



Gaze cues of isolated eyes facilitate the encoding and further processing of objects in 4-month-old infants

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ABSTRACT

We investigated young infants' object encoding and processing in response to isolated eye gaze cues on the neural and behavioral level. In two experiments, 4-month-old infants watched a pair of isolated eyes gazing towards or away from novel objects. Subsequently, the same objects were presented alone (i.e., without eyes). We measured event-related potentials (ERP) in response to object-directed and object-averted eye gaze as well as to the subsequently presented isolated objects. Using eye-tracking methods, we additionally measured infants' looking behavior in reaction to the subsequently presented isolated objects. The ERP data revealed an enhanced slow wave positivity for object-directed eye gaze, indicating increased encoding of observed gaze cues. Regarding the objects, we found an enhanced Nc amplitude and increased looking times in response to previously uncued objects, indicating a novelty response on the neural and behavioral level. The results suggest that isolated eye gaze stimuli are sufficient to trigger object encoding and facilitate further object processing.

1. Introduction

Eye gaze strongly affects communication and social interaction from early on in development (Bloom, 2000; Csibra and Gergely, 2006; Kampe et al., 2003). Within the first year of life, infants actively participate in episodes of joint attention that mainly rely on a shared gazing behavior. In such interactions, infants assess the relations between themselves, other individuals and external objects. This understanding is crucial for many aspects in infants' development and learning (e.g. Baldwin, 1995; Baron Cohen, 1995; Tomasello et al., 2005). Within natural play contexts, infants around the age of 6–9 months begin to follow gaze or point gestures of others before they initiate bids of joint attention themselves (Bakeman and Adamson, 1984; Butterworth and Jarrett, 1991). However, experimental studies using gaze stimuli indicate a sensitivity to joint attention that is already present in early infancy.

Behavioral studies with four-month-old infants using novelty preference tasks showed that infants' object-directed attention is affected by gaze-cues (Hoehl et al., 2013; Reid and Striano, 2005; Wahl et al., 2013). In these studies, infants watched a person first establishing eye contact and then shifting her gaze toward one of two laterally located objects. Consequently, one of the objects was gaze-cued and the other object was not gaze-cued. After a short delay, both objects were presented separately (i.e., without the person). Infants showed a novelty

preference for the previously uncued object as indicated by longer looking times for the uncued object compared to the cued object. The authors suggest that gaze cues trigger more efficient encoding of the gaze-cued object. Therefore, this object is more familiar to infants when they see it again. Conversely, the uncued object appears more novel, hence demanding more visual attention.

Studies measuring event-related potentials (ERPs) provide insight in the neural processing of gaze-cueing effects in 4-month-old infants (Hoehl et al., 2013; Wahl et al., 2013). In an adapted procedure, only one object was presented next to a person who either gaze-cued this object or gazed away. After a short blank-period, the previously gaze-cued or uncued object was presented again without the person and ERPs were measured. An enhanced amplitude of the negative central (Nc) component was found for previously uncued objects compared to previously gaze-cued objects. The Nc component is associated with the allocation of visual attention (Richards, 2003). Hence, the results indicate that more attentional resources are involved in the processing of uncued objects compared to cued objects. Gaze cues seem to facilitate object encoding, wherefore cued objects are more familiar to infants and require less attentional resources.

Several accounts are discussing the underlying mechanisms of this gaze-cueing effect on young infants' object processing. One account is based on the idea that gaze processing is integrated into the processing of the facial context. This is supported by results showing that infants'

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gaze processing is impaired when the facial configuration is disrupted (Farroni et al., 2005, 2004; Farroni et al., 2003, 2006). In contrast, according to another account eye gaze processing is rather specific to the eye stimuli themselves and mainly independent from any facial context (Baron-Cohen, 1994; Perrett and Emery, 1994). Supporting this account, a recent study on infants' behavior demonstrates that 4-month-old infants' attention towards objects is affected by previously demonstrated gaze cues of isolated eyes (Michel et al., 2017). Using a similar procedure as previous studies (Hoehl et al., 2013; Reid and Striano, 2005), infants first watched an isolated pair of eyes that shifted gaze towards one of two objects. Subsequently, they saw both objects presented alone. Infants looked longer at the previously uncued object, indicating a novelty preference. In line with previous work (Hoehl et al., 2013; Reid and Striano, 2005), the results suggest that young infants' object processing is facilitated by gaze cues. Moreover, this effect is elicited by gaze cues of isolated eyes.

