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The neural basis of perceptual category learning in human infants

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ABSTRACT

We measured looking times and event-related brain potentials (ERPs) to examine the cognitive and brain bases of perceptual category learning in 6-month-old infants. In Experiment 1, we showed that categorization and exemplar discrimination rely on different cortical processes. Specifically, the repetition of individual exemplars resulted in differential cortical processing at posterior channels at an early stage during object processing (100-300 ms), whereas discriminating amongst members of different categories was reflected in ERP differences over anterior cortical regions occurring later in time (300-500 ms) than the repetition effects. In Experiment 2, replicating the findings of Study 1, we found that infants engage the same cortical processes to categorize visual objects into basic level categories, regardless of whether a basic- (Bird vs. Fish) or global-level is crossed (Birds vs. Cars). This pattern of findings is consistent with perceptual accounts of infant categorization (Quinn & Eimas, 1996) and accords with recent adult neural-level models of perceptual categorization.

GENERAL INTRODUCTION

Categorization, the ability to recognize physically different objects as members of the same group, is a powerful process that helps us to structure and understand our environment. From insects to primates, categorization is evident across a broad range of animal species (Freedman & Miller, 2008). However, whereas in mammals and birds many categories are learned, in insects, reptiles and amphibia, adaptive categorization is genetically determined (e.g. Wyttenbach, May, & Hoy, 1996). The capacity to learn categories and to use this knowledge flexibly plays an important role in inference, prediction, decision-making, and language acquisition, and is thus integral to all kinds of human behavior.

One important aspect of categorization is our ability to group objects at different levels of abstraction. Adult category representations are organized hierarchically; while maintaining the ability to discriminate individual exemplars, we make basic-level distinctions as between birds and fish, global-level distinctions as between animals and vehicles, and subordinate-level distinctions as between robins and sparrows (Curran, Tanaka, & Weiskopf, 2002; Rosch & Lloyd, 1978). There is work to suggest that different brain and cognitive processes might allow for categorization at different levels of the hierarchy in adults (Tanaka, Luu, Weisbrod, & Kiefer, 1999).

While there is behavioral evidence that from very early in life human infants are able to learn new categories (see Mareschal & Quinn, 2001, for a review), little is known about the neural basis of perceptual categorization in infancy. Since disentangling bottom-up and top-down processing in adult category learning is notoriously difficult, studying category learning in prelinguistic infants that have little or no prior

knowledge of the many categories in their environment provides a unique way of exploring natural perceptual category learning (French, Mareschal, Mermillod, & Quinn, 2004). In the current study, we measured looking times and event-related brain potentials (ERPs) to systematically examine the cognitive and cortical mechanisms of object perceptual categorization in 6-month-old infants. Specifically, we asked (a) whether different neural signatures accompany basic-level perceptual category and exemplar distinctions in young infants, and (b) whether infants engage different brain processes when they make basic-level distinctions within or across taxonomic global-level boundaries.

At the neural level, studies with monkeys (Freedman, Riesenhuber, Poggio, & Miller, 2002; 2003) have provided support for a model of category learning in which neuronal populations in extrastriate visual cortex come to acquire higher degrees (sharper tuning) of selectivity for trained exemplars of stimuli within a category - a mechanism also hypothesized to underlie many developmental changes in infant categorization (Westermann & Mareschal, 2004). These exemplar-selective neurons provide input to higher cortical areas such as prefrontal cortex in which, after training, category-specific responses can be observed. Recently, in a functional magnetic resonance imaging (fMRI) study, Jiang et al. (2007) observed a very similar pattern of findings with human adults, providing further support for this model. Specifically, this study revealed a sharpening of representations coding for physical appearance of an object in lateral occipital cortex, and found an area in prefrontal cortex that selectively responded to explicit changes in category membership. Taken together, recent monkey and human neuroimaging studies support a general model in which dissociable, but possibly interdependent (see Jiang

et al., 2007), cortical processes enable exemplar-based representations in posterior cortex and category-based representations in anterior cortex.

Furthermore, ERP studies with adults have provided important insights into the dynamics of the brain processes involved in category learning and perceptual expertise. For example, in a series of category learning studies, Scott, Tanaka, Sheinberg, & Curran (2006, 2008) found that at the behavioral level, subordinate-level training but not basic-level training resulted in improved discrimination of trained exemplars, and that at the neural level the ERP data revealed that whereas training at both levels was associated with an increased N170 only subordinate-level training results in an enhanced N250 component at posterior channels. Global-level categorizations however have been shown to elicit an enhanced anterior negativity in adults' ERPs with a peak around 350 ms (Tanaka et al. 1999). This anterior ERP effect observed in adults and in older infants in picture-word matching tasks (12-month-olds; Friedrich & Friederici, 2005) has been interpreted as increased semantic processing. The pattern of these ERP findings suggests that brain processes related to discrimination of trained exemplars and (semantic) categorization are distinct in their timing (early versus late) and also differ with respect to their scalp topography (posterior versus anterior). Thus, these spatio-temporal characteristics of the brain processes identified in the adult brain provide an interesting framework in which infant ERP responses can be conceptualized.

Quinn and colleagues (2006) report the only existing ERP study of visual categorization in infants. In this study, 6-month-olds were familiarized with cat images and then tested with novel cat interspersed with novel dog images. Images from the novel category elicited an

enhanced Negative component (Nc) at anterior channels in infants' ERPs indicating that infants had learned the category successfully. Although this has been an important first step in illuminating the cortical bases of perceptual categorization in infancy, there are a number of vital questions that have not been addressed. First, given the neural model based on adult data presented above, it is important to directly compare the cortical processes related to exemplar-based representations (within-category) and to category-based representations (across-categories) to see whether, like in adults, these cortical processes are already dissociable in early human development. Second, Quinn et al. (2006) showed evidence of categorization in only one direction (discrimination of dogs from a newly acquired category of cats) but not bi-directionally (symmetrical) as would be expected from robust adult categorization (French, Mareschal, Mermillod, & Quinn, 2004). It is thus important to demonstrate symmetrical categorization in infants and investigate its underlying neural mechanisms. Third, it has not been tested whether (in young infants) making basic-level perceptual category distinctions across a global-level divide recruits different neural processes than making basic-level judgments within global-level boundaries. We tested all of these questions in the following two studies. In order to build upon and extend the previous infant ERP findings (Quinn et al., 2006) we also studied 6-month-old infants.

