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Infants perceiving and acting on the eyes: Tests of an evolutionary hypothesis

Teresa Farroni,^{a,b,*} Eileen M. Mansfield,^a Carlo Lai,^c
and Mark H. Johnson^a

^a *Centre for Brain & Cognitive Development, School of Psychology, Birkbeck College, University of London, 32 Torrington Square, London WC1E 7JL, UK*

^b *Dipartimento di Psicologia dello Sviluppo e della Socializzazione, University of Padua, Via Venezia 8, Padua 35131, Italy*

^c *Dipartimento di Psicologia, University of Rome "La Sapienza," Via dei Marzi 78, Rome 00185, Italy*

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Abstract

It has been hypothesized that an evolutionarily ancient mechanism underlies the ability of human infants to detect and act upon the direction of eye gaze of another human face. However, the evidence from behavioral studies with infants is also consistent with a more domain-general system responsive to the lateral motion of stimuli regardless of whether or not eyes are involved. To address this issue three experiments with 4-month-old infants are reported that utilize a standard face-cueing paradigm. In the first experiment an inverted face was used to investigate whether the motion of the pupils elicits the cueing effect regardless of the surrounding face context. In the second experiment pupil motion and eye gaze direction were opposed, allowing us to assess their relative importance. In a third experiment, a more complex gaze shift sequence allowed us to analyse the importance of beginning with a period of mutual gaze. Overall, the results were consistent with the importance of the perceived direction of motion of pupils. However, to be effective in cueing spatial locations this motion needs to be preceded by a period of direct mutual gaze (eye contact). We suggest that evolution results in information-processing biases that shape and constrain the outcome of individual development to eventually result in adult adaptive specializations.

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* Corresponding author. Fax: +44-20-7631-6587.

E-mail address: t.farroni@bbk.ac.uk (T. Farroni).

Young infants appear to have a particular interest in the eyes of other humans (Baron-Cohen, 1994; Gibson, 1969; Lasky & Klein, 1979; Samuels, 1985). In addition, the direction of eye gaze of another face can indicate an interesting target and provide the basis for “shared attention” with a caregiver (Butterworth & Jarrett, 1991). Due to the adaptive importance of detecting eye gaze early in life, Baron-Cohen (1994) proposed that there is an innate module within the brain specifically concerned with processing eye gaze, the “Eye Direction Detector” (EDD). Baron-Cohen further speculated that EDD is an evolutionarily ancient mechanism, shared with other primates, mammals, birds, or even reptiles. In humans EDD not only detects deviations in eye gaze but also constructs dyadic representations of their behavior. Baron-Cohen (1994) supported his claim, in three ways: (i) evidence from other species; (ii) evidence of specific neural mechanisms for processing eye gaze, and (iii) evidence of the ability to discriminate direction of eye gaze in early human infancy. In this paper we examine the third of Baron-Cohen’s lines of evidence. Specifically, we present results from three experiments with infants on perceiving and acting on another human’s direction of gaze. These experiments are designed to test whether a specific eye gaze mechanism, such as EDD, underlies infants behavior, or whether more domain-general processes are at work during infancy.

EDD has become an example of Evolutionary Psychology. While Evolutionary Psychology is a way of explaining psychological data rather than a directly testable theory, it anticipates that “the mind will be found to contain a large number of information-processing devices that are domain-specific and functionally specified” (Cosmides & Tooby, 1999, p. 15). A critical feature of Evolutionary Psychology arguments is that those domain-specific adaptations are the result of selective pressures during the evolution of humans. However, an alternative way to reach a domain-specific adult mind is through ontogeny (Elman & Bates, 1996). By this view, experiential and genetic factors combine during the development of the individual to result in a specified and adapted mind. The contrast between ontogenetic and phylogenetic causes of specialization is important for a number of reasons including the extent to which modern adult human specializations reflect the selective pressure on a primitive hunter–gatherer society. The ontogenetic view does not deny that evolution is one factor in adult brain specialization, but rather states that evolutionary pressure is reflected in newborn orienting and information-processing biases that, in turn, then shape and constrain the outcome of individual development.