Hence, young infants seem to be highly sensitive to referential information provided by gaze cues as it has been indicated by infants' looking behavior and brain responses. In contrast to behavioral evidence, it is not clear whether neural reactions to gaze cues are specific to eyes because there are no studies measuring neural processing of isolated eyes in young infants. We address this issue in the current study by investigating the neural processing of isolated eye gaze cues and corresponding effects on infants' object processing. This could help to better understand the underlying mechanisms of young infants' efficient processing of relevant aspects of the environment.

By measuring ERP's we investigated neural correlates of infants' object processing in response to gaze cues provided by isolated eyes. The age group of 4-month-olds was tested because latest research indicates a robust gaze-cueing effect on infants' object processing by this age. We used a similar procedure as it has been used in previous ERP-studies (Hoehl et al., 2013, 2012; Reid et al., 2004; Wahl et al., 2013): Infants first saw isolated eye stimuli that shifted gaze towards an object or away from an object. Then the same object was presented alone (i.e., without the eyes). As in previous studies using this paradigm, we measured ERPs during the presentation of the object alone. Additionally, we examined the epochs in which the eyes were actually gazing towards or away from the object. Data from this event have not been reported in the literature yet. Nevertheless, the main interpretation of the reported gaze-cueing effect on the infants' object processing is based on the actual event of gaze-cueing.

In a first step, we aim to replicate the effect of isolated eyes on infants' behavioral responses, as provided by Michel et al. (2017). This can provide convergent validity of the previous results on the behavioral level. In addition, it can help us to validate the stimuli used in the current study with respect to investigate the neural correlates of this effect. If isolated eyes are sufficient to trigger gaze-cueing effects similar to those provided by an intact face, we expect to find similar ERP-response for objects cued by isolated eyes as for those cued by eyes within intact faces. According to previous research (Hoehl et al., 2013; Wahl et al., 2013), we expect an enhanced Nc amplitude for objects that have previously not been gaze-cued by the isolated eyes, rendering a novelty response in the infant brain for uncued objects. For the actual event of object-directed eye gaze we expect to find a slow wave positivity (associated to encoding processes of visual stimuli, e.g. Nelson and Collins, 1992), suggesting memory encoding to be affected by observed gaze-cues.

The current study will provide valuable insight into gaze processing in response to isolated eyes free from the context of the face. More specifically, this study is the first that investigates neural response to isolated eye gaze cues for two crucial aspects of joint attention, the object-directed gaze and the processing of the involved object. ERPs have not been looked before to both, the object-directed gaze sequence and the sequence to the object alone in an object processing paradigm.

2. Experiment 1: validating behavioral responses

In order to validate the behavioral results provided by previous research (Michel et al., 2017), we applied an established procedure that has been used in several studies on this subject (Hoehl et al., 2013; Reid and Striano, 2005; Wahl et al., 2013). We measured infants' looking behavior in response to the presentation of two simultaneously shown objects. One of the objects has previously been gaze cued by an isolated eye stimulus. All data were assessed using eye tracking techniques.

2.1. Methods

2.1.1. Participants

A total of 17 infants (10 males) with an average age of four months and 21 days (10–30 days) were included. All infants were born full term (37–42 weeks).

