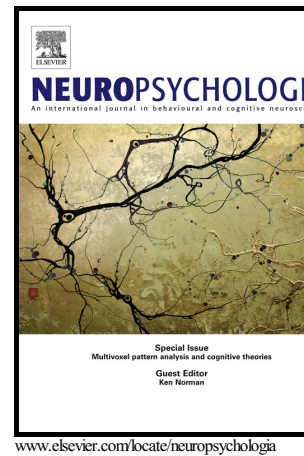


The development of category specificity in  
infancy—what can we learn from electrophysiology?

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The development of category specificity in infancy – What can we learn from  
electrophysiology?

Running title: Category specificity in infancy

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## Abstract

In this review I address the question why relatively little is currently known about the neural bases of category learning and beginning category identification in infancy. Electrophysiological research on infants' basic-level and global-level categorization has mainly focused on general measures of visual attention, not on specific neural processes underlying the development and identification of visual categories. Our knowledge on categorization processes in the infant brain is mainly limited to faces as categories. I will call for the use of EEG-based techniques such as rapid repetition ERP paradigms and fast periodic stimulation that have only rarely been used with infants in order to gain a better understanding of the development of category representations in the infant brain.

Keywords: Infancy; Faces; ERP; Categorization

The development of category specificity in infancy – What can we learn from electrophysiology?

From the moment infants are born they encounter a tremendous amount of visual input. One of the most important tasks within the first year after birth is to make sense of the various objects in the infant's visual environment. Which objects are foods? Which objects can be expected to start moving independently? Which objects are dangerous and which can be played with?

In this article I discuss research on the development of category specificity in the infant brain. The purpose of this article is not an exhaustive review of the literature, but rather to connect existing findings on visual categorization with findings on face processing in infancy, point out limitations of established research paradigms in these fields, and suggest future directions.

I start with a brief overview of behavioral research on infants' categorization in the first year. I then discuss event-related potential (ERP) studies on infants' category learning and category identification using familiarization experiments or oddball paradigms. Although these studies have complemented behavioral research, I argue that the relatively unspecific measures of attention in these studies have not allowed us to draw inferences on how and where category information is stored in the infant brain. Next, I review studies on infants' ERP responses to faces. This research has helped to identify several ERP components which are sensitive to the highly relevant category of human faces. In addition to classic ERP paradigms, the recent use of rapid repetition tasks has proven useful for studying the timing of categorization processes in the infant brain. I conclude with an outlook on future directions in this area of research and discuss the application of promising novel approaches such as rapid repetition and fast periodic stimulation to study category specificity in early development.

Behavioral studies of infant categorization have focused on the question at what age infants are capable of forming categories at different levels of abstraction. Based on the organization of object knowledge in adults (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976), distinctions are made between the ontological or global level (animate vs. inanimate), the superordinate level (e.g., vehicles, furniture, food), the basic level (e.g., cars, bikes, planes), and subordinate levels (e.g., trucks, convertibles, minivans). An exhaustive review of the infant categorization literature is beyond the scope of this article, but the interested reader is referred to several more comprehensive reviews (Mandler, 2004; Mareschal & Quinn, 2001; Oakes, Horst, Kovack-Lesh, & Perone, 2009; Rakison & Poulin-Dubois, 2001; Smith, 2005).

Visual categorization in infants has traditionally been studied using familiarization and detection-of-novelty paradigms. In these studies, infants are presented with a series of pictures or objects belonging to one object category (e.g., cats). Infants are thought to familiarize to one category if they spend less and less time looking at or exploring items of the same category during the course of the familiarization phase. At test, infants are then presented with a novel item of the familiarized category (e.g., a new cat) and a novel item belonging to a different category (e.g., a dog). If infants' attention recovers specifically at the sight of the novel item of the different category this is taken as evidence for a distinction between the two tested categories. In this case it is also inferred that infants' decline of attention during familiarization was not merely due to fatigue. An alternative task to study infant categorization on the behavioral level is the sequential touching task (Arterberry & Bornstein, 2012; Bornstein & Arterberry, 2010; Oakes, Plumert, Lansink, & Merryman, 1996). As this paradigm requires somewhat more elaborate motor skills, it is usually applied only with infants from the end of the first year onwards.

Research using looking times has shown that 3- to 4-month-olds are able to distinguish categories at the basic level (e.g., dogs vs. cats; Quinn, Eimas, & Rosenkrantz, 1993) as well as at a superordinate level (e.g., mammals vs. furniture; Behl-Chadha, 1996). Despite the great perceptual variety of items within superordinate or global-level categories, a global-to-basic level shift has been reported: Infants are able to discriminate between superordinate-level categories somewhat earlier than they are able to distinguish between different basic-level categories (Pauen, 2002).

Due to the use of a familiarization phase, infants' performance in these studies is usually interpreted in terms of online category learning during the experiment. One view is that infants abstract perceptual similarities between items of the same category during familiarization (Eimas, Quinn, & Cowan, 1994; French, Mareschal, Mermillod, & Quinn, 2004). However, prior real-world experiences also play a role. For instance, infants who live with a dog or cat at home are better able to discriminate between these two categories in an object examination task (Träuble, Babocsai, & Pauen, 2009) and respond differently to images of these animals (Hurley, Kovack-Lesh, & Oakes, 2010) than same-aged infants who do not have a pet. Thus, bottom-up processes of category learning and top-down processes of category recognition both seem to contribute to infants' performance in behavioral categorization tasks.

