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Does Early Perceptual Experience Influence Later Perceptual and Neural Discrimination in Children?

Hillary R. Hadley

University of Massachusetts - Amherst, hhadley@psych.umass.edu

DOES EARLY PERCEPTUAL EXPERIENCE INFLUENCE LATER PERCEPTUAL AND

NEURAL DISCRIMINATION IN CHILDREN?

A Thesis Presented

by

HILLARY R. HADLEY

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Approved as to style and content by:

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Lisa Scott, Chair

_____

Jennifer McDermott, member

_____

Maureen Perry-Jenkins, member

_____

Melinda Novak, Department Head
Department of Psychology

ABSTRACT

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HILLARY R. HADLEY, B.A., UNIVERSITY OF LOUISVILLE

M.A., UNIVERSITY OF MASSACHUSETTS, AMHERST

Directed by: Professor Lisa S. Scott

In infancy, the ability to tell the difference between two faces within a category (e.g., species, race) that is infrequently experienced declines from 6 to 9 months of age (Kelly et al., 2009, 2007; Pascalis et al., 2005; Pascalis, de Haan, & Nelson, 2002; Scott & Monesson, 2009). This decline in the ability to distinguish faces is known as "perceptual narrowing" and has recently been found to be absent when infants are given experience matching a face with an individual-level proper name between 6 to 9 months of age (Scott & Monesson, 2009). Additionally, individual-level experience between 6 and 9 months of age has led to neural changes at 9 months of age (Scott & Monesson, 2010). It is currently unclear whether brief, early experience between 6 and 9 months leads to sustained behavioral advantages and lasting neural changes. In order to answer these questions, the current study recruited and tested children who previously participated in a face training study when they were infants (Scott & Monesson, 2009, 2010). Findings revealed that individual-level experience with faces during the first year of life: 1) resulted in faster reaction time for faces outside of the trained category, and 2) led to more adult-like neural representations of faces outside of the trained category 3-4 years later. These results suggest that experience with individual-level learning in the first year of life is generalized to visually similar, but environmentally relevant face categories.

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CHAPTER 1

INTRODUCTION

The first year of life is one of the most important formative times in child

development. During this time, infants' sensory and motor capacities come online and

they begin to interact with the environment and build representations of the surrounding

world. This early experience shapes brain development by strengthening neural

connections and promoting extensive organization of perceptual systems (Greenough,

Black, & Wallace, 1987; Hensch, 2005; for review, see Shonkoff, 2000). Neural

connections that are made and strengthened early in development have been found to

influence later behavior (Anand & Scalzo, 2000; Greenough & Black, 1992; Lapiz et al.,

2003; for review, see Nelson, 1999). One important type of early experience that is

crucial to later social processing is experience with people. In particular, in the first year

of life infants learn to recognize and distinguish people within their environment (de

Haan, Johnson, Maurer, & Perrett, 2001; Pascalis, De Schonen, Morton, Deruelle, &

Fabre-Grenet, 1995).

Although a great deal has been learned about early infant capacities to recognize

people and objects, the process by which they build these capacities is still not well

understood. One model, "perceptual narrowing", suggests that during the first year of life,

infants' perceptual systems become increasingly tuned to categories of faces and

languages that they experience frequently in their environment (Kelly et al., 2007;

Lewkowicz & Ghazanfar, 2006; Pascalis et al., 2002; Werker & Tees, 1984). As part of

this process, the ability to make discriminations within categories with which infants

have limited experience declines from 6 to 9 months of age. This decline, known as

"perceptual narrowing", has been found to occur in multiple perceptual domains such as native and non-native speech perception (Werker & Tees, 1984), cross-species visual speech perception (Lewkowicz & Ghazanfar, 2006), cross-species face perception (Pascalis et al., 2005; Pascalis et al., 2002; Scott & Monesson, 2009), and other-race face perception (Kelly et al., 2007, 2009; Vogel, Monesson, & Scott, 2012). For instance, at 6 months of age infants are able to differentiate among monkey faces, but at 9 months of age, infants fail to discriminate among these faces (Pascalis et al., 2002). The process of perceptual narrowing guides concept learning in both perceptual and social domains and directs detailed attention towards environmentally relevant categories, such as human faces. For example, early experience with a mother's face teaches infants to associate their mother (versus strangers) with feelings of comfort and security, playing a significant role in attachment formation (Blehar, Lieberman, & Ainsworth, 1977). Furthermore, research across domains suggests that perceptual narrowing within a category (e.g., faces, language) is determined by experience with the category (Pascalis et al., 2005; Werker & Tees, 1984).

Recent work in cross-species face perception suggests that experience shapes perceptual discrimination abilities in infants, therefore determining the process of perceptual narrowing (Pascalis et al., 2005). One method of testing whether or not infants discriminate visual stimuli is the Visual Paired Comparison (VPC) task (for detailed methods, see Fantz, 1964). In this task, infants are briefly familiarized to a stimulus and following this familiarization period, infants are presented with the familiar stimulus alongside a novel stimulus. Discrimination is assessed through looking time; longer

looking toward one stimulus over the other (typically the novel stimulus) is indicative of the ability to tell apart the two stimuli.

To examine the role experience plays in the tuning of cross-species perceptual abilities, Pascalis and colleagues (2005) tested 6-month-old infants' discrimination of monkey faces before and after a 3-month training period. Prior to training, 6-month-old infants effectively discriminated among monkey faces. At 9 months of age, infants who received experience with monkey faces retained the ability to differentiate two monkey faces (novel exemplars). Nine-month-olds who received no training failed to discriminate among monkey faces, suggesting that experience is a key factor in the perceptual tuning that occurs between 6 and 9 months of age.

In the training study conducted by Pascalis and colleagues (2005), all infants were trained on monkey faces paired with unique names, making it unclear whether the specificity of labels played an important role in post-training discrimination. Scott and Monesson (2009) varied the level of monkey face labels in a follow-up study to specifically examine whether exposure to faces was sufficient for later discrimination or whether more specific types of learning were necessary, including labeled faces. As in the previous training study (Pascalis et al., 2005), infants completed a VPC task at 6 months of age before being sent home with training books of six monkey faces. Infants were randomly assigned to one of three training groups: 1) individual-level, where each face was labeled with a unique proper name (e.g. "Boris", "Fiona"), 2) category-level, where all faces were labeled with the same category name (e.g., "monkey"), or 3) exposure-level, where parents were not instructed to label the faces in any way. After 3 months of training, discrimination was tested again at 9 months of age. Similar to what

Pascalis and colleagues (2005) reported, 6-month-old infants successfully discriminated among monkey faces. At 9 months of age, only infants in the individual-level training group maintained the ability to differentiate monkey faces; infants in the category- and exposure-level groups failed to successfully discriminate among faces. These results suggest that visual perceptual narrowing is dependent on experience learning to match faces with individual-level proper names between 6 and 9 months of age.

Scott and Monesson (2010) investigated the role of experience on face-related neural activity using electrophysiological techniques (event-related potentials; ERPs). The N290 and P400, two infant ERP components associated with face perception (for review, see Halit, de Haan, & Johnson, 2003) were examined. Prior research suggests that these components are developmental precursors to the face-sensitive adult N170 component (de Haan, Pascalis, & Johnson, 2002). Additionally, these components become more specifically tuned to human faces across the first year of life, showing similar specificity as the adult N170 around 12 months of age (Halit, de Haan, & Johnson, 2003). Scott and Monesson (2010) showed infants images of upright and inverted, trained (from the training book) and untrained monkey faces while brain activity was recorded both before and after training. Inverted faces were included because face-sensitive ERP components have been found to exhibit differential amplitudes to upright and inverted human faces (Rossion et al., 1999). This "inversion effect" is considered a marker for holistic and expert perceptual processing and is not typically found for objects (Rossion & Curran, 2010).

Results revealed that at 6 months of age, infants exhibited no difference in response to upright versus inverted faces. However, at 9 months of age, infants trained at the

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individual level exhibited an inversion effect in the form of greater peak-to-peak

amplitude (N290 and P400 amplitudes) to inverted versus upright faces, as well as greater

amplitudes to inverted faces post-training relative to pre-training (Scott & Monesson,

2010). Nine-month-olds trained at the category level showed no difference in ERP

response between upright and inverted or trained and untrained faces. Finally, infants

trained at the exposure level also showed no differences in response to upright versus

inverted faces.

