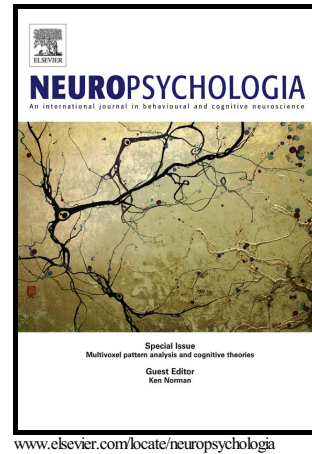


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1 Neural Correlates of Individuation and Categorization of Other-Species Faces in Infancy

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17 **Abstract**

18 The goal of this study was to investigate 9-month-old infants' ability to individuate and
19 categorize other-species faces at the subordinate level. We were also interested in examining the
20 effects of initial exposure conditions on infant categorization and individuation processes.

21 Infants were either familiarized with a single monkey face in an individuation procedure or
22 familiarized with multiple exemplars of monkey faces from the same species in a categorization
23 procedure. Event-related potentials were recorded while the infants were presented: familiar
24 faces, novel faces from the familiar species, or novel faces from a novel species. The
25 categorization group categorized monkey faces by species at the subordinate level, whereas the
26 individuation group did not discriminate monkey faces at the individual or subordinate level.

27 These findings indicate initial exposure to multiple exemplars facilitates infant processing of

1 other-species faces, and infants are efficient at subordinate-level categorization at 9 months of
2 age.

3 **Introduction**

4 Being able to recognize a familiar face based on its unique features and categorize groups
5 of novel faces based on their shared features is fundamental for human social interaction.
6 However, humans are not born face experts, and mastering the ability to categorize and
7 individuate faces is an important task of social development. Categorization is the process by
8 which individual exemplars are classified into groups based on shared characteristics (e.g.,
9 classifying an animal as a cat), whereas individuation is the process of discriminating among
10 exemplars of a category at the individual level (e.g., recognizing your family cat among a group
11 of cats; Hugenberg et al., 2010). Infants show gains in processing faces at the individual
12 (Mondloch, LeGrand, & Maurer, 2010) and categorical (Madole & Oakes, 1999) levels during
13 infancy. For example, infants begin to categorize faces based on gender (e.g., Rennels, Kayl,
14 Langlois, Davis, & Orlewicz, 2016), attractiveness (e.g., Ramsey, Langlois, Hoss, Rubenstein, &
15 Griffin, 2004), and race (e.g., Anzures, Quinn, Pascalis, Slater, & Lee, 2010).

16 The development of categorization moves from general to specific in the first year of life.
17 Superordinate (or global) categorization is the broadest level and has been seen in 2-month-olds
18 when forming a category for animate objects that excludes inanimate objects (mammals vs.
19 furniture; Quinn & Johnson, 2000). The next level, basic, is seen at 3-4 months of age, but not in
20 younger infants. Three- to four-month-olds can form categories for different types of animals; for
21 example, a category that includes cats but excludes horses (Eimas & Quinn, 1994). Subordinate-
22 level representations are formed around 6-7 months of age (Eimas & Quinn, 1994). For example,

1 6- to 7-month-olds demonstrate evidence of forming categorical representations for Saint
2 Bernards that excludes Beagles, which is a subordinate-level distinction among dog breeds
3 (Quinn & Tanaka, 2007).

4 Several factors affect infants' ability to form categories including initial exposure
5 conditions and prior experience. For example, Oakes and Ribar (2005) tested 4-month-old
6 infants' ability to distinguish between cats and dogs using different familiarization procedures.
7 One group was familiarized with paired presentations of two stimuli at the same time, and
8 another group was familiarized with sequential presentations of a single stimulus. Infants given
9 paired presentations of multiple stimuli were able to demonstrate basic-level categorization of
10 cats and dogs. In contrast, infants given sequential presentations of a single stimulus during
11 familiarization did not demonstrate basic-level categorization. Thus, exposure to multiple
12 exemplars during familiarization may lead infants to engage in a process of comparison which
13 likely facilitates infant categorization (also see: Casasola & Park, 2013; Oakes, Kovack-Lesh, &
14 Horst, 2009; Rose et al., 1982; Vukatana, Graham, Curtin, & Zepeda, 2015). Kovack-Lesh,
15 Oakes, and McMurray (2012) examined the impact of prior experience and visual scanning on
16 categorization for 4-month-olds. They found that infants were more likely to demonstrate basic-
17 level categorization of cats versus dogs if they had cats at home and exhibited high switch rates
18 in their looking behavior during testing, whereas infants were less likely to demonstrate basic-
19 level categorization if they did not have cats at home and exhibited low switch rates. This
20 finding indicates that regular exposure to individual members of other species (i.e., family pets)
21 facilitates infants' ability to form a basic-level category for that species that excludes other
22 species.

1 There has been a great deal of research documenting perceptual narrowing in infant face
2 processing, (for reviews, see Mauer & Werker, 2014; Scott, Pascalis, & Nelson, 2007).
3 Perceptual narrowing occurs as infants transition from having perceptual sensitivities that are
4 broadly tuned to a wide range of faces to being more narrowly focused and specialized for
5 processing faces encountered regularly in the native environment. The other-species effect
6 (OSE) is an example of perceptual narrowing in face processing. The body of behavioral
7 research on this effect suggests that there is maintenance of perceptual sensitivity for own-
8 species faces and a decrease in perceptual sensitivity for other-species faces (e.g, Pascalis et al.,
9 2005; Simpson, Varga, Frick, & Frigaszy, 2011).

10 In one of the earliest studies on the OSE in infancy, Pascalis, de Haan, and Nelson (2002)
11 tested infants at 6 and 9 months of age using a visual paired-comparison (VPC) task. The infants
12 were familiarized with either a single monkey or a single human face for 20s of accumulated
13 looking, and were then tested in VPC trials with the familiarized face paired with a novel face of
14 the same species. At 6 months of age, infants demonstrated evidence of discrimination of the
15 familiar face from the novel face in both the human and monkey conditions. In contrast, at 9
16 months of age, infants only demonstrated discrimination of the familiar face from the novel face
17 in the human face condition. This finding indicates that from 6 to 9 months of age, infants
18 maintain the ability to individuate own-species faces but show a decline in their ability to
19 individuate other-species faces. Simpson and colleagues (2014) have proposed a learned
20 attention model that states that with age, infants' sensitivity increases for facial dimensions
21 useful for identification, and this effect is strongest for own-species faces due to learned attention
22 that occurs with experience. Consistent with this proposal, research has shown that infants
23 trained with picture books of individually-labeled monkey faces between 6 to 9 months of age

1 (Pascalis et al., 2005; Scott & Monesson, 2009, 2010) maintain the ability to individuate other-
2 species faces at 9 months of age.

