | 1.19 | 15.5 | 244.94 | 35.5 |
| Primed | 6.41 | 12.7 | 235.57 | 28.3 |
| Male | 4.16 | 11.4 | 238.12 | 29.8 |
| Female | 2.08 | 12.5 | 240.04 | 31.5 |
| Unprimed | 2.16 | 11.6 | 241.81 | 36.1 |
| Male | 2.79 | 10.9 | 249.80 | 36.4 |
| Female | −2.80 | 11.4 | 245.49 | 37.9 |

analyses on this reduced sample conformed to the analyses performed on the complete sample.

At the level of the N160, faster processing of male than female faces was observed, $F(1, 16) = 9.462$, $p < .01$, $\eta^2 = .37$ (Male $M = 155.88$ ms, $SD = 17.8$; Female $M = 164.78$ ms, $SD = 14.8$). Additionally, male faces elicited smaller N290 amplitude (Male $M = 2.90$ $\mu$V, $SD = 8.3$; Female $M = 0.02$ $\mu$V, $SD = 8.5$; $F(1, 16) = 8.407$, $p < .05$, $\eta^2 = .34$) and larger P400 amplitude (Male $M = 16.98$ $\mu$V, $SD = 12.9$; Female $M = 12.6$ $\mu$V,

TABLE 4
Means and Standard Deviations (SDs) of the P400 Grand Average Response

| Condition | P400 Amplitude mean | P400 Amplitude SD | P400 Latency mean | P400 Latency SD |
|---|---|---|---|---|
| Repeated | 19.78 | 18.6 | 456.86 | 63.8 |
| Male | 12.80 | 15.1 | 446.51 | 65.9 |
| Female | 12.96 | 15.0 | 448.71 | 59.9 |
| Unrepeated | 17.97 | 14.2 | 458.45 | 60.2 |
| Male | 19.21 | 19.6 | 459.69 | 66.0 |
| Female | 11.70 | 17.3 | 459.06 | 56.6 |
| Primed | 18.87 | 14.5 | 457.66 | 50.9 |
| Male | 16.00 | 16.0 | 453.10 | 56.5 |
| Female | 12.33 | 14.2 | 453.88 | 45.3 |
| Unprimed | 16.82 | 10.8 | 451.14 | 66.3 |
| Male | 17.97 | 12.1 | 440.31 | 46.7 |
| Female | 12.87 | 9.9 | 434.27 | 45.4 |

TABLE 5
Means and Standard Deviations (SDs) of the Late Positivity Grand Average Response

| Condition | Late positivity amplitude mean | Late positivity amplitude SD |
|---|---|---|
| Repeated | 8.25 | 17.6 |
| Male | −0.16 | 15.9 |
| Female | 5.16 | 14.7 |
| Unrepeated | 5.07 | 13.4 |
| Male | 11.82 | 18.2 |
| Female | 0.58 | 16.1 |
| Primed | 6.66 | 12.1 |
| Male | 5.83 | 15.1 |
| Female | 2.87 | 12.7 |
| Unprimed | −1.53 | 10.2 |
| Male | 0.68 | 10.8 |
| Female | −4.27 | 9.7 |

$SD = 10.1$; $F(1, 16) = 6.964$, $p < .05$, $\eta^2 = .30$), but when a difference score was computed (amplitude at P400—amplitude at N290), the effect at the P400 was no longer significant, $F < 1$, $p = .54$.

## Summary

Primed and unprimed stimuli were treated differently in the infant brain. Primed stimuli elicited smaller P1 amplitude and latency and reduced N290 amplitude. Repetition effects on the P1, although in the other direction,

Complete group



Female faces



Male faces
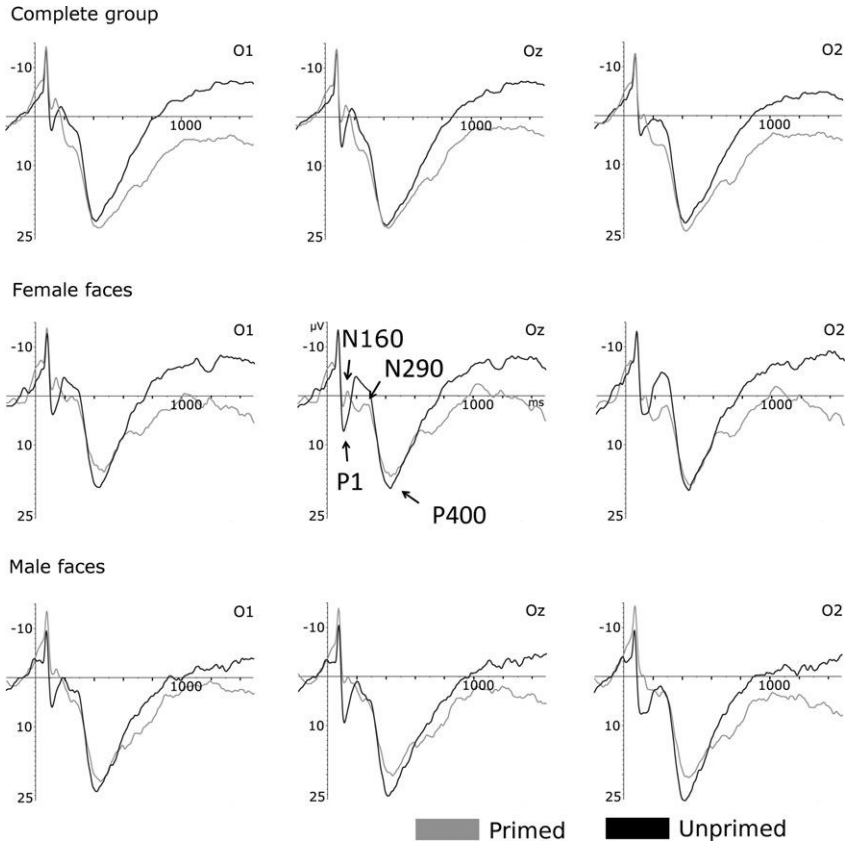


Primed    Unprimed

**Figure 2** Grand average ERP responses to Unprimed (black) and Primed (gray). The x-axis represents latency in milliseconds (ms), with tick-marks every 200 ms, and the y-axis, amplitude in microvolts (μV). Negative is plotted upward. P1 amplitude and latency were reduced for Primed. Moreover, N290 amplitude was reduced in response to Primed.

were also observed in previous work (Peykarjou et al., 2014) and suggest that categorical representations are activated very early during the stream of stimulus processing. Moreover, we observed differential processing of male and female faces at the level of the N160 and N290.

## Repeated versus unrepeated

In the next step, we focused on infants' ability to recognize individual faces. Similar to the Primed–Unprimed contrast, *r*epetition effects for indi-

vidual faces were examined by comparing Repeated and Unrepeated in a
2 (repetition condition: Repeated, Unrepeated) × 3 (electrode: O1, O2,
Oz) rmANOVA for each dependent variable (P1, N160, N290, P400, late
positivity). Waveforms are displayed in Figure 3.

### Complete sample

Latency of the N290 was reduced in response to repeated
($M = 227.74$ ms,   $SD = 29.8$)   compared   to   unrepeated   faces



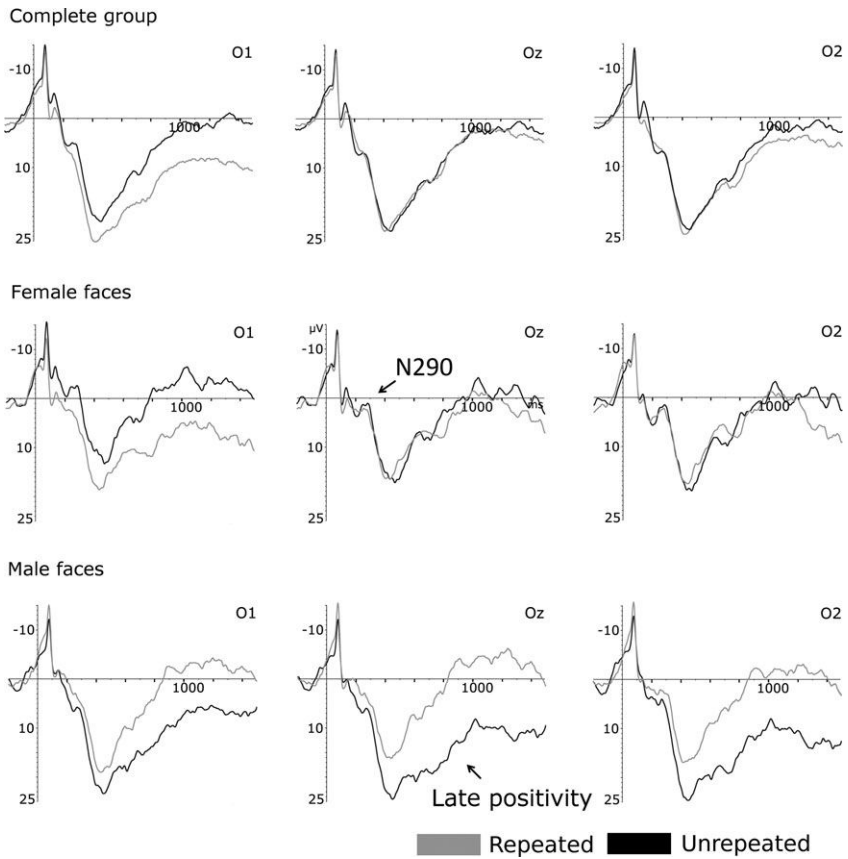**Figure 3**   Grand average ERP responses to Unrepeated (black) and Repeated (gray).
The *x*-axis represents latency in milliseconds (ms), with tick-marks every 200 ms, and
the *y*-axis, amplitude in microvolts (μV). Negative is plotted upward. N290 latency
was reduced for repeated faces. Only for male faces, unrepeated faces elicited
enhanced amplitude in a late time-range (late positivity from 600 to 1,500 ms).

($M$ = 243.40 ms, $SD$ = 33.6), $F(1, 30)$ = 9.164, $p$ = .01, $\eta^2$ = .23. None of the comparisons on the P1, N160 latency, N290 amplitude, the P400, or the late positivity provided significant results, however.

### Male–female contrast

Finally, we compared processing of male and female faces in 2 (face gender: male, female) × 2 (repetition condition: Primed, Unprimed) × 3 (electrode: O1, O2, Oz) rmANOVAs in the reduced sample of participants providing sufficient artifact-free trials ($N$ = 17). Again, we focused on significant results including face gender, as the general pattern of results conformed to the analyses within the complete sample.

Only at the level of the late positivity, an interaction between face gender and repetition condition was observed, $F(1, 16)$ = 10.883, $p < .01$, $\eta^2$ = .34. For male faces, amplitude was enhanced for unrepeated relative to repeated faces, $F(1, 16)$ = 9.500, $p < .01$, $\eta^2$ = .37 (Repeated $M$ = −0.16 μV, $SD$ = 15.9; Unrepeated $M$ = 11.82 μV, $SD$ = 18.2). For female faces, no difference between repeated and unrepeated faces was observed, $p$ = .30 (Repeated $M$ = 5.16 μV, $SD$ = 14.7; Unrepeated $M$ = 0.58 μV, $SD$ = 16.1).

### Summary

We observed evidence indicating that 9-month-old infants individuated male and female faces. Overall, N290 latency was reduced for repeated compared to unrepeated faces. In addition, only for male faces, the amplitude of the late positivity was enhanced for unrepeated relative to repeated faces.

## N160–N290 double-peaked negativity

As described in the previous paragraphs, we observed evidence for infants' ability to individuate faces across gender. Strikingly, although the N160 did not differentiate between repeated and unrepeated faces, visual inspection revealed that the N160–N290 double-peak was indeed primarily elicited for primed stimuli, and the N160 was nearly absent for unprimed stimuli. To confirm this observation statistically, we analyzed the time course of waveforms across conditions using a window analysis within the time-window of the N160 and N290 (120–300 ms) (Hoorrmann, Falkenstein, Schwarzenau, & Hohnsbein, 1998). We exported amplitude values for each time-point, averaged them across electrodes, and normalized the data using the mean across time-points of each condition. The resulting

values were compared in two separate rmANOVAs with 2 (condition: Primed, Unprimed, and Repeated, Unrepeated) * 45 (time-points: 120, 124…, 296) conditions. If the ERP waveform differs between conditions, a significant interaction between time-points and condition should be observed.

For the Primed–Unprimed contrast, a significant time-points-by-condition interaction was observed, $F(1, 44) = 3.041$, $p < .0001$, $\eta^2 = .09$, confirming that waveforms differed between primed and unprimed stimuli. In contrast, the waveforms of Repeated and Unrepeated did not differ from each other, $F(1, 44) = 1.037$, $p = .41$, $\eta^2 = .03$ (Greenhouse–Geisser corrected: $F(1.1, 43.9) = 3.041$, $p = .32$, $\eta^2 = .03$).

Restricting the analyses to the time-range of the N160 (120–200 ms) further confirmed that waveforms differed between Primed and Unprimed, $F(1.6, 19.4) = 5.472$, $p < .05$, $\eta^2 = .154$, but not between Repeated and Unrepeated, $F(1, 20) = 1.081$, $p = .307$, $\eta^2 = .035$. When including only 10 time-points in the time-window of the N160 and running consecutive analyses to examine the precise timing of differences, we found that they emerged in the time-range 160–196 ms ($F(1.45, 8.55) = 6.479$, $p < .01$, $\eta^2 = .178$, Greenhouse–Geisser corrected).

## DISCUSSION

The current study examined repetition effects for individual human faces in 9-month-old infants using ERPs as dependent measures. Our results provide evidence for infants' ability to perceptually encode and recognize unfamiliar faces individually, even though this task still seems to be difficult within the first year of life.

### Identity repetition effects

We observed repetition effects at the level of the N290, with shorter N290 latency for repeated compared to unrepeated faces. This is consistent with the assumption that the N290 is the main precursor of the adult N170 (de Haan et al., 2003; Hoehl & Peykarjou, 2012). In studies with adults, amplitude changes in the form of amplitude reductions have been reported following repetition of faces (Caharel et al., 2009; Eimer, Kiss, et al., 2010; Schweinberger et al., 2004). Consistent with the effect on N290 latency in the current study, reduced N170 latency for repeated faces has been observed as well (Itier & Taylor, 2002). Reduced N290 latency for repeated faces suggests that infants' brains mapped the two presentations of the same face and recognized their similarity. We conclude that the rep-

etition of an identical face accelerates processing at the level of the N290 in infants, in accordance with findings in adults (Itier & Taylor, 2002).

The absence of repetition effects on N160 or N290 amplitude, compatible with many studies in adults (Caharel et al., 2009; Eimer, Kiss, et al., 2010; Schweinberger et al., 2004), may indicate that infants' representation of individual faces was not comprehensive enough to reduce processing effort upon the second presentation. As discussed in the Introduction, behavioral paradigms allow the infant to accumulate visual experience with stimuli. Thus, infants may be well able to recognize unfamiliar faces when they have acquired a sufficient amount of familiarization time. However, it may still be difficult for them to recognize faces they have seen briefly. Increasing the presentation duration even further would likely allow infants to strengthen their representation of the single stimulus, and could induce repetition effects on N160/N290 amplitude.

On the P400, a component that has been discussed as another potential precursor of the N170 during infancy (de Haan & Nelson, 1999; de Haan et al., 2003), we did not observe any recognition-related repetition effects. This is in line with the two prior studies on repetition effects during infancy (Peykarjou et al., 2014; Righi et al., 2014), providing converging evidence against an association of the P400 with face individuation.

To our knowledge, this is the first infant study reporting a double-peaked negativity in the time-range of the adult N170–N250. Only for primed faces, we observed a negative peak, termed N160, preceding the N290 typically observed in infants (Cassia, Kuefner, Westerlund, & Nelson, 2006; de Haan, Pascalis, & Johnson, 2002; Peykarjou & Hoehl, 2013). The fact that a similar double-peak was not observed for unprimed faces indicates that this phenomenon cannot be attributed to mere sample characteristics. The sequence of trials in the current study was clearly structured. It consisted of a central attractor, a prime, and a target, and the main variation was the repetition or novelty of the target face. We suggest that this defined structure enhanced infants' focus on individual identities, thus inducing the N160.