In summary, only individual-level training from 6 to 9 months led to maintained

discrimination (Scott & Monesson, 2009) and an ERP inversion effect (Scott &

Monesson, 2010) for monkey faces. The authors concluded that experience with

individual-level labeling of an unfamiliar face category between 6 and 9 months of age

leads to holistic representations of that category and also no evidence of perceptual

narrowing. Moreover, the lack of individual-level experience results in the perpetuation

of the narrowing process and the associated decline in the ability to discriminate faces

within the category. Additionally, these results support the hypothesis that individual-

level learning with an unfamiliar face category leads to adult-like neural responses, akin

to what has been found in adult expertise investigations (Rossion, Gauthier, Goffaux,

Tarr, & Crommelinck, 2002; Rossion & Curran, 2010). However, it is currently unclear

whether learning during this early developmental period is sustained past infancy, as

evidenced by lasting changes in behavior or neural representations.

The current study sought to determine whether children who were given

experience with monkey faces between 6 and 9 months of age show lasting effects of this

early experience. This study serves as a direct follow-up to previous training studies

(Scott & Monesson, 2009, 2010). Children who participated in this training from 6 to 9 months of age returned to the laboratory between 4-5 years of age to complete a behavioral discrimination task and an ERP task investigating holistic processing, using stimuli from the previous training (monkey faces), a human face control condition, and a non-face object control condition (strollers). Previous work has found that young children are able to behaviorally discriminate among human faces of their own race (see control group in de Heering et al., 2010), thus the human face control condition was used as a comparison to assess "expert" performance. Research has shown that infants as young as 6 months of age exhibit an ERP inversion effect for human faces (de Haan, Pascalis & Johnson, 2002), thus a human face condition in the ERP task served as a basis for comparison for expert or holistic processing. The goal of bringing these children in for a follow-up visit was to assess whether information learned between 6 and 9 months of age is retained in early childhood.

First, we tested behavioral accuracy and reaction time to the previously trained category (monkey faces) in order to investigate any enduring gains in perceptual processing. Based on results from the prior training study (Scott & Monesson, 2009), we predicted that children trained at the individual level would exhibit faster reaction times and increased accuracy discriminating the trained category (monkey faces) compared to children trained at the category level or children with no prior training. We also expected all groups to exhibit increased accuracy and faster reaction times to human faces relative to the other conditions but we did not expect to find any group differences for the human face or non-face object control (stroller) conditions. If children in the individual-level training group exhibit processing advantages for the trained category (monkey faces)

relative to other groups, it would suggest that individual-level experience in infancy results in lasting effects for the trained category. However, since infants did not continue to learn about monkey faces past 9 months of age, it is possible that advantages gained through individual-level experience would be transferred to categories that infants continued to learn at the individual level, such as human faces. If individual-level gained in infancy is later applied to the environmentally relevant category of human faces, we would expect children trained at the individual level to exhibit faster reaction times and increased accuracy discriminating human faces compared to children trained at the category level and children with no prior training. These results would suggest that the experience of individual-level learning is more important than the category of faces involved in training.

Second, we measured ERPs in response to the trained category in order to identify any lasting neural changes. Evidence to support the idea of sustained changes comes from previous behavioral research in which Asian children adopted by Caucasian families between 2 and 26 months of age were tested on discrimination of Asian and Caucasian faces between the ages of 6 and 14 (de Heering, de Liedekerke, Deboni, & Rossion, 2010). Asian adoptees exhibited similar discrimination ability of Caucasian and Asian faces, suggesting that brief, early experience with Asian faces was sufficient for maintained discrimination. Additionally, the prior training study (Scott & Monesson, 2010) found that individual-level experience leads to changes in neural representations at 9 months of age. Therefore, we predicted that these neural changes will be retained for children trained at the individual level and will also facilitate behavioral discrimination later in childhood.

In order to investigate neural changes, we recorded and analyzed two ERP components: the N170 and the N250. The N170 is a negative deflection occurring around 170 msec post-stimulus onset. This component has been found to have a larger negative amplitude in response to human faces relative to animal faces and non-face objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier & Taylor, 2004), and is typically recorded at occipitotemporal and posterior temporal electrode sites (Bentin et al., 1996). The N170 component is considered an index of structural aspects of face encoding (Eimer, 2000). There are mixed findings as to whether the N170 exhibits differential amplitudes in response to face identity. Bentin and Deouell (2000) found no modulation of N170 amplitude due to face familiarity when participants were shown unfamiliar and familiar, famous faces. However, adults exhibited larger N170 amplitudes when they judged a face's identity to be different than that of a previous face as compared to when they judged identity to be the same (Jacques & Rossion, 2006), suggesting that N170 amplitude can sometimes be modulated by face identity. As previously mentioned, the N170 has been found to be modulated by face inversion. In studies with adults, the N170 was enhanced and delayed in response to inverted relative to upright faces (Rossion et al., 1999, 2000). This N170 "inversion effect" is taken as a marker for holistic perceptual processing.

While the N170 inversion effect is typically found in response to human faces, it has also been found in individuals responding to stimuli within a personal category of expertise (e.g., a dog expert looking at dogs, a bird expert looking at birds) (Tanaka & Curran, 2001). A comparable behavioral inversion effect has also been documented for objects of expertise, where experts but not novices exhibited decreased accuracy and

increased reaction times to categories of expertise (Diamond & Carey, 1986; Rossion & Curran, 2010). The N170 has been found to show increased amplitudes in response to novel objects after 6 days of training with the object category at both basic and subordinate levels (comparable to category and individual levels used in infant studies, respectively) (Scott, Tanaka, Sheinberg, & Curran, 2006), although N170 amplitude changes in response to a newly created category of expertise are not seen one week after training (Scott, Tanaka, Sheinberg, & Curran, 2008).

Although the N170 is most often studied in adults, the N170 has been found in children as young as 4 years old (Taylor, McCarthy, Saliba, & Degiovanni, 1999). In children, the N170 is also recorded over posterior temporal electrode sites, although children exhibit a longer latency to peak N170 relative to adults (Taylor et al., 1999). Further investigation of developmental changes in the N170 (Taylor, Batty, & Itier, 2004) indicated that in young children, the N170 component appeared to be bifurcated and contained two separate, identifiable peaks. The authors suggested that the second of these peaks was the N170, as it was more reliably present than the first peak. Similar to the work by Taylor and colleagues (Taylor et al., 2004, 1999), Kuefner and colleagues (2010) investigated the development of the N170 component in children between the ages of 4 and 17. The authors reported finding a large amount of variability in N170 latency, both between trials and between individual participants. Analyses of individual mean latencies revealed very little latency change across age. The apparent decrease in latency across development was due to longer latencies in the youngest age groups and these long latencies were in fact a result of a "bi-fid" N170 peak.

The prior training study (Scott & Monesson, 2010) found neural inversion effects following individual-level training in components thought to be developmental precursors to the N170 (de Haan et al., 2002). Based on these findings, we predicted that that if children exhibit lasting neural changes in response to early experience and learning in infancy we should see an N170 inversion effect in response to the trained category (monkey faces) for children trained with individual-level labels. However, it is also possible that in the absence of continued monkey face learning, the neural changes seen at 9 months of age after individual-level training will disappear and those neural resources will instead be recruited for learning other categories of faces or objects at the individual level. In this case, we might expect to see a benefit of early individual-level learning on human face processing.

The N250 component is a negative deflection occurring between 230 to 330 msec and peaking around 250 msec and is typically recorded over inferior temporal electrode sites (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002; Scott et al., 2006, 2008). When compared to other stimulus categories (e.g., monkey faces and cars), the adult N250 has been found to be greater in amplitude to human faces (Schweinberger, Huddy, & Burton, 2004). In particular, the N250 has been shown to respond to familiar faces, including one's own face (Tanaka, Curran, Porterfield, & Collins, 2006), famous faces (Schweinberger et al., 2002; Tacikowski, Jednoróg, Marchewka, & Nowicka, 2011), and newly familiar faces through familiarization or training (Tacikowski et al., 2011; Tanaka et al., 2006). It has been suggested that the N250 component therefore reflects individual-level processing and recognition (Schweinberger et al., 2004). The N250 is sensitive to face inversion, such that inverted faces elicit a smaller amplitude

response relative to upright faces (Schweinberger et al., 2004). Additionally, Scott, Tanaka, Sheinberg and Curran (2006) found that after subordinate (individual) level training with an unfamiliar category (birds), the N250 was enhanced to the trained category. The N250 was not enhanced after basic (category) level training however, further suggesting that the N250 component is related to individual-level recognition. A similar training study that used car stimuli found that, unlike the N170 effects, the training-related N250 changes were still present one week after training (Scott et al., 2008). In summary, the N250 appears to index face and object processing at the subordinate or individual level and training has been found to have lasting effects on the N250.