Behavioral tasks used to study categorization in infants have some limitations, however. Due to infants' limited attention span and relatively long presentation times for individual stimuli, only a very limited number of trials can be presented such that categories are typically represented only by a few (e.g., 8-10) different items. Furthermore, infants' control over their overt attention develops considerably over the first year (Posner & Rothbart, 1998) and may develop relatively independently from categorization skills. Thus, differences in behavioral task performances between different age groups may be affected by developments in overt attention control. In addition, all of the looking-time studies reported

above included familiarization phases and thus also involved infants' developing memory capacities. Studies assessing ERPs and applying passive viewing tasks are potentially less affected by these limitations and can be used to investigate different age groups across the lifespan with the very same task. The next section sums up electrophysiological studies on infants' categorization and concludes with pointing out the limitations of these studies.

What are the neural correlates of infants' visual categorization?

In the first ERP studies on infants' visual categorization, the same general approach as in the behavioral familiarization studies was used. Quinn, Westerlund, and Nelson (2006) presented 6-month-olds with a series of cat images during familiarization. During test, infants were then presented with images of novel cats (familiarized category) interspersed with images of dogs (novel category) while ERPs were recorded. Infants responded with increased amplitude of the Negative central (Nc) component to images of dogs after being familiarized with cats. The fronto-central Nc has been related to the amount of attention infants allocate toward a visual stimulus (Reynolds & Richards, 2005). Thus, as in behavioral studies, infants directed increased attention to items of a novel category as compared to items of a familiarized category. A similar effect was found when birds were contrasted with fish and cars (see Figure 1), suggesting that 6-month-olds are able to process categorical differences between two basic-level categories both when they belong to the same global-level category and also when they belong to different global-level categories (Grossmann, Gliga, Johnson, & Mareschal, 2009). These results are well in line with previous behavioral work and have been interpreted as reflecting perceptual category learning during the task.

In another set of ERP studies, adapted oddball paradigms were used and no familiarization phase was involved. Elsner, Jeschonek, and Pauen (2013) were interested in infants' global-level categorization of animals and furniture items. They presented 7-month-olds with one item (furniture or animal, varied between-subjects) at a frequency of 60%, one item of the same global-level category at 20% and one item of the other global-level category

at a frequency of 20%. The standard stimulus was perceptually similar to the oddball from the contrasting category (i.e., regarding shape, color, visibility of legs), but facial features were only present in animals. Infants responded with increased Nc amplitude to both oddball stimuli compared with the standard (see Figure 1). Differences between both oddballs were found in terms of Nc latency and infants' slow wave activity, suggesting increased processing demands for the out-of-category oddball. The latter finding suggests that infants did not only process the relative frequencies of the presented individual stimuli, but also detected the categorical contrast. Since no familiarization phase with multiple items from one category was applied in this study, the difference between infants' responses to the two oddballs may be attributed to processes of category identification. For instance, infants may have relied on facial features which were only present in the animals. This interpretation, however, is limited by the fact that only few exemplars from both categories were tested in this study.

Pauen, Wahl, and Hoehl (2011) introduced a categorical oddball paradigm to assess the same animal-furniture contrast in 4- and 7-month-olds. Instead of three different items, they presented infants with one hundred different items, among them 80 exemplars from one category (furniture or animal, varied between-subjects) and 20 exemplars from the other category. Exemplars were highly varied within each category. Nevertheless, both 4- and 7-month-old infants showed an increased Nc in response to oddball stimuli in the first half of the presentation sequence. This effect was found regardless of whether animals or furniture items served as standards. In the second half of the presentation, the effect disappeared in the 4-month-olds.

A connectionist model tested with the same categorical contrast suggested that both processes of online category formation and category identification contributed to the observed effects (Westermann, Pauen, Wahl, & Hoehl, 2014). The computational model was pre-trained with more or less experiences in order to simulate differences between 4- and 7-month-olds. The models were then subjected to the oddball task from the ERP study and



different hypotheses were tested. When the model was pre-trained with random dot patterns, the oddball effect arose gradually during test. When the pre-training involved different pictures of the same categories (animals and furniture), oddball effects were observed in both halves of the test. When adding an extra bit to the inputs (1 for animals, 0 for furniture) in the pre-training and test, simulating stable categorical representations, the oddball effect also occurred in both halves of the test. The model that best mirrored the Nc effects found in infants was one in which the extra bit was only added during pre-training, simulating the richer experiences infants make in the real world and supposing that infants continue learning from “impoverished” pictures in the oddball task. In this case the “older” model, simulating 7-month-olds, showed the oddball effect in both halves of the task, but the “younger” model, simulating 4-month-olds, showed the oddball effect only in the first half.

The same oddball task was used to test 4- and 7-month-olds’ discrimination of humans and animals, both depicted in full view of the whole body (Marinovic, Hoehl, & Pauen, 2014). Four-month-olds did not discriminate between the two categories within the global-level category of animates. Seven-month-olds, in contrast, responded with an increased Nc amplitude to the less frequent category, irrespective of whether standard items were humans or animals, suggesting robust discrimination of humans from other animals by this age (see Figure 1).

