Brief Report

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Efficient Human Face Detection in Infancy

ABSTRACT: Adults detect conspecific faces more efficiently than heterospecific faces; however, the development of this own-species bias (OSB) remains unexplored. We tested whether 6- and 11-month-olds exhibit OSB in their attention to human and animal faces in complex visual displays with high perceptual load (25 images competing for attention). Infants (n=48) and adults (n=43) passively viewed arrays containing a face among 24 non-face distractors while we measured their gaze with remote eye tracking. While OSB is typically not observed until about 9 months, we found that, already by 6 months, human faces were more likely to be detected, were detected more quickly (attention capture), and received longer looks (attention holding) than animal faces. These data suggest that 6-month-olds already exhibit OSB in face detection efficiency, consistent with perceptual attunement. This specialization may reflect the biological importance of detecting conspecific faces, a foundational ability for early social interactions. © 2015 Wiley Periodicals, Inc. Dev Psychobiol 58:129-136, 2016.

Keywords: own-species bias; attention capture; eye tracking; saliency; face learning; visual attention; infant; perceptual attunement; social orienting; face processing; face specialization

INTRODUCTION

Faces are biologically important for the formation and maintenance of social relationships; consequently, evolutionary pressures may have shaped infants' faceprocessing system (Leopold & Rhodes, 2010; LoBue & DeLoache, 2010; Parr, 2011; Pascalis & Kelly, 2009). A face detection system may be adaptive, directing infants to conspecifics' faces, ensuring face exposure during sensitive periods, supporting the formation of social bonds, and scaffolding social skill development (Johnson, 2005; Morton & Johnson, 1991; Murray, 2014; Schultz, 2005). Early disruptions to face detec-

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tion may impact later higher-level face skills, such as face recognition (Dalrymple & Duchaine, 2015). Given the importance of faces, infants may possess mechanisms that preferentially attract and engage attention to conspecifics, as conspecifics may indicate potential opportunities for social interactions, as well as potential threats (Di Giorgio, Méary, Pascalis, & Simion, 2012; Dupierrix et al., 2014; Heron-Delaney, Wirth, & Pascalis, 2011; Sanefuji, Wada, Yamamoto, Mohri, & Taniike, 2014; Simpson, Suomi, & Paukner, 2015). The superior processing of conspecifics relative to heterospecifics, known as own-species bias (OSB), is likely driven by experience (Scott & Fava, 2013). OSB is an example of perceptual attunement, a domain general developmental pattern of specialization in which infants, with age and experience, exhibit greater improvements in processing familiar compared to unfamiliar stimulus types (Maurer & Werker, 2014; Nelson, 2001).

OSB appears across numerous domains in infancy. For example, 3-month-olds spend longer looking at human compared to animal faces (Di Giorgio, Méary, Pascalis, & Simion, 2012a), and eyes (Dupierrix et al.,

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2014). By 9 to 12 months, infants are better at discriminating individual identities of human compared to animal faces (Pascalis, de Haan, & Nelson, 2002; Simpson, Varga, Frick, & Fragaszy, 2011) and voices (Friendly, Rendall, & Trainor, 2014). Recent work suggests infants may even discriminate intact and scrambled biological motion of conspecifics better than heterospecifics, suggesting OSB in processing kinematics (Simpson et al., submitted).

While these tasks shed light on the development of OSB in social information processing, in the real world infants are often confronted with more than two stimuli at a time. This challenge requires attention prioritization, processing some items but not others. When faced with this challenge, infants demonstrate impressive social detection capacities. For example, by 6 months of age, human faces attract and hold infants' attention more than non-face stimuli, even in complex visual displays (Di Giorgio et al., 2012a; Di Giorgio, Turati, Altoè, & Simion, 2012b; Elsabbagh et al., 2013b; Gliga, Elsabbagh, Andravizou, & Johnson, 2009; Gluckman & Johnson, 2013). However, studies thus far cannot determine whether these biases are due to general face properties (e.g., first-order relations of facial elements) or are exclusive to human faces, as face detection for human and animal faces has not been compared. In adults, animal faces engage similar visual processing as human faces (Diamond & Carey, 1986) and elicit similar neural activation (Blonder et al., 2004); therefore, comparisons of human and animal face processing can disentangle developmental patterns in face processing generally from human face processing specifically (Whyte, Behrmann, Minshew, Garcia, & Scherf, 2015). While adults exhibit an OSB in face detection (Simpson, Buchin, Werner, Worrell, & Jakobsen, 2014a), it is unclear when this bias emerges.