3 The event-related potential (ERP) has been widely used in research on face processing in
4 both infants and adults. The N290 and P400 have been identified as ERP components related to
5 face processing in infancy (de Haan, 2007; de Haan, Johnson, & Halit, 2003), and these
6 components are believed to be precursors to the adult N170 face processing component (Halit, de
7 Haan, & Johnson, 2003; Scott & Monesson, 2010). The N290 is a negatively polarized
8 component that occurs over midline and posterior electrodes with peak latency between 290 and
9 350 ms after stimulus onset (Halit et al., 2003). By 3 months of age, the N290 is greater in
10 amplitude to faces than noise (Halit, Csibra, Volein, & Johnson, 2004). The P400 is a positive-
11 going component that occurs over midline posterior electrodes and reaches peak amplitude
12 between 390 and 450 ms after stimulus onset. By 6 months of age, the P400 has a shorter latency
13 to peak in response to faces than objects (de Haan & Nelson, 1999), and by 12 months of age, the
14 P400 is shorter in latency to upright versus inverted human faces (Halit et al., 2003).

15 Scott, Shannon, and Nelson (2006) conducted one of the first ERP studies examining the
16 OSE in infancy. Two groups of 9-month-old infants were tested using both own- and other-
17 species faces. In the first condition, infants were familiarized with a human face in a frontal
18 orientation and then tested for recognition of the familiar face in a different orientation in
19 comparison a novel face in similar (frontal) and dissimilar (profile) orientations. The second
20 condition was identical except that monkey faces were used instead of human faces. In contrast
21 to the behavioral findings (Pascalis et al., 2002), 9-month-olds demonstrated recognition of
22 previously viewed human and monkey faces. Infants demonstrated greater amplitude N290 to
23 familiar compared to novel faces regardless of species. Furthermore, the P400 component was

1 greater in amplitude to novel compared to familiar monkey faces. However, infants
2 demonstrated differential amplitude of the P400 to human faces based on both familiarity and
3 orientation. The authors concluded that although the infants demonstrated evidence of successful
4 discrimination of novel and familiar monkey faces, the orientation effects found only in the P400
5 response to human faces indicated that the 9-month-olds were processing human faces at a more
6 specific and specialized level (Scott et al., 2006).

7 Stimulus inversion has also been used in research to examine depth of processing of
8 faces. The face-inversion effect (FIE) in which processing of inverted faces is impaired or
9 delayed compared to upright faces is believed to be a marker for configural processing of face
10 stimuli for infants and adults (Rossion & Curran, 2010; Yovel & Kanwisher, 2005). Although 9-
11 month-old infants do not typically show inversion effects in ERP responding to monkey faces,
12 Scott and Monesson (2010) found that 9-month-olds given three months of training with pictures
13 of monkey faces labeled at the individual level do show inversion effects on the averaged peak-
14 peak amplitude of the N290 and P400 components. This finding, coupled with the finding that 9-
15 month-old infants given similar training can demonstrate behavioral evidence of discriminating
16 monkey faces in the VPC task (Pascalis et al., 2005; Scott & Monesson, 2009), indicates that
17 regular exposure to monkey faces labeled at the individual level in infancy can lead to a
18 maintenance of face processing abilities at 9 months of age. However, these studies tested for
19 evidence of individuation of monkey faces, but did not test for evidence of categorization.

20 Grossman and colleagues (Grossman, Gliga, Johnson, & Mareschal, 2009) conducted one
21 of the first ERP studies examining infant categorization (see also, Leppänen, Richmond, Vogel-
22 Farley, Moulson, & Nelson, 2009). Six-month-old infants were shown a series of repeated and
23 non-repeated bird and object images. The authors found that differential amplitude of P1, an

1 early latency posterior component involved in basic visual processing, was associated with
2 repetition of an individual exemplar. The Negative central (Nc), a mid-latency anterior
3 component associated with attentional engagement (Courchesne, Ganz, & Norcia, 1981; de Haan
4 & Nelson, 1997, 1999; Reynolds 2016; Reynolds & Richards, 2005; Reynolds, Courage, &
5 Richards, 2010; Reynolds & Romano, 2016) was found to be greater in amplitude to exemplars
6 from a novel category. The authors concluded that the 6-month-olds had formed basic-level
7 categories for the familiar objects or vehicles, and the Nc effects reflected greater attention to
8 stimuli from novel categories.

9 Quinn, Doran, Reiss, & Hoffman (2010) recorded ERP data while 6- to 7-month-old
10 infants were familiarized with multiple exemplars of Saint Bernard images, and then shown a
11 series of novel Saint Bernard images interspersed with novel Beagle images. In addition to
12 analyzing the Nc and P400 components, the authors analyzed the positive slow wave (PSW).
13 Differential amplitude of PSW for familiar compared to novel stimuli has been utilized as an
14 electrophysiological index of recognition memory in infancy (de Haan & Nelson, 1999; Guy,
15 Reynolds, & Zhang; 2013; Reynolds, Guy, & Zhang, 2011; Nelson & Collins, 1991, 1992;
16 Snyder, Webb, & Nelson, 2002; Snyder et al., 2010; Wiebe et al., 2006). Quinn and colleagues
17 (2010) found that Nc amplitude was associated with novel category preference at the basic level.
18 Novel category preference at the subordinate level was associated with differential amplitude of
19 both the Nc and P400 components. It was concluded that the mechanisms involved in
20 subordinate-level categorization are supplementary to the mechanisms involved in basic-level
21 categorization, and that the P400 component is related to subordinate-level categorization.
22 Infants also demonstrated differential amplitude of the PSW based on basic- and subordinate-
23 level processing. The differences in PSW amplitude based on basic-level processing occurred at

1 an earlier latency than differences in PSW amplitude based on subordinate-level processing. The
2 authors proposed that these latency differences reflect a course-to-fine sequence of category
3 formation in 6- to 7-month-olds.

4 In a more recent study, Peykarjou, Pauen, and Hoehl (2014) used a rapid repetition
5 paradigm to examine 9-month-old infants' categorization of human and ape faces at three
6 different categorical levels – superordinate, basic, and individual. They found that infants first
7 identified the stimuli as “faces” (the superordinate level) as shown by a greater amplitude P1 to
8 faces than houses. They then categorized the faces as either ape or human as shown by
9 differential amplitude of the N290. Surprisingly, no individual-level responses were observed for
10 the human or ape faces. The authors concluded that the rapid repetition procedure may have
11 interfered with the 9-month-olds' ability to individuate human faces.

12 **The current study**

13 Taken together, the findings from the extant literature indicate that several factors,
14 including familiarization procedure, influence individuation and categorization of other-species
15 faces in infancy. The goal of the current study was to examine the effects of familiarization
16 condition on infants' individuation and subordinate-level categorization of other-species faces at
17 9 months of age. Although familiarization condition has been systematically manipulated in
18 behavioral research of infant categorization (e.g., Oakes & Ribar, 2005) and ERP research on
19 infant recognition memory (Reynolds & Richards, 2005), no study to date has examined the
20 impact of familiarization on neural correlates of subordinate-level categorization in infancy.
21 Additionally, although many studies have tested 9-month-olds on individuation and basic-level
22 categorization of monkey faces, their ability to categorize monkey faces at the subordinate level

1 has yet to be examined. We thus utilized ERPs to examine neural correlates of individuation and
2 subordinate-level categorization of other-species faces by 9-month-old infants. Infants were
3 divided into two groups: a categorization group and an individuation group. The participants in
4 the categorization group were familiarized with sequential presentations of multiple exemplars
5 from the same monkey species (similar to Quinn et al., 2010), whereas the participants in the
6 individuation group were familiarized with repeated presentations of the same individual
7 monkey face. Following familiarization, both groups were presented with equal probability
8 presentations of three different stimulus types: (1) novel faces from the same species as the
9 familiar category (i.e., novel-same trials), (2) novel faces from a different species than the
10 familiar category (i.e., novel-other trials), and (3) the face (or one of the faces) used during
11 familiarization (i.e., familiar trials). We also collected ERP data during the initial familiarization
12 trials (i.e., learning trials), and included this as the fourth stimulus type in our analysis.