Little research has examined the N250 component in children. Kuefner and colleagues (2010) have suggested that what has previously been referred to as a "bi-fid N170" in 4- to 6-year-old children (see Taylor et al., 2004) may in fact be the N250 component. The authors proposed that in young children the second of these "bi-fid N170" peaks was in fact the N250 component and that high levels of inter-trial variability in latencies caused the N170 and N250 components to overlap in time, resulting in a larger component that appeared to have two peaks. The authors suggest that the N250 seen in young children is comparable to what is seen in adults, although based on the task, the authors did not make explicit conclusions regarding the function of the N250 in children.

Based on the adult N250 literature, we predicted that if early learning resulted in lasting effects, the N250 amplitude should be larger in response to the trained category (monkey faces) for children trained at the individual level compared to children trained at

the category level or with no prior training. However, if the effects of early experience are not long lasting, we predicted that the N250 should be larger for human faces compared to monkey faces and non-face objects (strollers) for all groups of children.

In summary, the N170 and N250 components are associated with holistic or expert perceptual processing and individual-level recognition, demonstrated by larger amplitude responses to human faces relative to other stimuli and by differential responses to upright versus inverted faces.

If we find larger N170 and N250 amplitudes and an N170 inversion effect in response to the trained category (monkey faces) for children in the individual-level training group compared to children in the category-level training group or the no-training control group, this would suggest that early individual-level learning leads to lasting perceptual and neural changes relating to the trained category. Evidence of lasting effects would provide support for and highlight the importance of early learning and its effects on processing environmental events later in life. However, if we find larger N170 and N250 amplitude responses to human faces relative to the trained category (monkey faces) and non-face objects (strollers) for all groups, this would suggest that the effects of early, individual-level experience are not maintained for specific categories later into childhood. Evidence that brief, early learning with a category (between 6 to 9 months of age) does not lead to lasting effects would suggest that a continuation of experience is needed to facilitate long-lasting perceptual and neural change.

CHAPTER 2

METHODS

Participants

Participants were recruited through the University of Massachusetts Amherst Child Study Center Research Recruitment Database. Children with a history of neurological, visual or auditory impairments were excluded. Parents of participants were paid $10 and children received a small toy for their participation. Thirty-eight 4- to 5-year-old children (Mean age = 4.84 years, range = 4.00–5.33) were recruited (22 males, 16 females; 36 Caucasian, 1 Asian, 1 Asian/Caucasian). Twenty-one of these children participated in the previous training study (Scott & Monesson, 2009, 2010): 8 completed individual-level training as infants, and 13 completed category-level training[1]. Seventeen additional children served as age-matched controls who completed no prior training.

Final behavioral analyses for all behavioral trials (regardless of accuracy) included data from 33 children from the individual-level training group (n = 7), the category-level training group (n = 11) and the control group (n = 15). An additional 5 children were excluded from final analyses because their reaction times were more than 2 standard deviations away from the mean of all participants within their experimental group (n = 4), or their accuracy was 50% or less (n = 1).

Final electrophysiological analyses included data from 27 children from the individual-level training group (n = 7), the category-level training group (n = 10) and the control group (n = 10). An additional 11 children were excluded from final analyses

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[1] Two additional children who completed exposure-level training were recruited and tested. Due to the extremely low sample size for the exposure-level group, these children were not included in analyses.

because they did not tolerate the net (n = 4) or did not contribute enough artifact-free

trials per condition (n = 7).

Stimulus and apparatus

Stimuli consisted of 24 digitized color photographs of Barbary macaques

(*Macaca sylvanus*), 24 digitized color photographs of strollers and 18 digitized color

photographs of female Caucasian faces (Figure 1). The photographs of the Barbary

macaques and the strollers were used in the previous training studies (Scott, 2011; Scott

& Monesson, 2009, 2010). The photographs of female faces come from the NimStim Set

of Facial Expression database (Tottenham et al., 2009). Basic shapes were used as stimuli

for the practice rounds of the behavioral task. Stimuli were presented at a visual angle of

approximately 13°. In addition, color images and sound clips from *Finding Nemo* were

used to keep participants engaged during the tasks.

Procedure

Child participants completed a behavioral discrimination task and an ERP task.

The behavioral task included four stimulus conditions: (a) novel exemplars of monkey

faces from the previously training study; (b) the monkey faces specifically used in

previous training; (c) human faces (control); (d) strollers (non-face object control). The

ERP task included upright and inverted novel monkey faces, human faces, and strollers.

Children completed the behavioral and ERP tasks in the context of a *Finding Nemo*

game.

Prior training procedure. Child participants completed 3 months of face training when they were between 6 and 9 months of age (Scott & Monesson, 2009, 2010). At 6 months of age, infants were sent home with a training book of six monkey faces, which were either labeled at the individual level (e.g., "Boris"), the category level (e.g., "monkey"), or the exposure level (no label). For a period of three months, parents were instructed to look at the book with their infants for 10 minutes every day for the first two weeks, every other day for the following two weeks, every third day for the next two weeks and to continue with this pattern until the infants returned at 9 months of age.

Behavioral procedure. Discrimination ability was assessed using a match-to-sample paradigm (Lindsay, Jack, & Christian, 1991; Sangrigoli & De Schonen, 2004). Children were seated in front of a computer seat and given a Serial Response Box (i.e., button press; SR Box). An experimenter demonstrated how to perform the task and children had the opportunity to complete practice trials with basic shapes before starting the experiment. Children then completed twelve trials, completing three trials from each of the following conditions presented in random order: (a) novel monkey faces (b) familiar monkey faces; (c) human faces; (d) strollers. For each familiarization trial, children viewed one image from one of the four conditions for 5 seconds. A 5-second delay occurred between the familiarization phase and the test phase. The length of the delay was based on the delayed match-to-sample task in the Cambridge Neuropsychological Test Automated Battery (CANTAB; Sahakian et al., 1988), which has previously been used to study working memory in typically developing four- to eight-year-old children (Luciana & Nelson, 1998). After the delay, two side-by-side images were presented: the familiar (previously viewed) image and a novel image from the same

category (e.g., a novel monkey face was always be paired with another novel monkey face). Children were asked to indicate via button press which of the two images was the same as the previously shown image.

      Electrophysiological procedure. Children passively viewed upright and inverted images of novel monkey faces, human faces, and strollers. Familiar monkey faces (images used in prior training) were not shown in the ERP task due to constraints on a feasible number of trials children of this age will sit through. Further, prior training studies found evidence of generalization of the ERP inversion effect to unfamiliar exemplars (Scott, 2011; Scott & Monesson, 2010), thus the inversion effect for monkey faces was of interest. An experimenter presented trials only when children were looking at the screen. Each trial consisted of a 100ms baseline, a 500ms stimulus presentation and a 1000-1200ms inter-trial interval. Children completed an average of 207 (SD = 27.8) out of 216 possible trials[2]. The task was completed in the context of a game and children were told at the beginning of the ERP task that they would be looking for Nemo (from *Finding Nemo*), who was hiding throughout the presentation of stimuli. Children were asked to press a button on the SR Box when they "found Nemo" and received Nemo-related feedback and a short break. These additional "Nemo" breaks were used at the discretion of the experimenter to keep children interested in the task and children received an average of 15.2 (SD = 2.4) "Nemo" breaks throughout the testing session. Children were also given a break every 25 trials to encourage task completion. Additionally, children received a longer break halfway through the task to prevent fatigue.

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[2] Only 4 children did not complete all 216 trials.

ERPs were collected using a 128-channel Geodesic Sensor Net, which is linked to a DC-coupled 128-channel high input impedance amplifier (Net Amps 300 TM, Electrical Geodesics Inc., Eugene, OR). Amplified signals were low-pass filtered online at 100 Hz and were sampled every 2ms (at a rate of 500 Hz). During recording, all electrodes were referenced online to the vertex (Cz). Electrodes were adjusted until impedances were less than 50 kΩ.

ERP processing procedure. Data were processed using NetStation 4.3 (Electrical Geodesics Inc., Eugene, OR). Stimulus-locked ERPs were digitally low-pass filtered at 40 Hz and baseline-corrected with respect to a 100 ms pre-stimulus baseline. Segmented trials were scanned for artifacts and trials that contained eye blinks were detected and removed using NetStation's artifact detection ($\pm$ 160 µV threshold) and eye blink algorithms ($\pm$ 200 µV threshold). Segmented trials were also visually examined for excessive noise and/or drift. Individual trials were excluded from analyses if they contained more than 12 bad channels. Individual channels that were constantly marked bad (off-scale on more than 70% of trials) were replaced using a spherical interpolation algorithm. Participants who had less than 12 artifact-free trials per condition were also excluded from analyses (n = 4). Participants contributed an average of 21 (SD = 5.8) trials for each of the conditions (upright and inverted monkey faces, human faces, and strollers. An average reference was used in order to minimize reference site activity and to accurately estimate scalp topography.