We tested the nature of OSB in face detection efficiency during the first year of life, focusing on visual attention mechanisms overlooked in infant face perception studies (Frank, Anso, & Johnson, 2014). Three mechanisms—detection, attention capture, and attention holding—are fundamental, reflecting different but related aspects of visual processing (e.g., Cohen, 1972). Detecting information is evolutionarily primitive. Limited attentional resources require that information be filtered and not all stimuli are processed (e.g., Treisman, 1969). Attention capture is the extent to which a stimulus automatically elicits attention, measured with fixation response time (RT). Attention holding refers to attention maintenance, including look duration, reflecting interest, preference, and information extraction (Bronson, 1991). Face detection, compared to other face skills (e.g., discrimination), may be considered more foundational (Mondloch et al., 2013), present in rudimentary form from birth (Johnson, 2005). In addition, compared to face discrimination, face detection occurs early in the information-processing stream and requires fewer cognitive resources (e.g., memory; Palermo & Rhodes, 2007). Face detection is an important precursor to the development of higherlevel face skills, and disruptions to the face detection system may lead to face recognition difficulties (e.g., prosopagnosia: Dalrymple & Duchaine, 2015). While an OSB in face discrimination does not appear until 9 to 12 months, we predicted an earlier OSB in face attentional efficiency, given that detection is a more basic skill. Specifically, we predicted OSB in face detection, attention capture, and attention holding may already be present at 6 months of age, and will remain observable in 11-month-olds and adults. Unlike previous studies that measured human face detection in multi-item displays (e.g., Di Giorgio et al., 2012b) or compared preferences for human and animal faces in paired comparison tests (e.g., Duprierrix et al., 2014), we presented 25-item arrays of images, each with a human or animal face surrounded by nonfaces, and used eye tracking to measure visual attention efficiency.

METHODS

Participants

We recruited infants through emails at James Madison University, and adults through an undergraduate research participant pool. Poor calibration resulted in the exclusion of four 6-month-olds, leaving a final sample of 23 (M=6.1 months, SD=.31; range: 5.6 to 6.9 months; 11 females; 78% Caucasian); six 11-month-olds, leaving a final sample of 25 (M=11.1 months, SD=0.31; range: 10.4–11.8 months; 11 females; 84% Caucasian); and one adult, leaving a final sample of 43 (M=19.6 years; SD=1.48; 27 females; 81% Caucasian). Parents indicated their highest level of education: 4% completed high school, 6% completed partial college, 37% completed college, 29% completed a master's degree, 9% completed a professional degree, and 15% did not report. Families received monetary compensation and adults received course credit.

Materials

We recorded eye movements via corneal reflection using a Tobii T60 eye tracker, a remote 43 cm monitor (resolution 1280×1024 pixels), and a sampling rate of 60 Hertz. We collected and summarized data with Tobii Studio (Tobii Technology, Sweden).

Participants viewed 12 25-item arrays (5×5 matrices), subtending a visual angle of approximately 24° (Fig. 1A). Photos were in color, 4.4–4.9 cm (width) by 4.6–5.0 cm (height). Each array contained a unique neutral face of a

human, non-human primate (hereafter "primate"), or non-primate mammal (hereafter "mammal"). Faces were upright with visible and open eyes, visible noses and mouths, and were neutral expressions (Simpson et al., 2014a; Simpson, Mertins, Yee, Fullerton, & Jakobsen, 2014c). The remaining images were unique man-made and natural items. Rather than equating images on low-level characteristics, we chose heterogeneous images (Hershler & Hochstein, 2005; see Supplemental Materials).

Procedure

Participants sat 60cm from the monitor. After a 5-point calibration, participants viewed up to 12 trials. Prior to each trial, attention-getters directed gaze toward the center of the screen. Adults were told: "You will be viewing a series of pictures on each slide. Please look at each slide of pictures." Each array was displayed for five seconds for adults and eight seconds for infants, to provide each age group with enough time to explore some, but not all, of the images (see Supplemental Materials).