STUDY 1:

INTRODUCTION

In Study 1, we presented infants with either bird or fish images during the learning phase (familiarization), and then tested them with novel images from the familiar and unfamiliar categories (see Figure 1). In

addition, we presented 4 images during the familiarization repeatedly, which were then shown again during test, to assess infants' visual recognition of repeated exemplars. A first group of infants was tested behaviorally (Study 1a): (i) to see whether infants discriminate the newly learned category from an unfamiliar category as indexed by longer looking at images from the unfamiliar category when compared to images from the learned (familiar) category under the rapid presentation regime typical of ERP studies, and (ii) to assess whether after repeated presentation of exemplars during the familiarization, infants would discriminate those familiar exemplars from unfamiliar exemplars as indexed by longer looking at the unfamiliar exemplars. We measured ERPs in a second group of infants (Study 1b) and hypothesized that perceptual categorization and exemplar repetition will be associated with distinct cortical signatures in the infant brain. More specifically, on the basis of Quinn et al.'s (2006) findings, we predicted that the detection of a novel category will result in an enhanced fronto-central component (Nc) in infants' ERPs, whereas computations related to recognizing repeated objects within the familiar category will affect processes in posterior cortical regions (at occipital sensors over visual cortex, see e.g. Carver, Meltzoff, & Dawson, 2006).

METHODS

Participants.

Studies 1a & 1b:

Thirteen infants participated in the behavioral experiment of Study 1a. The final sample consisted of 12 infants (6 girls), aged between 167 and 192 days ($M = 179$ days). One of them was excluded because of completing too few trials. Twenty-two infants participated in the ERP experiment of Study

1b. The final sample consisted of fourteen infants (7 girls), aged between 169 and 188 days ($M = 177$ days). Eight of them were excluded because of excessive artifacts or completing too few trials.

Stimuli. The stimuli were digitized color photographs of visual objects from two different categories (birds and fish) (see Figure 1). For each category we developed a set of 28 images. Across the three categories, object images were matched for object size, luminance and color. The visual angle of the images subtended $20^\circ \times 13^\circ$ on average. Although screens of different sizes were used, visual angles of the object stimuli were kept constant across behavioral and ERP experiments.

Behavioral procedure and data analysis. The infants sat on their parent's lap at a 100 cm distance from a large flat screen monitor within an acoustically shielded and dimly lit room. A video camera mounted below the monitor and centered on the infant's face allowed us to record the infant's looking behavior. The first two trials were 15 s long and assessed the infant's prior preference for either of the two object categories in a visual paired comparison (VPC) task. In these two trials we presented two images (one exemplar of each category) side-by-side. Sides (left or right) of presentation were counterbalanced from the first to the second trial. This prior preference test was followed by the familiarization phase in which we presented infants with 40 1-s trials (images) from one category in pseudo-randomized order. This is substantially shorter than the typical 10-second presentation time of behavioral visual preference studies (see Mareschal & Quinn, 2001) but it was necessary in order to ensure that identical familiarization procedures were used across behavioral and ERP experiments. These 40 trials consisted of 24 different visual objects. Four of these 24 objects were randomly selected and presented five times and the

other 20 objects were presented only once.

After the familiarization, we presented infants with four 15-s long VPC test trials (see Figure 1). In the first two VPC test trials we assessed infants' ability to distinguish the familiar from an unfamiliar category. Infants saw a new image from the familiar category (i.e., an image that had not been presented during familiarization) presented side-by-side with an image from the new category. During the third and fourth VPC test trials we examined infants' ability to identify familiar exemplars from the familiar category and to discriminate them from unfamiliar exemplars from the familiar category. Infants saw a new image from the familiar category side-by-side with an image from the familiar category that had been repeated five times during familiarization. As in the prior preference test, sides of presentation (left and right) were counter-balanced during all four test trials. In between all trials a fixation stimulus (a flower) that was accompanied by sound effects was presented. From the video we coded infants' looking behavior and measured the cumulative duration of their looks during the VPC in the prior preference, the categorization and identification tests. Paired *t*-tests were used to compare looking time differences between conditions statistically.

ERP procedure. The infants sat on their parent's lap at a 60-cm distance from a 19" computer monitor within an acoustically and electrically shielded and dimly lit room. A video camera mounted below the monitor and centered on the infants' face allowed us to record their looking behavior. The experimental procedure in the ERP study was as closely matched to the behavioral study as possible. All object stimuli were presented for 1 s followed by a randomly varying (500-700 ms) inter-stimulus interval during which a fixation stimulus (flower) accompanied

by various sounds effects was presented. As in the behavioral study, during the familiarization phase, we presented infants with 40 trials (images) from one category in pseudo-randomized order (4 images were repeated during the familiarization 5 times). After the familiarization, infants watched three kinds of test trials: four familiar category-repeated images (which had been presented five times during familiarization), four familiar category-new images (not presented during familiarization), and eight new category images. Images were presented in a pseudo-randomized order with no more than two images from the same category presented in succession. Infants typically completed between 120 and 150 trials (including familiarization) before the session was concluded.