Time windows and electrode groupings were chosen based on previous research (Itier & Taylor, 2002; Rossion et al., 2000; Scott et al., 2006; Tanaka et al., 2006) and visual inspection of the data. Mean N170 amplitude was measured between 179 and 244

msec post-stimulus onset. Mean N250 amplitude was measured between 250 and 600 msec post-stimulus onset. Electrodes were grouped into left (64, 65, 66, 69, 70), middle (71, 74, 75, 76, 82), and right (83, 84, 89, 90, 95) regions (Figure 2). Responses were averaged across electrodes in each region for analysis.

CHAPTER 3

ANALYSES

Behavioral Analyses

Reaction time and accuracy were measured and averaged for all trials for each participant and then averaged across participants within each group. Each participant contributed three trials per condition to the computed averages. Based on our a priori hypotheses, analyses were conducted separately for each of the three conditions (human faces, monkey faces, strollers). Independent samples t-tests were conducted to examine overall accuracy and reaction time differences between training groups as well as accuracy and reaction time differences between training groups for each condition (i.e., human faces, monkey faces, strollers). T-tests were conducted based on our a priori hypotheses that 1) human faces would elicit higher accuracy and faster reaction time than other conditions, and 2) the individual-level training group would exhibit increased accuracy and faster reaction times to the trained category (monkey faces) compared to the category-level training group and the no-training control group. Paired samples t-tests were conducted to examine accuracy and reaction time differences between conditions within each training group. Independent samples t-tests were used to assess accuracy and reaction time differences between training groups for each condition.

Electrophysiological Analyses

Mean amplitude and latency of the N170 component was analyzed. Mean amplitude of the N250 component was also analyzed. Since the N250 component is not a

peaked component and there is difficulty pinpointing its peak in every participant, latency was not analyzed for the N250 (see Tanaka et al., 2006).

Analyses were first conducted to determine whether an inversion effect was present in response to human or monkey faces and if so, whether it differed across training group. In order to answer the first question, difference scores were computed between orientation (upright, inverted) for each condition and training group. Differences between upright and inverted stimuli have previously been found in the context of human faces (Bentin et al., 1996; Eimer, 2000; Rossion et al., 1999). Based on these results, we hypothesized that we would find differences between upright and inverted stimuli for the human face condition for all training groups. We also hypothesized that we would find differences between upright and inverted stimuli for the trained category (monkey faces) in the individual-level training group if training in infancy (see Scott & Monesson, 2010 for results) had lasting effects on the inversion effect. The purpose of creating difference scores was to examine the magnitude and direction of response difference between upright and inverted images. Difference scores were computed by subtracting the response to inverted stimuli within a condition from the response to upright stimuli in the same condition (e.g., upright human faces – inverted human faces). A negative difference score indicates that the response to upright stimuli was larger and a positive difference score indicates that the response to inverted stimuli was larger.

In order to investigate whether inversion effects were present and modulated by training group, difference scores between upright and inverted stimuli were submitted to a 3 x 2 mixed model MANOVA with factors of training group (individual-level training, category-level training, no-training control) and region (left, center, right) for each

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condition (human faces, monkey faces, strollers). As the inversion effect is typically seen in the N170 response (Bentin et al., 1996; Eimer, 2000; Rossion et al., 1999) and later in the N250 response (Schweinberger et al., 2004), difference scores were computed and analyzed for the N170 amplitude and latency, and the N250 amplitude.

In order to determine whether there were differential mean amplitude and latency responses to human faces, monkey faces, or strollers across training groups and whether there were differences in the distribution of neural activity across three defined regions of the scalp a 3 x 2 x 3 mixed model MANOVA with factors of condition (human faces, monkey faces, strollers), region (left, middle, right) and training group (individual-level training, category-level training, no-training control) was conducted in order to examine whether there were regional or condition-based differences across training group for the N170 and N250 components. Significant interactions were followed up with paired samples and independent samples t-tests. In the absence of a priori hypotheses, follow-up comparisons were Bonferroni corrected.

CHAPTER 4

RESULTS

Behavioral

Independent samples t-tests revealed no significant differences in accuracy between training groups. Additionally, paired samples t-tests revealed no significant accuracy differences between conditions.

Independent samples t-tests were conducted to compare reaction time averaged across all conditions between training groups. Children in the individual-level training group exhibited significantly faster overall reaction times than children in the category-level training group (t(16) = 2.26, p = .04) and no-training control group (t(20) = 2.09, p = .05). There were no significant overall reaction time differences between the category-level training and the no-training control groups.

Separate independent samples t-tests were conducted to compare reaction times for each training group within each condition. For the human face control condition, children in the individual-level training group (M: 3190.7 msec, SD: 738.4) exhibited significantly faster reaction times than children in the category-level training group (M: 5118.5 msec, SD: 2325.1) (t(16) = 2.11, p = .05) and the no-training control group (M: 4711.2 msec, SD: 1341.4) (t(20) = 2.79, p = .01) (Figure 3). The reaction times between category-level training and no-training control groups did not significantly differ in response to human faces. For the trained category condition (monkey faces), there were no significant differences in reaction time across groups (Figure 4). For the non-face object control condition (strollers), children without training (control group; M: 3928.64

msec, SD: 1153.94) had significantly faster reaction times compared to children in the

category-level training group (M: 5685.48 msec, SD: 2604.51) (t(24) = 2.33, p = .03).

Children in the individual-level training group (M: 3662.38 msec, SD: 1023.97) had

marginally faster reaction times in response to the non-face object control condition

(strollers) compared to children in the no-training control group (t(16) = -1.94, p = .07).

Reaction times for the non-face object control condition (strollers) did not differ

significantly between the individual-level training and category-level training groups

(Figure 5).

Paired samples t-tests were also conducted to compare reaction time between

conditions within each training group. No significant reaction time differences between

conditions were found.

Electrophysiological

N170

Inversion Effect. Differences between upright and inverted stimuli computed and

submitted to 3 separate 3 x 2 mixed model MANOVAs with factors of training group

(individual-level training, category-level training, no-training control) and region (left,

center, right) for each condition (human faces, monkey faces, strollers). Amplitude

analyses for the human face condition revealed a significant main effect of training group

$(F(2,24) = 5.22, p = .01, \eta^2 = .30)$. Follow-up analyses revealed that the individual-level

trained children exhibited the opposite pattern of difference scores than children trained

at the category-level during infancy (p = .04) and the children without training (p = .02).

The direction of the difference scores indicates that in the category-level training and no-

training control groups, upright human faces elicited a larger negative amplitude than inverted human faces. However, in the individual-level training group, inverted human faces elicited a larger negative amplitude than upright human faces (Figure 6 and Table 1). Across groups, no significant differences between upright and inverted stimuli were found in response to the trained category condition (monkey faces) or the non-face object control condition (strollers).

Latency differences between upright and inverted stimuli did not reveal any significant differences across conditions or groups.

Condition and Region Differences. Mean amplitude and latencies were submitted to a 3 x 2 x 3 mixed model MANOVA with factors of condition (human faces, monkey faces, strollers), region (left, middle, right) and training group (individual-level training, category-level training, no-training control). Amplitude analyses revealed no significant group differences for the N170. Analyses showed a significant main effect of condition ($F(2,23) = 83.38$, $p < .001$, $\eta^2 = .88$), where human faces elicited a greater amplitude N170 than the trained category (monkey faces) or the non-face object control (strollers) and the trained category (monkey faces) elicited a greater N170 than the non-face object control (strollers) (p's $< .001$) (Figure 7). There was also a main effect of region ($F(2,23) = 3.75$, $p = .04$, $\eta^2 = .25$), although follow-up comparisons showed no significant differences of theoretical interest. Analyses also revealed a significant interaction of condition and region ($F(4,21) = 22.10$, $p < .001$, $\eta^2 = .81$). However, follow-up comparisons primarily showed similar patterns across regions. Across all regions, human faces elicited a larger response compared to trained category (monkey faces) and the non-face object control (strollers), and the trained category (monkey faces) elicited a greater

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response than the non-face object control (strollers) (p's < .001). There was a significantly greater response to human faces and the trained category (monkey faces) in the left versus middle region (p's < .01). The trained category (monkey faces) also elicited a greater amplitude response in the left compared to right region (t(26) = -4.00, p < .001). Finally, the amplitude response to the non-face object control (strollers) was greater in the middle relative to left (t(26) = 3.35, p = .003) and right (t(26) = -3.60, p = .001) regions.