Two additionally tested infants were tested but excluded from the sample because they failed to provide a sufficient number of valid trials. Furthermore, some infants had to be excluded because no or too little fixations could be extracted from their gaze data. This was due to substantial tracking loss caused by extensive movements ($N = 2$) or technical problems ($N = 7$). Additional five infants were excluded because of a corrupted gaze recording. Written informed consent of all participants' parents was obtained. The Experiment has been carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.1.2. Stimuli and procedure

A similar procedure was applied as used by Michel et al. (2017), as well as by Hoehl et al. (2013). The stimuli in the current study were designed according to the proportions and location of the eyes as given in the intact female face stimulus used by Hoehl et al. (2013). Infants watched a film footage showing a pair of isolated eyes at the center of the screen. No other facial features were presented (Fig. 1). The eyes were true-to-life exemplars of human eyes, cut out at the outside of the eyelid using Adobe Photoshop. Two colorful objects (mostly small pet toys) were presented to the left or the right of the eyes. A trial began with the eyes gazing ahead for one second to establish eye contact with the infant. Next, the eyes shifted their gaze towards either the left or the right side in a natural motion (note that the gaze shifts were created as a true-to-life rotation of the eyeball rather than artificially shifting the pupil sideward). The eyes than remained statically gazing towards one side for another second. Consequently, one of the simultaneously presented objects was cued while the other one remained uncued. Then the screen was cleared and a central attractor was used to guide the infants' focus to the center of the screen. Subsequently, a paired preference test for the previously presented objects was applied for ten seconds.

A maximum of 12 trials was presented to the infants using Experiment Center 3.5 (Sensomotoric Instruments Inc.). In half of the trials, the location of the two objects was switched for the paired preference test. This way we could check whether the visual preference is due to the actual objects and not simply due to the location. We presented eye gaze direction of the isolated eyes as well as the change of object location in a semi-randomized order and balanced it across trials. Each trial consisted of a unique pair of objects. The objects were scaled to a maximum width or height of 5° visual angle (6.1 cm). We kept the relative size and position of the pair of eyes similar to that in Michel et al. (2017). Accordingly, the pair of eyes was scaled to a total width of 6.3° (7.7 cm) and a height of 1.1° (1.4 cm).

2.1.3. Eye tracking system and data processing

Infants watched the stimulus presentation on a 22-inch screen LCD monitor while sitting on their parent's lap. Binocular data was recorded at 120 Hz using a SMI RED 500 eye tracker and iViewX 2.8 firmware (SMI). The eye tracker unit was mounted below the screen (monitor integrated configuration). A webcam mounted on top of the monitor

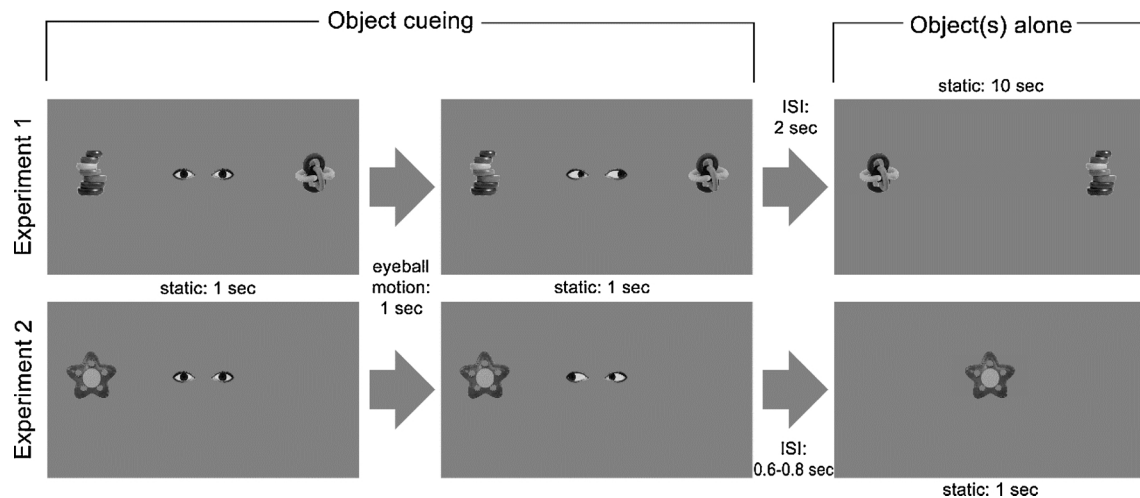


Fig. 1. Stimuli. Example of a trial presented in Experiment 1 (eye tracking) and Experiment 2 (event-related potentials). The objects, as well as the gaze direction and object location were counterbalanced across trials. Durations are presented in seconds for each segment of the trial. There is no picture presented for the eye gaze motion and the inter-stimulus interval (ISI).

was used to record the infants' behavior during the stimulus presentation. The eye tracking system provides a gaze position accuracy of 0.4° at a viewing distance of 70 cm. The recovery time to full tracking ability after an offset (e.g. because of excessive movements) was about 90 ms.