Vecera and Johnson (1995) demonstrated with schematic faces that 4-month-old infants can make direction of eye gaze discriminations, but, like adults, they are better when the eyes are presented in the context of an upright face than when they are presented within a scrambled face pattern. This evidence suggested that eye direction processing in infants is not the product of an encapsulated module, but rather reflects more general processing of faces (see Johnson, 1994). While the Vecera and Johnson (1995) study involved infants ability to discriminate between angles of gaze, it did not address the further question of whether infants use direction of gaze as a cue for directing their own attention.

Several recent studies with adults have demonstrated that the direction of gaze of a face can cue visuospatial orienting in a viewer (Driver et al., 1999; Friesen &

Kingstone, 1998; Langton & Bruce, 1999). In other words, adults are faster to respond to targets presented in locations congruent with the direction of eye gaze of a centrally presented face. This line of research has also been extended to infants. Hood, Willen, and Driver (1998) utilized a spatial cueing attention paradigm that has been used by several labs to study shifts of visual orienting and attention in infants (e.g., Hood, 1995). In the Hood et al. (1998) experiments the latency to make a saccade to a peripheral target was measured under conditions in which the location of the target was congruent or incongruent with the direction of gaze of a centrally presented video image of a face. According to Posner's (1980) model, when attention is focused to a particular location (such as, for example, the direction of the eyes), the visual processing of targets in that location is facilitated. Consequently, reaction times are faster if the target appears in the cued location and slower if the target appears in the opposite location. If the infants are able to use the preceding direction of the gaze as an attentional cue, the latency to make saccadic eye movements should be faster when the peripheral target appears in a location congruent with the direction of gaze. A group of infants varying from 10 to 28 weeks were found by Hood and colleagues to be faster to make a saccade toward the peripheral target located in the congruent than in the incongruent direction. The authors' interpretation of this finding was that infants' perception of an adult's deviated gaze induces shifts of attention in the corresponding direction because the direction of eye gaze can be used as attentional cue.

Farroni, Johnson, Brockbank, and Simion (2000) replicated the finding of Hood and colleagues with a narrower age range of infants (4–5 months). In addition to replicating the earlier study, Farroni et al. (2000) presented evidence that perceiving the motion of an eye gaze shift was critical for infants, and demonstrated that the cueing effect was not observed in situations where there was no motion, or apparent motion, of the eyes. These findings challenged the interpretation of a specific eye gaze detection process, such as EDD, and suggested that more general motion cueing effects were at work.

In the experiments in the present study, we investigate the issue of whether infant eye gaze cueing is the result of a domain-specific module or reflects the activity of domain-general processes. The EDD hypothesis predicts domain-specific processes from birth, whereas an ontogenetic view would be consistent with individual biases interacting with domain-general processes to eventually result in adult adaptive specialization. We used three manipulations of the procedure originally developed by Hood et al. (1998). First, in Experiment 1, we examine the effects of inverting the face on cueing. If infants are merely cued by motion, then an inverted face should produce the same cueing as an upright one. In Experiment 2 we presented infants with a face that was initially presented with an averted gaze that then shifted to the center. If infants are responding just to the motion of elements they should be cued in the direction opposite to that initially presented. Finally, in Experiment 3, a more complex eye gaze shift sequence was used in which the eyes shifted from center to averted, and then back to center. We ascertained whether infants would be cued by the direction of last motion, or by the direction in which the eyes were averted from center. In all of the above experiments we analysed saccades elicited by the presentation of the targets, and those directly triggered by the gaze shifts of the stimulus face.

Experiment 1

Farroni et al. (2000) produced evidence that the direction of perceived motion of stimulus elements is the most important factor in subsequently directing infants' attention to peripheral targets. For example, in their Experiment 2 they observed that infants were cued by the lateral motion of a face, rather than the direction of gaze of the eyes, and in their Experiment 3 they did not observe a cueing effect when only static eye gaze direction, and not motion, was available. In the present experiment we investigated this issue further by using the same paradigm employed to demonstrate the cueing effect by Hood et al. (1998, replicated by Farroni et al. 2000, Experiment 1) except that the face stimulus was inverted. A number of lines of evidence demonstrate that inverting a face leads to it being processed by different neural and cognitive mechanisms from an upright face (e.g., Tanaka & Farah, 1993; Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998). Thus, in this experiment we can ascertain the importance or otherwise of directed motion of stimulus elements without the surrounding context of an upright face. If the infants show the same cueing effect as with an upright face, this further bolsters the view that any lateral motion of elements is sufficient for the cueing effect. The specific prediction tested is that infants will be cued by the direction of motion of the pupils.