Although the perceived double-peak superficially matches the adult waveform for repeated faces, the observed components do not map one-to-one onto the adult components functionally. Whereas in adults the N170 is automatically generated for stimuli perceived as faces, the N250 is elicited when facial identity is important. Even though faces typically elicit a later-occurring component (N290) in infants, the repetition focus of the current study elicited an earlier peak (N160) not generally observed. It seems possible that the generally observed N290 is associated with the N250 rather than the N170 and that the N170 is only emerging later during development to become a distinct and early marker of face processing.

More studies using repetition paradigms across development are needed to test the functional association of the N160 and N290 with adult components.

## Face gender effects

Several studies have reported an advantage for processing and individuating female faces in infants (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002; Quinn et al., 2010; Righi et al., 2014). Therefore, we assessed ERP repetition effects separately for male and female faces in a subsample of infants that provided sufficient numbers of artifact-free trials. On typical face-related components, no gender-specific repetition effects were found. But, visual inspection of our data revealed a distinct positive ERP component starting around 600 ms to which we refer as "late positivity." This component was elicited with increased amplitude for novel compared to repeated male faces, potentially indicating that forming representations of male faces required increased and elongated processing effort. However, as the component was identified post hoc, this effect should be interpreted with caution. Future studies are needed to confirm differences in the development of representations of male and female faces, and to test how these might be related to other cognitive processes such as memory.

Reduced N160 latency and N290 amplitude for male compared to female faces may also be related to experience factors. It is possible that female faces triggered individuation attempts, requiring prolonged (N160) and increased (N290) processing of female compared to male faces.

Processing advantages for female faces have often been attributed to the larger amount of experience that infants gather with female caregivers (Rennels & Davis, 2008). However, other (experience-independent) factors may as well contribute to processing differences between male and female faces. Femalized faces are perceived as more attractive, and this holds for female as well as male faces (Perrett et al., 1998). This might interfere with recognition of individual faces, as superior recognition rates have been reported for highly attractive or unattractive faces (Shepherd & Ellis, 1973). To take this factor into account, we asked students to rate our stimuli blind to the experimental manipulation. These ratings confirmed that (1) gender could be inferred from the cropped faces and (2) there was no difference in perceived attractiveness or averageness of male and female faces. Thus, we did not find evidence indicating that the effect for male faces results from higher attractiveness or increased remarkability.

Why did infants then show increased processing effort for novel males? For both male and female faces, N290 latency was decreased by repetition, suggesting that infants processed face identity. The very prominent difference in processing repeated and unrepeated male faces may reflect later processing stages following initial perceptual analysis which are likely related to infants' limited experience with male faces. Unrepeated male faces may have been particularly difficult to compare to the previously seen faces, increasing the processing effort following early face-processing stages.

Our findings are only partially compatible with those reported in a recent study by Righi and colleagues (Righi et al., 2014) who observed a reduced N290 amplitude following repetition, but only for female faces. The 1-back design employed by Righi et al. (2014) may have required infants' short-term memory to a greater extent than our immediate repetition task, thus yielding a processing advantage for the more familiar female faces.

### Categorical repetition effects

Our findings suggest that infants less than 1 year of age quickly categorize faces versus nonfaces. P1 and N290 amplitude and P1 latency were reduced for faces preceded by faces relative to faces preceded by the central attractor. Hence, infants seem to recognize the presence of a face within ~100 ms after stimulus onset. They were able to form or activate a comprehensive representation of the human face category during presentation of the prime, and to reactivate it while they perceived the target. This fast-occurring repetition effect may in part rely on low-level cues associated with the face category. In the current study, categorical repetition was compared to an "unprimed" condition, in which a central attractor that clearly differed from faces in perceptual terms was presented. Future research should evaluate the role of low-level cues for the activation of categorical representations.

In a previous study on infants' face categorization (Peykarjou et al., 2014), the face category consisted of human and ape faces, preceded by houses in the unprimed condition. Under these more demanding circumstances, the P1 was elicited with reduced latency but enhanced amplitude for primed compared to unprimed faces, suggesting that a comprehensive face representation consisting of humans and apes was being built up. The P1 thus reflects categorical repetition, and the direction of repetition effects depends on the specific categorical context presented in the respective study. Together, these studies implicate that similar processes can be evoked in the infant as in the adult brain, with reduced amplitude

observed for easier perceptual mappings and repetition enhancement for more demanding mappings (Henson, 2003; Nemrodov & Itier, 2012).

## Limitations

The current study demonstrated perceptual recognition for a large number of faces, but tested only single faces at a time. Whether infants can also recognize single faces presented among distractors remains an interesting question for future research. Moreover, for repeated trials, the same image was presented as prime and target. It would be important to employ different images of faces to test recognition that is robust to changes in viewpoint or expression.

## CONCLUSIONS

In a rapid repetition ERP paradigm, we obtained evidence that 9-month-old infants are able to encode and recognize a large number of individual faces within a short amount of time. N290 latency was reduced for repeated faces, and a later-occurring positivity was enhanced for unrepeated male faces. The question of how much visual experience needs to be accumulated to represent a face, and how this changes with development, should be considered in future research by systematically varying (a) the number of different faces, (b) the presentation duration of each single stimulus, and (c) the familiarity with the given face category (i.e., unfamiliar faces, pre-experimentally familiar faces versus faces familiarized online). As demonstrated in this report, rapid repetition ERPs provide a suitable paradigm for this kind of research.

Together with a recent study (Peykarjou et al., 2014), the present results suggest that infants first classify faces broadly (as "faces") within 100 ms after stimulus onset and then process more fine-grained information such as basic-level category membership and face identity in subsequent steps. Future research should explore whether faces are processed in such a global-to-subordinate categorization sequence across development.

## ACKNOWLEDGMENTS

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## Manuscript II

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# At a Glance – Rapid Categorization of Ape vs. Human Faces in 9-Month-Old Infants

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## Abstract

The current study investigates categorization of human and ape faces in 9-month-old infants using a Fast Periodic Visual Stimulation (FPVS) paradigm while measuring EEG. In this paradigm, a categorization response is elicited only if infants discriminate between different categories and generalize across exemplars within each category. In study 1, infant categorization of upright and inverted human and ape faces was explored. Upright ape faces presented among human faces elicited a strong categorization response, whereas responses for upright human faces and inverted ape faces were smaller. Inverted human faces did not elicit categorization. The data were best explained by a model with main effects of species and orientation. However, variance of low-level image characteristics was higher for the ape than the human face category, providing a potential confound. Variance was matched to replicate this finding in an independent sample using highly controlled stimuli (study 2). Both human and ape faces elicited categorization in upright and inverted conditions, but again upright ape faces elicited the strongest responses. Like in study 1, data were best explained by a model of two main effects. These two experiments demonstrate that 9-month-olds rapidly categorize faces, and unfamiliar face categories elicit increased categorization responses.

Keywords: categorization, face processing, development, fast periodic visual stimulation (FPVS), electroencephalography (EEG)

**At a Glance – Rapid Categorization of Ape vs. Human Faces in 9-Month-Old Infants**

One of the most important visual challenges faced by young infants is to detect other human beings in their environment. Infants are surrounded by other humans most of the time, and are attracted by human faces in particular: For about 25% of their awake time, infants gaze at human faces [1]. Human faces form a homogeneous group of stimuli consisting of an oval shape with two eyes above a nose and a mouth. Given the high amount of exposure to faces and the homogeneity of exemplars of this category, it is not surprising that infants develop a categorical representation of faces from an early age [2]. However, the degree of specificity of this representation, in particular whether it differs for human and similarly looking nonhuman primate faces, remains unknown. The current study investigates this issue by testing visual categorization of human and ape faces in 9-month-old infants.

Perceptual categorization of human faces has been documented with brain and behavioural measures in adults. Human faces activate specialized regions along the ventral visual pathway with a right hemispheric advantage [3-5], and elicit a right-lateralized face-sensitive event-related-potential (ERP) response peaking at ~170 ms, the N170 [6]. It is increased in amplitude and/or latency for inverted faces [7-9]. Human individual face recognition is characteristically impaired for faces belonging to unfamiliar face categories, such as other species [10, 11] or other human groups [the "other-race" face effect, 12 for review, 13].

Several studies have compared the N170 in response to human and ape faces [14-16]. Carmel and Bentin [14] observed shorter N170 peak latencies for human than ape faces. A similar effect was obtained by Itier and colleagues [16], who also observed that the inversion effect was more pronounced for human faces in latency and absent for ape

faces in amplitude. Another study found smaller amplitude for human than monkey faces, and an inversion effect that was restricted to human faces [15]. The characteristics of the N170 for faces of different species have thus not been consistent across studies. Moreover, the N170 component is not present in infants, but two ERP components are considered as its precursors, the N290 and P400 [17, 18]. These components differ from the N170 in timing, scalp distribution, polarity (in case of the P400), and partly in response properties. This makes it difficult to predict how the species of faces may be reflected in infants' electrophysiological responses compared to adults'.

Processing of human and ape faces has been compared repeatedly during the first year of life. Newborns do not show a preference for human or ape faces, but a preference for upright faces irrespective of species [19]. Whereas young infants discriminate individual ape faces similarly to human faces, from 6 to 9 months of age individuation of ape faces declines [20, see 21, for similar results obtained with sheep faces, 22]. Experience in individuating ape faces helps infants to maintain their ability to discriminate them at 9 months [22]. When older infants are given more time to process the faces, discrimination of unfamiliar face categories is still possible [23].

Evidence for common categorization of human and ape faces (as primate faces) as well as distinct categorization (as human *vs.* ape faces) has recently been obtained in 9-month-old infants [24]. In this study, broad categorical repetition effects (face/non-face) were observed on the level of the early visual P1 component, and species-specific repetition effects on the level of the N290. In another line of research, the two potentially face-sensitive infant ERP components, N290 and P400, were compared for human and monkey faces [15, 25]. In all age groups tested (3-, 6-, and 12-month-olds), processing differences between the two face categories were observed, but they were

not consistent across age-groups. A human face-specific increase in N290 amplitude for inverted faces has been obtained only in 12-month-olds [25].

Several challenges make it difficult to draw conclusions from previous infant ERP studies on face species categorization [15, 25]. First, these studies suffered from relatively high drop-out rates of 63-81%, which raises the question whether their results can be generalized. Second, human and monkey faces were presented in a between-subjects design so that every infant viewed only faces from one species. Therefore, infants were not required to categorize faces at all. Third, processing differences between the different face species were observed at every age tested. One may wonder whether such differences truly reflect perceptual categorization. For instance, it has been suggested that the human face-specific inversion effect on N290 amplitude in 12-month-olds reveals expert face processing [17], but the inversion effect is no indication for categorical perception. To clearly demonstrate perceptual categorization, a paradigm is required that tests both discrimination between exemplars belonging to different categories, and generalization across exemplars belonging to the same category.

In addition, an expertise level at perceptual categorization requires that categorization happens fast and automatically [for a review, see 26]. Expert categorization in adults is very rapid: Broad categorization as animal/no animal takes place within 150 ms [27, 28], at about the same time as the onset of the N170. This ERP component reliably differentiates faces and various animal and object categories [6, 29, for a review, see 30]. Concrete [e.g., "face", "car", "dog"; 31, 32] and abstract [e.g., "living", "non-living"; 33, 34] categorization can even take place after having viewed an image for less than 50 ms. Moreover, face perception seems to be mandatory, that is, faces cannot be ignored even if it is required by the task [35-37], and face subcategory

(e.g., gender) judgements are not impaired by reduced attention [38]. Thus, it seems that face categorization occurs effortlessly in adults.

Recently, categorization in this sense (a rapid, automatic response including both discrimination and generalization) of human faces from many non-face visual objects has been demonstrated in adults with Fast Periodic Visual Stimulation [FPVS; 39] while measuring electroencephalography (EEG). In this paradigm, highly heterogeneous images of human faces were periodically presented between diverse images of different biological and non-biological objects including animals. In 4-6-monht-old infants, human faces elicited a strong right-lateralized occipito-temporal categorization response [2]. This response was driven by high-level representations, as it was not found for phase-scrambled images.

To evaluate whether infants have developed perceptual categories for human and ape faces, and to overcome limitations of previous ERP studies, we used a similar FPVS paradigm in the present study. FPVS has several advantages compared to standard ERP measures: (1) FPVS has a high signal-to-noise ratio, requiring short looking times so that only few trials are needed and few participants need to be excluded; (2) the different stimulus categories are embedded within one sequence and a categorization response will only be elicited if all (or most) exemplars are categorized, (3) and the categorization response can be defined and quantified objectively.

Here, we tested 9-month-old infants with sequences of human or ape faces as standard stimuli in which the respective other category was presented periodically as every $5^{th}$ image. At 9 months, behavioural work has demonstrated that individuation of ape faces has declined [20] and ERP work has indicated that the two categories are discriminated when stimuli were presented in an upright position [24]. Accordingly, we predicted that 9-month-olds show a categorization response when presented with

upright human versus ape faces. Whether categorization is similar for the two categories is an open question: Based on the assumption that real-world experience plays an important role even in early categorization [e.g., 40, 41], infants may find it easier to recognize deviant ape faces among human faces than vice versa. Extensive experience with processing of human faces might support and speed up the process of activating an already existing categorical representation and thus enhance novelty responses to exemplars that do not match the already established category (i.e., ape faces). Alternatively, categorization may be based on an innate mechanism specialized to recognize human faces [42]. In this case, infants may find it easier to detect human faces among ape faces. An exploration of infants' responses in both upright conditions will thus tell us more about the nature of cognitive processes underlying rapid visual categorization.

Moreover, this study explored the contribution of low-level image characteristics to face species categorization. If these cues were fully sufficient to discriminate both face categories, we would expect similar categorization performance in upright and inverted conditions because low-level cues are identical in both cases. However, if categorization were based on higher-level visual representations and previous real-world experience, infants should show a stronger categorization response when looking at stimuli presented upright than at faces presented in an inverted orientation.

The FPVS paradigm allows us to determine categorization performance not only at the group level but also at the level of individual infants. Study 1 provides an initial investigation of rapid processing of upright and inverted human and ape faces at 9 months of age. Based on this pilot study we then optimize the stimulus set and specify hypotheses to test with an independent sample in study 2. Findings of both studies provide the basis for our conclusions.

**2. Study 1**

**2.1 Material and Methods**

 **2.1.2 Participants.** Twenty-two 9-month-old infants were tested (10 female, mean

age = 9 months, 12 days, SD = 9 days) after obtaining verbal informed consent from

their caretaker. Two additional infants were tested but excluded (one due to excessive

crying, one due to insufficient data quality).

 **2.2.2 Stimuli/Presentation.** Infants were presented with sequences of human and

ape faces. Images were displayed in upright and inverted orientations in subsequent

trials. The presentation was similar to recent studies employing the FPVS technique [2,

43, 44]. Fifteen images each of human and ape faces were presented. Human face

images were taken from standard face databases [46][46][i.e., Radboud Face Database,

45, MacBrain Face Stimulus Set, 46]. Mean luminance was equalized across categories.

 Images were displayed on a light grey background. Infants sat at a looking distance

of 60 cm, and pixel size was 550 (width) x 607 (height), corresponding to

approximately 12 x 15 degrees of visual angle. Images changed size (+/- 10%) at every

stimulation cycle. MATLAB 7.8 (The Mathworks) with PsychToolbox

(http://psychtoolbox.org/) was used for stimulus display. Stimulus sequences were

presented at a fixed rate of 6.03 cycles per second (*F*=6.03 Hz; base stimulation

frequency) through sinusoidal contrast modulation [47]. Each cycle lasted 166 ms (i.e.,

1000 ms/6.033). Trials started with a uniform grey background from which an image

appeared as contrast increased. The stimulation was gradually faded in by progressively

increasing the modulation depth from 0% to 100% maximum contrast level (and faded

out vice versa). Each stimulus reached full contrast at 83 ms, then contrast was

decreased at the same rate. At fixed intervals of every 5th image, a stimulus from the

other category was introduced, creating a trial sequence containing category changes at

a frequency of 1.21 Hz (6.03 Hz/5; i.e., A= Ape; H = Human: HHHHAHHHHA.....).