Latency analyses showed no significant differences across training groups. Analyses revealed a main effect of condition (F(2,23) = 5.24, p = .01, η^2 = .31), such that there was a faster latency to peak to the non-face object control (strollers) than the trained category (monkey faces) (p = .01). The latency to peak was not significantly different to human faces compared to the trained category (monkey faces) or the non-face object control (strollers). Finally, there was also a main effect of region (F(2,23) = 4.99, p = .02, η^2 = .30), with a faster latency to peak recorded over the left than middle region (p = .01).

N250

Inversion Effect. Differences between upright and inverted stimuli computed and submitted to 3 separate 3 x 2 mixed model MANOVA with factors of training group (individual-level training, category-level training, no-training control) and region (left, center, right) for each condition (human faces, monkey faces, strollers). Analyses of the difference between upright and inverted stimuli showed no significant group differences for the human face control, the trained category (monkey faces) or the non-face object control (strollers).

Condition and Region Differences. Mean amplitude was submitted to a 3 x 2 x 3

mixed model MANOVA with factors of condition (human faces, monkey faces,

strollers), region (left, middle, right) and training group (individual-level training,

category-level training, no-training control).Amplitude analyses revealed no significant

group differences. Analyses showed a main effect of condition ($F(2,23) = 42.00$, $p <$

.001, $\eta^2 = .79$), where there was a greater N250 in response human faces relative to the

trained category (monkey faces) and the non-face object control (strollers) (p's < .001)

(Figure 7). There was also a main effect of region ($F(2,23) = 6.80$, $p = .01$, $\eta^2 = .37$), such

that there was a larger amplitude response in the left ($p = .05$) and middle ($p = .003$)

regions compared to the right region. Analyses also revealed a significant interaction of

condition and region ($F(4,21) = 7.95$, $p < .001$, $\eta^2 = .60$). Follow-up comparisons showed

that in all three regions, there was a larger amplitude in response to human faces relative

to the trained category (monkey faces) and the non-face object control (strollers) (p's <

.001). However, in the left region, there was also a larger amplitude in response to the

trained category (monkey faces) compared to the non-face object control (strollers) ($t(26)$

$= -5.41$, $p < .001$). In response to human faces, there was a larger amplitude response in

the left ($t(26) = -2.88$, $p = .01$) and middle ($t(26) = -2.47$, $p = .02$) regions compared to

the right region. In response to the trained category (monkey faces), there was a greater

amplitude in the left relative to middle ($t(26) = -2.17$, $p = .04$) and right ($t(26) = -4.51$, p

$< .001$) regions, as well as in the middle versus right region ($t(26) = -3.45$, $p = .002$).

Unlike the pattern seen for the trained category (monkey faces) and the human face

control, there was a greater amplitude response in the middle region relative to left ($t(26)$

= 4.06, p = .003) and right (t(26) = -4.44, p = .001) regions for the non-face object control

(strollers).

CHAPTER 5

DISCUSSION

The current study sought to examine whether experience with faces during the first year of life results in lasting perceptual and neural processing advantages for faces within or outside the trained face category as much as 3 years later. In order to answer this question, we recruited and tested children who previously participated in a face training study when they were infants (Scott & Monesson, 2009, 2010). In these previous studies, 6-month-old infants were randomly assigned to either an the individual-level training group, where each face was labeled with a unique proper name (e.g. "Boris", "Fiona") or the category-level training group, where all faces were labeled with the same category name (e.g., "monkey"). Infants were then trained over a 3-month period and were brought back at 9 months of age to assess learning. Results of these studies suggest that infants trained at the individual-level, but not category level, showed expert or holistic representations of the learned category and no evidence of perceptual narrowing. Based on the findings of these previous training studies, we predicted that if early learning in infancy leads to lasting processing advantages, children trained at the individual, but not the category level as infants should exhibit decreased reaction times and increased holistic processing in response to the trained category (monkey faces), relative to a control group of children who received no training as infants. However, it is also possible that in the absence of continued individual-level monkey face learning, the behavioral and neural changes seen at 9 months of age will disappear and those neural resources will instead be recruited for learning other categories of faces or objects at the

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individual level. In this case, we expected to see a benefit of early individual-level learning on human face processing.

The results from the behavioral task reveal differences in reaction time between training groups. Children in the individual-level training group exhibited faster reaction times in response to human faces compared to children in the category-level training group and children in the no-training control group (see Figure 2). There were no significant reaction time differences between training groups in response to the trained category (monkey faces). These findings suggest that early individual-level experience led to a facilitation in human face processing abilities 3 to 4 years later. Neither training group showed faster reaction times to the trained category (monkey faces), indicating that the category of face or object involved in the prior training may not be as important as the type of experience gained. Specifically, children in the individual-level training group received practice labeling at the individual level. The prior training studies demonstrated the importance of individual- relative to category-level labeling in promoting holistic/expert processing and discrimination of exemplars (Scott & Monesson, 2009, 2010). Therefore, we suggest that the facilitation of human face processing seen in the individual-level training group is due to an additional period of learning to label at the individual level, relative to children in the other groups. After the training period ended, these children continued utilizing individual-level labeling for human faces (and not monkey faces), thus honing their individual-level labeling to human faces alone.

Support for the idea of transferring or generalizing learning to a new, similar category comes from recent training studies conducted with bird species (Scott et al., 2006; Tanaka, Curran, & Sheinberg, 2005). Adults were trained to recognize birds either

at the basic level (bird family) or at the subordinate level (bird species). Findings revealed that after training, adults trained at the subordinate level showed a transfer of expertise to novel species categories. These results suggest that subordinate- or individual-level learning and experience can be transferred to similar, but novel categories. In the context of the current study, we propose that learning associated with individual-level labeling of monkey faces between 6 and 9 months was transferred to a perceptually similar, but environmentally-relevant category (human faces) after training ended.

To address the question of whether children trained at the individual-level during infancy exhibited sustained inversion effects for the trained category (monkey faces), we recorded ERPs while they viewed upright and inverted monkey faces, human faces, and a non-face control condition (strollers). We specifically examined the difference between upright and inverted stimuli across groups by computing the mean difference scores between responses to upright and inverted stimuli. For this analysis we found inversion differences for the N170, but not the N250 component in response to human faces. Specifically, the individual-level training group displayed a different pattern of inversion response to human faces compared to the category-level training group and the no-training control group. The category-level training group and the no-training control group exhibited larger N170 amplitudes to upright compared to inverted faces, while the individual-level training group displayed larger N170 amplitudes to inverted compared to upright faces. This finding is consistent with previous studies that report inversion effects for the N170 (Rossion et al., 1999, 2000). Although previous results have reported differential N250 responses to upright versus inverted faces (Schweinberger et al., 2004),

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our results suggest that in the current study, holistic processing was limited to the N170 component. It is possible that N250 inversion effects were not found in the current study because 4-year-olds' face-related responses are not completely adult-like (Kuefner et al., 2010). It is also possible that task-related differences account for the lack of N250 inversion effect in the current study. No differences between upright and inverted monkey faces were found, suggesting that training with monkey faces from 6 to 9 months of age did not lead to lasting ERP inversion effects. The typical adult N170 inversion effect reported in the literature is an enhanced and delayed N170 in response to inverted relative to upright faces (Rossion et al., 1999, 2000). Our findings suggest that children in the individual-level training group exhibit a more adult-like inversion effect than the other training groups, possibly reflecting increased holistic processing of human faces. However, it is difficult to determine the meaning of these differences at this time because later analyses revealed that although the pattern of results was significantly different across groups, both the category trained and no training control group did exhibit a significant difference between the upright and inverted human faces (Figure 8). This difference was in the opposite direction as the marginally significant difference between upright and inverted human faces for the individual-level training group. A small sample size may have contributed to the lack of significant inversion effect.

The finding that individual-level, but not category-level learning led to an adult-like inversion effect 3-4 years later further supports the importance of individual-level experience and learning. Additionally, these results suggest that individual-level learning not only facilitates behavioral response, but also leads to differential (and possibly more adult-like) neural processing. Similar to the behavioral results, individual-level training

with monkey faces led to changes in neural processing of human faces, suggesting that neural mechanisms related to holistic processing (the N170 inversion effect, see: Gauthier & Curby, 2005; Rossion et al., 1999) may generalize to similar perceptual categories.

To address the question of whether children trained at the individual-level during infancy exhibited larger N170 and N250 amplitude responses to the trained category (monkey faces) than children trained at the category-level or children with no prior training, we examined differences in component amplitude between groups. For this analyses we found no group differences for the N170 or N250 components between stimuli conditions or brain regions. However, we found expected amplitude patterns for both components across stimuli conditions. For the N170, all training groups exhibited amplitudes largest in response to human faces, followed by monkey faces, and finally strollers (see Figure 7). This finding is in line with past research indicating that the adult N170 amplitude is typically larger in response to human faces than animal faces or non-face objects (Bentin et al., 1996; Itier & Taylor, 2004). These results are also supported by prior findings that young children exhibit larger N170 amplitudes in response to faces versus non-face objects (cars, scrambled cars) (Kuefner et al., 2010; Taylor et al., 1999).