Method

Participants

Twenty-six babies participated in the experiment. Eleven were excluded from the final sample for various reasons: seven due to technical error, and four due to fussiness. Fifteen normal full term infants aged between 4 and 5 months, with a mean age of 18 weeks 5 days (range = 119–150 days; 8 male and 7 female) completed the study.

Apparatus and stimulus

Infants sat in an adapted infant car seat 70 cm distant from a $40.5\text{ cm} \times 30\text{ cm}$ ($30^\circ \times 23^\circ$) high resolution computer monitor. The infants' eye level was at the center of the screen. To attract the attention of the baby different sounds were emitted from speakers placed at the rear of the monitor. A video camera was placed above the monitor to enable video footage of the infants' eye movements to be obtained. The stimulus used was the same as that used in Farroni et al. (2000), but in this experiment the face was inverted (see Fig. 1). However, the eyes were still level with the middle of the monitor screen. The eyes opened and closed alternately every 500 ms to give the appearance of blinking and attract the watching infants' attention. The visual angle of the face subtended to $17^\circ \times 9^\circ$ and the eyes subtended to $2^\circ \times 1^\circ$. Targets stimulus (different cartoon pictures, $4^\circ \times 4^\circ$ of visual angle) appeared either to the right or left of the face at 11° of visual angle.

Procedure

Testing was carried out in a darkened sound attenuated room with the baby sitting in an adapted infant car seat facing the monitor screen. Trials began with the

presentation of an edited video image of a woman's face in the center of the screen, the eyes of which blinked every 500 ms to attract the infant's attention. When the infant was attending to the center of the screen the experimenter pressed a key and after 200 ms the pupils moved either right or left (0.5° of visual angle) where they remained for a further 1500 ms. After this time the face disappeared and a target was presented either in the same position as the averted gaze (congruent condition) or opposite the averted gaze (incongruent condition) and remained for 1000 ms (see Fig. 1). Trials were presented randomly, with 50% appearing in the congruent condition (i.e., the target was in the same direction as the eye gaze), and 50% in the incongruent condition (i.e., the target appearance was in the opposite direction to the eye gaze).

Data analysis

The onset and direction of the infants' eye movements were coded by the half frame (20 ms) by two independent coders from the videotape recorded of the session. Inter-coder reliability was high (0.95 Cohen's K). A total of 293 (46%) trials was excluded for the following reasons: the infant's head moved during the trial (71%), closed its eyes before target onset (18%), or a technical error occurred (11%). Saccades of under 60 ms latencies, after the appearance of the target, or over 800 ms were excluded from the analysis (4 under 60 ms and 4 over 800 ms), leaving a total of 341 scoreable trials.

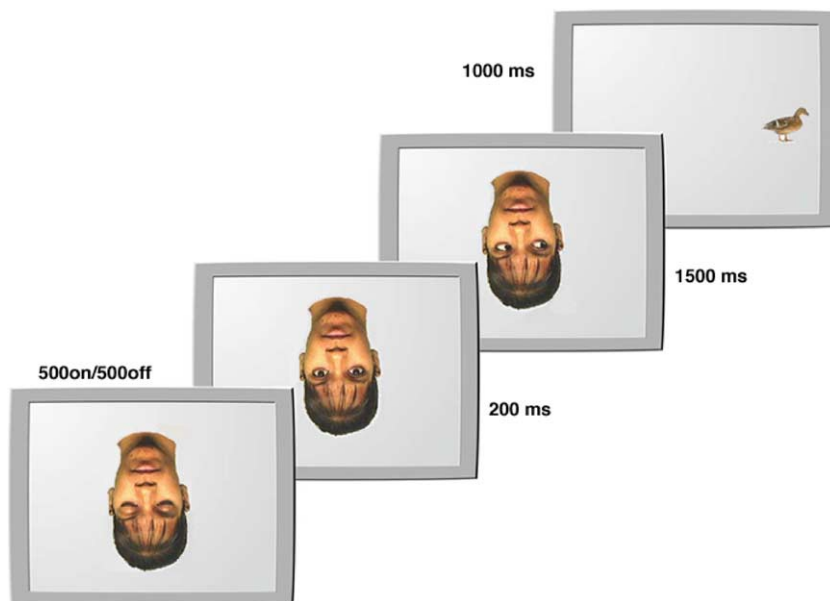


Fig. 1. Example of the edited video image illustrating the stimulus sequence for Experiment 1 (inverted face). In this trial the stimulus target appears on an congruent side. Reprinted by permission from B.M. Hood, J.D. Willen, & J. Driver, 1998, Adult's eyes trigger shifts of visual attention in human infants, *Psychological Science*, 9, 53–56, Blackwell Publishing Ltd.