EEG amplitude at this frequency ($F/5$ = 1.21 Hz) and its harmonics (i.e., $2F/5$ = 2.41

Hz, $3F/5$ = 3.62 Hz…) was used as an index of the visual system's categorization of

face species [48]. The schematic stimulation course is illustrated in Figure 1.

Four types of trials were presented: ape face deviant (with human face

standard), human face deviant (with ape face standard), and likewise versions of these

trials with pictures inverted. For half the sample, human faces served as standard, for

half the sample it was vice versa. Stimulus orientation was varied within-subject across

trials (four consecutive trials upright, then four trials inverted, four upright, four

inverted). Stimulus order was randomized for each trial with the exception that no

stimulus could be repeated immediately. Between trials, short breaks were provided if

needed. Overall, testing took about 10 minutes.

**2.2.3 Procedure**. Infants were seated at a looking distance of approx. 60 cm

from the computer screen on their caregiver's lap. Each trial consisted of a blank screen

(random, min. 5 seconds), a 2-second fade-in, a stimulation sequence for 20 seconds,

and a fade-out of 2 seconds. Stimulus fade-in and fade-out were introduced to avoid

surprise reactions, abrupt eye-movements or blinks.

Triggers were sent via parallel port at the start of the each sequence and at the

minimum of each cycle (grey background, 0% contrast). Trigger accuracy was

registered by a photodiode located in the upper left corner of the monitor. During the

entire stimulation, looking-behavior was video-taped and coded offline. Trials were

initiated manually when participants looked attentively at the screen and showed an

artifact-free EEG signal.

**2.2.4 EEG Recordings and Analyses.** EEG measures were obtained applying a

BrainProducts actiCap (Gilching, Germany) with 32 active Ag-AgCl electrodes

arranged according to the 10-10-system and a right mastoid reference. Sampling rate was set at 250 Hz and the EEG signal was amplified via a BrainAmp amplifier. Impedances were considered acceptable if < 20 kΩ. Recordings were acquired in a dimly-lit and quiet room.

EEG Preprocessing. All EEG processing steps were carried out using Letswave (http://nocions. webnode.com/letswave) and Matlab 2012b (The Mathworks) and followed the procedure described in several recent studies [e.g., 43, 49]. EEG data was first band-pass filtered at 0.1-100 Hz using a Butterworth filter with a slope of 24 dB/octet. Filtered data was then segmented 2 seconds before and after the sequence, resulting in 28-second segments (-2 s – 26 s). Next, noisy channels were identified and pooled from surrounding channels (for a maximum of 2 channels) and a common average reference computation was applied to all channels.

Frequency domain analysis. Preprocessed data segments were cropped to an integer number of 6.03 Hz cycles beginning 2 seconds after onset of the trial until approximately 20 seconds, just before the stimulus fade-out (120 cycles, 4973 time bins in total ≈ 19.892 s). The first two seconds of each trial were excluded to avoid any contamination by the initial transient responses. For each condition, trials were averaged in the time-domain for every individual participant. Averaging was performed to increase the signal-to-noise ratio (SNR) by reducing EEG activities non-phase-locked to the stimulus. Then a Fast Fourier Transform (FFT) was applied to these averaged segments to extract amplitude spectra for all channels (square root of sum of squares of the real and imaginary parts divided by the number of data points). Frequency analysis yielded spectra with a high frequency resolution of 0.0503 Hz (1/19.892 s).

To measure the magnitude of activity at pre-defined bins of interest, baseline corrected amplitudes were computed by subtracting the average amplitude of 12

surrounding bins (6 on each side, excluding the immediately adjacent bins) from every frequency bin [43, 49]. Z-scores were calculated as the difference between amplitude at the frequency of interest and mean amplitude of 12 surrounding bins divided by the standard deviation of the 12 surrounding bins [44]. Threshold of significance was placed at Z-score 1.64 ($p < 0.05$, one-tailed). SNRs were computed by dividing the signal by the amplitude at the 12 neighboring frequency bins. Note that in the current study, 12 rather than 20 bins as in previous studies [43, 44] were used to estimate noise variance. Due to shorter recording time in infants compared to adults (26 versus 66 second trials), the frequency resolution in this study is lower than in previous reports. In order to avoid including low parts of the spectrum that are inherently contaminated by higher levels of biological noise, the number of bins for noise variance estimation was reduced.

Only trials with a significant response at the base frequency (6.03 and/or its harmonic 12.07) were used. On average, participants viewed 10 trials ($M = 10.41$; $SD = 2.8$), of which one trial ($M = 1.36$; $SD = 1.7$) was excluded due to a non-significant base rate response. There was no difference in the number of trials in the human ($M = 10.4$; $SD = 3.4$) and ape conditions ($M = 10.4$; $SD = 2.1$; $p > .05$), but participants saw more upright ($M = 6.2$; $SD = 1.8$) than inverted trials ($M = 4.2$; $SD = 1.2$; $p < .001$). To ensure that results could not be explained by differences in trial numbers, additional analyses were performed using a matched number of upright and inverted trials (trials from the upright condition randomly excluded). The results pattern conformed to the analyses on all trials. Additionally, trials were selected based on looking time, which was coded offline from the video. 20% of trials were double-coded, with an intraclass correlation (ICC) coefficient of .98. When using only trials in which looking time was > 50%, the results pattern was similar to the main analyses.

Statistical analyses were performed using baseline corrected amplitudes (summed up to the highest consecutively significant harmonic; Retter & Rossion, 2016). For the categorization response, 1.21 Hz and harmonics were summed up to the 11th harmonic, but excluding the 5th and 10th harmonics which correspond to the base frequency. For the base stimulation response, 6.03 Hz and harmonics were summed up to the 6th harmonic. Channels of interest were defined based on scalp topographies: P7, P8, PO9, PO10, O1, O2, Oz for the categorization response and O1, O2, Oz for the base response.

Z-scores were used to determine whether a significant response was obtained in each condition. Responses were Greenhouse Geisser corrected. Conditions were compared using baseline corrected amplitudes in a JZS Bayes factor repeated measurement analysis of variance (rmANOVA) with default prior scales [50-52]. Factors were species (2: human deviant, ape deviant) * orientation (2: upright, inverted). Preliminary analyses indicated that there was no main effect or interaction with electrode, so an average of all seven electrodes (categorization response) or three electrodes (base response) was calculated and used in the statistical analyses. The Bayes factor rmANOVA provides a more conservative test than the standard rmANOVA and estimates probability for models based on the null and alternative hypotheses.

We hypothesized that upright images would elicit stronger categorization responses than inverted images. Differences in categorization of human and ape deviants were not expected.

**2.2 Results**

**2.2.1 Categorization Response.** The categorization response (response at 1.21 Hz and harmonics) was observable in the grand-averaged data when upright ape faces were presented as deviant stimuli among human faces (SNR 1.37, $Z > 3.11$, $p <$

.01; see Figure 2 and Table 1). It was spread over occipital channels, with a slight right-hemispheric advantage. When looking at single infants, a significant response was obtained in six out of 11 infants in that condition ($Zs > 3.11$, $ps < .001$). There also was a categorization response for upright human deviant faces (SNR 1.08, $Z > 2.33$, $p < .05$) and inverted ape deviants (SNR 1.20, $Z > 3.11$, $p < .01$). In analyses of individual responses, a categorization response was observed for inverted ape among human faces in six of 11 infants ($Zs > 2.33$, $ps < .01$), and for upright human among ape faces in seven of 11 infants ($Zs > 1.64$, $p < .05$). No categorization response was observed for inverted human deviant faces on grand-averaged data ($p > .05$), but one infant among 11 showed a categorization response for inverted human faces among ape faces ($Z > 1.64$, $p < .05$).

The Bayes rmANOVA revealed that the model with a main effect of orientation was preferred to the null model by a Bayes factor of 2.31. This provides marginal evidence [c.f. 53, Appendix B] for the hypothesis that categorization responses were stronger for upright images irrespective of species (upright $M = 3.08$ µV; $SD = 4.2$; inverted $M = .78$ µV; $SD = 3.3$). Moreover, the model with two main effects (species and orientation) was preferred to the null model by a Bayes factor of 3.07, providing moderate evidence that categorization responses differed between upright and inverted conditions and between human and ape deviants (ape face deviants $M = 3.15$ µV; $SD = 4.4$; human face deviants $M = .72$ µV; $SD = 3.0$). The difference between the model with a main effect of orientation and the one with main effects of species and orientation was only marginal (Bayes JZS = 0.75) but, unexpectedly, went in favor of the model with two main effects. The model with two main factors was also marginally preferred over a model with the main factor species (Bayes JZS = 2.27) and over a model with two main factors and an interaction term (Bayes JZS = 2.19).

**2.2.2 Base Response.** A strong response to the base visual stimulation was observed in all conditions (all SNRs > 2.1, all Zs > 10, see Table 2). It was centered on channel Oz and spread over O1 and O2. This response was significant in nine of 11 infants for upright ape faces ($Zs > 3.11$ $ps < .001$), in eight of 11 infants for inverted ape faces ($Zs > 3.11$, $ps < .001$), in all 11 infants for upright human faces ($Zs > 1.64$, $ps < .05$), and in nine of 11 infants for inverted human faces ($Zs > 2.33$, $ps < .01$).

The Bayes rmANOVA confirmed that there were no differences between conditions (JZS Bayes factors < 1 > .3).

| Response | deviant category | orientation | bca mean | bca SD | Z-score range | SNR range | N |
|---|---|---|---|---|---|---|---|
| categorization (1.21+ harmonics) | Ape | upright | 4.67 | 4.28 | .21 – 8.74 | 1.01 – 2.80 | 11 |
| | | inverted | 1.63 | 4.13 | -1.59 – 6.63 | .80 – 1.81 | 11 |
| | human | upright | 1.49 | 3.60 | -1.71 – 8.57 | .83 – 1.73 | 11 |
| | | inverted | -.06 | 2.02 | -1.76 – 2.01 | .80 – 1.35 | 11 |
| base (6.03 + harmonics) | Ape | upright | 2.79 | 2.22 | .21 – 36.45 | 1.05 – 8.91 | 11 |
| | | inverted | 2.46 | 2.67 | -.11 – 26.76 | .99 – 7.56 | 11 |
| | human | upright | 2.68 | 1.24 | 1.81 -17.64 | 1.31 – 5.00 | 11 |
| | | inverted | 3.11 | 1.77 | 1.08 – 21.95 | 1.18 – 6.04 | 11 |

Table 1. Baseline corrected amplitude (bca) means and standard deviations (SD), Z-score and signal-to-noise ratio (SNR) ranges for individual categorization and base rate responses in experiment 1. The categorization response was summed across harmonics 1-11 (excluding harmonics 5+10), the base response across harmonics 1-6.

**2.3 Discussion**

In study 1, we explored 9-month-old infants' rapid categorization of human and ape faces. As a group, infants showed a strong categorization response for upright ape faces presented among human faces, which was spread over the occipital cortex. Moreover, this response was observed in individual averages of six out of 11 infants. Categorization was also observed for upright human face deviants and inverted ape face

deviants. Categorization responses best fit a model with main factors of species and orientation, indicating that categorization of ape faces and upright images was stronger than of human faces and inverted images. Thus, this study reveals that 9-month-old infants' face species categorization relies on high-level visual perception and goes beyond mere perception of low-level image characteristics.

Moreover, this initial exploration of infant face categorization revealed an asymmetry, with stronger categorization responses for deviant ape faces. Before we can turn to discussing high-level explanations for this finding, however, low-level confounds should be ruled out. The asymmetry cannot be explained by a general difference of attention in human and ape standard trials. This was verified using two measures: (1) The response to the base stimulation frequency (6.03 Hz) did not differ between human and ape standard trials. (2) Video-coding confirmed that infants looked equally long at human ($M = 16.11$, $SD = 5$) and ape ($M = 15.49$ s, $SD = 3.7$) standard trials ($p > .6$). Therefore, we have no indication for differential attention to trials with different standard categories.

Likewise, categorization of ape from human faces cannot be attributed to low-level image characteristics, as inverting faces reduced categorization overall. Interestingly though, the categorization asymmetry was observed in inverted trials as well. Moreover, regarding individual infants' responses, six infants showed a categorization response for rarely presented inverted ape faces, whereas only one infant categorized rarely presented inverted human faces. This raises the question whether some low-level cues may have biased infants to categorize ape, but not human faces. Visual examination of our images indicated that the heterogeneity of ape faces was larger than that of human faces. Whereas human faces were taken from face databases, ape faces were collected from free images via google search, and were thus more likely

to vary. We extracted luminance and size values and statistical analyses confirmed that the standard deviations of both measures were larger for ape than human faces, while there was no difference in mean luminance and size. The larger variability of ape faces may have contributed to the asymmetrical categorization observed here: It might have been more difficult for infants to form a category of ape faces from which human faces could be distinguished. In comparison, detecting ape faces among the more homogeneous group of human faces might have been easier.

Therefore, we edited the images and matched the heterogeneity of face categories to examine categorization of those highly controlled stimuli in study 2. We based our hypotheses on study 1 and thus expected best model fit for a model with two main factors, orientation and species, reflecting stronger categorization responses for ape face deviants and upright conditions. These a priori hypotheses were evaluated using a rmANOVA. Thus, study 2 provides a test whether similar categorization patterns as in study 1 will be observed in an independent sample with highly controlled images.

## 2. Study 2

### 2.1 Material and Methods

**2.1.2 Participants.** Nineteen 9-month-old infants were tested (11 female, mean age = 9 months, 16 days, SD = 8 days) after obtaining verbal informed consent from their caretaker. Six additional infants were tested but excluded (three due to excessive crying, two due to insufficient data quality, and one due to rhythmic noise).

**2.2.2 Stimuli/Presentation.** The presentation was identical to study 1. From the stimuli presented in study 1, four images of ape faces were excluded because they were physically very different from the other ape faces, leaving 11 ape images. The number of human face images was matched by randomly excluding four images. Images were

edited so that luminance means and SDs as well as pixel size means and SDs were equalized between the two categories. Ten infants watched the presentation with human faces as standard, nine with ape faces as standard.

**2.2.3 Procedure**. Procedure was identical to study 1.

**2.2.4 EEG Recordings and Analyses.** EEG recordings and analyses were identical to study 1. On average, participants viewed 11 trials (Mean = 10.80, SD = 2.5), of which one trial (Mean = 1.32, SD = 1.2) was excluded due to a non-significant base rate frequency. There was no difference in the number of trials in the human standard ($M$ = 11.4; $SD$ = 2.8) and ape standard condition ($M$ = 10.1; $SD$ = 2.2; $p > .05$), but participants watched more upright ($M$ = 6.3; $SD$ = 1.6) than inverted trials ($M$ = 4.5; $SD$ = 1.3; $p < .001$). Similar to experiment 1, trials from the upright condition were randomly excluded to match the number of upright and inverted trials. The results pattern from this additional analysis conformed to the analyses on all trials, while giving a stronger effect of orientation.

Comparisons between conditions were performed in the same manner as in study 1. Baseline corrected amplitudes were summed up to the highest consecutively significant harmonic. For the categorization response, 1.21 Hz and harmonics were summed up to the 14th harmonic, but excluding the 5th and 10th harmonics which correspond to the base frequency.[1] For the base response, 6.033 Hz and harmonics were summed up to the 4th harmonic. Channels of interest were defined based on scalp topographies and conformed to the channels employed in study 1: P7, P8, PO9, PO10, O1, O2, Oz for the categorization response and O1, O2, Oz for the base response.