Data Analysis

We used the Tobii Fixation Filter (35 pixels). We created areas of Interest (AOI) around faces $(5 \times 5 \text{ cm})$ and arrays

 $(27 \times 27 \,\mathrm{cm})$. We defined face detection as the proportion of trials in which participants fixated on the face, out of the total number of trials in which there was at least one fixation on the array (see Supplemental Materials). We measured attention capture with RT (i.e., time from trial start to first face fixation). We defined attention holding as the proportion of face fixation time out of the total fixation time to the array. We explored the within-subjects factor of Species (human, primate, mammal) and between-subjects factor of Age (6 months, 11 months, adults). We employed Bonferroni corrections for t tests (3 comparisons, p = .0167).

RESULTS

Face Detection

A mixed-design ANOVA on the proportion of trials with a fixation to the face revealed main effects of Age (6-month-old, 11-month-old, adult), F(2, 58) = 13.10, p < .001, $\eta^2 = .45$, and Species, F(2, 116) = 14.73, p < .001, $\eta_p^2 = .25$, Figure 1B. There was no Age × Species interaction, F(4, 116) = .94, p = .44. Independent samples *t*-tests revealed that adults (M = 0.79,

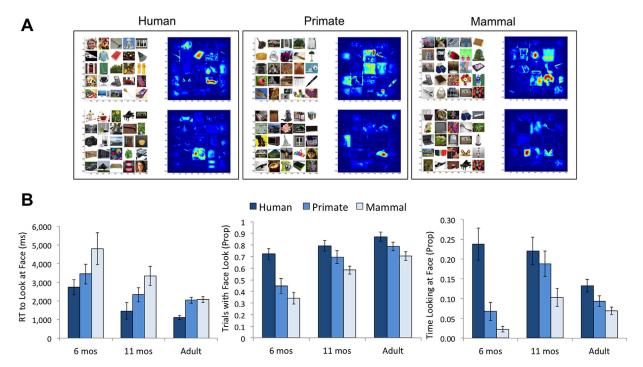


FIGURE 1 (A) Sample arrays and their salience maps, with the most salient regions in red (light gray) and the least salient regions in blue (dark gray). See Supplemental Materials for details. (B) Proportion of trials in which there was a fixation on a face (left graph), response times (RTs) to fixate on faces (middle graph), and proportion of time looking at faces (right graph). Faces were of humans (darkest bars), nonhuman primates (medium bar), or nonprimate mammals (lightest bars). Within each graph, 6-month-olds are shown on the left, 11-month-olds in the middle, and adults on the right. Error bars reflect within-subjects standard error of the mean.

SD = 0.17) were more likely to orient to faces compared to 6-month-olds (M = 0.58, SD = 0.19), t (61) = 4.24, p < .001, d = 1.16. There was no difference in the proportion of trials on which 6-month-olds and 11-month-olds oriented to the face, t(39) = 1.78, p = .08. There was a marginal difference in the proportion of trials on which 11-month-olds (M = 0.70, SD = 0.21)and adults oriented to the face, t(64) = 1.94, p = .056. Paired-samples t-tests revealed a greater proportion of trials received at least one face fixation when the trials contained human faces (M = 0.82, SD = 0.24) compared to primate faces (M = 0.70, SD = 0.27), t(70) = 3.50,p = .001, d = .42, and mammal faces (M = 0.63)SD = 0.27), t(65) = 5.58, p < .001, d = .70, and a marginally higher proportion of trials received at least one face fixation when the trials contained primate faces compared to mammal faces, t(61) = 2.42, p = .018, d = .31 (n.s. with Bonferroni).