Results and discussion

On average, infants made 11.4 target-driven saccades (range 9–38). A Wilcoxon Signed Rank Test was conducted to examine saccadic reaction times after the onset of the target for the two conditions. The analysis revealed no significant differences between the congruent and incongruent conditions ($M = 277$ ms, $SD = 63$ vs $M = 268$ ms, $SD = 60$). This result demonstrates that infants orienting to targets was not influenced by the cue when the face was inverted. Examination of target-driven saccades showed no significant cueing effect. This result is not consistent with the hypothesis that the lateral motion of elements is the only important factor giving rise to the cueing effect. Rather, it suggests that the context of an upright face may be important, and this issue is explored further in Experiment 2.

Experiment 2

In Experiment 3 of Farroni et al. (2000) we demonstrated that no cueing effect was observed when infants were presented with eye gaze direction in the absence of lateral motion. In that experiment the stimulus face eyes opened when already shifted to the left or right. In the present experiment we used a similar stimulus sequence, except that the averted eye gaze then shifted back to the central position to achieve mutual gaze with the viewer. If lateral motion of elements is the only important factor then infants should be cued by the direction of motion, and not by the initial direction of eye gaze. The specific prediction is that infants will respond to the direction of motion of the eyes (lateral to the center) rather than their initial direction.

Method

Participants

A total of 22 normal full term infants aged between 4 and 5 months (5 male and 10 female) with mean age 17 weeks 4 days (range = 116–134 days) were tested. Three babies were lost due to technical error, and four due to fussiness. Fifteen babies completed the experiment.

Apparatus and stimulus

The apparatus for this study was identical to that used in Experiment 1. The stimulus used was the same as in Experiment 1 (with the exception of the face being in an upright position), but the motion of the pupils was manipulated so that the infants did not see the movement of the pupils to the periphery, but perceived the motion of the pupils when they returned to the central position (see Fig. 2). The trials started with the eyes opening and closing alternately every 500 ms as in Experiment 1. The size of stimuli remained as in the previous experiment.

Procedure

Testing was carried out as in Experiment 1. Initially the blinking face was presented and when the baby was looking at the center of the monitor, the trial began.