EEG Recording and Data Analysis. The brain's electric activity was measured with the infant version of the Geodesic Sensor Net (64 Channel V2.0). The reference electrode was the vertex (Cz in the conventional 10/20 system). The electrical potential was amplified with 0.1–100 Hz bandpass, digitized at 250 Hz sampling rate and stored on computer disk for the off-line analysis. The behavior of all participants was initially coded from videotape so that only those trials in which the infants were fixating the center of the screen during the trial, without blinking or eye or head movements were included in the analysis of electrophysiological signals. Data from each sensor were removed if they contained artifacts created by movement or poor contact. The entire trial was excluded if data from more than 10 sensors had been removed or if the trial contained an eye blink or other artifact. Missing data for trials with 10 or fewer bad channels were interpolated using spherical spline interpolation. Data were re-referenced to average reference, baseline-corrected and then individual participant averages were computed for each trial type. Infants with less

than 10 artifact-free trials in the familiarization conditions, or less than 15 artifact-free trials in any of the test conditions, were excluded. The average number of trials was: (1) during familiarization: repeated trials $M = 14.5$ ($SD = 4.0$), not repeated trials $M = 15.8$ ($SD = 3.7$); (2) during test: familiar category trials $M = 21.4$ ($SD = 5.7$), new category trials $M = 23.1$ ($SD = 6.2$). Average ERPs were obtained time-locked to the onset of the object stimulus, ERP amplitude was assessed by averaging the data within two regions of interest (anterior channels [3,4,5,8,9,13,17,18,30,43,54,55,58,62]: electrodes over the frontal cortex; posterior channels [32,33,34,37,38,39,40,41,45]: electrodes over the occipito-posterior temporal cortex) (see Figures 3,4,6, and 7) for three consecutive time windows (100-300 ms, 300-500 ms, 500-1000 ms). These regions of interest and time windows were chosen on the basis of previous studies (Quinn et al., 2006; Carver et al., 2006) and the visual inspection of the data. Repeated measures ANOVAs with the within-subjects factors region (anterior, posterior) and condition (for within-category contrast: repeated, not repeated; for between-category contrast: new items new category, new items familiar category) were conducted to examine the ERP effects statistically. These ANOVAs were performed on transformed (vector scaled) data according to McCarthy and Woods (1985). Planned comparisons (within-category and between category) were conducted for posterior and anterior regions separately using paired sample t -tests.

RESULTS

Study 1: Basic-level categorization within a single global category

(Birds vs. Fish)

Behavioral results.

An overview of the behavioral results in Study 1 is shown in Figure 2. Our

analysis revealed that before familiarization infants had no prior preference for birds over fish images, $t(11) = 0.56, p = 0.59$. After familiarization to images of one category infants showed a preference for images from the novel category, i.e. they looked significantly longer at images from the new category when compared to new images from the old (familiar) category, $t(11) = 3.13, p = 0.01$. A significant novelty preference (longer looking) was also found for new (not repeated) images over repeated images from the familiar category, $t(11) = 2.28, p = 0.04$. There were no significant differences between the groups of infants that were familiarized to birds versus fish.

ERP results.

Within-category contrast:

Our analysis revealed a two-way interaction between region (anterior, posterior) and condition (repeated, not repeated) during the familiarization ($F [1, 13] = 6.82, p = 0.022$) and during the test ($F [1, 13] = 7.91, p = 0.015$) for the within-category comparison. As shown in Figure 3, during familiarization, repeated images when compared to non-repeated images elicited an enhanced early positive component (100 to 300 ms) at posterior channels, $t(13) = 2.71, p = 0.017$. However, during test, this effect was reversed, i.e., repeated images elicited an early positive component (100 to 300 ms) that was suppressed in its amplitude when compared to the non-repeated images, $t(13) = 2.93, p = 0.012$. No such effects were obtained at anterior channels. There were no significant differences between the groups of infants that were familiarized to birds versus fish.

Between-category contrast:

Our analysis revealed a two-way interaction between region (anterior, posterior) and condition (new items familiar category, new items new

category) for the between-category comparison during test ($F [1, 13] = 9.77, p = 0.008$). As shown in Figure 4, at anterior channels, images of the new category compared to images of the familiar category elicited a mid-latency (300 to 500 ms) negative component (Nc, Quinn et al., 2006) that was enhanced in its amplitude, $t(13) = 3.57, p = 0.003$. In addition, the results revealed that images of the familiar category when compared to the new category evoked an enhanced late positive component (500 to 1000 ms), whereas images from the new category resulted in a potential that returned to baseline, $t(13) = 3.14, p = 0.008$. The late positive component was also found to be greater in amplitude when the new items of the familiar category were compared to the repeated items of the familiar category, $t(13) = 2.47, p = 0.028$. No such effects were obtained at posterior channels. There were no significant differences between the groups of infants that were familiarized to birds versus fish.

DISCUSSION

In Study 1, we showed that repeating individual exemplars resulted in differential cortical processing at posterior channels at an early stage during object processing, whereas discriminating amongst members of different categories was reflected in ERP differences over anterior cortical regions occurring later in time than the repetition effects of individual exemplars. More specifically, the anterior component (Nc) did not differ between new and familiar instances of the familiar category, but was enhanced for new items of the unfamiliar category, providing ERP evidence that infants have categorized. This pattern of findings including the timing and the topography of the effects is in line with previous ERP work on perceptual category learning in adults (Scott et al., 2006, 2008; Tanaka et al. 1999), and it critically extends the one previous infant ERP

study on this topic (Quinn et al., 2006).

The timing of the ERP responses reported in this study with an earlier component for within-category discrimination and a later component for categorization in infants seem to be inconsistent with behavioral findings in adults showing faster categorization relative to object identification (Grill-Spector & Kanwisher, 2005). However, this difference might be explained by the fact that adults were explicitly instructed to specifically identify objects on the basis of linguistic subordinate labels, whereas infants in the current study had to simply detect the items that were repeated.