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[1] When analyzing an average of channels P7, P8, PO9, PO10, O1, O2, and Oz, harmonics 1 and 2 were not significant. In an additional analysis, these two harmonics were excluded and analyses were run using a sum of harmonics 3-14. The results pattern confirmed the one obtained with harmonics 1-14, while giving a stronger effect of orientation.

Preliminary analyses indicated that there was no main effect or interaction with electrode, so an average of all seven electrodes (categorization response) or three electrodes (base response) was calculated and used in the statistical analyses. The hypothesis that categorization responses would be strongest for upright ape deviants was tested using a Bayes rmANOVA and a standard rmANOVA with species (2: human deviant, ape deviant) * orientation (2: upright, inverted) as factors.

## 3.2 Results

### 3.2.1 Categorization Response
The categorization response (response at 1.21 Hz and harmonics) was observable in the grand-averaged data when upright ape faces were presented as deviant stimuli among human faces (SNR 1.59, $Z > 3.11$, $p < .01$; see Figure 3 and Table 2) spread over the occipital cortex. Moreover, a significant response was obtained in nine out of 10 infants ($Z$s $> 1.64$, $p$s $< .05$). There also were categorization responses in the other three conditions (upright deviant human faces SNR $= 1.26$, $Z > 3.11$, $p < .01$; inverted deviant ape faces SNR $= 1.21$, $Z > 3.11$, $p < .01$; inverted deviant human faces SNR $= 1.10$, $Z > 2.33$, $p < .05$). In analyses of individual responses, a categorization response was observed for upright human face deviants in seven of nine infants ($Z$s $> 2.33$, $p$s $< .01$), for inverted ape face deviants in five of 10 infants ($Z$s $> 1.64$, $p$s $< .05$), and for inverted human face deviants in one of nine infants ($Z > 1.64$, $p < .05$).

The Bayes rmANOVA revealed that the model with main effects of species and orientation was preferred to the null model by a Bayes factor of $> 100$. Compared to the model with a main effect of only orientation, it was preferred by a factor of 4.11, and compared to a model with only species by a factor of $> 100$. This provides conclusive evidence that the model of two main effects (species and orientation) fits the data better than the null model and the model with species only. Compared to the model

with only a main effect of orientation, the two main factors model was moderately

preferred. The model with two main factors was also conclusively preferred over a

model with the main factor species (Bayes JZS > 100), and marginally over a model

with two main factors and an interaction term (Bayes JZS = 2.42). Categorization

responses were stronger for upright images irrespective of species (upright $M = 4.67$

µV; $SD = 3.0$; inverted $M = 1.47$ µV; $SD = 2.8$) and for ape face deviants than human

face deviants irrespective of orientation (ape face deviants $M = 4.35$ µV; $SD = 3.4$;

human face deviants $M = 1.65$ µV; $SD = 2.6$).

**3.2.2 Base Response.** A strong response to the base stimulation was observed

in all conditions (all SNRs > 1.65, all Zs > 1.96, except for human faces inverted where

$Z = 1.54$, see Table 2). It was centered on channel Oz and spread over O1 and O2. This

response was significant in nine of 10 infants for upright ape faces ($Zs > 3.11$, $ps <$

.001), in nine of 10 infants for inverted ape faces ($Zs > 1.64$, $ps < .05$), in seven of nine

infants for upright human faces ($Zs > 1.64$, $ps < .05$), and in eight of nine infants for

inverted human faces ($Zs > 2.33$, $ps < .01$).

The Bayesian ANOVA confirmed that there were no differences between

conditions (JZS Bayes factors < 1 > .3).

| Response | deviant category | Orientation | bca mean | bca SD | Z-score range | SNR range | N |
|---|---|---|---|---|---|---|---|
| categorization (1.21+ harmonics) | ape | Upright | 5.97 | 3.19 | 1.39 – 26.84 | 1.18 – 3.13 | 10 |
| | | Inverted | 2.73 | 2.94 | -1.04 – 18.84 | .91 – 2.23 | 10 |
| | human | Upright | 3.23 | 2.24 | .05 – 4.75 | 1.00 – 1.52 | 9 |
| | | Inverted | .07 | 1.83 | -1.22 - 1.66 | .87 – 1.26 | 9 |
| base (6.03 + harmonics) | ape | Upright | 4.40 | 3.05 | 1.21 – 25.06 | 1.27 – 7.63 | 10 |
| | | Inverted | 3.86 | 3.55 | 1.32 – 22.01 | 1.29 – 8.03 | 10 |
| | human | Upright | 2.18 | 1.79 | -.99 – 20.67 | .87 – 4.72 | 9 |
| | | Inverted | 1.54 | 1.31 | .24 – 4.88 | 1.05 – 2.22 | 9 |

Table 2. Baseline corrected amplitude (bca) means and standard deviations (SD), Z-

score and signal-to-noise ratio (SNR) ranges for individual categorization and base rate

responses in experiment 2. The categorization response was summed across harmonics 1-14 (excluding harmonics 5+10), the base response across harmonics 1-4.

**3.3 Discussion**

We tested 9-month-olds' categorization of human and ape faces using an FPVS paradigm and observed categorization responses that were similar to study 1. Ape faces presented among human faces elicited a strong categorization response over occipital areas, and human faces elicited a smaller categorization response. Categorization of inverted images was much reduced, providing strong evidence that face species categorization in 9-month-old infants is not based on low-level cues.

Similar to study 1, we observed a categorization asymmetry where infants showed a stronger categorization response for rarely presented ape than human faces. Categorization in this study cannot be explained by low-level factors. The categorization response for inverted images was reduced, irrespective of face species. Moreover, the variance of luminance and size was matched in the two conditions, ruling out the possibility that increased variance of ape faces interfered with categorization of human faces, as might have been the case in study 1. The categorization asymmetry observed here cannot be explained by a general difference in attention for human and ape deviants, either, as there was no difference in the base rate response for respective trials. Alternative accounts for asymmetrical categorization will be considered in the General Discussion.

**4. General Discussion**

Together, the two studies presented here provide evidence that 9-month-old infants can categorize upright faces according to species at a high speed, that is, in less than 170 ms, allowing only one fixation on each image. In study 1, we ran an initial investigation

of human and ape face categorization and observed an occipital categorization response for upright face images. Categorization was stronger for ape than human deviant faces. As the ape face image set had larger variability of luminance and size, it might have been more difficult to detect deviant human faces among the ape faces than vice versa. Therefore, we matched low-level stimulus characteristics and ran study 2. The data from this independent sample confirmed that infants' rapidly categorized upright faces according to species. Again, deviant ape faces elicited stronger categorization responses than deviant human faces.

We took great care to evaluate the contribution of low-level image characteristics to categorization. Infants looked equally long at trials with ape and human deviants (and at upright and inverted trials), so we have no indication that attention was increased in any condition. Moreover, the base rate response, a direct measure of neural activation in response to general visual stimulation, did not differ between conditions. Most importantly, we ran inverted versions of trials in which low-level characteristics are exactly the same as in upright trials. Whereas infants also categorized inverted faces (only ape deviants in study 1, ape and human deviants in study 2), this response was smaller than for upright faces. However, the categorization asymmetry was observed in upright and inverted conditions, so despite all controls, we cannot fully rule out the possibility that low-level factors inherently associated with the two face species increased categorization of ape faces.

At 9 months of age, infants have acquired extensive experience with processing human faces, which leads them to individuate human, but not ape faces [20, 22; see 53, for a corresponding finding on same- and other-race faces]. Their experience with human faces may have allowed infants to categorize faces at a high speed in the current study, and may have enhanced categorization responses to the unfamiliar

category of ape faces. Extensive experience with human faces may speed up the process of activating a formerly developed categorical representation, whereas exemplars that do not match this well defined representation (i.e., ape faces) elicit strong novelty responses. Such a novelty response would not be reflected in looking time or the base rate response, as those measures reflect processing during complete trials and cannot be compared for single stimuli. To further explore whether familiarity with one of the face categories is sufficient to elicit skewed categorization, it would be helpful to compare categorization of two unfamiliar face categories, for instance other-race faces and ape faces at the end of the first year of life.

Moreover, infants' experience in recognizing human faces may have led them to individuate human faces, while sorting ape faces into a category, inducing the observed categorization asymmetry. However, in a study presenting human faces as deviants and different objects and animals as standards, 4-6-month-old infants showed a categorization response [2], demonstrating that infants generalized across human face exemplars. Compared to the current study, this study tested younger infants and presented highly diverse images as standard category. Thus, the context of many different kinds of categories together with infants' young age may have elicited categorization rather than individuation of faces.

Asymmetrical categorization of human stimuli has been reported before in behavioral tasks [55, 56]. In these studies, 3-4-month-old infants formed a category of humans (represented with head and body information) that included other animals, but formed a category of horses that excluded humans and other animals. This effect was restricted to conditions where head and body information was present, and not observed when only the head was presented [56]. Moreover, no asymmetry was observed in an ERP paradigm on human-animal categorization [57]. Thus, though asymmetrical

categorization of humans has been observed previously, these studies employed very different methods than the current study. However, similar to the current study, it was proposed that infants formed individual representations of human stimuli, whereas they formed categorical representations of other animal stimuli [55, 58]. Future work should use a similar approach to test whether younger infants who have not yet developed a specialized face processing system for human faces [i.e., 6-month-olds, 22] show similar categorization of human and ape faces.

Categorization in the current study occurred rapidly, that is, after seeing each image for only about 130 ms, with a stimulus onset asynchrony (SOA) of 170 ms. As a novel image faded in right after the previous one had faded out, stimulus processing was interrupted after 170 ms. Face species categorization was thus based on only gaze fixation by stimulus. Previous studies on human and ape face processing have employed presentation times of at least 500 ms [15], and image presentation was followed by an ISI so that processing could continue. Overall, behavioural and ERP studies on categorization require much longer presentation times [about 15 seconds in behavioral tasks; 41, 55, and between 500 and 1,500 ms in ERP tasks, 17, 58, 60]. Thus, the categorization response observed in the current study demonstrates that high-level representations can be activated much faster than previously suspected in the infant's brain, that is, within about 170 ms.

To sum up, the current study demonstrated rapid categorization of faces according to species in 9-month-old infants in two independent samples. Categorization was stronger for upright than inverted images, revealing that infant categorization is not based on low-level image characteristics but reflects high-level perception. While infants showed a strong categorization response for deviant ape faces, a smaller response was observed for deviant human faces. It seems likely that the greater novelty

of ape faces made it easier for infants to detect them among the more familiar human faces. Moreover, generalization across deviant human face images may have been impaired because 9-month-olds are inclined to individuate human faces. Thus, extensive experience with human faces enables infants to categorize even unfamiliar face categories at a single glance.

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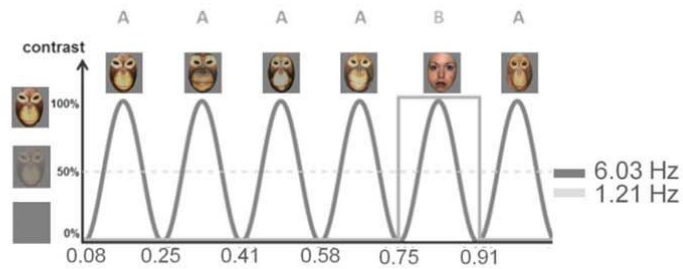## Acknowledgments

## Author contributions

St. P., S. H., S. P. & B. R. designed the studies. St. P. tested subjects. St. P. & B. R. analyzed the data. St. P., S. H., S. P. & B. R. wrote the manuscript.
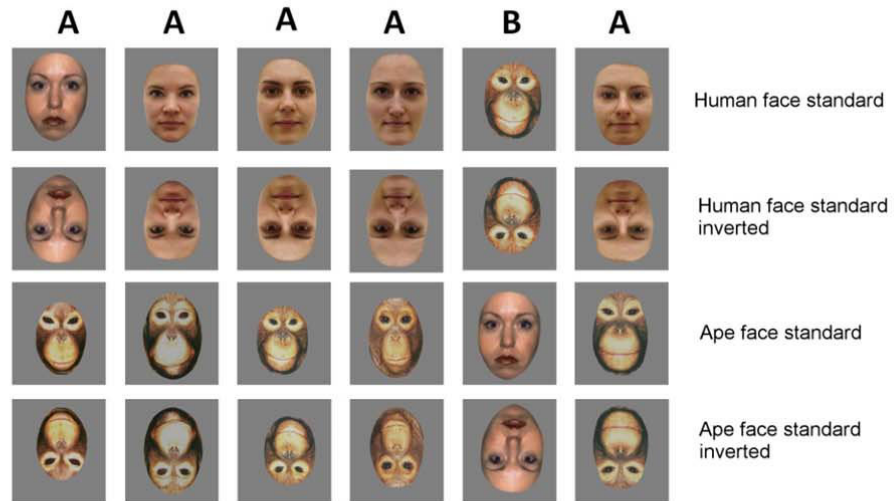
## Additional Information

We declare that we have no competing financial interests.
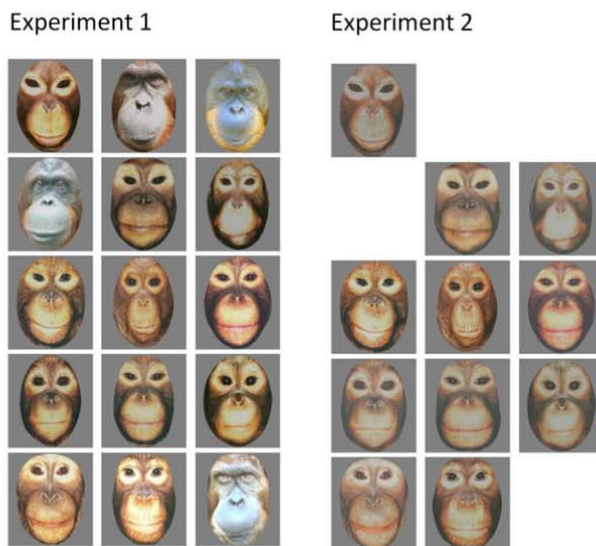
**Figures/Figure Captions**



Figure 1. Schematic illustration of the experimental paradigm, conditions and stimuli. 1.1 Experimental paradigm. Images were presented by sinusoidal contrast modulation at a rate of 6.03 cycles per second = 6.03 Hz (1 cycle ≈ 170 ms). Ape or

human faces stimuli were presented at every $5^{th}$ cycle (B) in subsequent trials (6.03/5 Hz = 1.21 Hz). The respective other category was presented as standard stimulus. Human faces images were not for publication and were thus replaced for this figure (except for the first face, taken from MacBrain Face Stimulus Set). 1.2 Conditions. The standard category (ape face, human face) was changed between-subjects. Note also that the stimuli changed size (range +/- 10%) at every stimulation cycle. The orientation of images (upright, inverted) was manipulated within-subjects. 1.3 Stimuli. Whole sets of ape face images used in the two experiments.