In sum, ERP studies on infants’ visual categorization have demonstrated that by 6-7 months of age infants are able to discriminate between several basic-level categorical contrasts as well as between the global-level contrast of animals vs. furniture items. The latter distinction is already observed in 4-month-olds and does not seem to require that infants first be familiarized with one of the categories. This suggests that infants are able to use their previously acquired knowledge of natural categories, e.g., regarding distinctive features of animates such as faces, to make this categorical distinction. In fact, behavioral research has demonstrated that the global contrast of animates vs. inanimates is one of the first to be made

in early infancy (Pauen, 2002; Quinn & Johnson, 2000). Thus, the finding that 4-month-olds are able to make this distinction in a categorical oddball task is in line with previous behavioral research (Pauen et al., 2011).

In all of the cited ERP studies, the Nc component was assessed (in addition to slow wave activity) as a marker of infants' increased attention to exemplars of the novel or relatively infrequent category. Although this measure has proven very useful, these ERP studies do not inform us about how and where category knowledge is represented in the infant brain due to the use of the Nc, i.e., a neural correlate of infants' attention. We can conclude that infants respond to the category change within 400-600 ms after stimulus onset (i.e., the latency of the Nc) but instead of telling us something about the processes of categorization, this research informs us about the outcome of these processes. Although the Nc is consistently increased in amplitude for items of the more novel or relatively infrequent category, Nc amplitude does not differ for items belonging to different categories that are presented at the same relative frequency (Elsner et al., 2013; Jeschonek, Marinovic, Hoehl, Elsner, & Pauen, 2010). Thus, the Nc is not likely involved in the process of categorization itself.

To conclude, though some of the limitations of behavioral studies could be overcome by using ERP measures, our knowledge of neural mechanisms underlying infants' categorization is still rather limited. Studies addressing the actual processes of categorization rather than general attention or memory processes signaling that categorization took place are needed. These might enable us to investigate the timing and sequence of categorization processes in the developing brain, i.e., allow us to gain information that is lost when only looking at the outcomes of visual processing and overt attention direction in the form of looking times. Since such processes have been primarily investigated with regard to faces, the next section will summarize ERP research on infants' processing of human faces.

- Insert Figure 1 about here -

Development of category-specific brain responses: Face-sensitive ERP components

The human face is one of the first and most frequently encountered visual stimuli for infants. Faces contain a large amount of relevant information, e.g., regarding a person's identity, emotional state, and attention focus. Infants preferentially follow faces and face-like schematic drawings with their gaze even hours after birth (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991). In addition, newborns are remarkably good at discriminating individual faces, given that they recognize both their mother's (Bushnell, Sai, & Mullin, 1989; Sai, 2005) and a stranger's face (Coulon, Guellai, & Streri, 2011) after relatively brief audiovisual exposure (see also Pascalis & de Schonen, 1994; Turati, Macchi Cassia, Simion, & Leo, 2006).

There has been considerable debate about the question whether there are specialized neural correlates or modules for face processing in the human brain (Kanwisher, McDermott, & Chun, 1997; Rossion, 2014) as opposed to more general neural mechanisms dedicated to the processing of highly trained visual object categories (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). From a developmental perspective there is evidence for qualitative differences in the processing of faces vs. other objects in addition to quantitative differences regarding the amount of experience obtained with faces as compared to other kinds of object (see Hoehl & Peykarjou, 2012, for a more thorough discussion of this issue and a more exhaustive review of the infant face processing literature). For instance, besides newborns' attention biases toward faces, there seems to be a sensitive period in infancy for building up a holistic face representation that, after being missed, cannot be wholly compensated for by later visual experience (Le Grand, Mondloch, Maurer, & Brent, 2004; Röder, Ley, Shenoy, Kekunnaya, & Bottari, 2013). Furthermore, perceptual narrowing<sup>1</sup> in the

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<sup>1</sup> Perceptual narrowing refers to the specialization of discriminatory abilities for frequently encountered kinds of auditory and visual stimuli at the expense of others during infancy. For instance, 6-month-old infants are able to discriminate between individual monkey faces as well as between human faces, whereas by 9 months of age, infants' ability to discriminate between individual monkey faces declines dramatically (Pascalis et al., 2002).

visual domain has only been demonstrated for faces but not other object categories (Pascalis, de Haan, & Nelson, 2002; Scott, 2011).

Electrophysiological research with adults has focused mostly on the N170 ERP component on posterior temporal electrodes that seems to represent face-sensitive neural processes (Bentin, Allison, Puce, Perez, & McCarthy, 1996). The N170 is larger in amplitude in response to faces as compared to other object categories (see Rossion & Jacques, 2008, for a review). Face-specific response properties of the N170 seem to depend on the conscious identification of a stimulus as a face (Bentin & Golland, 2002; Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002; George, Jemel, Fiori, Chaby, & Renault, 2005; Navajas, Ahmadi, & Quiñero, 2013). The N170 is delayed and/or enhanced by face inversion, but it is less affected by object inversion (Bentin et al., 1996; Itier, Latinus, & Taylor, 2006; Rossion et al., 1999; Rossion et al., 2000). This finding has been taken as evidence that the N170 reflects structural encoding of faces (Bentin et al., 1996; Eimer, 1998).