The repetition of exemplars within a category evoked an increase in amplitude during the learning (familiarization) phase and a decrease in amplitude during the test phase over the same posterior regions. Amplitude changes with repetition of a visual stimulus have been measured at the level of individual neurons in macaques (Desimone, 1996) and with brain imaging methods in human adults (for a review, see Grill-Spector, Henson, & Marin, 2006). Similar repetition effects have been observed in young infants for posterior ERP components (N290 and P400) in response to face stimuli (Gliga & Dehaene-Lambertz, 2007). The familiarity of the stimuli affects the direction of the repetition effects: an increase in response occurs for unfamiliar stimuli and a decrease with the repetition of familiar stimuli (Henson, Shallice, & Dolan, 2000). These dynamics are believed to correspond to an initial learning period when a representation of stimulus is created and more perceptual information is incorporated to represent an object (the response enhancement), followed by an adaptation of the response once a more robust object representation is formed (the response suppression). The current ERP findings with

infants reveal a very similar pattern of repetition enhancement and suppression depending on the familiarity of an object, suggesting that similar perceptual learning mechanisms as found in adults might be at work already early in human development. However, our design did not allow us to examine exactly how much experience (how many repetitions) is required to form a robust exemplar representation. Thus, studying repetition effects during infancy and correlating them with behavioral discrimination measures in future studies will provide important insights into the neural mechanisms and development of perceptual learning.

STUDY 2:

INTRODUCTION

In Study 2, we presented 6-month-old infants with either bird or car images during the learning phase (familiarization), crossing categories at a global level (animals versus vehicles), and then tested them with novel images from the familiar and unfamiliar categories. As in Study 1, we presented 4 images during the familiarization repeatedly, which were then repeated during test to assess infants' visual recognition (see Figure 1). We examined both behavioral (Study 2a) and ERP measures (Study 2b) in two separate groups of infants. On the basis of perceptual accounts of infant category learning (Quinn & Eimas, 1996; 2000), we hypothesized that infants at this age utilize similar cortical processes to categorize visual objects regardless of the level at which a category boundary is crossed (Study 1: basic-level within a single global level, or Study 2: basic-level across two global levels). Therefore we predicted that Study 2 would replicate the effects found in Study 1.

Participants.

Studies 2a & 2b:

Seventeen infants participated in the behavioral experiment of Study 2a. The final sample consisted of 16 infants (9 girls), aged between 166 and 194 days ($M = 181$ days). One infant was excluded because of completing too few trials. Twenty-five infants participated in the ERP experiment of Study 2b. The final sample consisted of fourteen infants (7 girls), aged between 170 and 192 days ($M = 178$ days). The remaining 11 were excluded because of excessive artifacts or completing too few trials.

Stimuli. The stimuli were digitized color photographs of visual objects from two different categories (birds and cars) (see Figure 1). The creation of the stimuli was otherwise kept identical to Study 1.

Behavioral procedure and data analysis, ERP procedure, and EEG Recording and Data Analysis.

All these aspects of Study 2 were kept identical to Study 1. The average number of trials was: (1) during familiarization: repeated trials $M = 13.2$ ($SD = 3.3$), not repeated trials $M = 14.1$ ($SD = 4.1$); (2) during test: familiar category trials $M = 22.7$ ($SD = 3.9$), new category trials $M = 24.3$ ($SD = 4.8$).

RESULTS

Study 2: Basic-level categorization across two global categories (Birds vs. Cars)

Behavioral results.

An overview of the behavioral results in Study 2 is shown in Figure 5. Our analysis revealed that before familiarization infants had no prior preference for cars over birds, $t(15) = 1.85$, $p = 0.09$. After familiarization to images of one category infants showed a preference for images from the novel category, i.e., they looked significantly longer at images from the new category when compared to new images from the familiar category, $t(15) = 3.50$, $p = 0.003$. The difference in looking time post familiarization

was significantly greater than the difference in looking time in the prior preference test $t(15) = 2.74, p = 0.015$. A significant novelty preference (longer looking) was also found for new (not repeated) images over repeated images from the familiar category, $t(15) = 5.97, p < 0.001$. There were no significant differences between the groups of infants that were familiarized to birds versus cars.

ERP results.

Within-category contrast:

Our analysis revealed a two-way interaction between region (anterior, posterior) and condition (repeated, not repeated) during the familiarization ($F [1, 13] = 7.13, p = 0.019$) and during the test ($F [1, 13] = 6.25, p = 0.026$) for the within-category comparison. As shown in Figure 6, during familiarization, repeated images when compared to non-repeated images elicited an enhanced early positive component (100 to 300 ms) at posterior channels, $t(13) = 2.57, p = 0.023$. During test, this effect was reversed, i.e. repeated images elicited an early positive component (100 to 300 ms) that was suppressed in its amplitude when compared to the non-repeated images, $t(13) = 2.83, p = 0.014$. No such effects were obtained at anterior channels. There were no significant differences between the groups of infants that were familiarized to birds versus cars.

Anterior channels (between-category contrast):

Our analysis revealed a two-way interaction between region (anterior, posterior) and condition (new items familiar category, new items new category) for the between-category comparison during test ($F [1, 13] = 11.51, p = 0.004$). As shown in Figure 7, at anterior channels, images of the new category compared to images of the familiar category elicited a mid-latency Nc (300 to 500 ms) that was enhanced in its amplitude, $t(13) = 3.38,$

$p = 0.005$. In addition, the results revealed that images of the familiar category when compared to the new category evoked an enhanced late positive component (500 to 1000 ms), whereas images from the new category resulted in a potential that returned to baseline, $t(13) = 2.93$, $p = 0.012$. The late positive component was also found to be greater in amplitude when the new items of the familiar category were compared to the repeated items of the familiar category, $t(13) = 2.25$, $p = 0.042$. No such effects were obtained at posterior channels. There were no significant differences between the groups of infants that were familiarized to birds versus cars.