Figure 2. Results of experiment 1. SNR of categorization response (1.21 Hz, 2.41 Hz, 3.62 Hz, 4.83 Hz) and of base response (6.03 Hz) and summed baseline corrected amplitude of categorization response (harmonics 1-11, excluding base response at $5^{th}$ and $10^{th}$ harmonic). Data has been averaged across electrodes (P7, P8, PO9, PO10, O1, O2, Oz) and grand-averaged across participants. There was no difference between conditions in the base response. The categorization response was observed for rarely presented upright ape faces, inverted ape faces, and upright human faces, but was strongest for upright ape deviants. * $p < .05$, ** $p < .01$, *** $p < .001$.
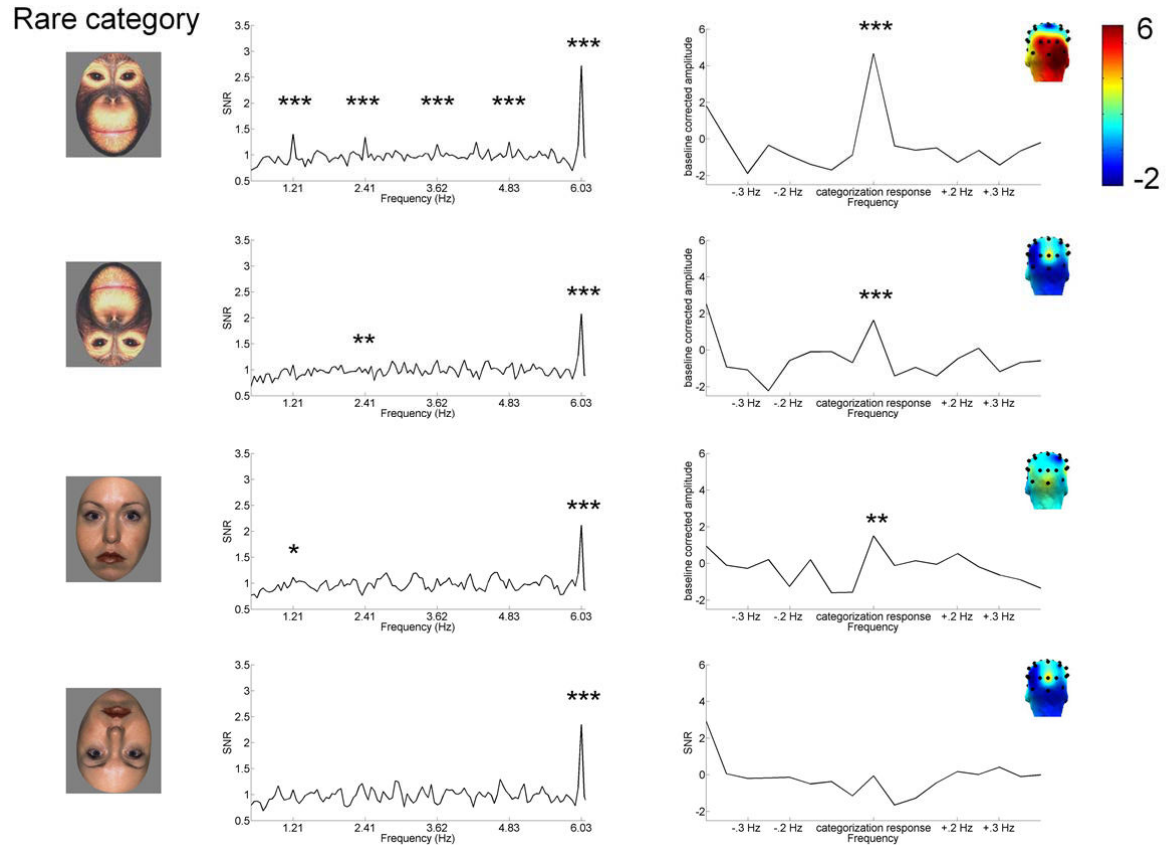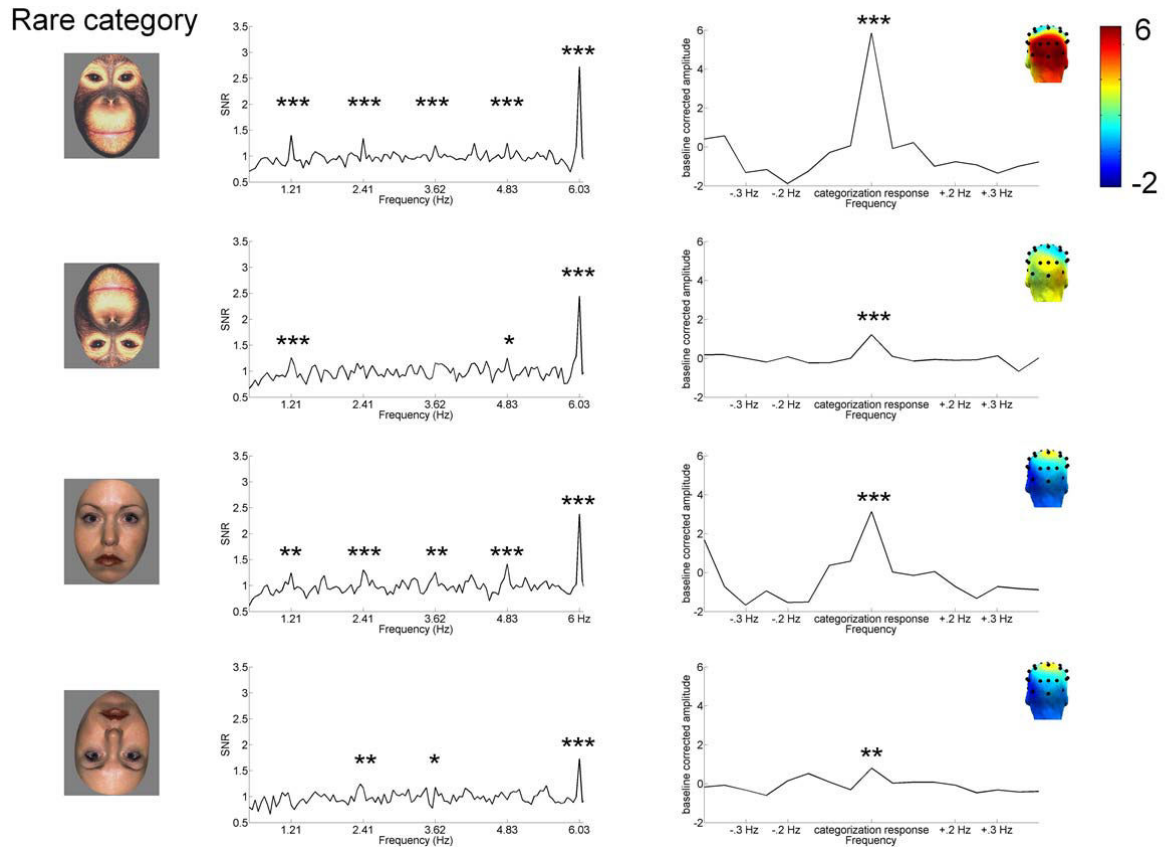
Figure 3. Results of experiment 2. SNR of categorization response (1.21 Hz, 2.41 Hz, 3.62 Hz, 4.83 Hz) and of base response (6.03 Hz) and summed baseline corrected amplitude of categorization response (harmonics 1-14, excluding base response at $5^{th}$ and $10^{th}$ harmonic). Data has been averaged across electrodes (P7, P8, PO9, PO10, O1, O2, Oz) and grand-averaged across participants. There was no difference between conditions in the base response. The categorization response was observed in all conditions, but was strongest for upright ape deviants. * $p < .05$, ** $p < .01$, *** $p < .001$.

# How do 9-month-old infants categorize human and ape faces? A rapid repetition ERP study

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## Abstract

The current study investigates how infants categorize human compared to ape faces. Nine-month-old infants were presented with priming stimuli related to human ($N = 24$) or ape ($N = 25$) face targets on different levels of categorization. Event-related potentials were recorded during a passive-looking rapid repetition paradigm. In a within-subjects design, priming effects of the same faces, different faces from the same basic-level category, different faces from the other basic-level category (human/ape faces), and house fronts were examined. Human and ape faces were first categorized on a superordinate level ("faces"), as indicated by enhanced P1 amplitude and reduced P1 latency for faces primed by any faces. Then, human and ape faces were categorized on a basic level. N290 amplitude and latency were larger for human and monkey targets primed by human faces. Neither human nor ape faces were categorized on the individual level.

Descriptors: Face processing, Categorization, Development, Infants, Event-related potentials

Infants are exposed to an immeasurable amount of diverse visual stimuli that compete for their limited processing capacities. Perceptual biases help them to focus attention on important stimuli by sorting them into categories. For example, a top-heavy bias guides infants' attention toward human faces (Macchi Cassia, Turati, & Simion, 2004), but also toward faces of other species (Di Giorgio, Leo, Pascalis, & Simion, 2011). However, it is highly important for infants to individuate human faces, whereas it may be less important for them to individuate exemplars of other-species faces. Although infants may perceive faces of different species as "faces," they may categorize human faces in a special way. To explore potential differences and similarities in infants' processing of human and other-species faces, the current study examined how 9-month-olds categorize human and ape faces in an event-related potential (ERP) rapid repetition paradigm.

Any given stimulus can be categorized on the superordinate level (e.g., animal, vehicle), the basic level (e.g., ape, cat), the subordinate level (e.g., chimpanzee, gorilla), or the individual level (e.g., the chimps "Bob" and "Ted" in the local zoo). Objects are preferentially categorized on the basic level by adults as well as by older children (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). For human faces, the individual level can be accessed as well as the basic level (Tanaka, 2001). In the following paragraphs, we review different ERP components that are associated with face processing of adults.

## Neural Correlates of Face Perception in Adults

**N170.** The N170 is an occipitotemporal ERP component that is consistently elicited by human faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996). It is usually found to peak earlier and with larger amplitude for faces than for other stimuli (Carmel & Bentin, 2002; Itier & Taylor, 2004b). The N170 is often linked to "structural face processing" (Eimer, 2000b; Rossion & Jacques, 2011), which may refer to holistic processing (perceiving the "gestalt" of the stimulus), elicited by human faces in particular (Maurer, Grand, & Mondloch, 2002). Structural face processing may also refer to processing of first-order relations (i.e., eyes over a nose over a mouth). The N170 is enhanced by stimulus inversion (Bentin et al., 1996; Rossion et al., 2000); thus, sensitivity to first-order relations may be part of structural face processing as reflected by the N170. Also, structural face processing may refer to processing of second-order relations, that is, the individual spacing among features. The N170 is sensitive to alterations in the spacing of features (Scott & Nelson, 2006). In addition, the N170 can be influenced by many other face characteristics, such as age or skin color (Balas & Nelson, 2010; Peykarjou, Westerlund, Macchi Cassia, Kuefner, & Nelson, 2013), and the role of the eyes for the N170 response to faces is still under debate (Eimer, 1998; Eimer, Gosling, Nicholas, & Kiss, 2010; Itier, Latinus, & Taylor, 2006). Thus, the term structural face processing may refer to a wide variety of phenomena.

Furthermore, the N170 is linked with categorization processes (see also Rossion & Jacques, 2011). As multiple studies show, the N170 also discriminates between nonface basic-level categories such as cars, shoes, or birds (Carmel & Bentin, 2002; Rossion et al., 2000). In addition, the N170 is modulated by perceived category membership. A recent study compared processing of Archimboldo paintings, which display faces composed of fruits

and vegetables, with realistic faces. N170 amplitude for upright Archimboldo paintings was similar to the N170 for upright faces (Caharel et al., 2013). The N170 amplitude for inverted Archimboldo paintings was similar to the N170 for inverted objects, and much smaller than for inverted faces. In priming or habituation paradigms, N170 amplitude is reduced in response to faces that were preceded by faces compared to faces preceded by nonface stimuli (Eimer, Gosling et al., 2010; Eimer, Kiss, & Nicholas, 2010; Itier & Taylor, 2002; Kovacs et al., 2006). In some studies, the N170 is also reduced for repeated individual faces (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Itier & Taylor, 2002), but this effect is not observed consistently (Schweinberger, Huddy, & Burton, 2004; Schweinberger, Pfütze, & Sommer, 1995). Thus, the N170 seems to reflect categorization on the basic rather than on the individual level.

**N250.** Following the N170, the N250 can be observed. This negative deflection over occipitotemporal cortices seems to be associated with recognition of individual faces. It is consistently elicited for familiar faces (Schweinberger et al., 1995, 2004; Tanaka, Curran, Porterfield, & Collins, 2006). N250 amplitude is increased in response to one's own face and for personally familiar cars and dogs compared to novel stimuli, suggesting that it reflects processing of individuated stimuli regardless of category (Pierce et al., 2011). In repetition paradigms, the N250r can be observed if the same face is presented repeatedly (Begleiter, Porjesz, & Wang, 1995; Pfütze, Sommer, & Schweinberger, 2002; Schweinberger et al., 1995; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). Whereas the N250r is consistently elicited for faces, a diminished N250r has been observed for repeated familiar words (Pfütze et al., 2002) and ape faces (Schweinberger et al., 2004).

**P1.** The P1 is an occipital ERP component peaking around 100 ms. It is susceptible to low-level stimulus characteristics (Dering, Martin, Moro, Pegna, & Thierry, 2011; Rossion & Caharel, 2011; Rossion & Jacques, 2008), but it is also sensitive to the presence of faces in some studies (Eimer, 1998, 2000a). These early differences between faces and nonfaces may reflect categorization based on low-level statistical cues (Rossion & Jacques, 2011). Specifically, parameters such as color and energy distribution, shape, local contrast, and luminance may contribute to the fast discrimination of face and nonface stimuli. However, P1 also differentiates well-controlled scrambled from intact faces (Herrmann, Ehlis, Ellgring, & Fallgatter, 2005). A recent independent component analysis study demonstrated that P1 face effects are driven by single subjects, whereas N170 face effects are consistent across participants (Desjardins & Segalowitz, 2013). Thus, at least some participants may discriminate faces from other categories as early as ~100 ms after stimulus onset.

To sum up, adults are equally well able to categorize human faces on the individual as on the basic level, whereas they preferentially categorize objects on the basic level. The N170 can be considered as a neural correlate for basic-level categorization and shows larger amplitude and shorter latency for human faces. The N250/N250r can be interpreted as neural correlates for individual-level categorization and are elicited for familiar or repeated faces.

### Developmental Changes in Object Categorization and Face Classification

Within the first year of life, infants develop their abilities to categorize visual stimuli on the basic and on the superordinate level.

Regarding neural correlates of superordinate-level categorization, 7-month-old infants distinguished between human and animal stimuli in a categorical oddball paradigm (Marinovic, 2011; Marinovic & Pauen, 2010). They showed an enhanced negative central (Nc) response for the infrequent category regardless of species, indicating increased attention allocation to oddball stimuli (Reynolds & Richards, 2005; Richards, 2003). In a study contrasting animals and furniture items, 7- to 8-month-old infants showed a decreased positive slow wave (PSW) in response to items preceded by stimuli from the same superordinate-level category compared with items preceded by stimuli from the other superordinate-level category (Jeschonek, Marinovic, Hoehl, Elsner, & Pauen, 2010). The PSW reflects stimulus encoding or memory updating (de Haan & Nelson, 1997, 1999; Webb, Long, & Nelson, 2005), which seems to be facilitated for items preceded by exemplars from the same superordinate category. Regarding neural correlates of basic-level categorization, 6-month-old infants who were familiarized with one basic-level category (e.g., birds or fish) allocated more attention, as indexed by the Nc, to exemplars of a different category (Grossmann, Gliga, Johnson, & Maeschal, 2009).

Concerning the categorization of human faces in infancy, two potentially face-sensitive ERP components have been identified. The N290 and P400 are observed in response to static faces over occipitotemporal cortices and may reflect basic-level categorization like the N170 in adults (de Haan, Johnson, & Halit, 2003; Hoehl & Peykarjou, 2012). Compared to the N170, both components have a longer latency and are more medially distributed (de Haan et al., 2003). N290 amplitude is larger for human than ape faces (de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003). Inverted human faces elicit increased N290 amplitude when compared with upright human or inverted monkey faces in 12-month-old infants (Halit et al., 2003) and compared with upright human faces in 3-month-old infants (Peykarjou & Hoehl, 2013). Moreover, P400 latency is shorter for human faces than toys in 6-month-old infants (de Haan & Nelson, 1999). Four-month-old infants showed categorical repetition effects for eye stimuli primed by face-related images (i.e., bodies, profile faces) in contrast to stimuli primed by inanimate images (i.e., houses or cars) at the level of the N290 and the P400 (Gliga & Dehaene-Lambertz, 2007). The P1 has also been sensitive to the presence of faces in several infant studies (Itier & Taylor, 2004a; Macchi Cassia et al., 2006; Melinder, Gredebäck, Westerlund, & Nelson, 2010).