Face Attention Capture

A mixed-design ANOVA on RTs revealed main effects of Age, F(2,55) = 10.85, p < .001, $\eta^2 = .28$, and Species, F(2,110) = 21.41, p < .001, $\eta_p^2 = .37$, and a mar-Age \times Species interaction, F(4,110) = 2.40, p = .055 Figure 1B. Independent samples *t*-tests revealed that adults were faster ($M = 1,722 \,\mathrm{ms}$, SD =543 ms) than 6-month-olds (M = 3,425 ms, SD =1,727 ms), t(60) = 5.89, p < .001, d = 1.62, and marginally faster than 11-month-olds ($M = 2,339 \,\mathrm{ms}$, SD =1,560 ms), t(65) = 2.36, p = .021, d = .60 (n.s. with Bonferroni). Eleven-month-olds were marginally faster than 6-month-olds, t(41) = 2.16, p = .036, d = .66 (n.s. with Bonferroni). RTs were faster to human faces $(M=1,553 \,\mathrm{ms}, SD=1,600 \,\mathrm{ms})$ compared to primate faces $(M = 2,356 \,\mathrm{ms}, SD = 1,418 \,\mathrm{ms}), t(69) = 5.91,$ p < .001, d = .71, and mammal faces $(M = 2.766 \,\mathrm{ms})$ SD = 1,821 ms, t(62) = 6.12, p < .001, d = .77, but there was no difference between primate and mammal faces, t(57) = 1.09, p = .28. We followed up the marginal Age × Species interaction with an ANOVA within each species, across age. This revealed main effects of Age, $Fs \ge 5.38$, ps < .007, $\eta_p^2 \ge .130$. Independent samples t tests revealed equally fast RT for each species, for 6- and 11-month-olds, ps > .05 (see Fig. 1B for descriptive statistics). While adults were faster than 6-month-olds for all species, $ps \le .001$, $ds \ge .96$, adults were faster than 11-month-olds only for mammal faces, p = .004, d = .82, but not human or primate faces, ps > .05. We next explored RT within each age across species, which revealed main effects of Species, $Fs \ge 3.72$, ps < .05, $\eta_p^2 \ge .24$. Paired t tests revealed that, for each age group, RTs were faster to human compared to mammal faces, ps < .017, $ds \ge .75$. However, only 6-month-olds and adults had faster RTs to human compared to primate faces, p = .014, d = .84, and p < .001, d = .80, respectively, while 11-montholds had only a trend (n.s. with Bonferroni) of faster RTs for human compared to primate faces, p = .047, d=.54. For all ages, primate and mammal faces did not differ, ps > .05.

Face Attention Holding

A mixed-design ANOVA on the proportion of time looking to the face, out of the total time looking to the array, revealed main effects of Age, F(2,78) = 5.15, p = .008, $\eta^2 = .13$, and Species, F(2,156) = 47.57, p < .001, $\eta_p^2 = .38$, qualified by an Age × Species interaction, F(4,156) = 4.30, p = .003, Figure 1B. Independent samples t tests revealed that 11-month-olds looked for a greater proportion of time (M = .17,SD = .10) than adults (M = .10, SD = .08), t(66) = 3.36,p = .010, d = .85, but 6-month-olds (M = .12, SD = .16)did not differ from 11-month-olds, t(45) = 1.30, p = .038 (n.s. with Bonferroni) or adults, t(65) = .80, p=.42. Paired-samples t-tests revealed a greater proportion of time looking at human faces (M=.18,SD = .15), compared to primate (M = .11, SD = .12), t(81) = 4.59, p < .001, d = .51, and mammal faces (M = .07, SD = .08), t(83) = 7.35, p < .001, d = .80, andgreater time looking at primate compared to mammal faces, t(82) = 4.41, p < .001, d = .49. One-way repeated measures ANOVAs on each age group, to follow up the Age × Species interaction, each revealed a main effect of Species (6-months: F(2,32) = 24.11, p < .001, $\eta_p^2 = .601$; 11-months: F(2,40) = 7.02, p = .002, $\eta_p^2 = .002$.260; Adults: F(2,84) = 20.58, p < .001, $\eta_p^2 = .329$). Paired-samples t-tests comparing Species within each age group revealed that 6-month-olds spent a greater proportion of time looking at human faces (M=.24,SD = .18) compared to primate (M = .07, SD = .10) or mammal faces (M = .02, SD = .03), t(16) = 3.99,p = .001, d = .97, and t(18) = 6.47, p < .001, d = 1.48,respectively, but exhibited only a trend of more looking to primate than mammal faces, t(17) = 2.61, p = .018, d=.61 (n.s. with Bonferroni). In contrast, 11-montholds looked more to both human (M = .22, SD = .16)and primate faces (M=.19, SD=.16) compared to mammal faces (M = .10, SD = .11), t(21) > 2.81,ps < .010, ds > .60, but looked equally to human and primate faces, t(20) = 1.45, p = .163. Finally, adults looked more to human (M=.13, SD=.10), than primate (M = .09, SD = .09), t(43) = 4.14, p < .001,d = .62, or mammal faces (M = .07, SD = .07), t(42) =5.72, p < .001, d = .87, and looked more to primate than mammal faces, t(24) = 2.70, p = .010, d = .41. There were no other differences, ps > .05.