Comparison of ERP findings of Study 1 and 2:

In order to compare statistically the pattern of ERP findings between Study 1 and 2, we calculated (1) the ERP amplitude differences between the experimental conditions, and (2) the peak latency of this difference for each infant. For these two dependent measures, we then conducted repeated measures ANOVAs with between-subjects factor *Study* (two levels: Study1, Study 2) and within-subjects factor *ERP effect* (four levels: familiarization posterior channels, test posterior channels, test anterior channels Nc, test anterior late positive component). This analysis revealed no main effect of the factor *Study* (ERP amplitude: $F[1, 26] = 0.35$, $p = 0.559$, $\eta_p^2 = 0.079$; peak latency: $F[1, 26] = 0.18$, $p = 0.675$; $\eta_p^2 = 0.063$) and no interaction between the factors *Study* and *ERP effect* (ERP amplitude: $F[3, 78] = 0.19$, $p = 0.903$, $\eta_p^2 = 0.017$; peak latency: $F[3, 78] = 0.32$, $p = 0.811$, $\eta_p^2 = 0.038$) for either of the dependent measures (ERP amplitude difference and peak latency), indicating that there were no significant differences in the ERP findings across studies.

DISCUSSION

In Study 2, we contrasted basic-level categories (birds and cars) that crossed a taxonomic global-level boundary (animals and vehicles) and replicated the behavioral and ERP effects reported in Study 1, indicating that perceptual categorization processes can be reliably elicited in these young infants. As predicted, there were no differences in the brain processes that 6-month-old infants engage when they discriminate between basic-level categories within (Study 1) or across the global-level (Study 2) of an abstract hierarchy. This suggests that in our study infants do not employ any additional or different brain processes when they tease apart basic-level perceptual categories that belong to different global-level categories (i.e., Animals and Vehicles). Finally, in the current study, this distinction was assessed by contrasting two basic-level perceptual categories instead of two global-level categories consisting of various basic-level exemplars (e.g., Animals: fish, birds, horse, etc.) because using global-level categories would have introduced additional perceptual variance across categories, thereby introducing a confound between perceptual variability and level of categorization in any comparison of the ERP effects across Study 1 and Study 2 (see Thierry, Martin, Downing, & Pegna, 2007).

GENERAL DISCUSSION

Event-related brain potentials measured in 6-month-olds in a perceptual category learning paradigm revealed that (a) perceptual categorization and exemplar discrimination rely on cortical processes that are distinct in timing and spatial distribution and (b) that at this age, infants utilize similar cortical processes to categorize visual objects at the basic level regardless of whether the distinction is within or across taxonomic global-level domains.

Previous work with human adults and monkeys has revealed category-based representations in prefrontal cortex (see Freedman & Miller, 2008, for a review). Similarly, we found that in 6-month-olds an ERP component (Nc) over anterior cortical regions was sensitive to category information. In prior work the cortical sources of this infant ERP component have been localized in prefrontal cortex (including inferior, medial and superior frontal gyri, and the anterior cingulate cortex; see Reynolds & Richards, 2005). The similarity between the adult and monkey findings and the current data seems striking but one has to be careful in interpreting this similarity since different methods were used across studies. Furthermore, the infant Nc component is associated with a wide range of attention-recruiting tasks (Csibra, Kushnerenko, & Grossmann, in press) and may therefore not be a category-specific response *per se* but could rather be interpreted in terms of increased attention allocation towards the out-of-category exemplar. However, this would not undermine the fact that only the out-of-category exemplars, not the new exemplars of the familiar category, grabbed the infants' attention, as reflected in the specific modulation of this ERP component.

Following the Nc, we observed a late positive component (LPC) in response to new items of the familiar category, whereas items of the new category resulted in a return to baseline. This infant ERP component is thought to be involved in the updating of an existing memory representation (Nelson & Collins, 1991; see also Nelson, 1994; Nelson, Thomas, de Haan, & Wewerka, 1998, for discussion of the response properties of this component) and might thus reflect processes related to the integration of new exemplars into an already existing representation (possibly prototype) of the familiar category. This interpretation is also

consistent with (a) the finding that novel exemplars of the familiar category elicited a larger LPC than repeated exemplars of the familiar category, and (b) the notion that this component might be an index of category learning as suggested by Quinn and colleagues (2006). It is interesting to note that although the LPC occurred later in the ERP than the Nc, both components showed a very similar scalp topography, which might indicate that out-of-category detection and updating of category representations relies on similar brain processes but differs with respect to its timing.

Another line of work that might help to interpret our current findings has compared implicit to explicit category learning in adults using fMRI. Reber, Gitelman, Parrish, and Mesulam (2003) observed decreased occipital activity for novel categorical stimuli compared with non-categorical stimuli following implicit learning. In contrast, after explicit (instructed) learning, novel categorical stimuli evoked increased activity in the prefrontal cortex (and some other regions), suggesting that category knowledge depends on how it is learned. This pattern of findings in adults may suggest that infants, who showed a category-sensitive component over anterior brain regions in the current study, are actively engaged in organizing the stimuli they were presented with into categories.

Another important finding of our study was that, for both behavioral and ERP measures, it did not seem to matter whether the basic-level categories contrasted crossed a global-level divide or not. Birds were considered as far apart from fish as they were from cars, as suggested by the similar Nc responses evoked by the new category exemplars in Study 1 and Study 2. This is consistent with perceptual account of early infant categorization, at least at the age we have tested (Quinn & Eimas, 1996,

2000; Quinn, Johnson, Mareschal, Rakison, & Younger, 2000). In future work the paradigm developed in this study could be used to (a) examine older infants who are known to have acquired conceptual category knowledge to see how this affects the brain processes involved in object categorization (see Mandler, 2004), and (b) to assess global-level categorization directly by contrasting, for example, animals (fish, birds, etc.) and vehicles (cars, boats, etc.).