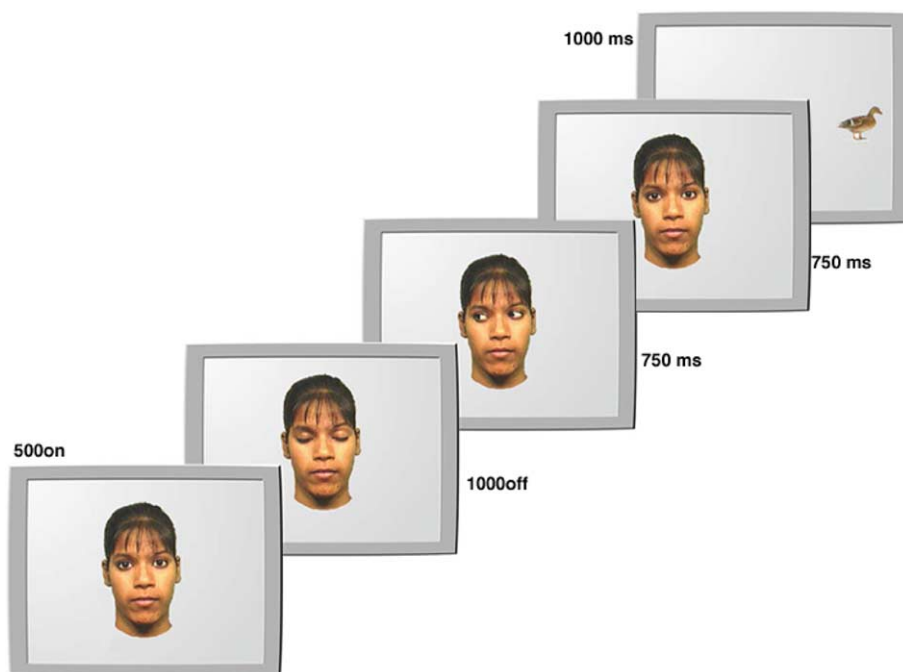


Fig. 2. Example of the edited video image illustrating the stimulus sequence for Experiment 2. Reprinted by permission from B.M. Hood, J.D. Willen, & J. Driver, 1998, Adult's eyes trigger shifts of visual attention in human infants, *Psychological Science*, 9, 53–56, Blackwell Publishing Ltd.

The eyes opened already oriented either to the right or to the left where they remained for 750 ms before shifting back to a central position for the next 750 ms. After this time the face disappeared and a target was presented either in the same position as the averted gaze (congruent condition), or opposite (the incongruent condition) and remained for 1000 ms (see Fig. 2). Note the terms “congruent” or “incongruent” correspond to the direction of the averted gaze.

Data analysis

The onset and direction of the infants' eye movements were coded by the half frame (20 ms) by two independent coders from the recorded videotape of the session. Inter-coder reliability was high (0.93 Cohen's Kappa). A total of 346 trials was excluded for the following reasons: the infant's head moved during the trial (60%), or closed its eyes before target onset (34%), or a technical error occurred (6%). Saccades under 60 ms latencies or above 800 ms were excluded from the analysis.

Results and discussion

On average, infants made 13.6 target-driven saccades (range 12–52). Forty-nine percent of the scoreable trials were in the congruent condition. Wilcoxon Signed

Rank Test revealed no significant difference between the congruent and incongruent conditions ($M = 277$ ms, $SD 56$ vs $M = 282$ ms, $SD 49$). This shows that the static gaze direction was not conducive to shifting the infants' attention when the target was presented.

In this experiment no cueing effect was observed in the target-driven saccades. This negative result does not support the hypothesis that direction of motion of elements is the only determining factor for the cueing effects. Instead, it raises the alternative hypothesis that the directed motion of elements needs to be preceded by a phase of mutual eye gaze contact between the viewing infant participant and the stimulus face. This hypothesis is investigated in Experiment 3.

Experiment 3

The target-driven results from Experiments 1 and 2 were not consistent with the hypothesis advanced by Farroni et al. (2000) that lateral motion of stimulus elements is the only factor in determining where infants direct their spatial attention. However, all of the results obtained with this paradigm so far are consistent with the alternative hypothesis that lateral motion of elements needs to be preceded by a period of mutual gaze between the watching infant and an upright stimulus face. Hains and Muir (1996) argued that when adults engage in face-to-face interactions with 3- to 6-month-olds, adult eye contact cues infants to engage in communicative exchanges. This engagement may be necessary before attentional cueing can take place. For this reason, in Experiment 3 we test this latter hypothesis by studying infants' responses to a more complex gaze shift sequence. In this sequence the eyes open with direct gaze before shifting to the right or left and then moving back to center (see Fig. 3). This sequence was identical to that in Experiment 2, except that it was preceded by a short (200 ms) phase of direct gaze followed by lateral motion of the pupil from the center. Therefore, it allows us to test the hypothesis that a brief period of mutual gaze is sufficient to engage the attentional mechanisms that are then subsequently directed by pupil motion. Specifically, we predict that infants will be cued by one of the direction of motions of the pupils in this experiment.

Method

Participants

Thirty normal full term infants aged between 4 and 5 months participated in the experiment (age = 18 weeks 4 days, range 114–148 days; nine male and seven female). Nine babies were lost due to technical error, and 5 due to fussiness. Sixteen babies completed the experiment.