DISCUSSION

Given the social and ecological importance of faces for infants, and their early exposure to conspecifics, biases to detect conspecific faces may be evident in the first year of life (Simpson et al., 2015). In adults, conspecific faces are detected more efficiently than heterospecific faces (Simpson et al., 2014a; 2014c). The present study explored whether this OSB in face detection is present in 6- and 11-month-old infants. While previous work reported that human faces, compared to non-faces, were more likely to capture and hold infants' attention (e.g., Gluckman & Johnson, 2013), the present study compared attentional efficiency to human and animal faces in complex 25-item visual displays. We found that, by 6 months of age, human faces, compared with primate and mammal faces, were more likely to be detected, were detected more quickly, and held attention longer, supporting the proposal that own-species faces are biologically important in infancy (e.g., Sanefuji et al., 2014). Critically, our stimulus analysis (see Supplemental Materials) revealed that these results are unlikely to be due to low-level salience (Gluckman & Johnson, 2013; Hershler & Hochstein, 2005; Ho-Phuoc, Guyader, & Guérin-Dugué, 2010; Walther & Koch, 2006).

We also found age-related improvements in face detection, regardless of the species. This finding may indicate a general improvement in face processing with age, consistent with a report that adults outperformed infants in discriminating human, monkey, and sheep faces (Simpson et al., 2014b). Alternatively, this developmental improvement in detection for all animal faces may reflect age-related increases in information processing speed (Rose, Feldman, & Jankowski, 2002). Nonetheless, there is a strikingly similar pattern across all ages, in which human faces were more likely to be detected than animal faces.

Human faces, compared with primate and mammal faces, captured attention more quickly across all ages. This finding is notable given that 6-month-olds do not yet appear to show OSB in facial identity discrimination (e.g., Pascalis et al., 2002). This study presents evidence that, by 6 months, infants already exhibit adult-like OSB in attentional efficiency. In addition, while we found broad improvement in face attention capture for all species from 6 months to adulthood, by 11 months, infants already exhibited adult-like speed for human and primate faces. This suggests that mechanisms to efficiently locate conspecific faces may already be fully functioning by 11 months.

Finally, all age groups looked longer at human than mammal faces, suggesting OSB in attention holding. This finding is consistent with previous reports that, in paired preference tests, 3-month-olds look longer to human compared to animal faces (e.g., Di Giorgio et al., 2012a). In addition, primate faces appear to be processed more similarly to human faces than mammal faces. While 6-month-olds and adults clearly looked longer to human than primate faces, 11-month-olds looked equally to human and primate faces. In fact, it appears that there may be a developmental increase in attention holding to animal faces from 6 to 11 months, while attention to human faces remains equivalently high between 6 and 11 months. These results are consistent with those exploring the own-race effect, in which older infants look more to novel (i.e., less familiar) other-race faces compared to faces of familiar races (Liu et al., 2015). Nonetheless, here the pattern is strikingly similar across development for all three attentional measures.

While previous studies report that infants as young as 3 months already exhibit preferences for own-species faces and eyes in tasks with two images (Di Giorgio et al., 2012a; Dupierrix et al., 2014), the present study extends these findings in a paradigm with 25 concurrently presented images. Even with this high perceptual load, with many items competing for attention, we found that 6-month-old infants were faster to look, more likely to look, and looked longer at conspecific relative to heterospecific faces.