13 **Predictions**

14 A summary of our hypotheses is presented in Table 1. Given Grossman and colleagues'
15 (2009) research indicating P1 represents early visual processing sensitive to basic stimulus
16 repetition, we predicted that the individuation group would show reduced P1 amplitude for
17 familiar trials in comparison to learning trials. Based on the finding that 9-month-olds
18 demonstrate differential amplitude of the N290 based on familiarity regardless of species (Scott
19 et al., 2006), we predicted that infants would demonstrate greater amplitude N290 on familiar
20 trials in comparison to learning, novel-same, and novel-other trials. Because 6- to 7-month-olds
21 demonstrate subordinate-level categorization of other-species through greater amplitude Nc and
22 P400 to exemplars from novel categories (i.e., Beagles compared to Saint Bernards; Quinn et al.,
23 2010), we predicted that the categorization group would show greater amplitude Nc and P400 to

1 novel-other species monkey faces in comparison to novel-same species and familiar monkey
2 faces representing greater attention to the novel category of faces. Findings have been mixed on
3 9-month-olds' ability to individuate monkey faces with 20 s of exposure and most of the relevant
4 ERP work using monkey faces has not focused on Nc. Because the bulk of the literature
5 indicates relatively poor individuation of monkey faces for 9-month-olds without supplemental
6 training (e.g., Pascalis et al., 2002, 2005; Scott & Monesson, 2009, 2010), we predicted that the
7 individuation group would likely show equivalent Nc and P400 amplitude across all stimulus
8 types. Our prediction that the categorization group would demonstrate differential Nc and P400
9 based on stimulus type and the individuation group would not was also based on research
10 indicating that exposure to multiple exemplars during familiarization facilitates categorization
11 (e.g., Cassosola & Park, 2013; Oakes & Ribar, 2005). Finally, based upon Quinn and colleagues'
12 (2010) finding that PSW activity may reflect both basic- and subordinate-level categorization
13 processes, we predicted that infants in the categorization group would display reduced amplitude
14 PSWs on familiar, novel-other, and novel-same trials in comparison to learn trials. Because the
15 bulk of the extant literature indicates relatively poor individuation of monkey faces for 9-month-
16 old infants and poor performance on recognition memory tasks for infants familiarized with a
17 single stimulus (Oakes et al., 2009; Rose et al., 1982), we predicted no differences in PSW
18 amplitude across stimulus types for the individuation group indicating a lack of recognition of
19 the familiar face.

20 **Method**

21 **Participants**

1 A sample of 29 infants (14 female, 15 male) were tested within 2 weeks of their 9-month
2 birthdate. The mean age of infants at testing was 278 days ($SD = 4.94$, $range = 266 - 288$). Only
3 infants who were born full-term (at least 38 weeks gestation) with no complications and a normal
4 birth weight were recruited. Participants were drawn from a predominantly Caucasian and
5 middle-class population. The racial distribution of infants included in the final dataset was: 26
6 Caucasian, 1 African American, 1 Asian, 1 Hispanic. An additional 28 infants were tested, but
7 not included in the final sample due to distractibility/fussiness, insufficient number of artifact
8 free ERP trials (i.e., minimum of 8 per condition), or technical problems. This attrition rate falls
9 within a normal range for infant ERP studies (DeBoer et al., 2007).

10 **Apparatus**

11 Participants were seated in their parents' lap in a sound-attenuated room, 55 cm away
12 from a 27" color LCD monitor (Dell 2707 WFP). To limit distraction during testing, the testing
13 area was surrounded by black curtains on all sides except for the side located behind the
14 participant. Room lighting was dimmed throughout testing. A digital camcorder (Sony DCR-
15 HC28) was located just above the monitor for judging infant visual fixations. Fixations were
16 judged online for the purpose of experimental control. The video was also recorded through use
17 of Netstation software produced by Electrical Geodesics Incorporated (EGI; Eugene, Oregon).
18 The Netstation was used to record EEG data and to synchronize this data with the video. The
19 experimental procedure was controlled using E-Prime 2.0 software (Psychology Software Tools,
20 Inc.; Sharpsburg, PA.). The E-Prime program sent experimental events to the Netstation and
21 utilized a single-clock system to time-lock these experimental events with the EEG and video
22 data.

1 **Visual Stimuli**

2 **Other-species faces.** Digital oval-shaped color photographs of adult capuchin and
3 macaque faces were presented sequentially on the monitor (see Figure 1). The macaque images
4 were drawn from the same database used in previous research in the area (Pascalis et al., 2005;
5 Scott & Monesson, 2009, 2010). Images of capuchin faces were provided by Catherine F. Talbot
6 with permission from the Georgia State University Language Research Center. Faces subtended
7 a 20° square visual angle on the monitor from the position of the participant, and were centered
8 on the screen against a white background.

9 **Attractor stimuli**

10 During the familiarization phase, an orange star was used as an attractor to ensure that the
11 infant was centrally fixated prior to every stimulus presentation. The orange star subtended a 15°
12 square visual angle and was presented in the middle of the screen against a white background.

13 **Sesame Street clips:** Video clips (with audio) of Sesame Street characters were used to redirect
14 infants' interest and attention to the monitor during the second phase of testing if they became
15 distracted. The video covered a 15° square area centered on the monitor.

16 **Procedure**

17 After informed consent was obtained, infants were seated on a parent's lap in the testing
18 room. An appropriately sized EGI sensor net was then selected and placed on the infant. Net
19 application took about 5-10 minutes. During the application of the net, a second experimenter
20 interacted with the infant using infant-directed speech, silly faces, and/or rattles or other toys as a
21 distraction to decrease the likelihood of fussiness.