An animated stimulus (contracting disk) coupled with a moderate sound was used to calibrate the infants before recording. The disk was covering $0.5\text{--}2.8^\circ$ at its minimum and maximum expansion and appeared at 5 locations on the screen. The calibration process did not continue until a sufficient amount of gaze data was gathered for all five locations. Raw data was processed with Matlab (Mathworks Inc.) using a customized procedure. Missing coordinates were interpolated linearly for gaps up to 80 ms of duration. The grand average of two averages across the samples before and after each data point was used to reduce noise. Fixations were determined using a dispersion filter with a radius of 1° within a minimum duration of 100 ms. To assess infants' looking time towards the objects during the paired preference test, the fixations for each object were cumulated within non-overlapping rectangle areas of interest (AOIs) covering these objects.

For statistical analysis, only trials were included in which the infants attended to critical aspects of the stimulus presentation besides the paired preference test: the display of the eyes as they were gazing ahead and as they were gazing towards one of the objects. For each trial, the infants had to obtain at least 500 ms of cumulated fixations to the whole object display. Additionally, only infants were included that contributed at least two valid trials for each, the switched object location, and the same object location during the paired preference test. The infants contributed an average of 8 trials to the analysis ($SD = 2.8$, ranging between 4–12 trials).

2.2. Results

A repeated measures ANOVA was applied to examine the visual preference for one of the objects during the paired preference test. Two within-subject factors were applied: Object (previously cued object, previously uncued object) and Location (same location as during the cueing phase, switched location). A main effect for the factor Object was found, $F(1, 16) = 9.226$, $p = .008$, $\eta^2 = .366$. Infants looked significantly longer at the previously uncued objects (mean: 2229 ms, standard error: 255 ms) compared to the previously cued objects (mean: 1714 ms, standard error: 188 ms). No other effects were found.

The results are in line with previous research (Hoehl et al., 2013; Reid and Striano, 2005; Wahl et al., 2013) using gaze cues provided by an intact person's face. Accordingly, infants examined previously uncued objects significantly longer as compared to previously cued

objects. Furthermore, the current data validate those reported by Michel et al. (2017). Gaze cues of isolated eyes lead to a similar effect as it has been found for gaze cues provided by an intact face.

3. Experiment 2: neural responses

Experiment 2 investigates the effect of isolated eyes on infants' object processing on the neural level, with Experiment 1 and Experiment 2 being conceptualized as a between-subjects study design.

The eye stimuli from Experiment 1 were used within a similar procedure that was adapted to measure ERPs. This procedure has already been used in several studies on this subject and age-group before (Hoehl et al., 2012, 2013; Wahl et al., 2013). Referring to Hoehl et al. (2013), we expect an enhanced Nc amplitude for objects that have previously not been gaze-cued by the isolated eyes compared to previously gaze-cued objects. For the actual event of object-cueing, an enhanced positive slow wave is expected indicating the involvement of encoding processes in response to object-directed eye gaze compared to object-averted gaze.

3.1. Methods

3.1.1. Participants

A sample of 19 infants (10 males) with an average age of four months and 19 days (12–30 days) was analyzed. All infants were born full term (37–42 weeks). Eight infants were excluded from the analysis because they did not contribute the minimum number of trials for averaging. Six further infants were tested but not included because of distress (e.g. extensive movements or crying).