Infants' ability to represent individual exemplars seems to depend on the global-level category examined. For the inanimate domain, 4-month-old infants' attention to individual objects can be increased through social cues (Kopp & Lindenberger, 2012; Reid, Striano, Kaufman, & Johnson, 2004; Wahl, Michel, Pauen, & Hoehl, 2012). Moreover, 3-month-old infants notice if an object previously cued by a fearful face is exchanged for another exemplar (Hoehl, Wiese, & Striano, 2008). They showed enhanced attention only if the same object was presented again, not if a different object was presented. Therefore, in ERP paradigms, infants individuate objects from 3–4 months of age.

Stimulus individuation has been observed even earlier within the animate domain. Newborns preferentially look at faces, both the mother's and an unfamiliar female's, if the face previously talked to them (Coulon, Guellai, & Streri, 2011; Sai, 2005). One- and 3-month-old infants can recognize one of four static faces with which they have previously been familiarized (de Haan, Johnson, Maurer, & Perrett, 2001). However, the scope of familiarization or preference paradigms is limited. Recognition of single exemplars from a category represented through very few exemplars, following

a familiarization phase, does not necessarily indicate that infants will also individuate exemplars if the category is represented more broadly, and no familiarization procedure is involved.

To date, no specific ERP component for the repetition of individual exemplars like the N250r (Schweinberger et al., 2004) in adults has been reported in the infant literature, but the N290 and P400 have been associated with individual-level processing during the first year of life. Familiarization with a 3D face model influences 3-month-olds' P400 to the familiar compared with a novel face (Moulson, Shannon, & Nelson, 2011). The P400 also discriminates the mother's and a stranger's face in 6-month-old infants (de Haan & Nelson, 1997). At 9 months, habituation with a two-dimensional face stimulus induces larger N290 amplitude to the familiar compared with a novel face (Moulson et al., 2011). Individual-level rapid repetition effects have been observed at the level of the Nc and PSW for images of toys, pets, and people in 4-month-old infants (Snyder, Garza, Zolot, & Kresse, 2010). In a study examining identity priming for human faces with a lag of 6–12 items, the Nc was reduced for repeated stimuli in 6-month-old infants (Webb & Nelson, 2001). Thus, individual-level repetition effects have been observed on ERP components indexing attention and memory updating so far.

Experience seems to play an important role in the development of individual-level categorization. Using a preference-for-novelty-design, Pascalis, de Haan, and Nelson (2002) showed that 6- and 9-month-old infants as well as adults were able to discriminate human faces. However, only 6-month-old infants, not 9-month-olds or adults, were able to discriminate ape faces. This process of "perceptual narrowing" similarly takes place for processing of sheep faces (Simpson, Varga, Frick, & Fragaszy, 2011) and other-race faces (Kelly et al., 2007). Individuation training with ape (Scott & Monesson, 2009) or other-race faces (Herone-Delaney et al., 2011) between 6 and 9 months of age prevented perceptual narrowing, but categorization training did not. This suggests that experience with individuating exemplars is crucial for maintaining the ability to categorize on the individual level.

To sum up, building on behavioral findings, ERP studies have provided evidence for infants' abilities to categorize visual stimuli on the superordinate, basic, and the individual level. The N290 and the P400 are potential precursors of the N170 as neural correlates of basic-level categorization. A specific ERP component as neural correlate for individual-level categorization has not been identified so far. Developmental studies suggest that experience shapes infants' sensitivity to perceptual differences among various kinds of faces.

### Aims and Hypotheses of the Current Study

The current study sought to determine how 9-month-old infants categorize faces when they are presented with a large variety of individual exemplars related to the target images on different levels of abstraction. This age group was chosen because at 9 months, following a phase of perceptual narrowing, individuation has been observed for human faces but not for ape faces in behavioral paradigms (Pascalis et al., 2002). Therefore, testing 9-month-olds provides the potential to reveal distinct categorization processes for human and ape faces.

Priming effects of the same or related images on target stimuli were examined in an ERP rapid repetition paradigm. According to a model put forward by Henson (2003), repetition enhancement is elicited when additional processes are recruited for the target relative to the prime, and repetition suppression is elicited when fewer

processes are evoked for the target. Repetition suppression (Naccache & Dehaene, 2001) may thus be observed when an existing memory trace is reactivated, whereas repetition enhancement (Eimer, Kiss, & Nicholas, 2010; Nemrodov & Itier, 2011, 2012) may be observed when a memory trace is built up.

Superordinate- as well as basic-level categorization for human, animate, and inanimate stimuli can be observed in infants less than 8 months of age (Grossmann et al., 2009; Jeschonek et al., 2010; Pauen, 2002a; Quinn, 2004; Quinn, Doran, Reiss, & Hoffman, 2010). Thus, we expect 9-month-olds to activate preexisting superordinate- and basic-level categories. Repetition suppression is predicted for categorical priming, that is, for targets primed by faces compared to nonfaces (superordinate-level categorization) and for targets primed by the same relative to the other basic-level category (basic-level categorization). Categorization on different levels may occur on different ERP components, which would inform us about categorization timing in the infant brain.

Concerning priming of individual faces, infants are expected to represent unfamiliar human faces individually (Kelly et al., 2007; Pascalis et al., 2002). They will likely build up a representation for the individual face during prime presentation, but given the short stimulus presentation (1,000 ms), this representation may not be comprehensive. If a comprehensive representation is developed, repetition suppression for identical faces will be observed; if the representation is further developed during target presentation, repetition enhancement is predicted. If, however, infants do not represent unfamiliar faces individually, the activation of the categorical representation (human face) by both prime and target may also be reflected by repetition suppression. In the latter case, repetition suppression at the individual level is expected to mimic the effect of basic-level repetition. In contrast, in the case of individual-level representation of faces, repetition suppression will likely occur on a different level of processing, thus affecting another ERP component. Based on prior behavioral research, 9-month-old infants are not expected to represent ape faces individually (Pascalis et al., 2002), so repetition suppression is expected for ape targets primed by the same relative to another ape face reflecting basic-level priming.

Importantly, the categorical ERP repetition paradigm allows us to investigate the fine-grained time course of categorization processes. Thus, it is possible to determine whether categorization effects on different levels of abstraction can be observed in any specific time sequence.

### Materials and Method

#### Participants

The final sample consisted of 49 infants with an average age of 9 months and 12 days (age range 8 months, 30 days–9 months, 29 days, $SD = 15$ days). Twenty-eight participants were male, 21 female. All infants were born full term (> 37 weeks of gestation) without a known record of neurological problems. Participants mainly belonged to a Caucasian middle class. An additional 43 infants were tested but not included in the final analyses due to fussiness (21 participants), failure to reach the minimum number of trials required for adequate ERP averaging (21 participants), or experimenter error (1 participant). This exclusion rate is well within the typical range in visual infant ERP research (Stets, Stahl, & Reid, 2012). To be included in the sample, a minimum of 10 trials per condition had to be contributed.

**Figure 1.** Examples of stimuli. 1: House fronts. 2: Human faces. 3: Ape faces.

**Stimuli/Presentation**

One group of infants saw a presentation with human face targets, another group watched a presentation with ape faces targets. Ape faces were chosen for comparison to human faces because they belong to a different basic-level category, but resemble human faces in terms of both first-order (organization of facial features) and second-order (spacing of facial features) relations (Maurer et al., 2002). Priming effects were examined on the individual level of categorization (same, other), on the basic level (same basic, other basic, i.e., same species faces vs. other species faces), as well as on the superordinate level (same superordinate, other superordinate, i.e., faces vs. nonfaces). Thus, we employed a mixed design with target category (human, ape) manipulated between subjects and priming conditions (same, other, other basic, other superordinate) manipulated within subjects.

Stimuli were 80 pictures of each face category (humans, apes) and 120 pictures of house fronts (all colorful). The human face category consisted of 40 male and 40 female faces with a neutral facial expression. To enhance variability within the human face category, 20 (10 male, 10 female) faces belonged to a non-Caucasian race (i.e., Asian, African). The human face stimuli were taken from standard face databases (i.e., MacBrain Face Stimulus Set[1]; Radboud Face Database, Langner et al., 2010). A minor proportion (i.e. = 10) of all pictures were taken in our lab to increase

perceptual variability. All pictures were taken in full front view with a neutral expression and in high quality.

The ape face category was broad and consisted of four subordinate-level categories: chimpanzees, gorillas, orangutans, and smaller mixed monkeys. For each subcategory, 20 pictures were included. Ape and house pictures were taken from the Internet and supplemented with photos taken by the authors. All pictures of all categories were cropped to a face-shaped oval of the same size, extending $15.5 \times 22.5$ cm on the screen (see Figure 1 for exemplary stimuli of all three categories).

The presentation consisted of 120 trials, with each trial comprising stimulus triplets: one nonface stimulus (i.e., a house), followed by two subsequently presented face stimuli. Each stimulus within a given triplet was presented for 1,000 ms, with a blank screen of 600–800 ms between stimuli. The interstimulus interval between triplet trials was 800–1,200 ms.

Given that the first stimulus in each trial was always a house front, the face presented next served as target for other superordinate. This face also served as prime for the subsequently presented third stimulus (i.e., the second face). In the human condition, one of 40 different human faces was presented as third stimulus in a given trial. Similarly, in the ape group, 40 ape faces were presented as third stimulus (see Figure 2 for an exemplary trial sequence).

There were three different priming conditions with respect to the third stimulus (second face) of the triplet: primed by the same face (same), primed by another face belonging to the same subordinate-level category (other; together same and other formed same basic), and primed by a face from the other basic-level category (other basic; together same, other, and other basic formed same superordinate). Thus, the 40 target faces were presented three

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1. Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development (Tottenham et al., 2009).
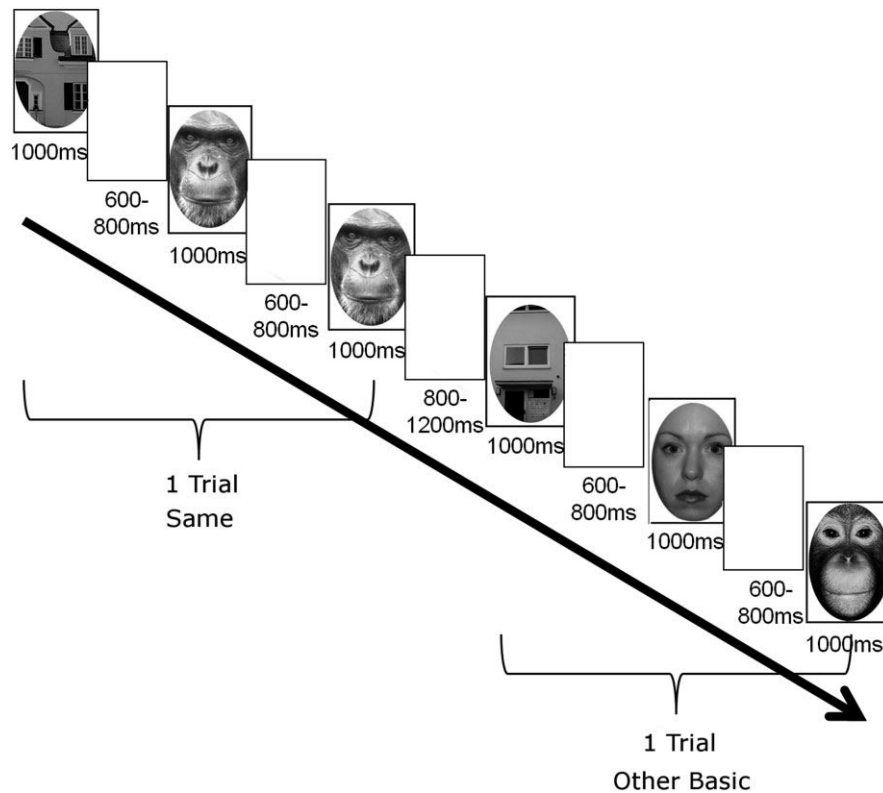
**Figure 2.** Examples of trials for the ape group. Each trial consisted of a stimulus triplet including one house front and two faces. The first face was used as target in the other superordinate condition and as prime for the second face. The second face was analyzed as target.

times as targets and once as prime. All other pictures were presented only once. Within each triplet, stimuli were matched for mean luminance.

Trials were presented in blocks of 40 triplet trials so that each target face appeared once per block in one of the three priming conditions. The reason for structuring each trial as a triplet containing house front, prime, and target face was mainly to provide a de-prime at the beginning of each trial as the presentation of multiple faces in succession potentially might have multiplied priming effects. Priming conditions were presented in semirandomized order with the restriction that no condition was directly repeated and that each priming condition appeared with equal probability within each presentation block.

### Procedure

The infants were placed on their parents' lap in front of a 17″ TFT (thin film transistor) presentation screen at a distance of approximately 45 cm. The screen and the chair in front of it were both surrounded by a dark blue folding screen to minimize distraction by the lab furnishings. Parents were asked not to interact with their infant during data collection. The stimuli were presented while the infants' looking behavior was monitored on video. When the infants started to fuss, they were offered a short break in which a black-and-white rotating spiral accompanied by a short attention-grabbing sound appeared on the screen. Sessions were terminated when infants' attention could no longer be directed to the presentation.

### ERP Recording and Analyses

Electroencephalogram (EEG) measures were obtained applying a Brain Products actiCAP (Gilching, Germany) with 32 active Ag-AgCl electrodes arranged according to the 10-10 system and a right mastoid reference. Sampling rate was set at 250 Hz, and the EEG signal was amplified via a BrainAmp amplifier. Impedances were considered acceptable if < 20 kΩ. Offline, filters were applied at 0.3–30.0 Hz. To maximize the distinctness of the visual ERP components, data were rereferenced to an average reference, excluding horizontal and vertical ocular channels. Prior to averaging, up to 4 channels with data loss (if they were not channels of interest, see below) were interpolated by computing the mean of four surrounding channels. EEG was time-locked to target onset and segmented into epochs from 200 ms before stimulus onset to 1,500 ms past stimulus onset. A baseline correction was applied using the average voltage of the 200 ms prior to stimulus onset.

Components were analyzed using BrainVision Analyzer over occipital cortices at three electrode sites: O1, O2, Oz. These electrode sites correspond to electrode clusters in which the components of interest have been recorded in previous studies (Parise, Handl, & Striano, 2010; Scott & Monesson, 2010). Compared to the N170, which is most prominent at P8/ PO8 in adults, infant face-specific responses are more medially distributed (Hoehl & Peykarjou, 2012).

Infants' looking behavior was inspected offline to exclude trials in which the infant's eyes were not directed to the screen. In addition, artifacts caused by eye and body movements were rejected offline using automatic artifact detection methods of ERPLAB (electrical artifacts: voltage change > 200 μV within 100 ms, blink detection: normalized cross-covariance threshold of electrooculogram data 0.7 within a 400-ms time period). The first criterion was applied only on channels of interest (O1, O2, Oz).

Individual averages for each of the four conditions (same, other, other basic, other superordinate) were computed. In the human

**Table 1.1.**  *Human Group: Means and Standard Deviations (SD) of the P1 Grand Average Response*

| Condition | P1 amplitude Mean | P1 amplitude SD | P1 latency Mean | P1 latency SD |
|---|---|---|---|---|
| Same | 15.61 | 11.2 | 162.72 | 28.8 |
| Other | 17.06 | 12.4 | 169.83 | 30.6 |
| Same basic | 16.33 | 10.8 | 166.28 | 23.6 |
| Other basic | 18.90 | 12.9 | 173.83 | 24.5 |
| Same superordinate | 16.33 | 10.8 | 168.80 | 20.9 |
| Other superordinate | 12.52 | 8.0 | 176.44 | 21.2 |

condition, on average 79.4 trials were included (same $M = 16.3$, $SD = 5.5$; other $M = 16.3$, $SD = 5.6$; other basic $M = 16.9$, $SD = 5.4$; other superordinate $M = 30.0$, $SD = 9.2$). In the ape condition, on average 83.6 trials were included (same $M = 16.8$, $SD = 4.2$; other $M = 16.6$, $SD = 3.5$; other basic $M = 18.8$, $SD = 4.4$; other superordinate $M = 31.4$, $SD = 8.8$). For further analyses, a category same basic was averaged combining trials from same and other. Similarly, a category same superordinate was averaged using same, other, and other basic. $F$ tests provided evidence that there were no differences in variance for the measured ERP components between categorical contrasts, all $ps > .05$, so trial numbers were not artificially reduced to the level of the other conditions.