1 The experiment had two stages (see Figure 1). The first stage was the familiarization
2 phase of the experiment (i.e., learning trials). The individuation group ($n = 15$; 5 female/10 male)
3 was familiarized through repeated presentations of a single monkey face presented twenty times.
4 The image was presented centrally for 1000 ms following the presentation of an attractor
5 stimulus used to ensure central fixation. When the infant was judged to be centrally fixated on
6 the attractor stimulus, the experimenter initiated a stimulus presentation through a button press.
7 The 1000 ms stimulus presentation was preceded by a 200 ms blank white screen (used for
8 prestimulus ERP baselines) and followed by a blank white screen that varied randomly in
9 duration from 1000 – 1500 ms. The categorization group ($n = 14$; 9 female/5 male) was shown
10 10 different monkey faces during familiarization, each face was presented twice for a total of 20
11 stimulus presentations. The timing of each stimulus presentation was identical to the timing of
12 presentations in the individuation condition. The 10 monkey faces used for each categorization
13 participant were drawn from the same species (either capuchin or macaque). For both the
14 individuation and categorization conditions, the use of either capuchin or macaque faces for the
15 familiarization condition was counter-balanced across participants to control for potential species
16 effects. The second stage began immediately after the completion of the familiarization stage.
17 The second stage consisted of ERP test trials consisting of presentations of three stimulus types:
18 novel individual faces from the same species as the familiar faces (novel-same), novel faces from
19 the other species than the familiar faces were from (novel-other), and faces used in the
20 familiarization phase (familiar). The presentation of faces from these stimulus conditions was
21 done in pseudo-random order, with equal probability. If an infant became distracted, dynamic
22 Sesame Street video clips with accompanying sound tracks were played to regain the infant's
23 attention. Looking behavior was analyzed offline to ensure infants were looking during each

1 trial. Trials in which infants were not looking or looked away during stimulus presentation were
2 excluded from analyses. Testing continued until the infant was no longer on task, and typically
3 lasted about 10 minutes. On average, infants completed 126 trials for both the 1st and 2nd stage.
4 ($SD = 28$).

5 **EEG Recording**

6 The Electrical Geodesics Incorporated (EGI) Geodesic EEG System 300 (GES 300) 128
7 channel EEG recording system was used. This system consisted of infant-sized HydroCel
8 Geodesic Sensor (HCGSN) nets, a GES 300 amplifier, and the Netstation recording program.
9 The HCGSN sensor nets are arranged in a configuration of electrode pedestals on which 124
10 electrodes are mounted within electrolytic sponges. The net was soaked in an electrolyte solution
11 before use. The elasticity of the net maintains the spacing between electrodes once it is placed,
12 using the mastoid, nasion, and vertex locations to find the correct position on the participant. The
13 average interelectrode distance of the electrodes on the scalp is 21 mm. Electrode impedances
14 were measured prior to testing, and generally ranged from 10 to 50 k Ω . If during sensor net
15 application, the impedance of an electrode was deemed as high (>100 k Ω), the electrode was
16 repositioned until impedance values reached an acceptable level. A Dell Workstation was used
17 to control the experimental protocol and to send time-locked experimental events to the EEG
18 acquisition computer. The delay between the timing of the stimulus presentation initiated by the
19 E-Prime computer and the actual display of the stimulus on the presentation monitor was
20 determined using a photoreceptor and verified to have no drift across testing sessions. This
21 stimulus display offset was corrected for during ERP segmenting. The EEG was sampled at 250
22 Hz with 20K amplification. The EEG recordings were band-pass filtered from 0.3 to 30 Hz.

1 The EEG was edited using the Netstation software to identify saccades, blinks, movement
2 artifact, and poor recording. Artifact was defined as $\Delta > 250\mu\text{V}/250\text{ms}$. EEG channels were
3 marked bad if artifact was found. Trials in which over 10% of the channels were marked bad due
4 to excessive artifact or noise were excluded from the analysis. For trials that were retained for
5 the ERP analysis, individual channels marked bad were replaced using a spherical spline
6 interpolation (Perrin, Pernier, Bertrand, Giard, & Echallier, 1987; Srinivasan, Tucker, & Murias,
7 1998). Only those participants who contributed a minimum of 8 artifact-free ERP trials per
8 condition for stable ERP averages were included in the final dataset (Farroni, Johnson, & Csibra,
9 2004; Reynolds, Guy, & Zhang, 2011; Reynolds & Richards, in press). The average number of
10 trials contributed per condition were: 15.28 trials ($SD = 3.40$) in the learning condition, 16.00
11 trials ($SD = 4.44$) in the familiar condition, 15.38 trials ($SD = 3.80$) in the novel-other condition,
12 and 16.07 trials ($SD = 3.94$) in the novel-same condition.

13 ERP averages were calculated from 200 ms before stimulus onset to 1500 ms after
14 stimulus onset. The latency, duration, and electrode locations used to analyze each component of
15 interest were determined primarily based on previous findings (Nc and PSW components: Guy,
16 Reynolds, Mosteller, & Dixon, 2017; Quinn et al., 2010; Reynolds & Richards, 2005; N290 and
17 P400 components: Peykarjou et al., 2014; Quinn et al., 2010; Reynolds, Bahrick, Lickliter, &
18 Guy, 2014; Scott et al., 2006) as well as inspection of the grand average waveforms (averaged
19 across experimental groups) to determine the electrode locations where each component was
20 most prominent (DeBoer, Scott, & Nelson, 2007). The P1 was analyzed as the mean amplitude
21 of the ERP from 75 - 175 ms following stimulus onset at midline occipital electrodes (81, 74, 82,
22 75, 73, and 88). The N290 was analyzed as the mean amplitude of the ERP from 225 – 325 ms
23 following stimulus onset at the same midline occipital electrodes as the P1, and the P400 was

1 also analyzed at these electrodes as the mean amplitude of the ERP from 350 – 600 ms following
2 stimulus onset. Nc was analyzed as the mean amplitude of the ERP from 350 – 650 ms
3 following stimulus onset at midline central electrodes (7, 106, 13, 6, and 112). The PSW was
4 analyzed as the mean amplitude of the ERP from 600 – 1500 ms following stimulus onset at left
5 frontal electrodes (24, 27, 28, and 20), and right frontal electrodes (124, 117, 118, and 123).

6 **Design for Statistical Analysis**

7 The ERP component averages were analyzed for experimental effects using 2 x 2 x 4
8 multivariate analysis of variance (MANOVA) with familiarization condition (2: categorization,
9 individuation) and sex (2: female, male) as between-subjects factors, and stimulus type (4:
10 learning, familiar, novel-other, novel-same) as a within-subjects factor. We also analyzed
11 hemisphere (Guy et al., 2013, 2017; Reynolds et al., 2014) as a within-subjects factor for the
12 PSW (2: left frontal, right frontal). For significant interaction effects, follow-up analyses were
13 done using ANOVAs and the least significant differences test (LSD) as recommended by Saville
14 (1990). The Greenhouse-Geisser correction was used in cases of violations of the assumption of
15 sphericity. Effect sizes (η_p^2) are reported on all significant effects, and all significant tests are
16 reported at $p < .05$.