Written informed consent of all participants' parents was obtained. The Experiment has been carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

3.1.2. Stimuli and procedure

Infants watched the same film footage showing isolated eyes as it was used in Experiment 1. In Experiment 2, only one object was presented next to the eyes. Similar to Experiment 1, the eyes first gazed ahead before they shifted to the left or to the right side for one second. ERPs were measured while the eyes looked either at the object (i.e., object-directed event) or away from it (i.e., object-averted event). After a short blank-period the previously cued or uncued object was then presented alone at the center of the screen while ERPs were constantly measured. As in previous studies (Hoehl et al., 2013; Wahl et al., 2013), we used this epoch to examine the effect of gaze-cues on the further

processing of objects.

Infants were presented to a maximum number of 160 trials. Different objects as in Experiment 1 were used and every trial consisted of a novel object. Trials were presented in a semi-randomized order. Gaze direction, object location, and the constellation of gaze direction and object location was counterbalanced across every 40 trials. Additionally, the successive presentation of the same gaze direction, object location, or their constellation was restricted to 3 times in a row.

3.1.3. EEG recording and data processing

Infants sat on their parents' lap in front of a 24-inch screen LCD monitor. Infants' behavior was recorded by a high resolution webcam for later examination. EEG data were recorded at a sampling rate of 200 Hz using 32 Ag-AgCl active scalp electrodes (10–20 system) and an actiCHamp amplifier (Brain Products GmbH, Munich, Germany). During recording, data were filtered using a bandpass filter of 0.1–100 Hz and referenced to the right mastoid. An offline filter of 0.3–30 Hz was applied and data were referenced to the linked mastoids. The vertical and horizontal electrooculogram (EOG) was referenced bipolarly. The continuous data was segmented and baseline corrected (200 ms before event onset). Two epochs of 1200 ms duration were analyzed: one epoch is covering the event of object-cueing and is time-locked to the static display of the object-directed or object averted eye gaze. The second epoch is covering the display of the previously gaze-cued or uncued object alone.

The infants' behavior during the experiment was coded offline. Only trials were included in which the infant attended the entire sequence of the trial and performed no obvious or repetitive movements during the ERP measurement. To control for electrical artifacts, segments were rejected semi-automatically in which all data within a moving time window of 200 ms differed more than 200 μ V. Visual inspection was performed to reject further segments due to artifacts.

Data were averaged for each condition (cued vs. uncued). Regarding the cueing and uncueing events (with eyes), infants contributed a mean of 30 valid trials to their average for cued ($M = 15$, $SD = 5.7$, ranging between 10 and 29 trials) and uncued ($M = 15$, $SD = 7.1$, ranging between 10 and 30 trials) objects. Regarding the subsequent presentation of object alone (without eyes), the infants contributed a mean of 35 valid trials to their average for previously cued ($M = 17$, $SD = 7.2$, ranging between 10 and 30 trials) and uncued ($M = 18$, $SD = 6$, ranging between 10 and 29 trials) objects. As dependent variable, the mean amplitudes on fronto-central channels were assessed and averaged for 3 regions of interest (ROI): a left ROI involving F3, F7, FC5 and C3, a right ROI involving F4, F8, FC6 and C4 and a center ROI involving Fz, FC1, FC2 and Cz. These regions were chosen, because the examined ERPs are most prominent at these scalp locations. The channels were reduced to the ROI to minimize the number of factor levels and to detect potential differences between hemispheres.

3.2. Results

Visual inspection of the grand average of the object-directed or object-averted gaze revealed differences in slow wave activities at fronto-central channels between 300 and 1200 ms (Fig. 2). We conducted a repeated measures ANOVA with the within-subject factors Cueing (object-directed eye gaze, object-averted eye gaze) and ROI (left, center, right). For the factor Cueing, a significant main effect was found, $F(1, 18) = 5.109$, $p = .036$, $\eta^2 = .221$. There was a significantly more positive slow wave activity for object-directed eye gaze ($AM = 7.393 \mu$ V, $SE = 2.003 \mu$ V) compared to object-averted eye gaze ($M = 1.032$, $SE = 3.291 \mu$ V). No effect for the factor ROI or interaction effect was found.