In conclusion, 6-month-olds may not entirely be face generalists, possessing only a coarse face template; rather, 6-month-olds already appear to exhibit some own-species face specialization. These results do not call into question the reports that younger infants more easily discriminate individual faces of novel face categories (e.g., unfamiliar races and species) than older infants and adults (e.g., Kelly et al., 2007; Pascalis et al., 2002). Our data, rather, suggest a more nuanced view of face specialization. While 6-montholds may be broadly tuned face generalists for some face skills (e.g., discrimination), the present findings suggest that, when considering attentional mechanisms (detection, attention capture, attention holding), by 6 months, infants already exhibit OSB in attentional efficiency. Indeed, face detection and preferences may precede other face skills (e.g., discrimination), which may depend upon these more basic capacities (Dalrymple & Duchaine, 2015; Mondloch et al., 2013; Schultz, 2005). For example, infants exhibit face specialization for own-species and own-race faces earlier in pairedcomparison preference tests, by around 3 months (Bar-Haim et al., 2006; Liu et al., 2015; Sanefuji et al., 2014), while such biases in face discrimination are not observed until about 6 to 9 months (Anzures, Quinne, Pascalis, Slater, & Lee, 2010; Kelly et al., 2007; Pascalis et al., 2002).

Although speculative, this own-species detection may be possible through a perceptual template for own-species faces (Heron-Delaney et al., 2011), potentially created or refined through perceptual attunement (Maurer & Werker, 2014). The present data are consistent with an experience-driven developmental pattern of perceptual attunement. However, 6-montholds have had much experience with conspecific faces; therefore, future work must explore whether this face template is present at birth or requires experience. Infants with controlled or limited postnatal social environments, such as infants treated for bilateral congenital cataracts (Mondloch et al., 2013) or face nave infant monkeys (Sugita, 2008), will be useful in this regard.

Future work must determine whether the present findings are domain general, or reflect a phenomenon only at the species-level (i.e., processing of own-species vs. other species). Attentional mechanisms for other types of face specialization—e.g., race, sex, age—might, like the OSB, emerge at or before 6 months of age. For example, in adults, cross-race faces are located more quickly than own-race faces, suggesting a detection advantage for cross-race faces (Levin, 2000); however, to date, the development of other-race face detection remains unknown.

Finally, infants' face attentional efficiency—detection, attention capture, and attention holding—may hold promise for identifying early abnormalities which may indicate heightened risk for disorders (e.g., autism: Elsabbagh et al., 2013a, 2013b; Schultz, 2005; prosopagnosia: Dalrymple & Duchaine, 2015). While neurotypical populations find human faces more rewarding than animal faces, autistic populations exhibit the reverse (Whyte et al., 2015). Assessing the development of OSB in these populations may prove insightful.

AUTHOR CONTRIBUTIONS

K.V. Jakobsen and E.A. Simpson developed the study concept and design. L. Umstead collected the data, under the supervision of K.V. Jakobsen. K.V. Jakobsen and E.A. Simpson performed the analysis, interpretation, and drafted the manuscript. All authors provided critical revisions and approved the final version of the manuscript.

NOTES

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REFERENCES

- Anzures, G., Quinn, P. C., Pascalis, O., Slater, A. M., & Lee, K. (2010). Categorization, categorical perception, and asymmetry in infants' representation of face race. Developmental Science, 13(4), 553–564. DOI: 10.1111/j.1467-7687.2009.00900.x.
- Bar-Haim, Y., Ziv, T., Lamy, D., & Hodes, R. M. (2006). Nature and nurture in own-race face processing. Psychological Science, 17(2), 159–163.
- Blonder, L. X., Smith, C. D., Davis, C. E., Kesler, M. L., Garrity, T. F., Avison, M. J., & Andersen, A. H. (2004). Regional brain response to faces of humans and dogs. Cognitive Brain Research, 20(3), 384–394. DOI: 10.1016/ j.cogbrainres.2004.03.020.
- Bronson, G. W. (1991). Infant differences in rate of visual encoding. Child Development, 62(1), 44–54. DOI: 10.1111/ j. 1467-8624. 1991.tb01513.x.
- Cohen, L. B. (1972). Attention-getting and attention-holding processes of infant visual preferences. Child Development, 43(3), 869–879. DOI: 10. 2307/1127638.
- Dalrymple, K. A., Duchaine, B. (2015) Impaired face detection may explain some but not all cases of developmental prosopagnosia. Developmental Science. Advance Online Publication. Doi: 10.1111/desc.12311.
- Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. Journal of Experimental Psychology: General, 115(2), 107–117. DOI: 10.1037/ 0096-3445.115.2.107.
- Di Giorgio, E., Méary, D., Pascalis, O., & Simion, F. (2012a). The face perception system becomes species-specific at 3 months: An eye-tracking study. International Journal of Behavioral Development, 37(2), 95–99. DOI: 10.1177/ 0165025412465362.
- Di Giorgio, E., Turati, C., Altoè, G., & Simion, F. (2012b). Face detection in complex visual displays: An eye-tracking study with 3-and 6-month-old infants and adults. Journal of Experimental Child Psychology, 113(1), 66–77. DOI: 10.1016/j.jecp.2012.04.012.
- Dupierrix, E., de Boisferon, A. H., Méary, D., Lee, K., Quinn,
 P. C., Di Giorgio, E., ... Pascalis, O. (2014). Preference for human eyes in human infants. Journal of Experimental Child Psychology, 23, 138–146. DOI: 10.1016/j. jecp.2013.12.010.
- Elsabbagh, M., Fernandes, J., Webb, S. J., Dawson, G., Charman, T., & Johnson, M. H. (2013a). Disengagement of visual attention in infancy is associated with emerging autism in toddlerhood. Biological Psychiatry, 74(3), 189–194.