In summary, the current study provided important insights into the brain dynamics of perceptual learning and categorization in infancy. It further provided developmental support for an existing neural-level model of perceptual categorization that was thus far based on neuroimaging work with adults and monkeys (Freedman & Miller, 2008; Scott et al. 2006, 2008; Tanaka et al. 1999). Thus, this study demonstrates how cognitive neuroscience and developmental cognitive psychology can cross-fertilize each other and thereby contribute to the progress in the new field of developmental cognitive neuroscience (Johnson, 2005).

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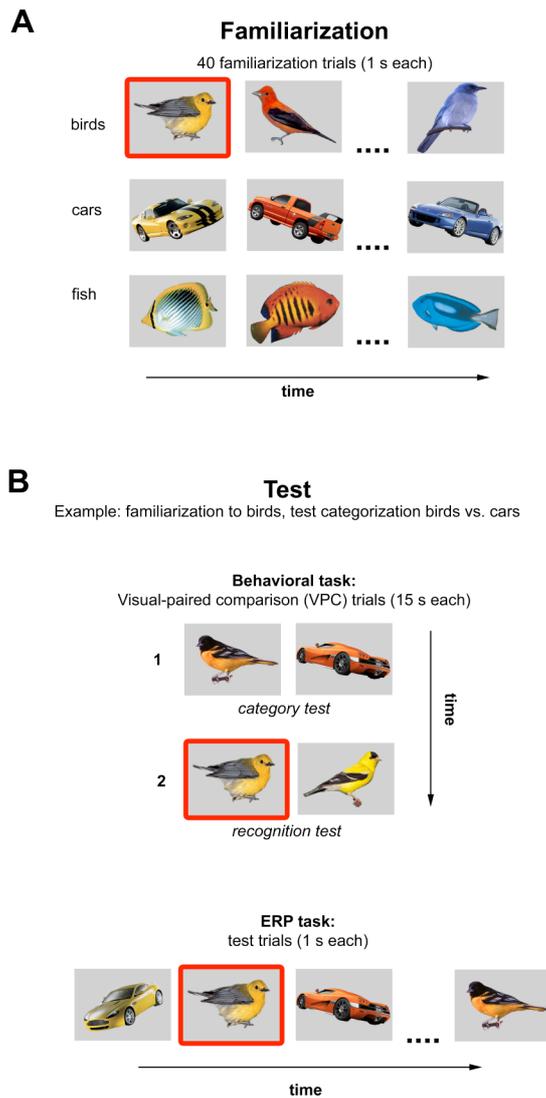


Figure 1: This is an illustration of the procedures (A: Familiarization; B: Test) used in the behavioral and ERP tasks using example stimuli from all three categories (birds, cars, and fish). As shown here, the familiarization phase was identical for behavioral and ERP tasks. Please note that for illustration purposes an example item that was repeated during familiarization and test is marked by a red frame. This was not the case during the presentation to the infants. For further procedural details see Method sections of Study 1 and 2.

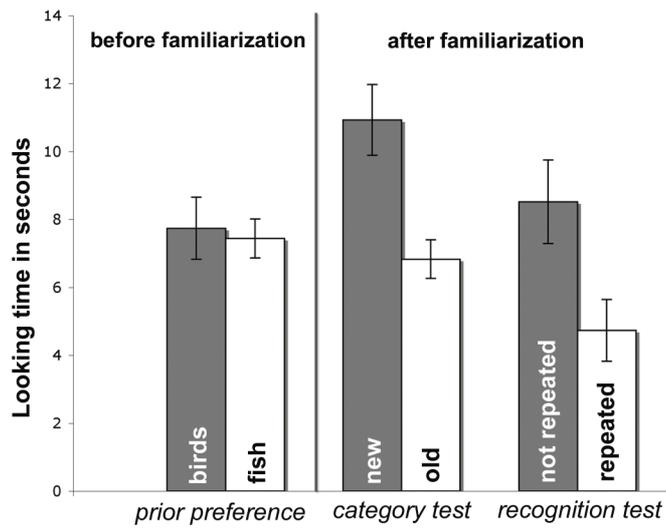


Figure 2: Overview of behavioral looking time results for the prior preference, category and visual recognition tests of Study 1.

