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How do neural responses to eyes contribute to face-sensitive ERP components in young infants? A rapid repetition study

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ABSTRACT

Several face-sensitive components of the event-related potential (ERP) have been identified in infants, such as the posterior N290 and P400 components. The contribution of eye-sensitive neurons to these components is still unclear, however. A rapid repetition ERP paradigm was used to test 4-month-olds' responses to faces with and without eyes (preceded by houses, i.e., unprimed) and faces with eyes that were preceded by faces with or without eyes (i.e., primed). N290 latency was reduced and P400 amplitude was increased for unprimed faces without eyes compared to intact faces. In addition, N290 latency was reduced for faces preceded by intact faces compared to faces preceded by faces without eyes. Thus, processing speed at the level of the N290 and amplitude of the P400 are affected by the absence of eyes in a face supporting the notion that eye-sensitive neurons contribute to these components in infancy. Findings are discussed in relation to the early development of face processing and infant and adult ERP responses to faces and eyes.

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1. Introduction

People are remarkably good at discriminating and recognizing human faces (Bruce & Young, 1986). Even newborn infants are able to recognize their mother's face only hours after birth (Sai, 2005) and they can recognize a stranger's face after familiarization (Coulon, Guellai, & Streri, 2011). One of the most important facial features to allow for face identification is the eye region (Sinha, Balas, Ostrovsky, & Russell, 2006). Removing the eyes and/or eyebrows of a face makes it extremely hard to recognize even highly familiar faces (Sadr, Jarudi, & Sinha, 2003). It has therefore been suggested that the eyes are the most informative and most attended features in the human face (Itier & Batty, 2009). The current study investigates how the eye region and, in particular, its absence in a face affects infants' neural responses to face stimuli.

Neurophysiological research has revealed components of the event-related potential (ERP) that are involved in processing faces and eyes in infants, children, and adults (Hoehl & Peykarjou, 2012). The N170 on lateral posterior channels is reliably larger and faster in response to faces compared to other object categories in adults (Rossion & Jacques, 2008). It is also delayed and sometimes enhanced by face inversion, which disrupts configural visual processing, but it is less affected by object inversion (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier, Latinus, & Taylor, 2006). This has been taken as evidence that the N170 reflects structural encoding of faces (Bentin et al., 1996).

Interestingly, it seems to be the information presented in the eye region that determines whether a stimulus is processed as a face. No face inversion effect is found on the N170 for schematic faces with line drawings of objects substituting the eyes, but it is found for schematic faces with little faces at the position of the eyes (Bentin, Golland, Flevaris, Robertson, & Moscovitch, 2006). Amplitude of the N170 in response to isolated eye stimuli is equal or even larger than N170 amplitude to complete faces, which has lead to the suggestion that the N170 might reflect the operation of an eye processor (Bentin et al., 1996). However, amplitude of the N170 does not differ in response to intact faces vs. faces with the eye region removed (Eimer, 1998). Thus, the N170 does not merely reflect activity of neurons sensitive to the presence of eyes, but may rather be induced by neurons responding to faces and, in addition, neurons responding selectively to eyes (Itier, Alain, Sedore, & McIntosh, 2007; Itier & Batty, 2009; Itier et al., 2006).

There is evidence that the role of the N170 in the processing of eyes may change across development. The N170 in children from 4 to 15 years is much larger in amplitude and faster in latency in response to eyes alone compared to intact faces (Taylor,

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Edmonds, McCarthy, & Allison, 2001). Furthermore, while the N170 to faces develops until adulthood, the N170 response to isolated eyes has a mature morphology already by 11 years of age.

In infants, the N290 component has been identified as a potential precursor of the N170. It has been observed in response to static faces in infants from 3 months of age and it is comparable to the adult N170 with respect to its topography and polarity, though it is a little delayed, more medially distributed and smaller in amplitude (de Haan, Johnson, & Halit, 2003). The N290 is enhanced for faces relative to matched visual noise in 3-month-olds (Halit, Csibra, Volein, & Johnson, 2004). At the same age, N290 amplitude is specifically enhanced by inversion of a face but not a car (Peykarjou & Hoehl, 2013). In addition, a posterior P400 is typically observed in infants' ERP responses to faces. In 6-month-olds this component peaks at a shorter latency for faces than objects (de Haan & Nelson, 1999) and it is larger for upright as compared to inverted human and ape faces (de Haan, Pascalis, & Johnson, 2002). In 3-month-olds P400 amplitude is greater for intact faces as compared to scrambled faces whereas the N290 does not differ in response to these stimuli (Gliga & Dehaene-Lambertz, 2005).

Notably, the infant N290 is enhanced by direct eye gaze in static faces compared to averted gaze in 4-month-olds (Farroni, Csibra, Simion, & Johnson, 2002), which is not the case for the N170 component in adults (Taylor, Itier, Allison, & Edmonds, 2001). Furthermore, faces deviating from a standard face only with respect to the eye region elicit an increased N290 in 9-month-olds in an oddball paradigm, which is not the case if it is the mouth region that differs from the standard face (Key, Stone, & Wiliams, 2009). Thus, the infant N290 seems to be particularly sensitive to information from the eye region of a face. It is an open question, however, to what extent this component is sensitive to the presence or absence of eyes in a face stimulus. If the N290 predominantly responds to eyes, removing the eye region of a face stimulus should considerably reduce its amplitude, which is not the case for the adult N170 (Eimer, 1998).