Apparatus and stimulus

The apparatus for this study was identical to that used in Experiments 1 and 2. The stimulus used was the same as the previous experiment but the motion of the pupils was manipulated so that the infants saw movement of the pupils to the

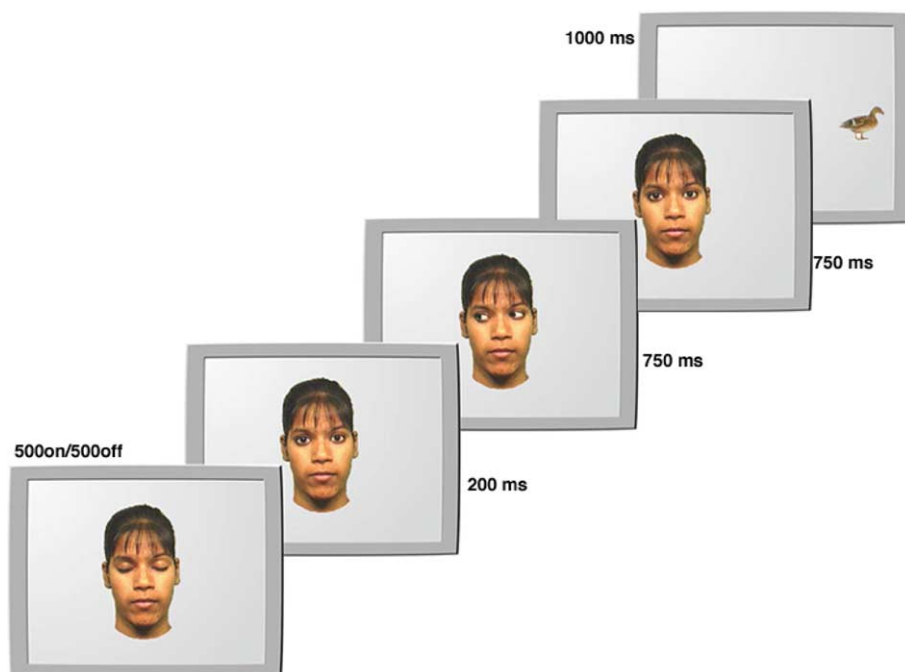


Fig. 3. Example of the edited video image illustrating the stimulus sequence for Experiment 3. Reprinted by permission from B.M. Hood, J.D. Willen, & J. Driver, 1998, *Adult's eyes trigger shifts of visual attention in human infants*, *Psychological Science*, 9, 53–56, Blackwell Publishing Ltd.

periphery and then returned to the central position (for timing see Fig. 3). The trials started with the eyes opening and closing alternately every 500 ms (as in Experiments 1 and 2). The size of the stimuli remained as in the previous experiments.

Procedure

Testing was carried out as in Experiments 1 and 2. When the infant was attending to the center of the screen the experimenter pressed a key to start a trial. Trials began with the eyes facing the baby for 200 ms and then a movement either right or left (0.5° of visual angle) where they remained for 750 ms giving the impression that the face was averting its eyes before going back to the central position for the following 750 ms.

After this time the face disappeared and a target was presented either in the same position as the averted gaze (congruent condition) or opposite the averted gaze (the incongruent condition) and remained for 1000 ms. The next trial then began with the blinking face centrally presented. Note that the term “congruent” or “incongruent” always corresponds to the position of the averted gaze.

Data analysis

The onset and direction of the infants' eye movements were coded by the half frame (20 ms) by two independent coders from the recorded videotape of the session. The reliability between coders was good (0.84 Cohen's K). A total of 338 (44%) trials was

excluded for the following reasons: the infant's head moved during the trial (72%) or closed its eyes before target onset (18%), or a technical error occurred (10%). Saccades under 60 ms latencies or above 800 ms were excluded from the analysis.

Results and discussion

On average, infants made 16.1 target-driven saccades (range 10–41). Half of scoreable trials were in the congruent condition. A second Wilcoxon Signed Rank Test revealed a difference between the congruent and incongruent conditions, ($Z = 2.12$, $p = .03$; $M = 286$ ms, $SD 73$ vs $M = 265$ ms, $SD 61$, respectively). This result indicates that infants were influenced by the second movement of the pupils.

The results of this experiment are consistent with the hypothesis that even a brief period of mutual gaze is sufficient to engage the attentional mechanisms that are then guided by the direction of motion of the pupils. In contrast to Experiment 2, in which there was no directly preceding phase of mutual gaze (due to 1000 ms eyes closed), target-driven saccades were significantly faster in the direction cued by the last motion (from averted to center).