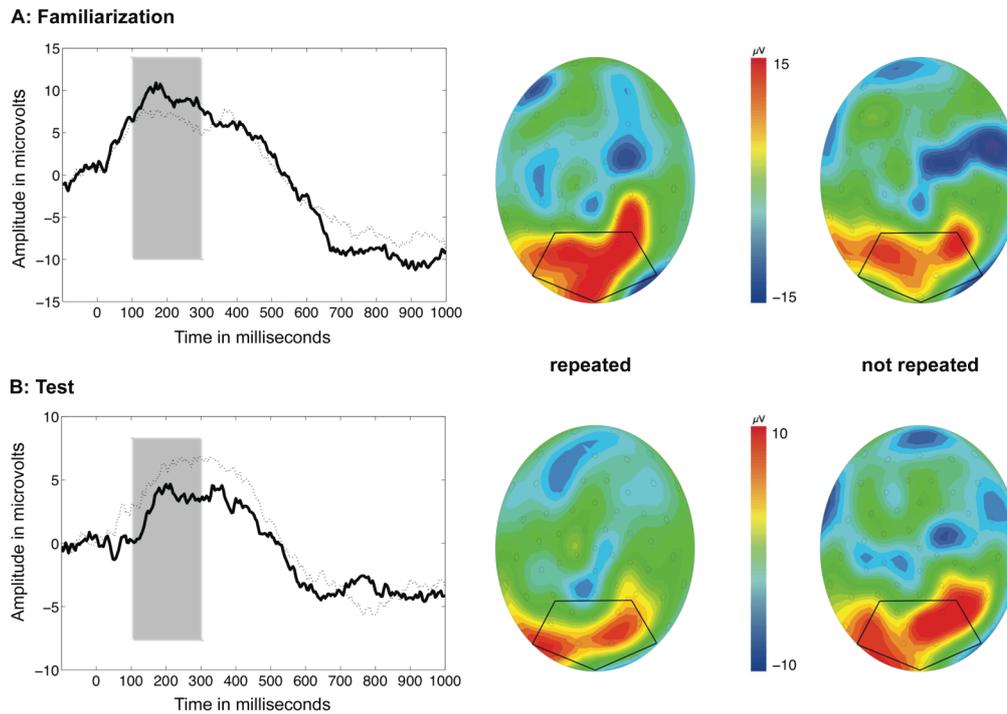


Figure 3: This graph depicts the ERPs measured in Study 1 at posterior channels during familiarization and test (left) in response to repeated items (solid line) and not repeated items (dotted line) and the scalp topography of the ERPs (right). Selected channels used for calculating the ERPs on the left were within the region marked on the scalp topography map by the black frame. The time window (100 to 300 ms) during which statistically significant differences between conditions were found is marked in gray. The scalp topography is an average for a time window from 160 to 240 ms.

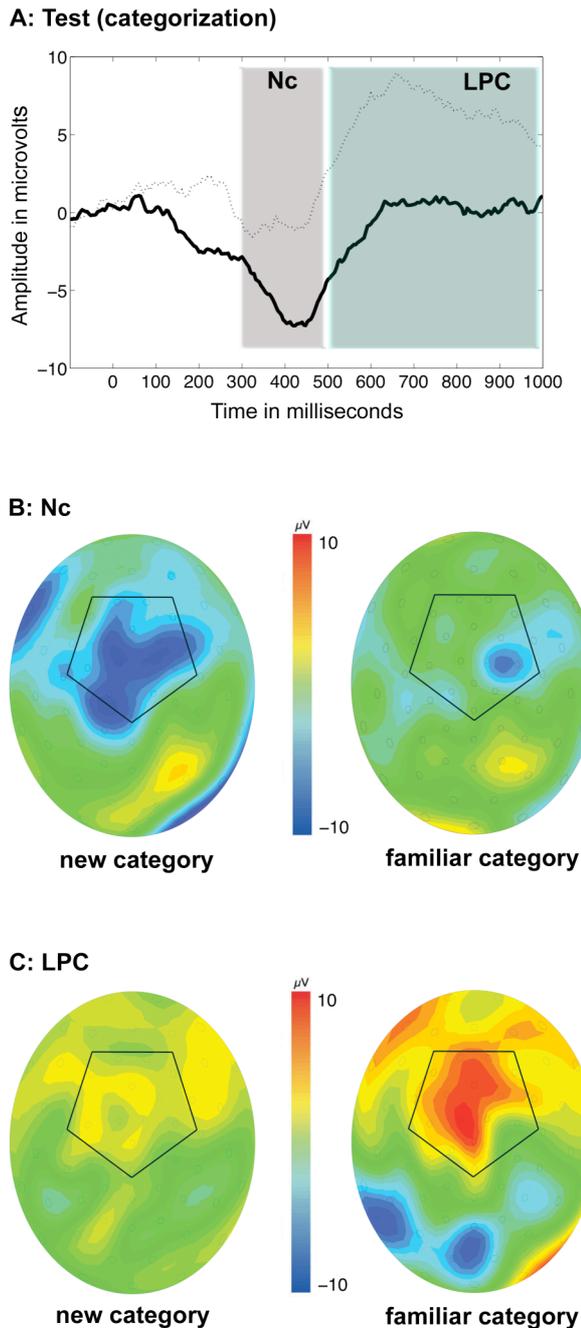


Figure 4: This graph depicts the ERPs measured in Study 1 at anterior channels during test (top) in response to new items from the new category (solid line) and new items from the familiar category (dotted line) and the scalp topography of the ERPs (right). Selected channels used for calculating the ERPs on the left were within the region marked on the scalp topography map by the black frame. The time windows (Nc: 300 to 500 ms; LPC: 500 to 1000 ms) during which statistically significant differences between conditions were found are marked in gray and green respectively. Nc scalp topography is an average for a time window from 360 to 440 ms. LPC scalp topography is an average for a time window from 640 to 720 ms.

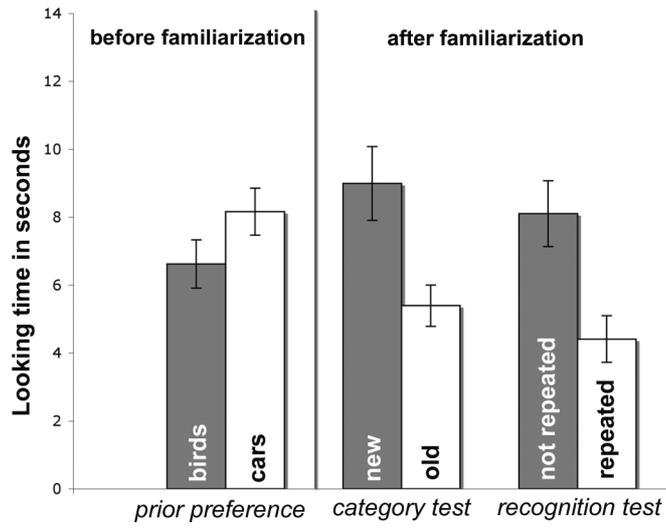


Figure 5: Overview of behavioral looking time results for the prior preference, category and visual recognition tests of Study 2.