For the presentation of the previously gaze-cued or uncued object alone, the Nc component was assessed between 400 and 800 ms. Object (previously gaze-cued, previously uncued) and ROI (left, center, right) were applied as within-subject factors. The analyses revealed a

significant main effect for the factor Object, $F(1, 18) = 6.875$, $p = .017$, $\eta^2 = .276$. The Nc amplitude was significantly larger for the previously uncued objects ($AM = -8.843 \mu$ V, $SE = 2.5 \mu$ V) compared to the previously gaze-cued objects ($M = -1.788 \mu$ V, $SE = 1.84 \mu$ V). No other effects were found. Fig. 2 shows the grand average ERPs of the left, center, and right ROI. Fig. 3 displays the distribution of the ERPs across the fronto-central channels.

4. Discussion

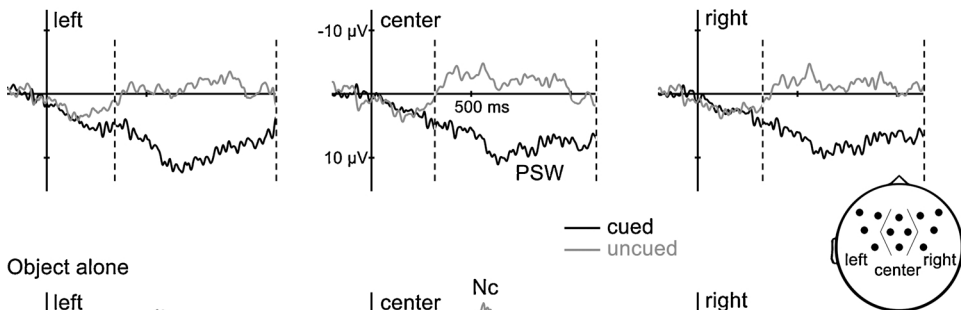
The aim of the current study was to investigate behavioral and neural mechanisms of gaze-cueing effects on object processing in early infancy. Particularly, we examined the role of the eye stimulus itself by presenting isolated eyes. In a first step, we replicated recent data providing evidence for gaze-cueing effects in response to isolated eyes on infants' looking behavior (Michel et al., 2017). In line with this study and previous studies that used eye gaze cues within intact human faces (Hoehl et al., 2013; Reid and Striano, 2005; Theuring et al., 2007; Wahl et al., 2013), we found an attentional bias for previously uncued objects, rendering a novelty preference for uncued objects. This suggests that gaze cues of isolated eyes facilitate the processing of objects. Consequently, previously cued objects appear more familiar to the infants. However, the current data does not provide information about the stability of this novelty effect. Theuring et al. (2007) found a rather short-term novelty effect in 12-month-old infants using a slightly different object cueing paradigm. Further studies are needed to clarify the temporal characteristics of the novelty effect in younger infants.

In a second step, we investigated neural responses to the event of gaze-cueing and to the subsequent presentation of the previously cued or uncued objects. For the event of gaze-cueing, we found an enhanced slow wave positivity for the object-directed gaze compared to the object-averted gaze. Since a slow wave positivity in infants is associated with encoding processes of visual stimuli (Nelson, 1994; Nelson and Collins, 1992; Snyder, 2010), this suggests that gaze cues of isolated eyes affect memory encoding. This is in line with the previous assumptions of gaze-cueing effects on young infants' object processing (Hoehl et al., 2013; Michel et al., 2017; Reid et al., 2004; Reid and Striano, 2005; Wahl et al., 2013). However, the current study is the first to provide direct evidence for this assumption.

In response to the subsequent presentation of previously gaze-cued or uncued objects, we found an enhanced Nc amplitude for the uncued objects. This suggests that previously uncued objects appear more novel to the infants, thus requiring more attentional resources for further processing compared to previously cued objects. The previously cued objects, on the other hand, appear more familiar to the infants. These results are in line with previous studies that using comparable stimulus presentations and reporting similar ERP responses to objects that have previously been gaze-cued by an intact person or face, respectively (Hoehl et al., 2013; Wahl et al., 2013). This suggests that isolated eyes affect infants' object processing on neural level similar to eye gaze within a human face. However, whether there are subtle differences in the neural processing of eye gaze within a human face or in isolation cannot be evaluated on the basis of the current data.