In addition to measuring infants' responses to faces with and without eyes, a valid approach to test the contribution of eye-sensitive neurons to the N290 is using a rapid repetition ERP paradigm. Here, the response to a target stimulus is assessed depending on the preceding prime stimulus. The advantage of rapid repetition or priming paradigms is that ERPs are recorded in response to physically identical stimuli (i.e., the same targets preceded by different primes), such that low-level perceptual differences between stimuli are no confound. Repetition suppression of an ERP component is typically taken as evidence that prime and target stimulus activate a common representation in the brain at the processing step of the affected component (e.g., Gliga & Dehaene-Lambertz, 2007). Whereas repetition *suppression* is taken to signal neural adaptation, repetition *enhancement* indicates that additional processing is recruited for the target relative to the prime, for instance, because a neural representation is still being built up (Henson, 2003; Peykarjou, Pauen, & Hoehl, 2014).

Only few priming studies have examined face processing in infants (e.g., Stolarova, Whitney, Webb, deRegnier, Georgieff, & Nelson, 2003; Webb & Nelson, 2001), and only one study using a rapid repetition paradigm has been published (Peykarjou et al., 2014). In one priming study isolated eyes were presented embedded within a sequence of face or object stimuli (Gliga & Dehaene-Lambertz, 2007). In 3- to 4-month-olds the N290 response to isolated eyes was reduced in the context of frontal view faces vs. houses but not in the context of profile view faces with closed eyes vs. cars (Gliga & Dehaene-Lambertz, 2007). Thus, similar or overlapping neural populations underlying the N290 response seem to respond to isolated eyes and intact frontal view faces featuring eyes in 3-month-olds (a weaker effect was found for frontal faces with closed eyes).

Here, 4-month-olds' ERP responses for intact faces and faces with the eye region removed are investigated. Based on previous research (e.g., Farroni et al., 2002), it is assumed that the infant N290 is sensitive to information from the eye region to a greater extent than the N170 in adults. Therefore, differing from the adult N170 (Eimer, 1998), we predict reduced amplitude of the N290 for (unprimed) faces without eyes compared to intact faces. In addition, greater repetition suppression of the N290 is expected to occur for faces preceded by intact faces featuring eyes as compared to faces without eyes. Finally, responses to unprimed faces with eyes will be compared with responses to primed faces that were preceded by faces with or without eyes in order to assess to what extent both kinds of priming affect face processing relative to the unprimed condition. It is expected that responses to primed faces preceded by intact faces differ more from unprimed faces than responses to faces preceded by faces without eyes because the latter are expected to elicit less priming effects.

2. Material and methods

Four-month-old infants took part in this rapid repetition ERP study. In a within-subject design infants' responses to unprimed faces with eyes (unprimed-with eyes) and without eyes (unprimed-no eyes) were tested. Furthermore, we tested infants' responses to intact faces primed by faces with eyes (primed-with eyes) and intact faces primed by faces without eyes (primed-no eyes). All experiments were conducted with the understanding and informed consent of each participant's parent.

2.1. Participants

All participating infants were born full term (37–41 weeks) and were in the normal range for birth weight. Thirteen infants were included in the sample (8 females, age range: 4 months, 1 day to 4 months, 26 days; average age: 4 months and 18 days). Another 34 infants were tested but excluded from the sample because they failed to reach the minimum requirement of 10 artifact free trials per condition for averaging ($N = 29$) or because of technical problems ($N = 5$). Our criterion for inclusion and the resulting attrition rates are within the normal range for visual infant ERP studies (DeBoer, Scott, & Nelson, 2007; Stets, Stahl, & Reid, 2012).

2.2. Stimuli

Stimulus material consisted of portrait photographs of 40 male and 40 female Caucasian faces and 160 pictures of house fronts (all colorful). The face stimuli were taken from standard face databases (Langner, Dotsch, Bijlstra, Wigboldus, Hawk, & van Knippenberg, 2010; Tottenham, 1998). Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development (Tottenham, Tanaka, Leon, McCarry, Nurse, Hare, & Nelson, 2009). Forty of the face pictures (half female) were only used as target stimuli that were preceded by other faces (i.e., in the primed conditions). These were always intact, i.e., presented with eyes. The other forty faces served as primes for these targets and were also used as stimuli in the unprimed conditions because they were always preceded by a house front. From these latter 40 face pictures (20 male, 20 female) the eye regions, including the eyebrows, were removed and replaced by smooth skin using Adobe Photoshop CS2. In half of the trials the original intact faces were presented as primes and in the other half of the trials the same faces with the eye region removed were presented as primes. House pictures were taken from the internet. All pictures were cropped to a face-shaped oval

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