For the N250 component, human faces elicited a larger amplitude response than monkey faces or strollers for all training groups. These results are in agreement with similar findings that the adult N250 amplitude is largest for human faces, smaller but present for monkey faces, and not present for non-face objects (cars) (Schweinberger et al., 2004). These findings may reflect the N250 component's role in individual-level processing. Specifically, the N250 amplitude response may be larger to human faces compared to monkey faces or non-face objects (strollers) because in the current study,

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only human faces were processed at the individual-level. It is somewhat difficult to relate the current N250 results to previous developmental literature, as only one study has reported an N250 response in young children (Kuefner et al., 2010). Comparison to the previous developmental N250 study is also difficult because, although the authors proposed the "bi-fid N170" to be the N250 component, they did not offer an interpretation of the N250 in relation to the experimental task. However, Kuefner and colleagues (2010) reported the "split N170" in response to both human faces and cars, a finding which was not reproduced with the non-face objects (strollers) in the present study. Thus, more research is needed to determine the specificity of the N250 component in young children.

Researchers have suggested that the period from 6 to 9 months of age may constitute a "sensitive period" during which specialized cortical regions are formed or enhanced in response to environmental experience (Lewkowicz & Ghazanfar, 2009; Scott, Pascalis, & Nelson, 2007). Sensitive periods have previously been found for perceptual systems (e.g., visual system: Hubel & Wiesel, 1970) and serve the general purpose of creating a window of time in which environmental input or experience can shape associated cortical structures while these structures are developing. Moreover, cortical systems are thought to be highly plastic during sensitive periods and though these systems can be reshaped later in life by environmental experience, later plasticity is more limited (Sengpiel, 2007). The timing of perceptual narrowing for faces coincides with a proliferation of synaptic connections followed by the pruning of these connections to adult numbers (Huttenlocher, 1984; for review, see Scott et al., 2007). It is possible that perceptual experiences during this important time in brain development may have lasting effects

relative to perceptual experiences after synaptic connections reach adult levels. The advantage of additional experience labeling at the individual level may be specifically important in the period between 6 to 9 months of age. Processes related to brain development, including synaptic overproduction and pruning, combined with experience may work to create lasting neural and behavioral processing advantages. While the current study cannot directly address the question of whether 6 to 9 months of age constitutes a sensitive period, it is the first step in attempting to answer such a question and shows that learning during this period has lasting effects on behavior and brain processes. Future research should examine the long-term impact of individual-level training implemented within different age ranges. For example, it would be interesting to know whether or not additional experience with individual-level labeling lead to lasting effects when training occurs after the purported sensitive period (e.g., 9 to 12 months) or whether individual-level learning would be maintained if it occurs earlier in infancy (e.g., 3-6 months).

The current study was constrained by two major limitations. The first limitation resulted from a longitudinal design, which required recruiting participants 3-4 years after initial testing. The upper limit of the sample size for each training group available for recruitment was small (n = approximately 15 per group), but successfully used in the prior training studies (Scott & Monesson, 2009, 2010). However, only a proportion of these children were successfully contacted and recruited (individual-level group n = 8; category-level group n = 13) for the present investigation. The second limitation was methodological in nature. Event-related potential research requires participants to sit still through a large number of trials in order to collect enough data free from noise and

artifacts (e.g., large muscle movements, blinks). Although the majority of children in the current study successfully completed all ERP trials, a large number of artifacts resulted in a smaller sample size. In summary, a limited participant pool in conjunction with methodological constraints related to testing a child population, resulted in small group sample sizes. The small sample sizes reduced our statistical power.

However, despite these limitations, the current study found evidence that early, individual-level experience leads to lasting advantages in perceptual and neural processing. Children trained at the individual-level as infants exhibited faster reaction times to human faces compared to children trained at the category-level and children with no prior training. Additionally, children trained at the individual-, but not the category-level, displayed a differential, more adult-like ERP inversion effect in response to human faces compared to children who received no training as infants. Interestingly, the behavioral and neural processing advantages seen after individual-level training occurred in response to human faces, but not in response to the trained category (monkey faces). These results suggest that the experience of labeling faces at the individual level, and not the category of faces used during training, is important in facilitating later processing. Furthermore, learning related to individual-level labeling is generalized to perceptually similar, but environmentally relevant categories (human faces).

Future research should investigate the whether 6 to 9 months of age constitutes a sensitive period during which individual-level learning leads to lasting advantages relative to other periods in development by conducting training studies within different developmental windows (e.g., 9 to 12 months of age). Future work should also investigate whether generalization of individual-level learning is specific to categories of

faces, or whether learning can be transferred from non-face categories that are

perceptually dissimilar to faces.

Tables

Training Group	N170 amplitude: Human Upright (µv)	N170 amplitude: Human Inverted (µv)	Difference Score: Upright-Inverted (µv)
Control	- 4.41	- .62	- 3.79
Category	- 5.17	- 1.94	- 3.24
Individual	- 2.41	- 3.91	1.51

Table 1. Difference scores for N170 amplitude response to upright – inverted Human faces. Negative difference scores reflect a larger N170 amplitude to upright faces, positive difference scores reflect a larger N170 amplitude to inverted faces.