17 **Results**

18 **The P1 component**

19 Table 2 presents a summary of the significant findings from our analyses. The results of
20 the MANOVA done on P1 amplitude at midline occipital electrodes (Oz area) revealed a
21 significant main effect of stimulus type, $F(3, 25) 10.42$; $p < .01$; $Wilks \Delta = .444$; $\eta_p^2 = .556$.
22 Infants demonstrated significantly greater amplitude P1 during learning trials ($M = 17.$, $SE =$

1 1.92) in comparison to the familiar ($M = 3.34$, $SE = 1.55$), novel-other ($M=5.31$, $SE = 1.85$), and
2 novel-same ($M = 6.05$, $SE = 1.17$) trials. This main effect was qualified by a significant
3 interaction of stimulus type and familiarization condition, $F(3, 25) 3.09$; $p < .05$; $Wilks \Delta = .729$;
4 $\eta_p^2=.271$. Follow up tests indicated there was a significant effect of stimulus type for the
5 individuation group, $F(1, 14) 29.50$; $p < .01$; $\eta_p^2=.678$. As can be seen in Figure 2, infants in the
6 individuation group showed significantly greater amplitude P1 on learning trials ($M = 19.83$, SE
7 $= 2.66$) in comparison to familiar ($M = 5.98$, $SE = 1.38$), novel-other ($M = 2.46$, $SE = 1.87$), and
8 novel-same trials ($M = 4.37$, $SE = 1.71$). In contrast, the effect of stimulus type was not
9 significant for the categorization group ($p > .05$ for all comparisons).

10 **The N290 component**

11 There were no significant main or interaction effects found from the MANOVA on mean
12 amplitude of the N290 at midline occipital electrodes (Oz area). However, given the significant
13 main and interaction effects described above on the amplitude of the P1 component, which
14 preceded the N290 at occipital electrodes (see Figure 2), we carried out a supplementary peak-to-
15 trough analysis on the change in amplitude of the ERP from the time window of the analysis of
16 the P1 to the time window of the analysis of the N290. Similar to the standard analysis of mean
17 amplitude reported above, no significant main or interaction effects were found in the MANOVA
18 for the peak-to-trough analysis. The interested reader is referred to Picton and colleagues (2000)
19 for points regarding the advantages of baseline-to-peak analyses over peak-to-peak and peak-to-
20 trough analyses.

21 **The P400 component**

1 The results of the MANOVA run on P400 amplitude at midline occipital electrodes (Oz
2 area) revealed a main effect of stimulus type, $F(3,23) 3.98; p < .05; Wilks \Delta = .658; \eta_p^2 = .342$.
3 This main effect was qualified by a significant interaction of familiarization condition and
4 stimulus type, $F(3,23) 3.95; p = .05; Wilks \Delta = .660; \eta_p^2 = .340$. Follow-up ANOVAs run
5 separately for each familiarization condition indicated no differences based on stimulus type for
6 the individuation group ($p = .97$). In contrast, as illustrated in Figure 2, infants tested in the
7 categorization condition demonstrated significantly greater amplitude P400 (all $ps < .05$) on
8 novel-other trials ($M = 35.35, SE = 4.98$) in comparison to learning trials ($M = 20.42, SE = 4.44$),
9 familiar trials ($M = 21.07, SE = 4.89$), and novel-same trials ($M = 27.90, SE = 3.05$).

10 **The Nc component**

11 A MANOVA run at midline central electrodes (Cz area) indicated a significant
12 interaction of familiarization condition and stimulus type on Nc amplitude, $F(3,25) 3.81; p = .02$;
13 $Wilks \Delta = .686; \eta_p^2 = .314$. Similar to the analysis of the P400 component, follow-up ANOVAs
14 run separately for each familiarization condition indicated no differences based on stimulus type
15 for the individuation group ($p = .69$). In contrast, as can be seen in Figure 3, the categorization
16 group demonstrated significantly greater amplitude Nc (all $ps < .05$) on novel-other trials ($M = -$
17 $12.73, SE = 2.02$) in comparison to learning trials ($M = -6.64, SE = 1.70$), familiar trials ($M =$
18 $-7.75, SE = 1.90$), and novel-same trials ($M = -8.43, SE = 1.48$).

19 **The PSW component**

20 For the MANOVA conducted on PSW amplitude, we included hemisphere as a factor,
21 using left frontal (F3 area) and right frontal (F4 area) electrodes. The MANOVA revealed a
22 main effect of stimulus type, $F(3,23) 3.27; p = .04; Wilks \Delta = .701; \eta_p^2 = .299$. This main effect

1 was qualified by a significant three-way interaction of familiarization condition, stimulus type,
2 and hemisphere, $F(3,23) 4.54$; $p = .012$; $Wilks \Delta = .628$; $\eta_p^2 = .372$ (see Figure 4) .

3 To follow-up on this interaction, two-way ANOVAs were run separately for each
4 familiarization group. For the individuation group, there were no differences in PSW amplitude
5 based on stimulus type ($p = .78$), and no PSW amplitude differences based on the interaction of
6 stimulus type and hemisphere ($p = .93$). For the categorization group, there was a significant
7 main effect of stimulus type, $F(3, 39) 4.98$; $p < .01$; $\eta_p^2 = .277$. This main effect was qualified by
8 a significant interaction of stimulus type by hemisphere, $F(3,39) 5.78$; $p = .03$; $\eta_p^2 = .308$. At left
9 frontal electrodes, infants in the categorization group demonstrated significantly greater
10 amplitude PSW on learning trials ($M = 7.68$, $SE = 1.46$) in comparison to novel-other trials ($M =$
11 0.39 , $SE = 2.22$) and novel-same trials ($M = 1.49$, $SE = 2.54$). Additionally, infants in the
12 categorization group demonstrated significantly greater amplitude PSW on familiar trials ($M =$
13 6.79 , $SE = 1.67$) in comparison to novel-other trials. At right frontal electrodes, infants in the
14 categorization demonstrated significant greater amplitude PSW on learning trials ($M = 7.24$, SE
15 $= 1.69$) in comparison to familiar trials ($M = -0.71$, $SE = 1.28$) and novel-other trials ($M = -1.41$,
16 $SE = 1.99$). Additionally, infants demonstrated greater amplitude PSW on novel-same trials (M
17 $= 3.52$, $SE = 2.93$) in comparison to novel-other trials.

18 Discussion

19 The present study examined 9-month-old infants' ability to individuate and categorize
20 monkey faces when familiarized to either an individual face or a selection of exemplar faces
21 from the same monkey species. We expected exposure to multiple exemplars to facilitate infants'
22 processing of faces, and thus predicted that infants in the categorization group would show

1 evidence of subordinate-level categorization. In contrast, we predicted that infants in the
2 individuation group would only demonstrate evidence of basic repetition effects on early visual
3 processing, but that they would show no evidence of recognition memory in later latency ERP
4 components associated with attention and recognition memory.

5 **The P1 component**

6 The P1 is an early latency component associated with early visual processing. Grossman
7 and colleagues (2009) examined 6-month-old infants' basic-level categorization of birds and
8 vehicles and found that the P1 is sensitive to stimulus repetition with greater amplitude P1 to
9 repeated stimuli in comparison to non-repeated stimuli during familiarization trials, and greater
10 amplitude to non-repeated stimuli in comparison to repeated stimuli during test trials. This led
11 the authors to conclude that the P1 is associated with basic repetition effects during early visual
12 processing. Peykarjou and colleagues (2014) examined superordinate- and basic-level
13 categorization of human and monkey faces for 9-month-old infants. They found that P1 was
14 reduced in amplitude to primed stimuli that followed a prime from the same category. This was
15 interpreted as representing categorical repetition effects early in the visual processing stream.