In infants, two ERP components recorded over medial occipital regions have been discussed as potential precursors of the adult N170: the N290 and P400 (see de Haan, Johnson, & Halit, 2003, for a review of face-sensitive ERP components in infants). N290 amplitude is increased for faces relative to matched visual noise in 3-month-old infants (Halit, Csibra, Volein, & Johnson, 2004). In 3-, 6-, and 12-month-olds, N290 amplitude is greater for human faces as compared to monkey faces (de Haan, Pascalis, & Johnson, 2002; Halit, de Haan, & Johnson, 2003). Peykarjou and Hoehl (2013) observed increased N290 amplitude in response to inverted faces relative to upright faces but not cars in 3-month-olds (see Figure 2). A similar adult-like inversion effect specifically for human but not monkey faces has been reported for 12-month-olds (Halit et al., 2003). At 4 months the N290 is also increased in amplitude for faces with scrambled inner features as compared to intact human faces (Parise, Handl, & Striano, 2010). Thus, the N290 displays some specificity for human faces and seems to share some functional properties with the adult N170 which is also increased by face

inversion (Itier et al., 2006; Rossion et al., 1999) and distortion of the configuration of inner facial features (George, Evans, Fiori, Davidoff, & Renault, 1996; Macchi Cassia, Kuefner, Westerlund, & Nelson, 2006).

- Insert Figure 2 about here -

In 6-month-olds, the P400 is of larger amplitude for upright vs. inverted faces, but this effect was found both for human faces and monkey faces (de Haan et al., 2002). Furthermore, the P400 is larger for intact faces as compared to faces with scrambled inner features, though this effect was also observed for intact vs. distorted human bodies (Gliga & Dehaene-Lambertz, 2005). Thus, the P400 seems to be sensitive to the configuration of visual stimuli, but not exclusively with regard to human faces. The P400 does, however, seem to discriminate between different object categories in 6-month-olds as it is of shorter latency for faces compared to toys when upright stimuli are used (de Haan & Nelson, 1999). Further evidence for the P400 as a precursor of the adult N170 comes from a study showing similar sensitivities of both components to featural and configural changes to previously familiarized faces in 8-month-olds and adults, respectively (Scott & Nelson, 2006).

Both the N290 and P400 are affected by visual expertise, in particular individual-level training. Nine-month-olds who received visual experience with individually-labelled monkey faces between 6 and 9 months responded with increased P400 amplitude for inverted monkey faces vs. upright monkey faces (Scott & Monesson, 2010). This effect was not found following exposure to monkey faces without labels or with basic category labels (i.e., “monkey”). Training with individually-labelled strollers between 6 and 9 months led to increased N290 amplitude for upright vs. inverted strollers, whereas category level training did not have this effect (Scott, 2011). While impressively demonstrating the effects of individual-level training on infants’ visual object processing, these studies leave open how the reported effects relate to infants’ larger N290 for inverted vs. upright human faces (Halit et al., 2003; Peykarjou & Hoehl, 2013).

Together, the reviewed studies suggest that the infant N290 and P400 possess some functional commonalities with the adult N170, which has led to the suggestion that both components become integrated into the mature N170 across development (de Haan et al., 2002). By 3-4 months the N290 is to some extent human face-specific as it discriminates between human and monkey faces (Halit et al., 2003) and is sensitive only to the inversion of human faces but not cars (Peykarjou & Hoehl, 2013). Thus, the infant N290 may represent the identification of a visual stimulus as a human face, but it may also relate more generally to processes of basic-level categorization (Scott, 2011; Scott & Monesson, 2010). In fact, it is likely that the N170 as well as the N290/ P400 represent activations of several neural sources (Bötzel, Schulze, & Stodieck, 1995; Deffke et al., 2007; Itier & Taylor, 2004; Johnson et al., 2005; Schweinberger, Pickering, Jentsch, Burton, & Kaufmann, 2002; Shibata et al., 2002) and the engagement of more than one process related to face perception and categorization (Eimer, Kiss, & Nicholas, 2010; Rossion, 2014). The same face can always be categorized at different levels of abstraction, e.g., at a global level as “face”, at a more basic level as “human face” and at the individual level as “Bill”. These different processes are difficult to disentangle within the above-mentioned studies. ERP repetition paradigms take advantage of the high temporal resolution of ERPs and can help to investigate the timing and sequence of categorization processes in the developing brain.

Timing and sequence of categorization processes in the infant brain: ERP repetition studies

Effects of stimulus repetition on neural activations have been investigated with single-cell recordings, EEG/MEG, and neuroimaging techniques in order to gain a better understanding of visual processing and semantic representations in the brain (Grill-Spector, Henson, & Martin, 2006). Depending on the study, responses to identical repeated stimuli were recorded or responses to stimuli that differed in one stimulus dimension or that were semantically related (Grill-Spector et al., 2006). When a prime or adaptor stimulus influences neural responses to a target this is can be interpreted as signaling that adaptor and target

activate a common neural representation at the affected processing step (e.g., faces and eyes at the level of the N170/ N290: Gliga & Dehaene-Lambertz, 2007). When a target differs from a prime stimulus in only one particular dimension (e.g., size, position, viewpoint), changes in neural activation are usually taken as evidence that the affected brain region or ERP component is sensitive to the stimulus dimension in question (Henson, 2003).