- Elsabbagh, M., Gliga, T., Pickles, A., Hudry, K., Charman, T., & Johnson, M. H. (2013b). The development of face orienting mechanisms in infants at-risk for autism. Behavioural Brain Research, 251, 147–154.
- Frank, M. C., Amso, D., & Johnson, S. P. (2014). Visual search and attention to faces during early infancy. Journal of Experimental Child Psychology, 118, 13–26. DOI: 10.1016/j.jecp.2013.08.012.
- Friendly, R. H., Rendall, D., & Trainor, L. J. (2014). Learning to differentiate individuals by their voices: Infants' individuation of native- and foreign-species voices. Developmental Psychobiology, 56(2), 228–237. DOI: 10.1002 /dev.21164.
- Gliga, T., Elsabbagh, M., Andravizou, A., & Johnson, M. (2009). Faces attract infants' attention in complex displays. Infancy, 14(5), 550–562. DOI: 10.1080/15250000903144199.
- Gluckman, M., & Johnson, S. P. (2013). Attentional capture by social stimuli in young infants. Frontiers in Psychology, 4(257), 1–7. DOI: 10.3389/fpsyg.2013.00527.
- Heron-Delaney, M., Wirth, S., & Pascalis, O. (2011). Infants' knowledge of their own species. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1571), 1753–1763. DOI: 10.1098/rstb.2010.0371.
- Hershler, O., & Hochstein, S. (2005). At first sight: A high-level pop out effect for faces. Vision Research, 45(13), 1707–1724. DOI: 10.1016/j.visres.2004.12.021.
- Ho-Phuoc, T., Guyader, N., & Guérin-Dugué, A. (2010). A functional and statistical bottom-up saliency model to reveal the relative contributions of low-level visual guiding factors. Cognitive Computation, 2(4), 344–359. DOI: 10.1007/s12559-010-9078-8.
- Johnson, M. H. (2005). Subcortical face processing. Nature Reviews Neuroscience, 6(10), 766–774. DOI: 10.1038/ nrn1766.
- Kelly, D. J., Quinn, P. C., Slater, A. M., Lee, K., Ge, L., & Pascalis, O. (2007). The other-race effect develops during infancy evidence of perceptual narrowing. Psychological Science, 18(12), 1084–1089. DOI: 10.1111/j.1467-9280.2007.02029.x.
- Leopold, D. A., & Rhodes, G. (2010). A comparative view of face perception. Journal of Comparative Psychology, 124(3), 233. DOI: 10.1037/a0019460.
- Levin, D. T. (2000). Race as a visual feature: Using visual search and perceptual discrimination tasks to understand face categories and the cross-race recognition deficit. Journal of Experimental Psychology: General, 129, 559–574. DOI: 10.1037/0096-3445.129.4.559.
- Liu, S., Xiao, W. S., Xiao, N. G., Quinn, P. C., Zhang, Y., Chen, H., Ge, L., Pascalis, O., ... Lee, K. (2015). Development of visual preference for own-versus otherrace faces in infancy. Developmental Psychology, 51(4), 500–511. DOI: 10.1037/a0038835.
- LoBue, V., & DeLoache, J. S. (2010). Superior detection of threat-relevant stimuli in infancy. Developmental Science, 13(1), 221–228. DOI: 10.1016/j.dr.2013.07.005.
- Maurer, D., & Werker, J. F. (2014). Perceptual narrowing during infancy: A comparison of language and faces.