16 In the current study, we predicted that infants in the individuation group would
17 demonstrate greater amplitude P1 on learning trials in comparison to familiar trials indicative of
18 repetition effects (Grossman et al., 2009; Peykarjou et al., 2014). We did not expect this effect
19 for the categorization group since infants in that group were shown multiple exemplars during
20 familiarization instead of a single exemplar. The results supported our prediction for the P1.
21 Infants demonstrated greater P1 amplitude on learning trials in comparison to all other trials.
22 There was also a significant interaction of familiarization group and stimulus type on P1

1 amplitude. Infants in the individuation group showed greater amplitude P1 on learning trials in
2 comparison to all other stimulus type trials.

3 The finding that the learning trials were significantly greater in P1 amplitude than both
4 the novel-same and novel-other trials indicates this effect was not simply due to the novelty of
5 the monkey faces at the start of testing. Instead, this general reduction in P1 amplitude from the
6 first 20 (learning) trials to the subsequent test trials is most likely an effect of trial order. Past
7 research has shown similar reductions in amplitude across testing sessions for the Nc component
8 (Wiebe et al., 2006) and the PSW (Snyder, Webb, & Nelson, 2002). It is worthwhile to note that
9 this effect was only significant for the P1 component. We did not find general amplitude
10 reductions from learning trials to test trials for the later latency components. The Nc, P400, and
11 PSW were affected by more specific effects driven by interactions of stimulus type and
12 familiarization condition which indicates that the P1 may represent a more basic response
13 associated with early visual processing and perhaps super-ordinate level categorization (Pekarjou
14 et al., 2014) whereas the mid-latency (Nc and P400) components and PSW are most likely
15 involved in higher-level processing related to attention, subordinate-level categorization, and
16 recognition.

17 **The N290 Component**

18 The N290 is a face-sensitive ERP component that may be a precursor to the adult N170
19 component (de Haan et al., 2002, 2003, 2007; Halit et al., 2003; Reynolds et al., 2014). The
20 N290 increases in specificity with age, and shows inversion effects for both human and monkey
21 faces by 12 months (de Haan, Pascalis, & Johnson, 2002; Halit et al., 2003). Furthermore,
22 infants demonstrate differential amplitude N290 to monkey faces in comparison to human faces

1 (de Haan et al., 2002; Peykarjou et al., 2014). These findings indicate that the N290 may be
2 related to basic-level category distinctions (inverted versus upright; human versus monkey).

3 For the N290, we predicted that infants would demonstrate greater amplitude N290 on
4 familiar trials in comparison to all other trials. The results of the current study did not support
5 our prediction. No significant experimental effects were found in our analysis of the N290. The
6 lack of a significant effect of stimulus type on N290 in the current study was unexpected given
7 Scott and colleagues' (2006) finding that 9-month-old infants demonstrate greater amplitude of
8 the N290 for familiar compared to novel monkey faces. The contrasting findings may have been
9 due to procedural differences across studies. Scott and colleagues (2006) presented infants with
10 repeated presentations of the familiar monkey in multiple orientations, which may have
11 facilitated the infants' individuation of the familiar from novel faces. We also found no N290
12 effects for our categorization group. In contrast, Peykarjou and colleagues (2014) found
13 differential amplitude of the N290 for 9-month-olds in response to human compared to monkey
14 faces which indicates that the N290 may be associated with basic- or superordinate-level
15 categorization as opposed to the subordinate-level our categorization procedure was focused on.
16 Previous infant ERP work on subordinate-level categorization (e.g., Quinn et al., 2006) has
17 focused on the Nc, P400, and PSW components. Therefore, further research is needed to
18 determine exactly what level(s) of categorization the N290 may be associated with throughout
19 infancy.

20 **The Nc and P400 components**

21 Past research has found the Nc and P400 to be associated with attention and
22 categorization (e.g., Hoehl, 2016; Grossman et al., 2009; Quinn et al., 2010). For the Nc and

1 P400, we predicted that the categorization group in the current study would demonstrate greater
2 amplitude Nc and P400 to novel-other faces in comparison to novel-same and familiar faces
3 indicative of subordinate-level categorization. We also predicted that the individuation group
4 would demonstrate equivalent Nc and P400 amplitude across conditions indicating an inability to
5 fully process monkey faces at the individual level when only given 20 s of familiarization. The
6 current findings were consistent with these hypotheses. The categorization group demonstrated
7 greater amplitude Nc and P400 to novel-other species faces in comparison to all other stimulus
8 types. This indicates greater attention to monkey faces categorized at the subordinate-level.
9 Importantly, the individuation group showed no differences in Nc or P400 amplitude based on
10 stimulus type indicating that this group did not discriminate novel monkey faces from the
11 familiar face at either the individual level or the species level. The null findings for the
12 individuation group indicate the categorization group's greater amplitude Nc and P400 to novel-
13 other faces in comparison to the familiar and novel-same faces was not simply due to the
14 distinctiveness of cross-species comparisons. Thus, 9-month-old infants are quite efficient at
15 categorizing other-species faces at the subordinate level when given exposure to multiple
16 exemplars during category learning, whereas, they show no evidence of individuating monkey
17 faces when exposed to repeated presentations of a single exemplar during learning.

18 **The Positive Slow Wave**

19 Based on Quinn and colleagues (2010) findings indicating the PSW may reflect both
20 basic- and subordinate-level categorization processes, we predicted that infants in the
21 categorization group would show significant differences in PSW amplitude on learning trials in
22 comparison to the familiar, novel-other, and novel-same trials. We predicted no differences in
23 PSW amplitude based on stimulus type for the individuation group. The results partially

1 supported our predictions. For the individuation group, there were no differences in PSW
2 amplitude based on stimulus type, again indicating the infants were unable to individuate
3 monkey faces in this procedure. However, for the categorization group, there was an interaction
4 of stimulus type and hemisphere. At left frontal electrodes, the PSW was significantly greater in
5 amplitude on learning and familiar trials in comparison to novel-other trials. Additionally, the
6 PSW was greater in amplitude on learning trials than novel-same trials. At right frontal
7 electrodes, the categorization group had greater amplitude PSW on learning trials in comparison
8 to familiar and novel-other trials, and greater amplitude PSW on novel-same trials in comparison
9 to novel-other trials. Although this three-way interaction is difficult to interpret, these findings
10 could reflect both a reduction in amplitude of the PSW from early (learning) trials to subsequent
11 test trials as well as categorization effects (familiar compared to novel-other).

12 **Conclusion**

13 It is interesting to note that experimental effects became increasingly complex with later
14 latency components in the processing stream. The results of the analyses of the Nc and P400
15 were remarkably similar, with infants in the categorization group demonstrating greater
16 amplitude Nc and PSW on novel-other trials in comparison to all other stimulus types. The
17 consistency in the effects of stimulus type, coupled with the similar latency of these two
18 components, indicates that Nc and P400 may reflect similar processes related to attention (Guy,
19 Zieber, & Richards, 2016; Scott et al., 2006). We believe these findings clearly demonstrate that
20 attention plays a fundamental role in subordinate-level processing of other-species faces. Finally,
21 the effects of familiarization condition and stimulus type on the PSW were complex and
22 potentially driven by both repetition suppression (Snyder et al., 2010) and categorization
23 processes. Quinn and colleagues' (2010) proposal that infant ERPs reveal a course-to-fine

1 processing sequence during subordinate-level categorization is consistent with the overall pattern
2 of effects found across ERP components for the categorization group in the current study.