Time windows for the components of interest were selected based on previous reports and visual inspection: P1, 100–200 ms; N290, 200–350 ms; P400, 350–550 ms (Balas et al., 2010; Scott, Shannon, & Nelson, 2006). Mean amplitude and latency to peak were extracted. Visual inspection of waveforms revealed that potential amplitude differences at the level of the N290 may be driven by differences at the preceding P1 component, and, similarly, differences at the level of the P400 may be driven by differences at the preceding N290. In order to control for these differences, difference scores using mean amplitude of the preceding component were computed (Kuefner, de Heering, Jacques, Palmero-Soler, & Rossion, 2010; see also Peykarjou et al., 2013). Analyses were conducted using both uncorrected and adjusted values. In the Results section, adjusted analyses are reported and supplemented with the uncorrected analyses. In addition to the analyses on P1, N290, and P400, analyses on attention- and memory-related ERP components, the Nc and PSW, were carried out. However, those analyses did not yield any significant results, so they are not discussed further.

In order to test our hypotheses that effects of prime category on ERPs for targets will be observed on the superordinate, the basic, and the individual level, we ran mixed model analyses of variance (ANOVAs) for the P1, the N290, and the P400. First, we looked at categorization on the superordinate level by comparing repetition

effects by same superordinate (averaged from same, other, and other basic) with other superordinate (houses). In a next step, we examined repetition effects on the basic level by comparing same basic (averaged from same, other) with other basic. Finally, we looked at repetition effects on the individual level by comparing same and other.

## Results

### Same Superordinate Versus Other Superordinate

First, superordinate-level categorization was examined by comparing same superordinate (computed as average from same, other, and other basic) and other superordinate. For each of the dependent variables a 2 (Group: human, ape) $\times$ 2 (Priming Condition: same superordinate, other superordinate) $\times$ 3 (Electrode: O1, O2, Oz) mixed model ANOVA was carried out. All statistical tests were conducted on a .05 level of significance (two-tailed). Bonferroni and Greenhouse-Geisser corrections were performed if applicable. All means and standard deviations ($SD$s) for the different priming conditions are reported in Table 1 (human condition) and Table 2 (ape condition). Waveforms are displayed in Figure 3. Table 3 provides a summary of the main findings of the ANOVA across conditions and groups.

P1 amplitude was enhanced for same superordinate relative to other superordinate, $F(1,47) = 18.96$, $p < .001$, $\eta^2 = .29$ (same superordinate $M = 21.35 \mu V$, $SD = 15.0$; other superordinate $M = 15.25 \mu V$, $SD = 12.3$). In addition, amplitude was larger in the ape compared to the human group, $F(1,47) = 4.64$, $p < .05$, $\eta^2 = .09$ (human $M = 14.40 \mu V$, $SD = 8.2$; ape $M = 21.41 \mu V$, $SD = 14.9$).

P1 latency was reduced for same superordinate ($M = 163.73$ ms, $SD = 21.7$) relative to other superordinate ($M = 173.74$ ms, $SD = 24.8$), $F(1,47) = 8.84$, $p < .01$, $\eta^2 = .16$.

There were no effects on N290 amplitude in the adjusted analyses. However, in the uncorrected analyses, N290 amplitude was enhanced for same superordinate ($M = 29.38 \mu V$, $SD = 18.2$) relative to other superordinate ($M = 22.94 \mu V$, $SD = 15.4$), $F(1,47) = 13.97$, $p < .01$, $\eta^2 = .23$.

**Table 1.2.**  *Human Group: Means and Standard Deviations (SD) of the N290 Grand Average Response*

| Condition | N290 amplitude Mean | N290 amplitude Mean corrected | N290 amplitude SD | N290 latency Mean | N290 latency SD |
|---|---|---|---|---|---|
| Same | 22.06 | 6.45 | 16.8 | 235.06 | 26.4 |
| Other | 25.64 | 8.58 | 17.7 | 251.33 | 43.7 |
| Same basic | 23.44 | 7.51 | 16.4 | 243.19 | 26.0 |
| Other basic | 29.77 | 10.87 | 20.1 | 227.78 | 25.7 |
| Same superordinate | 26.61 | 7.51 | 17.6 | 238.06 | 22.6 |
| Other superordinate | 19.80 | 7.27 | 13.9 | 252.44 | 39.3 |

**Table 1.3.** *Human Group: Means and Standard Deviations (SD) of the P400 Grand Average Response*

| Condition | P400 amplitude Mean | P400 amplitude Mean corrected | P400 amplitude SD | P400 latency Mean | P400 latency SD |
|---|---|---|---|---|---|
| Same | 37.56 | 15.50 | 20.7 | 453.00 | 54.8 |
| Other | 38.76 | 13.12 | 19.0 | 446.22 | 52.2 |
| Same basic | 37.75 | 14.31 | 18.2 | 449.61 | 45.1 |
| Other basic | 46.34 | 16.57 | 20.1 | 444.39 | 44.3 |
| Same superordinate | 42.05 | 14.48 | 18.6 | 447.87 | 39.6 |
| Other superordinate | 34.43 | 14.63 | 15.6 | 464.44 | 55.7 |

N290 latency was shorter in the ape compared to the human group, $F(1,47) = 6.52$, $p < .05$, $\eta^2 = .12$ (human $M = 245.25$ ms, $SD = 25.5$; ape $M = 229.00$ ms, $SD = 18.7$).

In the corrected analyses, P400 amplitude was larger in the human compared to the ape group, $F(1,47) = 5.27$, $p < .05$, $\eta^2 = .10$ (human $M = 14.55$ μV, $SD = 5.9$; ape $M = 10.13$ μV, $SD = 7.4$). No such effect was observed in the unadjusted analyses, $p > .05$, but P400 amplitude was enhanced for same superordinate ($M = 41.64$ μV, $SD = 18.6$) relative to other superordinate ($M = 35.56$ μV, $SD = 16.8$), $F(1,47) = 9.20$, $p < .01$, $\eta^2 = .16$.

P400 latency was shorter in the ape compared to the human group, $F(1,47) = 5.64$, $p < .05$, $\eta^2 = .11$ (human $M = 456.16$ ms, $SD = 41.3$; ape $M = 427.47$ ms, $SD = 43.2$).

**Summary.** As expected, we observed evidence for superordinate-level categorization. Irrespective of group, superordinate-level categorization was elicited very early during processing, as indicated by enhanced P1 amplitude and reduced latency for same superordinate compared with other superordinate (i.e., for faces preceded by other faces compared with faces preceded by houses). In the unadjusted analyses, enhanced amplitude for same superordinate carried over to the N290 and P400.

**Same Basic Versus Other Basic**

In the next step, basic-level categorization was examined by comparing priming for same basic (computed as average of same and

**Table 2.1.** *Ape Group: Means and Standard Deviations (SD) of the P1 Grand Average Response*

| Condition | P1 amplitude Mean | P1 amplitude SD | P1 latency Mean | P1 latency SD |
|---|---|---|---|---|
| Same | 22.57 | 19.4 | 161.76 | 29.5 |
| Other | 25.06 | 16.9 | 153.55 | 34.7 |
| Same basic | 25.61 | 17.6 | 157.65 | 26.8 |
| Other basic | 25.60 | 17.4 | 161.28 | 29.1 |
| Same superordinate | 26.16 | 17.0 | 158.86 | 21.6 |
| Other superordinate | 17.88 | 15.0 | 171.15 | 28.1 |

**Table 2.2.** *Ape Group: Means and Standard Deviations (SD) of the N290 Grand Average Response*

| Condition | N290 amplitude Mean | N290 amplitude Mean corrected | N290 amplitude SD | N290 latency Mean | N290 latency SD |
|---|---|---|---|---|---|
| Same | 32.01 | 9.44 | 19.9 | 221.97 | 22.4 |
| Other | 33.38 | 8.32 | 21.7 | 223.25 | 28.7 |
| Same basic | 32.90 | 8.88 | 19.6 | 222.61 | 22.5 |
| Other basic | 31.20 | 5.60 | 20.8 | 240.43 | 32.9 |
| Same superordinate | 32.05 | 7.80 | 18.8 | 228.55 | 19.7 |
| Other superordinate | 25.96 | 8.09 | 16.5 | 229.44 | 27.9 |

**Table 2.3.** *Ape Group: Means and Standard Deviations (SD) of the P400 Grand Average Response*

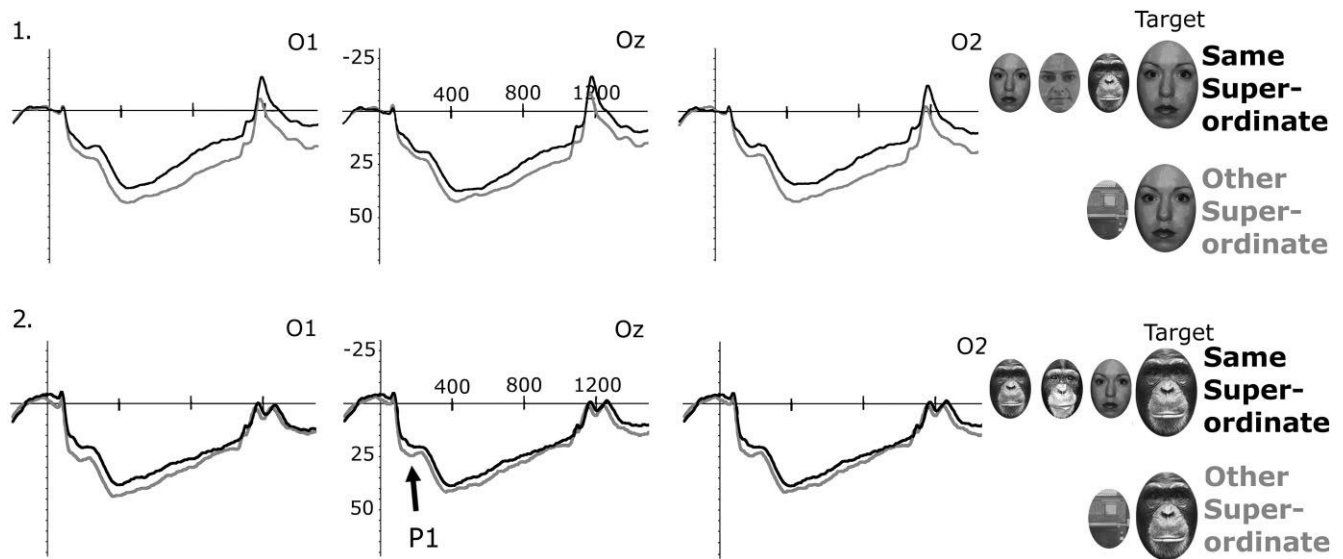| Condition | P400 amplitude Mean | P400 amplitude Mean corrected | P400 amplitude SD | P400 latency Mean | P400 latency SD |
|---|---|---|---|---|---|
| Same | 41.80 | 9.79 | 19.5 | 431.09 | 63.1 |
| Other | 45.11 | 11.73 | 20.9 | 430.24 | 68.3 |
| Same basic | 43.66 | 10.76 | 18.1 | 430.66 | 56.5 |
| Other basic | 38.83 | 7.63 | 22.9 | 419.63 | 52.2 |
| Same superordinate | 41.24 | 9.55 | 19.0 | 426.99 | 47.4 |
| Other superordinate | 36.67 | 10.71 | 18.2 | 427.95 | 55.7 |

**Figure 3.** Grand average ERP responses to same superordinate (black) and other superordinate (gray). 1: Human group. 2: Ape group. The *x* axis represents latency in milliseconds (ms), the *y* axis amplitude in microvolts (µV). Negative is plotted upwards. P1 amplitude was enhanced and P1 latency reduced for same superordinate.

other) with other basic in a 2 (Group: human, ape) $\times$ 2 (Priming Condition: same basic, other basic) $\times$ 3 (Electrode: O1, O2, Oz) mixed model ANOVA for each dependent variable. Waveforms are displayed in Figure 4.

Neither for P1, nor for P400 latency, was any significant main effect or interaction observed.

In the corrected analyses, for N290 amplitude, an interaction of priming condition and group was observed, $F(1,47) = 10.70$, $p < .001$, $\eta^2 = .18$. In the human group, amplitude was reduced for other basic compared to same basic, $F(1,23) = 8.04$, $p < .01$, $\eta^2 = .26$. In the ape group, amplitude was enhanced for other basic compared to same basic, $F(1,24) = 4.05$, $p = .056$, $\eta^2 = .14$. Interestingly, in the human target group, other basic ($M = 10.87$ µV, $SD = 12.3$) was less negative compared to the unprimed condition (other superordinate: $M = 7.27$ µV, $SD = 13.9$), which did not differ from same basic ($M = 7.51$ µV, $SD = 9.5$). In the ape target group, other basic ($M = 5.60$ µV, $SD = 8.5$) was more negative than the unprimed condition (other superordinate: $M = 8.09$ µV, $SD = 16.5$), which was similar to same basic ($M = 8.88$ µV, $SD = 8.8$). Thus, relative to the unprimed condition, the effect of basic-level prime

category seems to be driven by the other basic condition, rather than the same basic condition with effects going in opposite directions in both groups.

In the uncorrected analyses, an interaction between priming condition and group was also observed, $F(1,47) = 4.72$, $p < .05$, $\eta^2 = .09$. For the human group, N290 amplitude was less negative for other basic than same basic, $F(1,23) = 9.00$, $p < .01$, $\eta^2 = .28$. Here, the effect was driven by other basic ($M = 29.77$ µV, $SD = 20.1$) as well, which was less negative than the unprimed condition (other superordinate: $M = 19.80$ µV, $SD = 13.9$) and same basic ($M = 23.44$ µV, $SD = 16.4$). In the ape group, only a marginal effect of electrode was observed, $F(2,23) = 2.78$, $p = .083$, $\eta^2 = .19$. The differences between electrodes failed to reach significance in the post hoc analyses.