Most often stimulus repetition leads to reduced neural activity in response to the target as compared to the adaptor stimulus or an unprimed target. This response pattern is commonly referred to as repetition suppression (Grill-Spector et al., 2006). However, repetition enhancement has also been reported under certain circumstances (Henson, Shallice, & Dolan, 2000). According to Henson (2003), repetition suppression reflects processes that occur for both prime and target stimulus whereas repetition enhancement is found when additional processes operate on the target as compared to the prime. The latter may be the case, for instance, when new representations are build for previously unfamiliar stimuli (Henson et al., 2000). It should be noted though that ERPs cannot easily be used to ascertain whether repetition suppression at a given component is actually due to neural adaptation or the superimposition of a positivity/negativity at the same latency. This uncertainty regarding the underlying neural processes is a limitation of ERP studies in general that also concerns repetition paradigms.

Several studies using stimulus repetition paradigms have shown reduced N170 amplitude (or M170 amplitude in MEG studies) for faces that were preceded by faces compared to non-face stimuli (Eimer, Gosling, Nicholas, & Kiss, 2010; Eimer, Kiss, et al., 2010; Harris & Nakayama, 2007, 2008; Itier & Taylor, 2002; Kovacs et al., 2006). Repetition suppression of N170 amplitude for repeated faces of the same identity occurs across changes of viewpoint for upright faces (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009), but this effect is considerably reduced and delayed for inverted faces (Jacques, d'Arripe, & Rossion, 2007).

The degree to which repetition suppression effects on the N170 are specific to faces and facial features still remains unclear. One study found similar repetition suppression on the N170 in response to hands preceded by hands vs. faces as for faces preceded by faces vs. hands (Kovacs et al., 2006), suggesting that shape-selective mechanisms but not necessarily face-selective mechanisms may be involved. When using long lags between identical adaptor and target stimuli, the N170 is reduced for repeated familiar faces as well as for repeated line drawings of objects (Guillaume et al., 2009). Other studies, however, reported differential repetition effects for faces as compared to objects or words on the N170 (Maurer, Rossion, & McCandliss, 2008; Mercure, Cohen Kadosh, & Johnson, 2011). Thus, repetition suppression effects on the level of the N170 may to some extent be category-specific.

Only very few ERP studies on infant face processing using repetition paradigms have been published so far. Webb and Nelson (2001) found increased Nc amplitude in 6-month-olds for faces that were repeated following a lag of 6-12 other images. Gliga and Dehaene-Lambertz (2007) reported that in 3- to 4-month-olds the N290 response to isolated eyes is reduced in the context of frontal view faces vs. houses but not in the context of profile view faces with closed eyes vs. cars. The authors concluded that frontal view faces activate to some extent the same neurons as isolated eyes at the processing stage of the N290 whereas profile view faces with closed eyes and objects do not (a weaker effect was found for frontal faces with closed eyes). Thus, in contrast to adults, a view-invariant representation of human heads that is independent of the presence of visible eyes has not been developed at this age (see Kobayashi et al., 2011, for evidence from functional near-infrared spectroscopy that a view-invariant representation of faces develops by 7-8 months).

Further evidence for the involvement of the N290 in the processing of eyes in 4-month-olds comes from a rapid repetition study in which intact faces were preceded by faces with or without eyes (Hoehl, 2015). The only ERP component affected by the different



adaptor stimuli was the N290, albeit only in terms of latency, which was reduced for faces preceded by intact faces compared to faces preceded by faces without eyes.

Peykarjou, Pauen, and Hoehl (2014) tested 9-month-olds' repetition effects for faces that were categorically related to prime stimuli at different levels of abstraction. One group of infants saw human faces as targets whereas another group was tested with ape faces as targets. On a global level, the authors compared infants' responses to target faces preceded by faces in general (human and ape) to faces preceded by non-face objects (i.e., houses). Regardless of target face category (human or ape), faces preceded by faces elicited increased P1 amplitude (100-200 ms) and reduced P1 latency on occipital channels. This finding suggests a rather rapid global-level identification of a stimulus as a face or non-face. In adults face-sensitive responses have also been reported on the level of the P1 (Herrmann, Ehlis, Ellgring, & Fallgatter, 2005), but have been attributed to differences in low-level properties (e.g. amplitude spectrum, color) of the stimulus categories (Rossion & Caharel, 2011).

On a more basic level, effects of the species of prime stimuli were assessed. In the human target group, N290 amplitude and latency were reduced following ape face primes compared to human face primes. In contrast, in the ape face target group N290 amplitude and latency were increased following human face primes compared to ape face primes (see Figure 3). According to the model by Henson (2003), repetition suppression for human target faces indicates that infants' representation of human faces was activated but not modulated by the ape primes. Repetition enhancement for ape faces seems to imply, in contrast, that infants' representations of ape faces, which were presumably less stable to begin with, were updated following the presentation of a human face prime. Thus, the basic-level contrast of human vs. ape faces affected processing at the level of the N290. It will be important to examine in further research to what extent this effect is face-specific or whether the N290 is similarly sensitive to other basic-level categorical contrasts. Neither in the human target group nor in

the ape target group did any effects of face identity repetition occur within the respective species.