3 The individuation group in the current study failed to demonstrate differential responding
4 based on familiarity and novelty of monkey faces in the current study. Daily experience likely
5 serves to maintain infants' ability to individuate own-species faces. For example, Sugden,
6 Mohamed-Ali, and Moulson (2013) utilized head mounted cameras on 1- and 3-month-old
7 infants in their home environments, and found that 25% of the infants' waking time was spent
8 exposed to faces. Thus, by 9 months of age, the typical human infants have had extensive
9 experience with human faces, and the maintenance of the ability to individuate human faces is
10 likely driven by extensive daily interaction with conspecifics. Given that we only tested 9-
11 month-old infants in the current study, our results do not provide insight into potential effects
12 related to perceptual narrowing in infant face processing. However, our findings do indicate that
13 initial exposure conditions play an important role in 9-month-old infants' performance on face
14 processing tasks. The finding that exposure to multiple exemplars facilitates infant face
15 processing and categorization is consistent with previous behavioral work showing that
16 comparison fosters both categorization and recognition memory (Cassosola and Park, 2013;
17 Oakes & Ribar, 2005; Oakes et al., 2009; Rose et al., 1982). Future studies should be aimed at
18 examining the effects of familiarization condition on processing of both own- and other-species
19 faces across a broad age range in early development.

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2 Table 1 *Hypotheses for ERP Components by Familiarization Condition*

Component	Categorization group	Individuation group
P1	No differences	Greater amplitude on learning trials in comparison to familiar
N290	Greater amplitude to familiar in comparison to all other trials	Greater amplitude to familiar in comparison to all other trials
Nc	Greater amplitude to novel-other in comparison to novel-same and familiar	No differences
P400	Greater amplitude to novel-other in comparison to novel-same and familiar	No differences
PSW	Reduced amplitude on familiar, novel-other, and novel-same in comparison to learn trials	No differences

3 Table 2 *Analysis Results for ERP Components by Familiarization Condition*

Component	Categorization group	Individuation group
P1	No differences	Greater amplitude to learning trials as compared to familiar
N290	No differences	No differences
Nc	Greater amplitude to novel-other in comparison to novel-same and familiar	No differences
P400	Greater amplitude to novel-other in comparison to novel-same and familiar	No differences
PSW	At left frontal electrodes: <ul style="list-style-type: none"> • Greater amplitude to learning and familiar in comparison to novel-other • Greater amplitude to learning trials in 	No differences

- comparison to novel-same
At right frontal electrodes:
- Greater amplitude to learning trials in comparison to familiar and novel-other
 - Greater amplitude to novel-same trials in comparison to novel-other
-

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2 Figure 1. Diagram of Experimental Procedure. A diagram of the experimental procedure
3 including examples of the face stimuli used in the study is shown. The left panel provides a
4 diagram of the categorization procedure, and the right panel presents a diagram of the
5 individuation procedure. The face stimuli are presented in grayscale for publication purposes.

6 Figure 2. The P1, N290, and P400 Components by Familiarization Group and Stimulus
7 Type. The P1, N290, and P400 components are presented by familiarization group and stimulus
8 type. The left panel shows ERP waveforms for the individuation group at Oz (75), and the right
9 panel shows ERP waveforms for the categorization group at Oz. The midline occipital electrode
10 cluster used in the analyses is indicated in the sensor net layout shown to the bottom left. The
11 open rectangles indicate the time window of the analyses for each component.

12 Figure 3. The Nc Component by Familiarization Group and Stimulus Type. The Nc
13 component is presented by familiarization group and stimulus type. The left panel shows ERP
14 waveforms for the individuation group at lead 6, and the right panel shows ERP waveforms for
15 the categorization group at lead 6. The midline central electrode cluster used in the analyses is
16 indicated in the sensor net layout shown to the bottom left. The open rectangles indicate the time
17 window for the analysis of Nc.

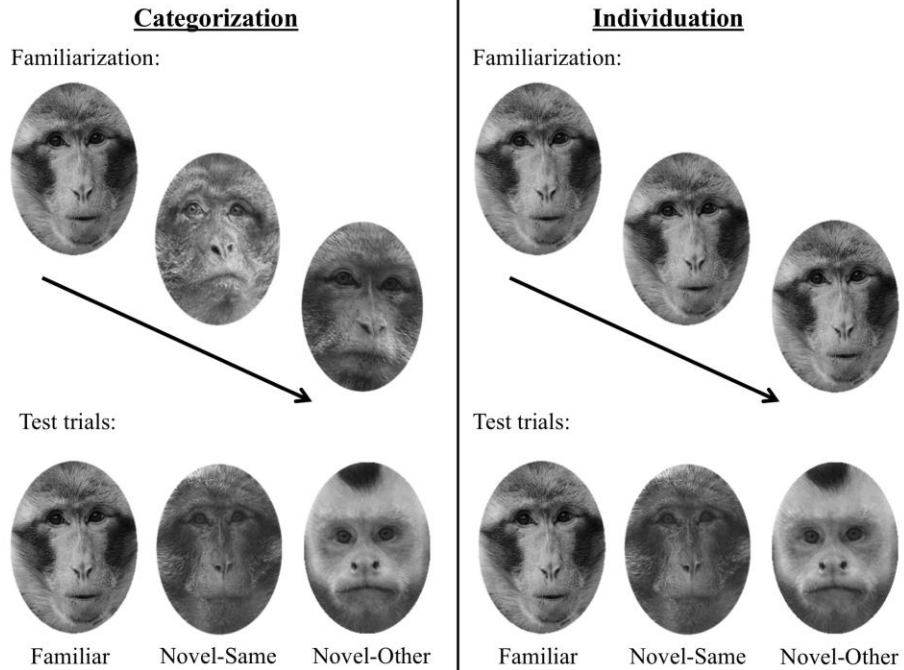
1 Figure 4. The PSW Component by Familiarization Group, Stimulus Type, and
2 Hemisphere. The PSW is presented by familiarization group, stimulus type, and hemisphere. The
3 left panel shows ERP waveforms by group at F3 (24), and the right panel shows ERP waveforms
4 by group at F4 (124). The left and right frontal electrode clusters used in the analyses are
5 indicated in the sensor net layout shown in the center. The open rectangles indicate the time
6 window of the analyses of the PSW.