Other studies using slightly different procedures provide additional insight in this regard. One study that investigated the neural response of four-month-old infants to static gaze displays reports an enhanced Nc amplitude for displayed object-averted gaze cues of a person (Hoehl et al., 2008). This suggests, that observing object-directed eye gaze is processed with less effort compared to object-averted gaze and therefore, that more resources are available for encoding the entities of the object-directed gaze display, like the gazed-at object. Another study provides information about further encoding of objects that previously have not been gaze-cued (Reid et al., 2004). These findings suggest that previously uncued objects require additional encoding due to their novelty compared to previously gaze-cued objects. In line with the current results, this supports the assumption that eye gaze of a person

Object cueing



Object alone

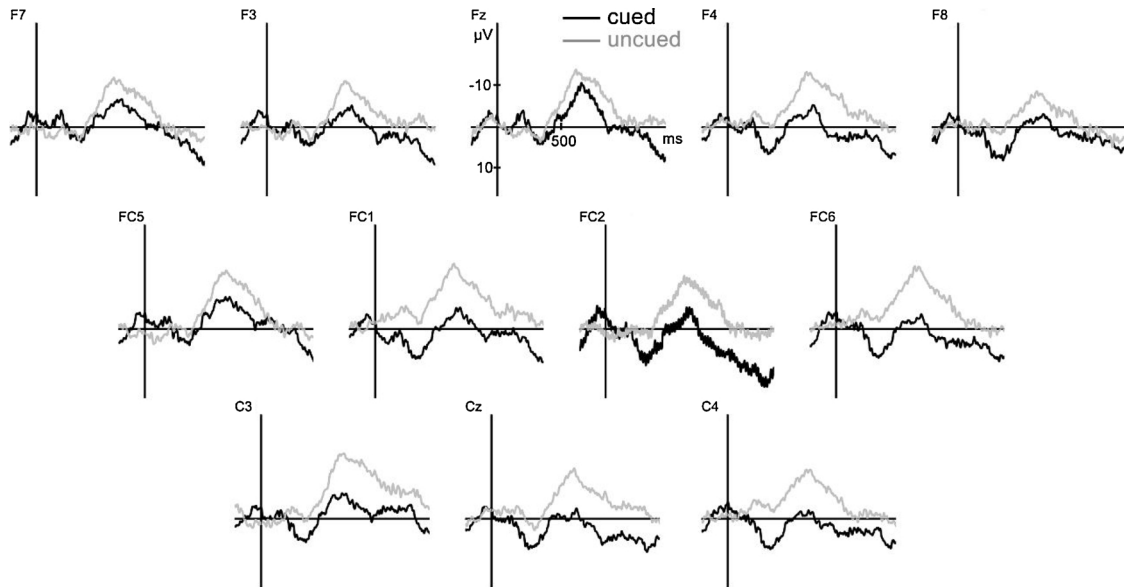
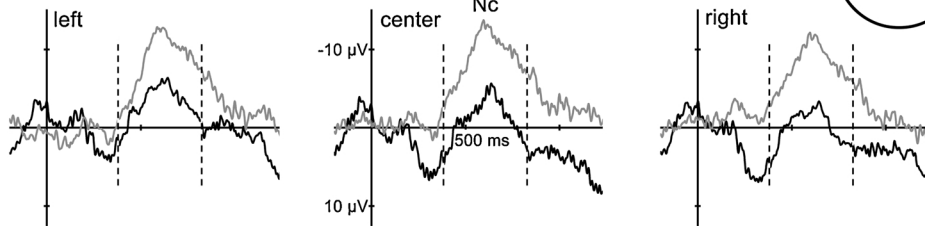


Fig. 3. Distribution of the Nc component across fronto-central channels (Experiment 2). Grand average ERPs for the previously cued object (black line) or uncued Object (gray line) are displayed. Negative is plotted upwards.

functions as a cue to facilitate the processing of the gazed-at object. On the other hand, objects that are not the target of a person's eye gaze are processed less efficiently and, therefore, require more subsequent processing.