- Insert Figure 3 about here -

Given that infants are remarkably good at discriminating individual faces even hours after birth (Bushnell et al., 1989; Coulon et al., 2011; Sai, 2005), it seems surprising that no repetition effects of face identity were found in the study by Peykarjou, Pauen, et al. (2014). One possibility is that the rather short presentation times (1,000 ms) made it impossible for infants to build up individual face representations. In addition, the inclusion of faces from another species in the stimulus presentation may have shifted the task focus toward categorization rather than individuation of faces. In a subsequent experiment, face primes and targets were therefore presented for 1,500 ms and only human faces were shown (Peykarjou, Pauen, & Hoehl, in press). In this study, reduced N290 latency for repeated faces as compared to faces preceded by another face was observed, speaking for a facilitatory effect of stimulus repetition at the level of the N290. When responses to male and female target faces were analysed separately, only for male faces increased late slow wave positivity on occipital channels was found for unrepeated faces. The latter finding indicates specifically increased processing demands for unrepeated male faces, in line with infants' greater difficulties at processing male faces on the behavioural level (Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002).

Together, infant studies using stimulus repetition suggest that faces are first discriminated from other categories on a global level at the early processing step of the P1. Basic-level contrasts are then registered at the level of the N290. Individual face discrimination seems to require longer stimulus presentation and affects N290 latency rather than amplitude. Especially for male faces, face identity repetition effects were observed on a late occurring positive slow wave component on occipital channels. Thus, a processing sequence from global-level categorization to individual face recognition was observed. The

specificity of the reported response patterns for faces and the contribution of low-level perceptual differences between categories has yet to be determined.

#### Future directions

ERP repetition paradigms enable us to investigate the timing of visual object categorization in the infant brain. However, studies have so far been limited to the use of face stimuli (Peykarjou, Pauen, et al., 2014; Peykarjou et al., in press). It will be important to extend this research to other object categories. In human adults, so called “concept neurons” (Quiroga, 2012) that respond specifically to object categories other than faces (e.g., animals) exist in the medial temporal cortex (Kreiman, Koch, & Fried, 2000), but no particular ERP component has been related to the processing of an object category other than faces. Only one study has reported categorical priming effects for animal and furniture items on a right frontal positive slow wave component in 7-month-olds, but this study had a very small sample and was not initially designed to test repetition effects (Jeschonek et al., 2010).

Therefore, one important avenue for further research on category specificity in the infant brain will be to test repetition effects for stimuli other than faces which are related to each other at different levels of abstraction. For instance, effects of the same animal, another animal, and a furniture item on ERP responses to an animal target could be assessed. One hypothesis might be that the P1 on occipital channels is sensitive to global category membership and thus distinguishes between animal primes (same global category) and furniture primes (other global-level category) by 4 months of age. In this context it will also be important to assess whether effects on the P1 can be attributed to low-level perceptual differences between categories, for instance, by using phase-scrambled control stimuli. It will be particularly interesting to test whether the N290 displays sensitivity to basic-level category contrasts and perhaps even stimulus identity (in terms of latency) for categories other than faces.

It is also possible that at the time when a particular categorical contrast is build up during early infancy it is registered at later processing steps or different electrode sites than after it is firmly established. In adults objects are usually first recognized at the basic level (Rosch et al., 1976), yet categorical distinctions on the basic level develop later than global-level categorization in ontogeny (Pauen, 2002). Thus, a switch in the neural processing sequence from global-before-basic to basic-before-global might be observed at some point in development. In fact, the “entry level” at which perceptual input makes contact with stored semantic information shifts toward more subordinate levels with increasing expertise (Tanaka & Taylor, 1991) and available semantic knowledge (Anaki & Bentin, 2009). Alternatively, the basic-level advantage observed in many tasks in adults may be due to the fact that lexical representations at the basic level are the most accessible, although visual stimuli are first processed in a coarse manner at the superordinate level (Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009). In this case a switch in the processing sequence would not be expected during development. Testing preverbal infants along with children at different levels of language proficiency with the very same task is possible with ERPs and may provide useful information regarding the potential effects of lexical representations on visual categorization.

Besides rapid repetition, another EEG-based technique that can be used in different age groups to investigate category discrimination and that is especially feasible for infant studies is fast periodic stimulation. Here, stimuli are presented at a fixed rate (e.g. 6 Hz), thus inducing a response of the visual system at the exact same frequency, the so-called steady state visual evoked potential (SSVEP, Regan, 1989). This method provides a robust and objective measure of stimulus discrimination, for instance, the discrimination of individual faces (Rossion & Boremanse, 2011). The first study using this method to study infants’ higher level visual processing demonstrated 4- to 6-month-olds’ sensitivity to global structure in face and object images by presenting alternating intact and scrambled images (Farzin, Hou, &

Norcia, 2012). Fast periodic stimulation can also be used to obtain an objective index of object categorization by presenting two stimulus categories at different rates (e.g., different face races, Peykarjou, de Heering, Hoehl, Pauen, & Rossion, 2014). One advantage of this technique when compared to classic ERP measures is that SSVEPs are relatively immune to artifacts and yield a high signal-to-noise ratio, such that only a few minutes of stimulation are required to obtain a robust effect in individual infants and dropout rates are extremely low.