7

8 Highlights

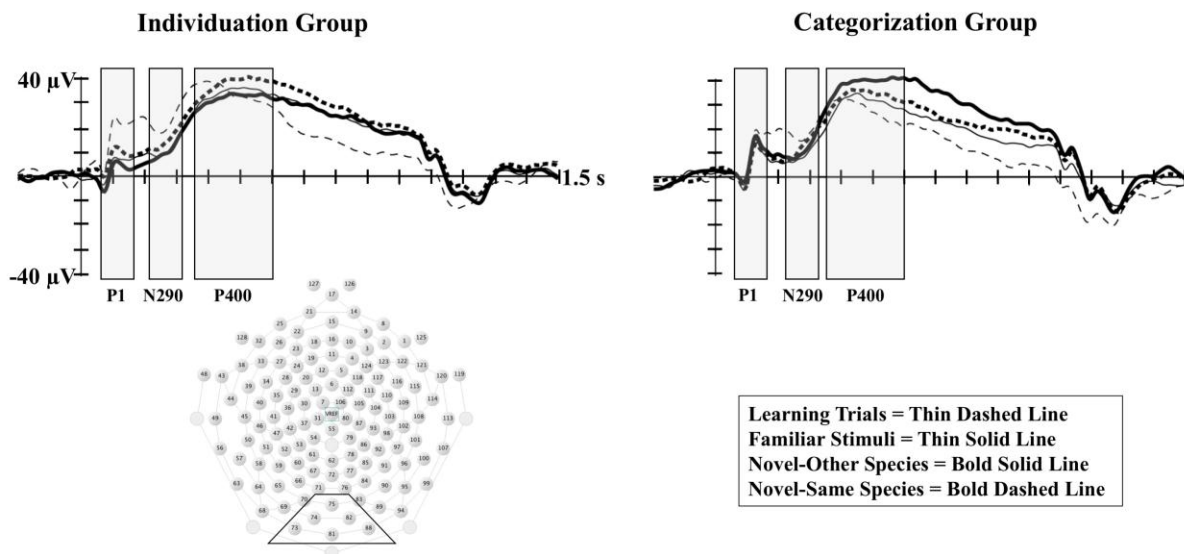
- 9 • The results indicate that human infants are efficient at categorizing other-species faces at
10 9 months of age.
11 • Exposure to multiple exemplars facilitated 9-month-olds subordinate-level categorization
12 of other-species faces.
13 • The Nc and P400 ERP components are associated with subordinate-level categorization
14 of other species faces.
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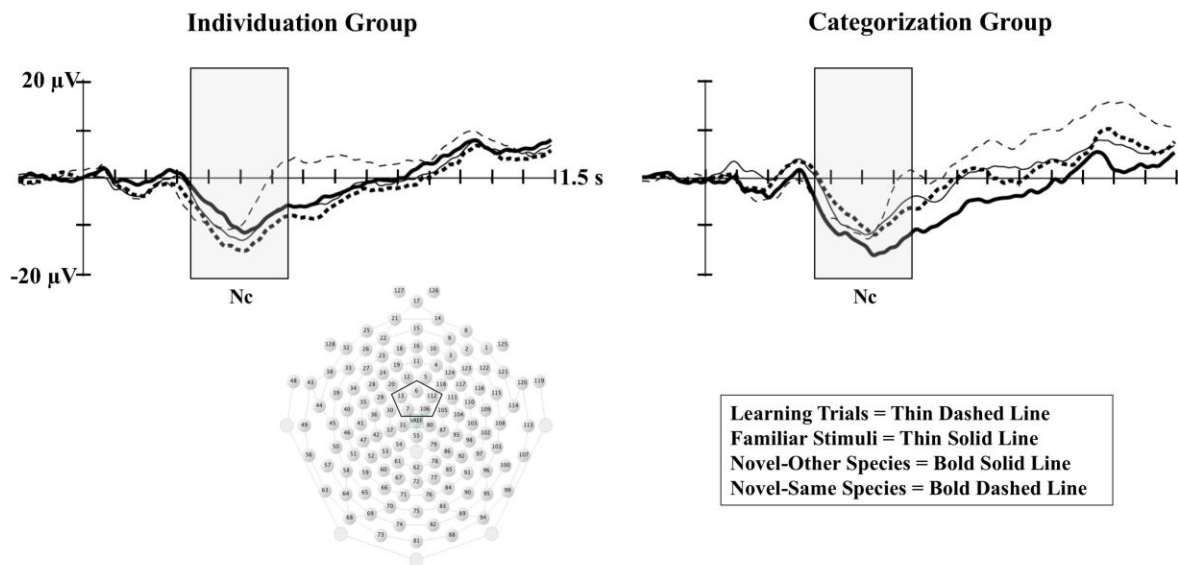
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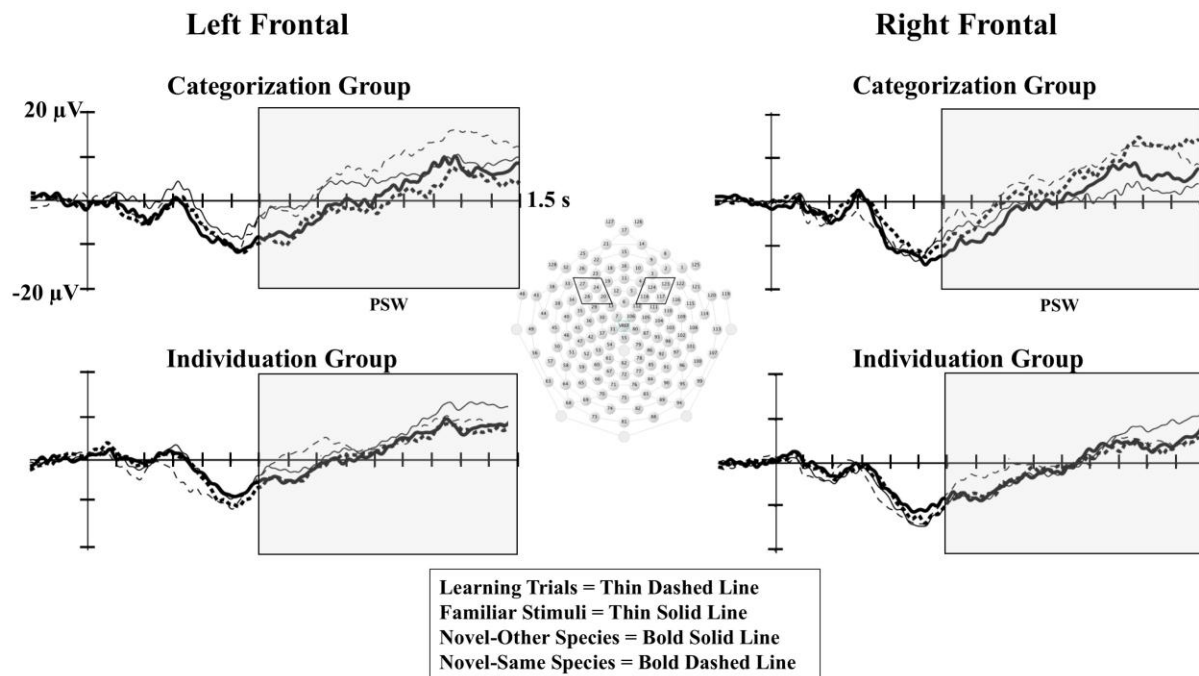
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