Cue-driven saccades

To examine any direct effects of the motion of the pupils of the stimulus face on saccades made by the watching infant, saccades made just after the onset of the averted gaze, and before the appearance of the target were recorded. These saccades were defined as cue-driven saccades, and are presented separately from target-driven saccades for clarity (see Table 1). In the first experiment, infants made a significantly higher number of cue-driven saccades in the direction of the pupil shift than in the opposite direction (see Table 1 for details). This result indicates that the motion of the pupils can directly elicit a saccade in the direction of the cue even though the face was inverted. This finding suggests that any lateral motion of elements is sufficient for inducing this direct effect on saccades.

In Experiment 2 there were two different cues during the 1500 ms before the target appearance (see Fig. 2). The first cue was during the first 750 ms due to the position

Table 1
Characteristics of cue-driven saccades in Experiments 1–3

Experiment	Number of first cue-driven saccades (range)	To the cue (<i>SD</i>)	Opposite to the cue (<i>SD</i>)	<i>P</i> (Wilcoxon Signed Rank Test)	To the second cue (<i>SD</i>)	Opposite to the second cue (<i>SD</i>)	<i>P</i> (Wilcoxon Signed Rank Test)
1	0–14	5.7 (3.4)	3.0 (3.4)	.002	—	—	—
2	0–9	2.47 (2.2)	1.8 (1.2)	n.s.	1.8 (2.1)	1.7 (1.9)	n.s.
3	0–20	5.3 (4.7)	2.6 (2.1)	.02	4.6 (4.7)	2.3 (1.7)	n.s.

of the pupils of the averted gaze being either right or left. Saccades could be made either in response to the eye gaze position or in the opposite direction. The second cue was the motion cue that occurred during the second 750 ms where there is a visible movement of the pupils back to the central position.

No significant difference between the mean number of saccades made in direction of the position cue and in the opposite direction was found. This result indicates that the position of the pupils without the motion does not cause saccades in the direction of the gaze. During the second 750 ms the movement of the pupils back to the central position did not elicit an orientation from the infant either (see Table 1).

In Experiment 3, there were also two phases that could directly elicit saccades (see Fig. 3): first a shift from direct to averted gaze, and second a shift back from averted to direct gaze. Analysis showed more saccades in the direction of the initial pupil motion (direct to averted). This result indicates that the first motion of the pupils can elicit saccade in the direction of motion and is consistent with the results from Experiment 1 where the saccades were elicited by the initial movement of the pupils from center to averted. No significant difference between the mean number of saccades made in direction of the second motion cue and in the opposite direction was found (Table 1).

In summary, in both Experiments 1 and 3 apparent motion of the pupils was perceived, and this directly elicited a saccade in some trials from the viewing infants. This effect was not observed in Experiment 2 where there was no initial apparent motion. In addition, the movement from averted to straight-on gaze in this experiment did not elicit cue-driven saccades either. Cue-driven saccades appear to be elicited in infants under conditions where a central element (pupils) shifts to the right or left. Whether the moving elements need to resemble eyes is unclear, but these elements do not need to occur within the context of an upright face. This suggests that the conditions for eliciting cue-driven effects are broader than those for target-driven effects.

General discussion

In three experiments we analysed the specificity or otherwise of eye gaze cueing effects in infants. Only in Experiment 3 was a significant target-driven cueing effect observed. Taken together with the results from Farroni et al. (2000), this suggests that target-driven cueing effects are observed only following a period of mutual gaze with an upright face. In other words, eye contact with an upright face may engage mechanisms of attention such that the infant is more likely to be cued by any subsequent motion. While in natural interactional situations the next motion following mutual gaze is frequently a shift of the eyes, other motions may suffice. For example, in Farroni et al. (2000, Experiment 2), following a period of mutual gaze with an upright face, the whole face except the pupils shifted laterally giving the impression of an eye gaze shift in the direction opposite to that of the face motion. Infants were cued in the direction of the face motion, rather than the apparent eye gaze shift. This shows that after attention mechanisms are engaged by a period of mutual gaze with

an upright face, the motion cue need not be eye specific. However, just mutual gaze without motion is not sufficient (see Farroni et al., 2000, Experiment 3).