A limitation of virtually all of the discussed behavioral and ERP studies on visual categorization in infancy is that stimulus images were segmented from their background. Extremely little is known about figure-ground segregation in infancy (Hayden, Bhatt, Kangas, & Zieber, 2011). One important avenue for future research is therefore to study whether infants' performance in categorization tasks is changed when stimuli are presented with natural backgrounds. One recent study used fast periodic visual stimulation in 4- to 6-month-olds infants. Participants were presented with images of multiple different objects interspersed with highly variable faces appearing as every 5<sup>th</sup> stimulus (de Heering & Rossion, 2015). In contrast to the above-reviewed studies, all images were shown in front of their natural background. A response at exactly the stimulation rate of the face stimuli was observed over right occipito-temporal sites, indicating the activation of face-specific neurons that generalized across faces shown from different view-points, with different expressions, ages and genders. No such effect was found using phase-scrambled images. Thus, the effect is not merely due to low-level perceptual differences between stimuli. It is a matter of future research to determine whether other object categories presented at a certain rate among stimuli from different categories elicit a similar response, especially when complex non-segmented images are used.

Despite the fact that much research has been conducted on category learning in infancy and also on the neural bases of categorization in adults, we know relatively little about the neural processes and brain areas that are involved in categorization in early

development. On the one hand this is due to the fact that the initial neurophysiological studies on infant categorization focused on a general measure of attention, the Nc, instead of exploring the timing, sequence, and topography of categorization processes in the developing brain. On the other hand, studies on categorization-specific neural processes in infancy have mainly used face stimuli and have rarely included other object categories. In conclusion, I propose that two EEG-based techniques, rapid repetition and fast periodic stimulation, will be particularly informative regarding the development and neural bases of category representations in infants.

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Figure captions.

Figure 1. Nc responses over central channels in the studies by Grossmann et al. (2009; top panel), Elsner et al. (2013; middle), and Marinovic et al. (2014; lower panel). The Nc is consistently increased in amplitude for stimuli of the novel or relatively infrequent (oddball) category. The Nc does not differ in amplitude for categories presented at the same relative frequency (see also Jeschonek et al., 2010). Reprinted with permissions.

Figure 2. ERPs in response to upright faces (black line) and inverted faces (grey line) in 3-month-olds over PO9 (Peykarjou & Hoehl, 2013). Negative is plotted upwards.

Figure 3. ERP responses for human (upper panel) and ape faces (lower panel) preceded by items of the same basic level category (black line) or items of the other basic level category (grey line). Items of the same basic category could have the same or a different identity than the target. Negative is plotted upwards. N290 amplitude and latency were enhanced for both kinds of targets primed by human faces. Reprinted with permission from Peykarjou et al. (2014).