Taken together, the current study provides evidence that isolated eyes are sufficient to function as cues that facilitate object encoding, which in turn facilitates the subsequent processing of gaze-cued objects. However, there is still little known about the underlying mechanisms. Recent literature discusses electrophysiological markers that index processes of learning about objects in a social context during infancy. One marker represents alpha-band activity, which is associated with automatic processes of attention allocation towards relevant stimuli (Ward, 2003). By an age of 4 months, alpha-oscillations are found to be modulated in response to observed object-looker-relations, like object-directed versus object-averted eye gaze of a person (Michel et al., 2015). This indicates a rudimentary mechanism that facilitates attention allocation in response to gaze cues in young infants. According to the current findings, modulations in alpha activity could also be expected in response to isolated eye gaze cues. In a recent study on 11-month-old infants, Begus et al. (2015) found modulations in theta

Fig. 2. ERP results (Experiment 2). Grand average ERP responses for the Object cueing (object-directed or object-averted gaze) and for the Object alone (the subsequent presentation of the previously gaze-cued or uncued object). Grand averages were assessed for three regions of interest (ROI) on fronto-central channels: a left ROI (F3, F7, FC5 and C3), a right ROI (F4, F8, FC6 and C4) and a center ROI (Fz, FC1, FC2 and Cz). The black line displays responses to cued objects, the gray line displays responses to uncued objects. Note that negative is plotted upwards.

activity during object examination to predict the successful encoding of the examined objects. Modulations in theta oscillations are suggested to be linked to memory processes and executive control of attention. Examining theta activity may provide a deeper insight in the social object learning. For younger infants, however, modulations in theta activity are found to be rather inconsistent in response to observed object-looker-relations (Michel et al., 2015). This may be due to the limited ability of executive control of attention in younger infants, rendering the gaze-cueing effect on young infants' object processing as a rather rudimentary mechanism of automatic attention allocation.

The current results suggest that gaze-cueing effects in early infancy rely on specific stimuli that indicate another person's attention like the eyes rather than the presence of an intact person. Baron Cohen (1995, 1994) proposed the existence of a brain module (Eye Direction Detector, EDD) that specifically reacts to perceived eyes, involving the allocation of the observer's attention in accordance to perceived gaze direction. The current study cannot provide sufficient evidence for the existence of such a module. Nevertheless, the current findings support the assumption that the infant brain is able to process eye gaze independently (i.e., without the face). The current results, moreover,

provide additional insight in eye-specific brain mechanisms that goes beyond the conception of an EDD. That is, the perceived eye gaze does not only bias attention according to the gaze direction, but, furthermore, affects the processing of the environment as shown by the current ERP results.

Several questions arise with regard to the underlying mechanisms of the gaze-cueing effect of isolated eyes on young infants. One question refers to the perceptual properties of human eyes, especially to the contrast polarity of the white sclera and the dark pupil. Reports about single cell recordings of the macaque brain showed neurons in the superior temporal sulcus that respond specifically to the changing proportion of the white and dark area during gaze shifts (e.g. Langton et al., 2000; Perrett and Emery, 1994; Perrett et al., 1992). While there is no prove of such specific neurons in the human brain, several studies provide evidence for a contrast-sensitive processing of human eye gaze by inverting the contrast of the eye stimuli (Jessen and Grossmann, 2014; Michel et al., 2017). However, present studies are using eyes or eye-like stimuli in a rather natural shape and configuration that fit nearly perfect into a human face. It is unclear whether the rounded and pairwise appearance of the eyes or eye-like stimuli contribute to the processing of isolated eyes or whether this is even mandatory in this regard. Thus, it cannot be ruled out that eye gaze processing may rely on more than just perceptual features like the contrast polarity. This issue has to be addressed in future research.

Declarations of interest

None.

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