The conclusion that a period of mutual gaze with an upright face facilitates the direction of attention differs in at least two respects to Baron-Cohen's EDD hypothesis. First, infants do not appear to be sensitive to direction of eye gaze other than after a short period of direct (mutual) gaze. Second, at least at the young ages we have examined, there is no evidence yet that dyadic representations are formed. Having noted some differences between our findings and Baron-Cohen's hypothesis, we also note similarities. Specifically, in a recent study we demonstrated that even newborns are sensitive to direct gaze (Farroni, Csibra, Simion, & Johnson, 2002). This result establishes a clear evolutionary adaptation with multiple neural, cognitive, and behavioral consequences. In terms of evolutionary psychology, the results obtained so far about the development of eye gaze perception are consistent with an ontogenetic explanation in which the result of evolutionary selection is a number of newborn biases and preferences that help shape subsequent development. The finding that a sensitivity to direct gaze is present from birth, and that it may engage particular neural systems, suggests mechanisms selected by evolutionary pressure. In contrast, the cueing of attention in infants appears to be a more general system, not yet dedicated to eyes, which may only become eye-specific through ontogenetic experience. In other words, we suggest eye gaze cueing in infants engages general mechanisms that become incorporated into a more specific system by adulthood. Thus a specific image of averted gaze can elicit shifting of eye gaze in adults but not in infants (Driver et al., 1999; Friesen & Kingstone, 1998; Langton & Bruce, 1999).

Neuroimaging work with adults has indicated that mutual gaze, particularly with faces rated as attractive, causes activation of the right anterior cingulate, and the ventral striatum (Kampe, Frith, Dolan, & Frith, 2001). Whether specific neural activity is also elicited in infants following mutual gaze has recently been investigated (Farroni et al., 2002). Specifically, using high-density ERPs in 4-month-olds we observed that faces with direct gaze elicited a larger amplitude response at a time and scalp location consistent with face processing as compared to faces with averted gaze. One interpretation of this result is that general face processing is enhanced when accompanied with mutual gaze. The significance of mutual gaze in the development of human relationships has been shown in many studies, demonstrating that gaze provides information to regulate adult–infant interactions and to exercise social control (Blass & Camp, 2001; Kleinke, 1986). An early sensitivity for such signals, as demonstrated in these studies, facilitates this development. Furthermore, interpretation of eye gaze signals as referential communicative acts is essential for developing a rich understanding of others' mental states (Frith & Frith, 1999), whereas the absence of sensitivity to mutual gaze may provide a causal factor in developmental disorders of social understanding, such as autism (Baron-Cohen, Cambell, Karmiloff-Smith, Grant, & Walker, 1995). Finally, the current behavioral evidence indicates that mutual gaze engages attentional mechanisms that make infants more likely to orient to cued target locations.

As with other aspects of the human social brain (Johnson & Morton, 1991), we believe that most Evolutionary Psychology theories have underestimated the impor-

tance of ontogeny. The typical approach to Evolutionary Psychology entails the assumption that specific “modules” within the brain support particular cognitive functions that can be modulated or selected relatively independently of the rest of the brain. Unfortunately, these assumptions are inconsistent with recent work in neuroscience for at least two reasons. First, in analyses of the size of brain structures of over 131 different species, Finlay and Darlington (1995) concluded that the relative size of different brain structures in different brain species can be predicted from a function of the overall rate of brain development. This overall rate could be controlled by only a few genes. In general, their results were not consistent with independent genetic regulation of individual brain structures, a conclusion that extends to human brain development data (Clancy, Darlington, & Finlay, 2000). A second reason for questioning assumptions critical to the typical Evolutionary Psychology approach is that in contemporary human adult functional neuroimaging, it is no longer assumed that particular brain regions house certain cognitive functions. Rather, cognitive functions are viewed as being supported by interactions between many brain regions (e.g., Friston & Price, 2001). Both of these lines of evidence are consistent with an “interactive specialization” view of human functional brain development (Johnson, 2001) during which functions such as eye gaze cueing become increasingly specific through the specialized interaction between several brain regions (see Johnson & Farroni, 2003).

In conclusion, we suggest that eye gaze processing provides an example of how selective pressure in evolution has biased the behaviour of human newborns in such a way that their subsequent brain development is preferentially channelled to the social domain. Thus the human “social brain” is constructed afresh in each individual, rather than being the result of pre-specified modules.

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