Figures
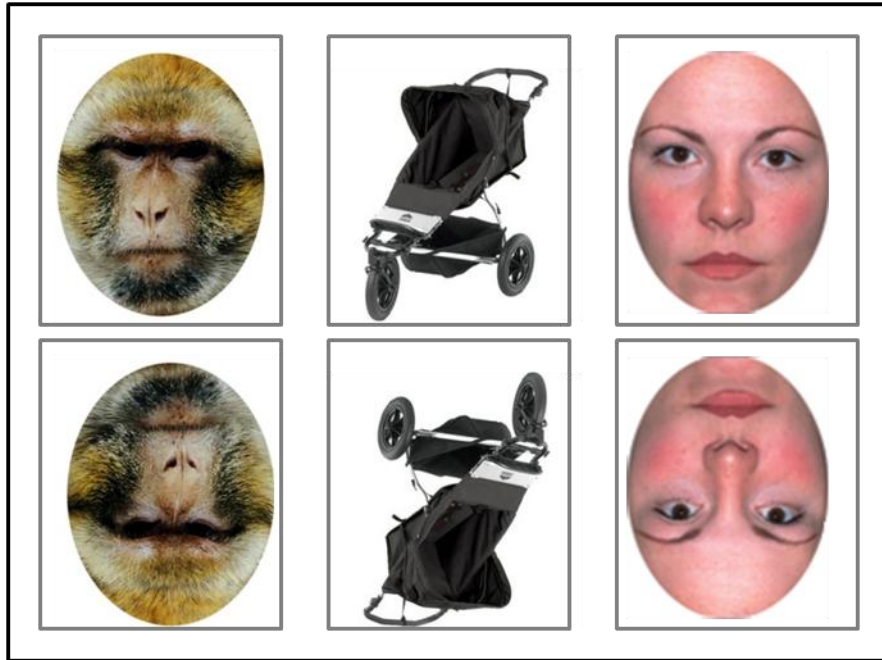
Figure 1. Examples of Barbary macaque, stroller, and human stimuli
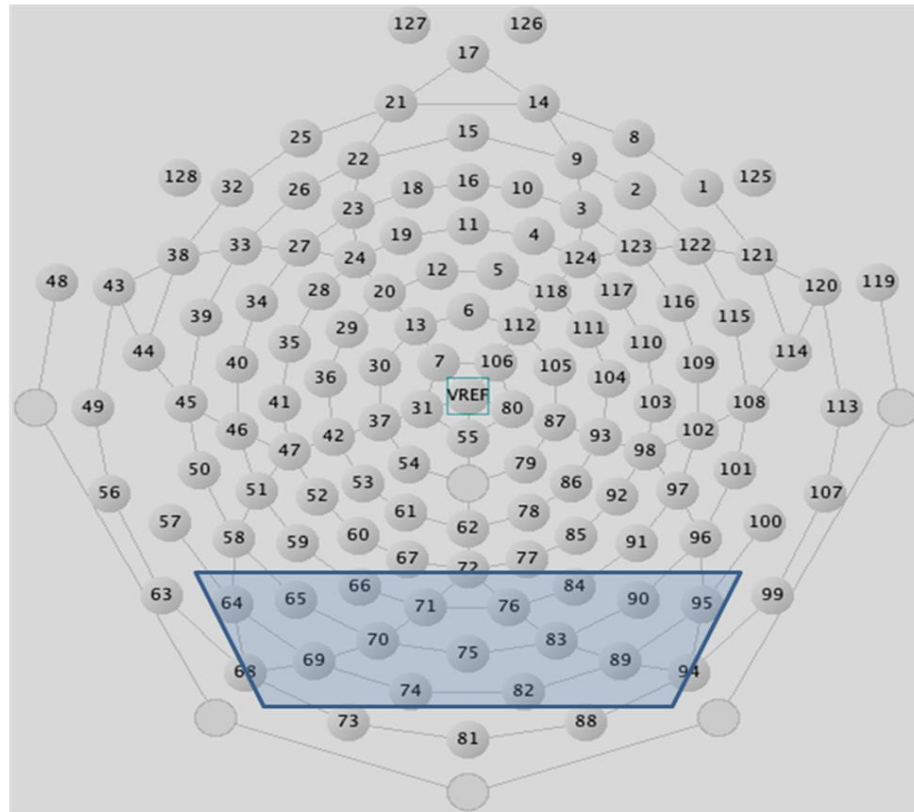
Figure 2. Electrodes used in analyses. Electrodes were grouped into left (64, 65, 66, 69, 70), middle (71, 74, 75, 76, 82), and right (83, 84, 89, 90, 95) regions. Responses were averaged across electrodes in each region for analysis
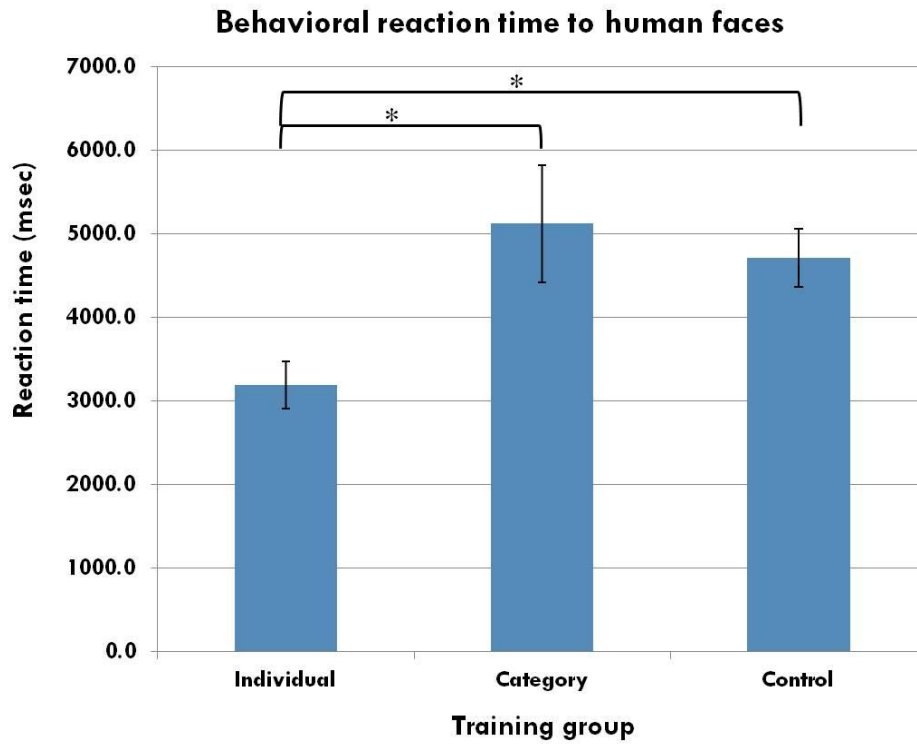
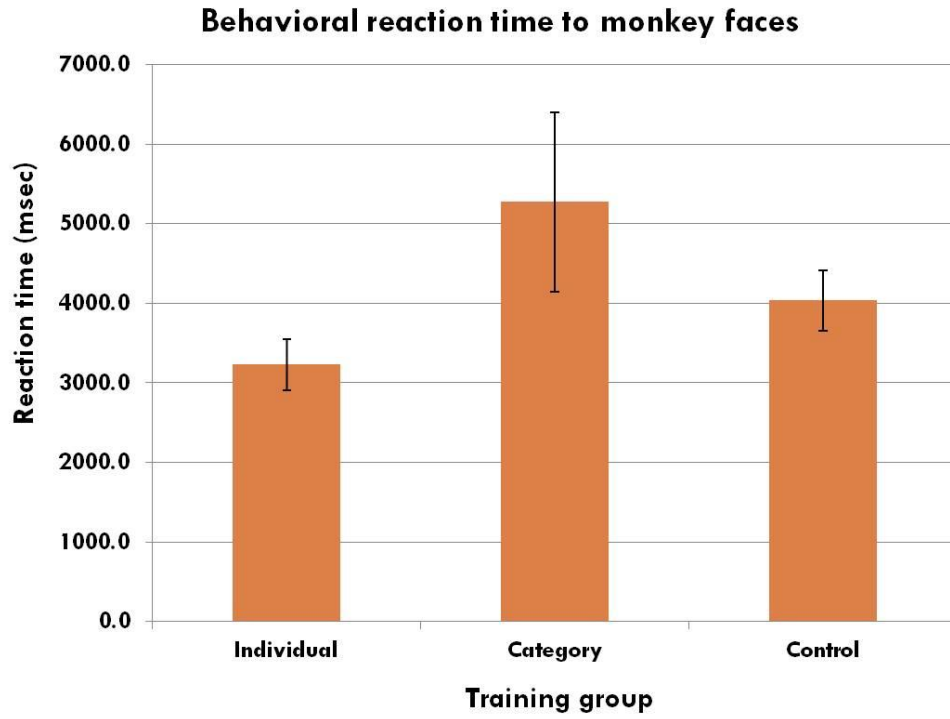Figure 3. Reaction time to human faces for each training group.

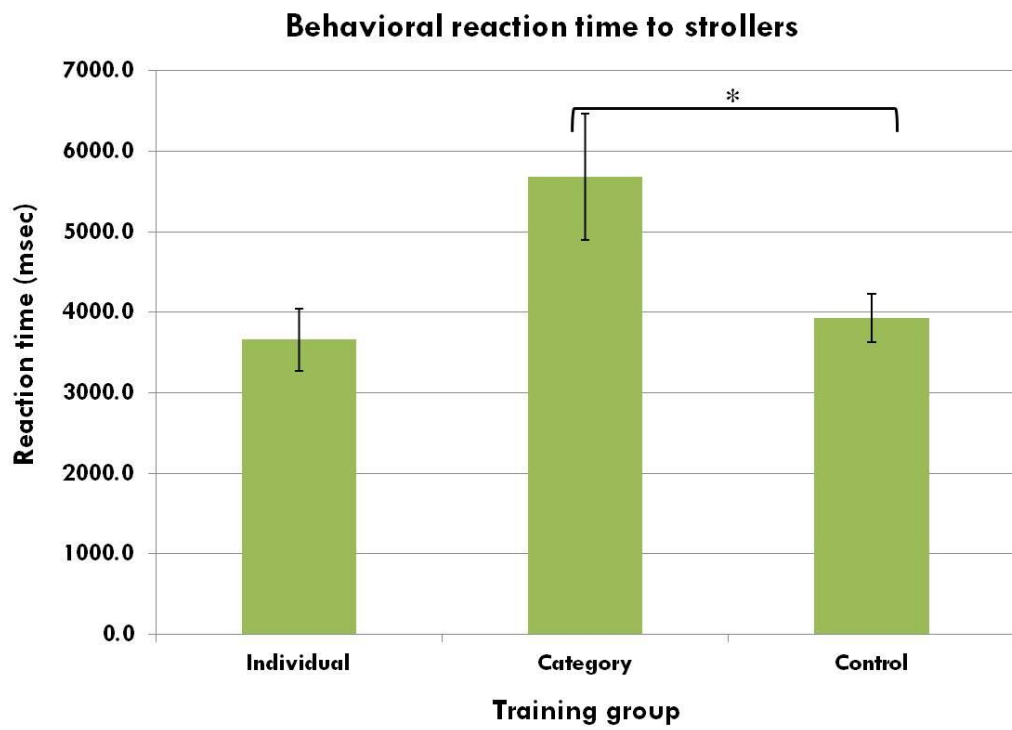Figure 4. Reaction time to monkey faces for each training group.