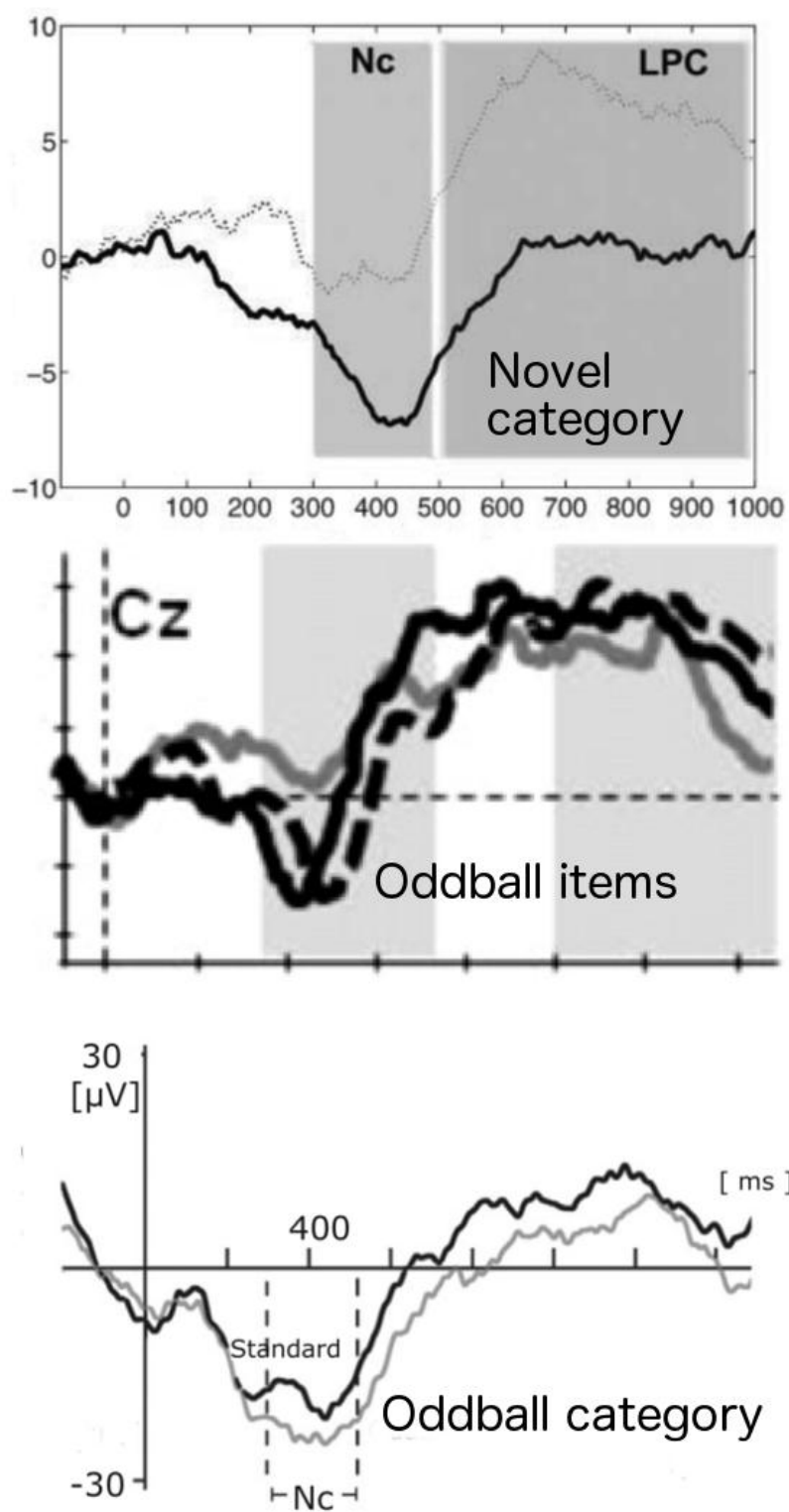


fig1

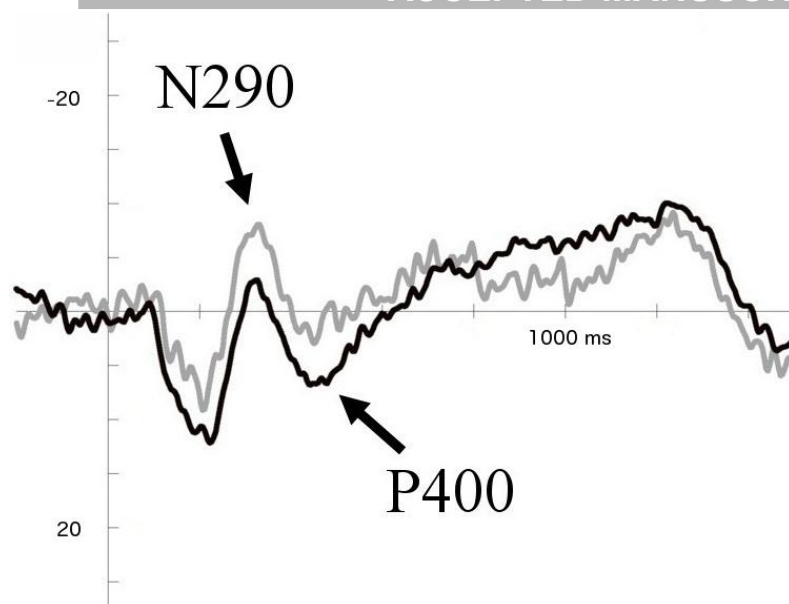


fig2

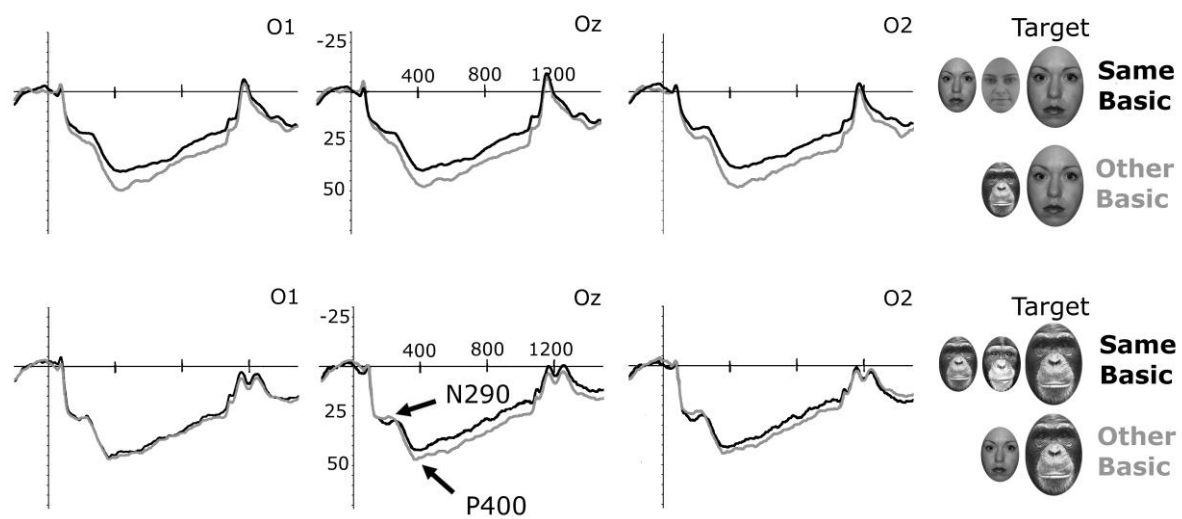


fig3

### Highlights

- Behavioral and EEG research on infant categorization is reviewed.
- Infants accomplish global-level categorization before basic-level categorization.
- ERPs reveal a similar sequence of categorization processes in the infant brain.
- Rapid repetition and fast periodic stimulation inform about infant categorization.