For N290 latency, an interaction between priming condition and group was observed, $F(1,47) = 12.17$, $p < .01$, $\eta^2 = .21$. In the human group, latency was reduced for other basic ($M = 227.78$ ms, $SD = 25.7$) compared to same basic ($M = 243.19$ ms, $SD = 26.0$), $F(1,23) = 7.92$, $p < .05$, $\eta^2 = .26$. In the ape group, latency was enhanced for other basic ($M = 240.47$ ms, $SD = 32.9$) compared

**Table 3.** *Summary of Main Findings of ANOVAs for Different ERP Components and All Categorical Contrasts*

| | Categorical contrast | | |
|---|---|---|---|
| ERP components | Superordinate level | Basic level | Individual level |
| P1 amplitude | Higher for same than for other | *n.s.* | *n.s.* |
| P1 latency | Shorter for same than for other | *n.s.* | *n.s.* |
| N290 amplitude | *n.s.* | Human group: Smaller for other basic than same basic | *n.s.* |
| | | Ape group: Larger for other basic than same basic | |
| N290 latency | *n.s.* | Human group: Longer for same basic than other basic | *n. s.* |
| | | Ape group: Shorter for same basic than other basic | |
| P400 amplitude | *n.s.* | Ape group: Higher for same basic than other basic | *n.s.* |
| P400 latency | *n.s.* | *n.s.* | *n.s.* |

*Note*. *n.s.* = not significant.
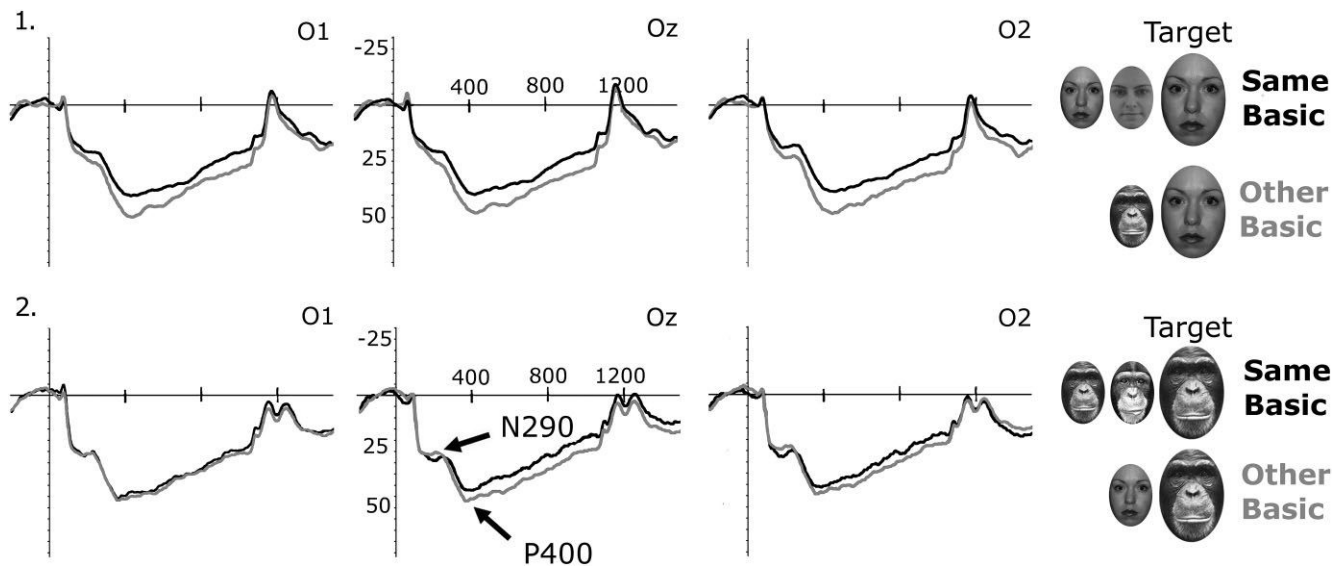
**Figure 4.** Grand average ERP responses to same basic (black) and other basic (gray). 1: Human group. 2: Ape group. The *x* axis represents latency in milliseconds (ms), the *y* axis amplitude in microvolts (μV). Negative is plotted upwards. N290 amplitude and latency were enhanced for targets primed by human faces. In the ape group, P400 amplitude tended to be larger for same basic.

to same basic ($M = 222.61$ ms, $SD = 22.5$), $F(1,23) = 5.67$, $p < .05$, $\eta^2 = .19$.

In the corrected analyses, for P400 amplitude, priming condition interacted with group, $F(2,46) = 5.95$, $p < .05$, $\eta^2 = .11$. In the ape group, a marginal effect of priming condition was observed, $F(1,24) = 4.16$, $p = .052$, $\eta^2 = .15$. Amplitude was slightly larger in response to same basic ($M = 10.76$ μV, $SD = 6.5$) than other basic ($M = 7.63$ μV, $SD = 9.5$). In the human group, no main effect of priming condition was observed, $p > .10$. Across groups, there was an electrode effect, $F(2,46) = 6.04$, $p < .01$, $\eta^2 = .11$. In the follow-up analyses, no differences between electrodes were observed. P400 amplitude was larger in the human ($M = 15.44$ μV, $SD = 6.9$) than in the ape group ($M = 9.20$ μV, $SD = 7.3$), $F(1,47) = 9.54$, $p < .01$, $\eta^2 = .17$.

In the uncorrected analyses, priming condition also interacted with group, $F(1,47) = 12.08$, $p < .01$, $\eta^2 = .20$. In the human group, P400 amplitude was larger for other basic ($M = 46.34$ μV, $SD = 20.12$) than own basic ($M = 37.75$ μV, $SD = 18.25$), $F(1,23) = 18.83$, $p < .001$, $\eta^2 = .45$. No significant effects were observed in the ape group.

**Summary.** Consistent with our hypothesis, evidence for basic-level categorization of human and ape faces was found, particularly at the level of the N290. Considering the adjusted analyses, N290 amplitude and latency were reduced for human targets preceded by ape faces. In contrast, N290 amplitude and latency were enhanced in response to ape targets preceded by human faces (see Figure 4). For the ape group only, P400 amplitude was marginally larger in response to same basic.

### Same Versus Other

We then tested whether faces were also categorized on the individual level, as indicated by differential priming effects for same versus other. For each dependent measure, a 2 (Group: human,

ape) × 2 (Priming Condition: same, other) × 3 (Electrode: O1, O2, Oz) mixed model ANOVA was carried out.[2] Waveforms are displayed in Figure 5.

In both the adjusted and uncorrected analyses, no significant main effects or interactions were found for the P1, for N290 amplitude, or the P400. In the adjusted analyses, N290 latency was shorter in the ape than in the human group, $F(1,47) = 8.78$, $p < .01$, $\eta^2 = .16$ (human $M = 243.19$ ms, $SD = 26.0$; ape $M = 222.61$ ms, $SD = 22.5$). No effect was observed in the uncorrected analyses, $p > .05$.

**Summary.** Contrary to our initial hypothesis, no individual-level rapid repetition effects were observed at the level of the P1, N290, or P400 (see Figure 5) in the human group. The absence of individual-level priming effects for the ape group was consistent with our expectations.

### Discussion

The results of the current study indicate that 9-month-old infants categorize human and ape faces first on a superordinate level and then on a basic level, as suggested by the temporal sequence of rapid repetition ERP effects. P1 amplitude was enhanced and P1 latency was reduced for same superordinate (i.e., faces preceded by faces, averaged across same, other, and other basic) compared with other superordinate (i.e., faces preceded by houses). This indicates that human and ape faces were at first not differentiated at the categorical level, but rather treated as belonging to a common superordinate-level category (e.g., "faces"). Initially, we had

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2. As the stimulus set included 25% of other-race faces for which individual-level categorization was not expected (Kelly et al., 2007), analyses were also carried out for trials showing own-race faces only. There were no differences regarding individual-level categorization between analyses on all trials and those on own-race trials.
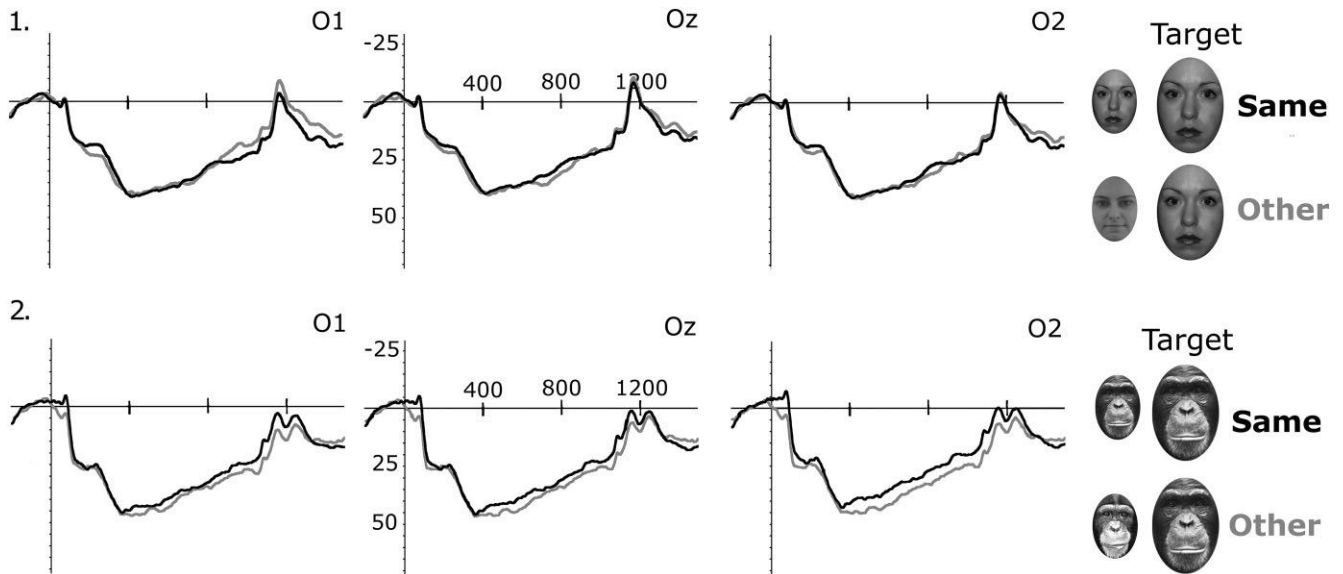
**Figure 5.** Grand average ERP responses to same (black) and other (gray). 1: Human group. 2: Ape group. The *x* axis represents latency in milliseconds (ms), the *y* axis amplitude in microvolts (μV). Negative is plotted upwards. There were no significant differences between priming conditions.

expected that primes and targets from the same superordinate-level category would activate a comprehensive pre-existing representation of "faces," leading to repetition suppression. The finding that P1 amplitude was enhanced for targets primed by the same superordinate level indicates that the categorical representation was updated during target presentation.

This early differentiation of superordinate-level categories may result from the differential association of face and nonface stimuli with low-level visual cues (Rossion & Jacques, 2011). These perceptual characteristics may have differed more strongly between faces and house fronts than between the faces presented. It seems important to note that low-level perceptual differences were also inherent in the comparison of ape and human faces, as well as between individual faces of the same species (human or ape faces). Given that P1 did not differ between same basic and other basic, our findings indicate that human and ape faces were treated as one category by 9-month-olds who clearly discriminated them from house fronts during early phases of stimulus processing. To clarify the role of the P1 as a potential ERP component reflecting processes of categorization at higher-order levels, future studies should assess whether the P1 also differentiates between broader animate-inanimate stimuli contrasts (e.g., animals vs. vehicles) but not between basic-level contrasts (e.g., birds vs. fish).

In a processing step following superordinate-level categorization, stimuli were categorized on a basic level. We base our interpretation of the N290 and P400 amplitude effects on the adjusted analyses to control for potential carryover effects that might obscure results. In the human target and in the ape target condition, faces belonging to the other basic level category induced repetition effects on N290 amplitude.

For human targets (but not ape targets), repetition suppression was induced by ape faces. In accordance with the model by Henson (2003), this may indicate that infants' representation of human faces was activated but not modulated by ape primes. Rather, we suggest that their representation was already distinct so that a clear differentiation between human and ape faces was possible. In contrast, enhanced N290 amplitude following human primes in the ape

group may indicate that infants' representation of ape targets was updated. Given infants' limited experience with apes, it does not seem surprising that their basic-level representation of ape faces is not as stable as that of human faces. From the current data, we cannot infer with any certainty how human faces influence the categorical representation of ape faces. However, our results show that the N290 is sensitive to the basic-level category membership of subsequently presented faces, consistent with the assumption that the N290 is a functional precursor of the adult N170 (de Haan et al., 2003; Peykarjou & Hoehl, 2013). It remains to be determined whether the N290 is also sensitive to the basic-level category membership of nonface stimuli.

There was no evidence for individual-level categorization in the current paradigm, although the exact same pictures were presented twice in succession. This finding can be explained in two ways: Either infants did not build up a representation of the individual faces during prime presentation, or the initial representation was not reactivated during target presentation. Though this is consistent with our hypothesis for the ape group, for the human group we initially expected to find evidence for individual-level categorization. In behavioral paradigms, recognition of individual human faces is consistently observed in 9-month-old infants (Kelly et al., 2007; Pascalis et al., 2002). These paradigms generally differ from the present study in multiple ways. Perhaps most importantly, only few exemplars from one basic-level category are presented for a much longer period of time each. This may lead to brain processes that differ substantially from those elicited in a rapid repetition ERP-priming task with only very short presentation intervals and a large number of different exemplars of each category. Consequently, these studies are not directly comparable to the current paradigm.

Some ERP studies have provided evidence for stimulus repetition effects in infants (Snyder et al., 2010; Webb & Nelson, 2001). In those studies, stimulus presentation was shorter (500 ms), and the intertrial interval was longer (1,800–2,800 ms). Moreover, a smaller number of individual exemplars was presented, and face stimuli were not cropped to an oval shape. These differences may

have contributed to the absence of individual-level repetition effects in the current study. It seems possible that the complexity of the current design did not support individual-level categorization. Presenting three different basic-level categories belonging to two superordinate-level categories may have emphasized categorization rather than individuation processes. To investigate whether individual-level categorization can be observed in infants using rapid repetition, a facilitated paradigm should be employed with faces from one basic-level category only and maybe a different time course allowing for longer presentation of each individual stimulus.

In our paradigm, P1 response properties were consistent with superordinate-level categorization, and N290 response properties were consistent with basic-level categorization. Only very few studies conducted with adults so far have analyzed repetition effects on the P1 for face stimuli (Kovacs et al., 2006; Schweinberger et al., 1995). The studies using houses as primes for human faces did not analyze priming effects on the P1 (Eimer, Kiss, & Nicholas, 2010; Nemrodov & Itier, 2012), and to our knowledge, no rapid repetition study has investigated categorization on different levels of abstraction in adults so far.

The N290 basic-level repetition effect observed here endorses the view that the N290 is a precursor of the N170 in adults, which can also be regarded as an indicator for basic-level categorization (Carmel & Bentin, 2002; Rossion et al., 2000). We did not observe an ERP component specific for the repetition of individual faces like the N250r in adults (Schweinberger et al., 1995).

The current study provides evidence that 9-month-old infants are able to categorize stimuli on different levels of abstraction within a short period of time. In this paradigm, larger samples of stimuli related to the targets on different levels of categorization were presented, and the cascade of very fast categorization responses could be analyzed. This allowed for a more comprehensive investigation of categorization processes than behavioral paradigms. Including subordinate-level primes would also help to understand the hierarchy of categorical representations. Priming through faces from the same and other gender, race, or age could be contrasted. However, given infants' limited attention span, it was not possible to include more levels of categorization in the current study. Even with the four conditions tested here, we had to use a mixed model design with human target faces in one group and ape target faces in the other group. As a result of employing a partly between-subjects design, we cannot fully exclude the possibility that the differences we found between the human and ape targets in fact reflect differences between the groups tested.

In everyday life, infants see many human faces and may also see several pet faces, for example, while watching the street from their stroller. From the current study, we can infer that they will categorize the faces they encounter into superordinate and basic level groups. Our results do not provide evidence for infants' ability to individuate unfamiliar faces, however. Whether this reflects a general limit at 9 months of age or results from the specific task demands remains to be clarified by future research.

Depending on the category membership of the preceding stimulus, 9-month-olds' responses to both human and ape faces were altered. From this, we received clues about the timing of categorization processes in the infant brain: When another kind of face preceded a face compared to a house, the priming effect occurred earlier (P1: 100–200 ms) than when effects of same species versus other species primes were compared to each other (N290: 200–350 ms). Our data support the idea that infants sorted the faces presented at the categorical level very fast. When aided by additional cues such as hair contour, sound, or motion information, categorization may be even faster in everyday life. The observed cascade of categorization, as indicated by brain correlates, reflects the development of categorization levels during infancy: Despite the larger perceptual diversity, superordinate categories are discriminated earlier in life than basic-level categories, as has been demonstrated in different behavioral paradigms (e.g., Behl-Chadha, 1996; Mandler & McDonough, 1993, 1998; Pauen, 2002b; Quinn & Johnson, 2000). It has been speculated that this global-to-basic level shift may reflect the importance of agency. Only animate beings can act as agents and thus provide potential aid or threat. It is of vital importance for infants to identify those agents. In fact, it may be so important that categorization prevails over individuation in young infants. The present study is a first attempt to explore this issue using brain correlates and a rapid repetition paradigm with 9-month-olds. We introduce a novel paradigm that may be used in future studies with various kinds of categories at different levels of categorization during development.

## Conclusions

In this rapid repetition ERP paradigm, 9-month-old infants first categorized faces as "faces" as indicated by the P1, and then as "human faces" or "ape faces" as indicated by the N290. However, infants did not categorize faces individually. We conclude from these results that, within a very short period of time, infants group visual stimuli first on a broader, and then on a more specific categorical level.

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