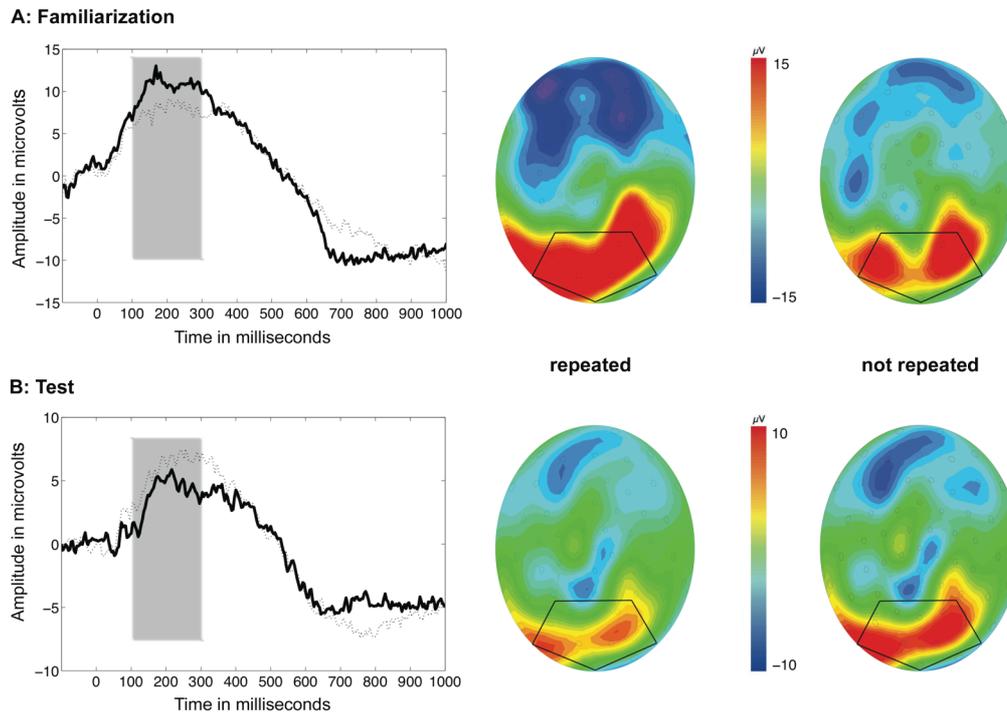


Figure 6: This graph depicts the ERPs measured in Study 2 at posterior channels during familiarization and test (left) in response to repeated items (solid line) and not repeated items (dotted line) and the scalp topography of the ERPs (right). Selected channels used for calculating the ERPs on the left were within the region marked on the scalp topography map by the black frame. The time window (100 to 300 ms) during which statistically significant differences between conditions were found is marked in gray. The scalp topography is presented for a time window from 160 to 240 ms.

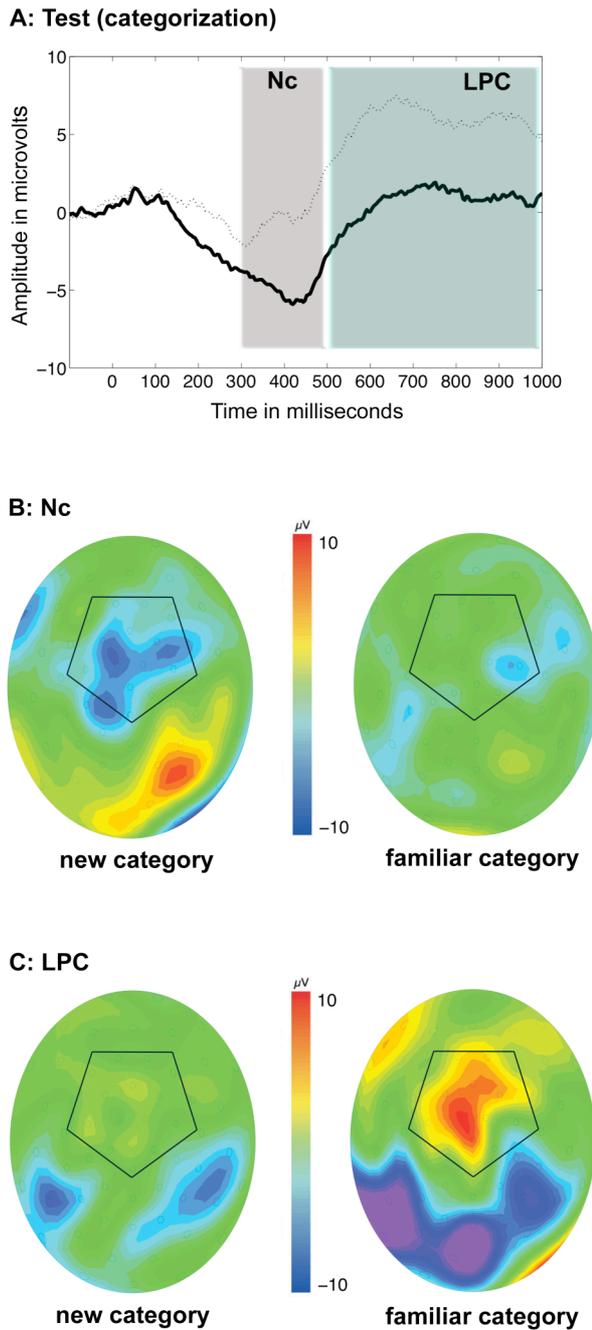


Figure 7: This graph depicts the ERPs measured in Study 2 at anterior channels during test (top) in response to new items from the new category (solid line) and new items from the familiar category (dotted line) and the scalp topography of the ERPs (right). Selected channels used for calculating the ERPs on the left were within the region marked on the scalp topography map by the black frame. The time windows (Nc: 300 to 500 ms; LPC: 500 to 1000 ms) during which statistically significant differences between conditions were found are marked in gray and green respectively. Nc scalp topography is an average for a time window from 360 to 440 ms. LPC scalp topography is an average for a time window from 640 to 720 ms.