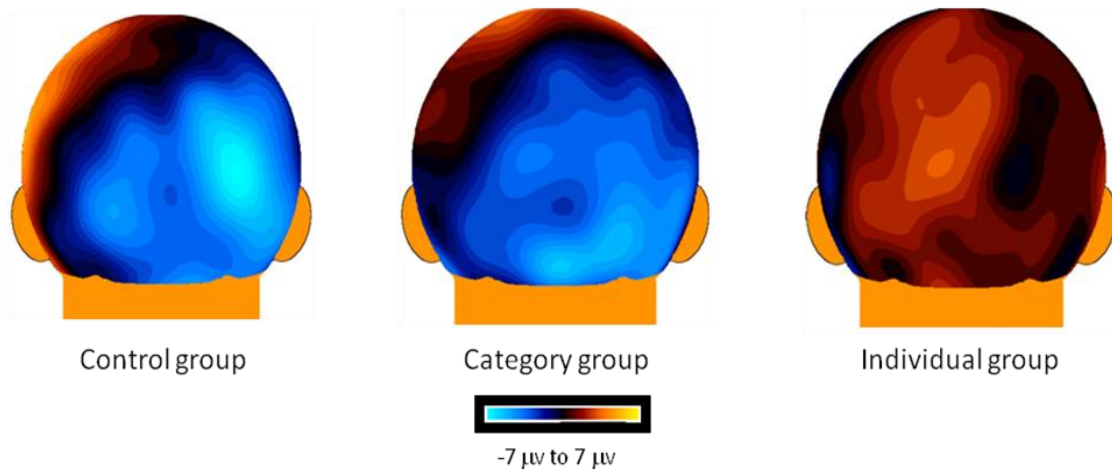Figure 5. Reaction time to strollers for each training group.

Figure 6. Head plots of N170 amplitude difference scores for Upright – Inverted Human faces. More negative activity indicates a larger amplitude response to upright Human faces, while more positive activity indicates a larger amplitude response to inverted Human faces.
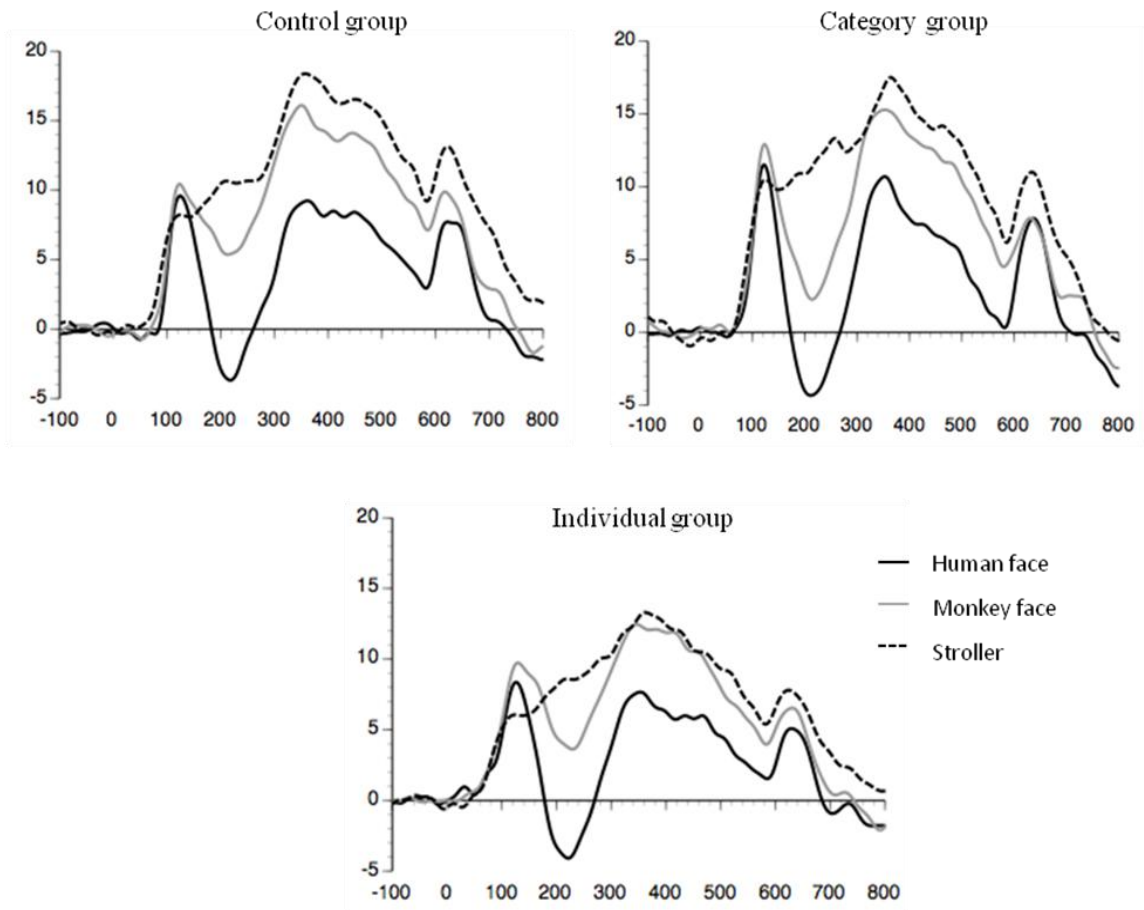
Figure 7. Responses to human face, monkey face and stroller conditions. The N170 amplitude is largest in response to human faces, followed by monkey faces, then strollers, for all three groups. The N250 amplitude is larger in response to human faces relative to monkey faces and strollers in all three groups.
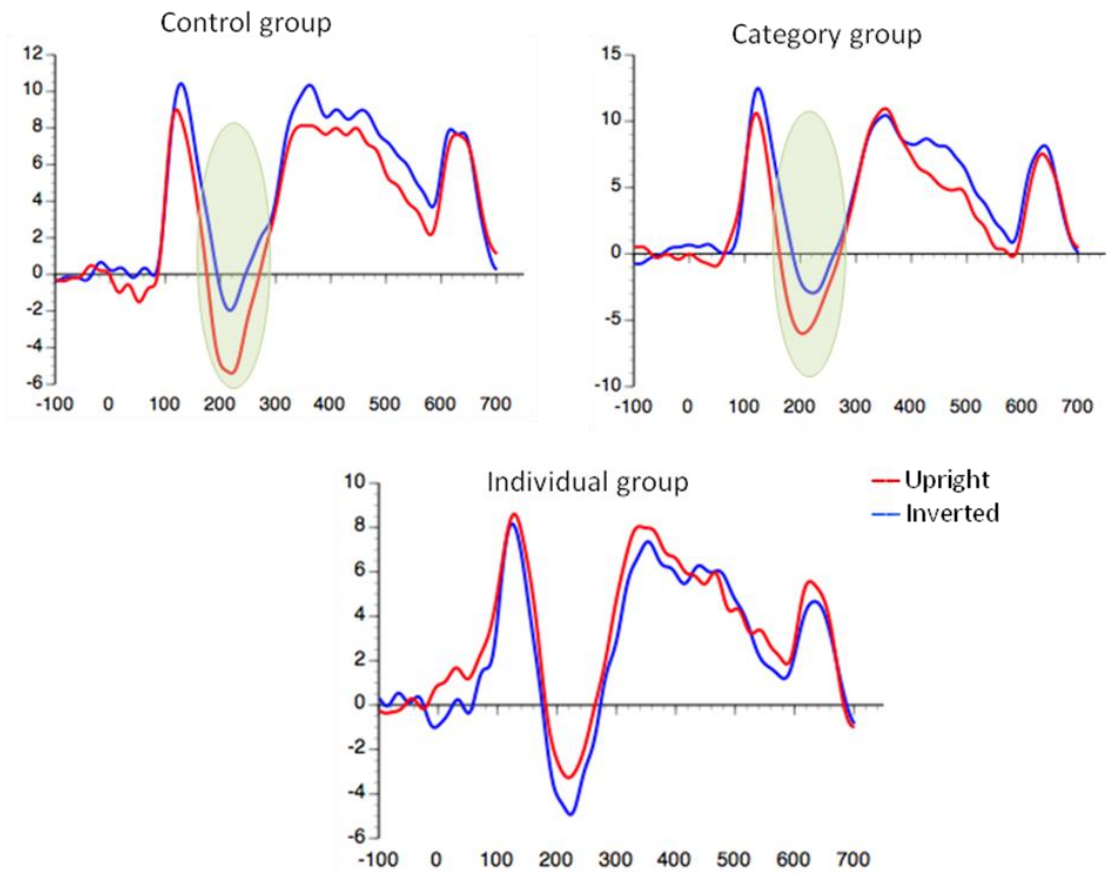
Figure 8. Responses to upright versus inverted Human faces. The N170 amplitude is larger in response to upright than inverted faces in Control and Category groups, while the N170 amplitude is larger is response to inverted than upright faces in the Individual group.

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