- Developmental Psychobiology, 56(2), 154–178. DOI: 10.1002/dev.21177.
- Mondloch, C. J., Segalowitz, S. J., Lewis, T. L., Dywan, J., Grand, R., & Maurer, D. (2013). The effect of early visual deprivation on the development of face detection. Developmental Science, 16(5), 728–742.
- Morton, J., & Johnson, M. H. (1991). CONSPEC and CONLERN: a two-process theory of infant face recognition. Psychological Review, 98(2), 164–181. DOI: 10.1037/ 0033-295X.98.2.164.
- Murray, L. (2014). The Psychology of Babies: How relationships support development from birth to two years. Robinson Publishing.
- Nelson, C. A. (2001). The development and neural bases of face recognition. Infant and Child Development, 10, 3–18.
- Palermo, R., & Rhodes, G. (2007). Are you always on my mind? A review of how face perception and attention interact. Neuropsychologia, 45(1), 75–92.
- Parr, L. A. (2011). The evolution of face processing in primates. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1571), 1764–1777. DOI: 10.1098/rstb.2010.0358.
- Pascalis, O., de Haan, M., & Nelson, C. A. (2002). Is face processing species-specific during the first year of life?. Science, 296(5571), 1321–1323. DOI: 10.1126/science.1070223.
- Pascalis, O., & Kelly, D. J. (2009). The origins of face processing in humans: Phylogeny and ontogeny. Perspectives on Psychological Science, 4(2), 200–209.
- Rose, S. A., Feldman, J. F., & Jankowski, J. J. (2002). Processing speed in the 1st year of life: A longitudinal study of preterm and full-term infants. Developmental Psychology, 38(6), 895–902.
- Sanefuji, W., Wada, K., Yamamoto, T., Mohri, I., & Taniike, M. (2014). Development of preference for conspecific faces in human infants. Developmental Psychology, 50(4), 979–985. DOI: 10.1037/a0035205.
- Schultz, R. (2005). Developmental deficits in social perception in autism: The role of the amygdala and fusiform face area. International Journal of Developmental Neuroscience, 23, 125–141. DOI: 10.1016/j.ijdevneu.2004.12.012.
- Scott, L. S., & Fava, E. (2013). The own-species face bias: A review of developmental and comparative data. Visual Cognition, 21(9-10), 1364–1391. DOI: 10.1080/ 13506285.2013.821431.
- Simpson, E. A., Buchin, Z., Werner, K., Worrell, R., & Jakobsen, K. V. (2014a). Finding faces among faces: Human faces are located more quickly and accurately than other primate and mammal faces. Attention, Perception, & Psychophysics, 76(8), 2175–2183. DOI: 10.3758/s13414-014-0744-x.
- Simpson, E. A., Jakobsen, K. V., Fragaszy, D. M., Okada, K., & Frick, J. E. (2014b). The development of facial identity discrimination through learned attention. Developmental Psychobiology, 56(5), 1083–1101. DOI: 10.1002/dev.21194.
- Simpson, E. A., Mertins, H. L., Yee, K., Fullerton, A., & Jakobsen, K. V. (2014c). Visual search efficiency is greater

- for human faces compared to animal faces. Experimental Psychology, 61(6), 439–456. DOI: 10.1027/1618-3169/a000263.
- Simpson, E. A., Paukner, A., Jakobsen, K. V., Ferrari, P. F., Suomi, S. J., Jastorff, J. (submitted). Infant macaques exhibit own-species bias in biological motion perception.
- Simpson, E. A., Suomi, S. J., & Paukner, A. (2015) Evolutionary relevance and experience contribute to face discrimination in infant macaques (*Macaca mulatta*). Journal of Cognition and Development, DOI: 10.1080/15248372.2015.1048863.
- Simpson, E. A., Varga, K., Frick, J. E., & Fragaszy, D. M. (2011). Infants experience perceptual narrowing for non-primate faces. Infancy, 16(3), 318–330. DOI: 10.1111/j.1532-7078.2010.00052.x.
- Sugita, Y. (2008). Face perception in monkeys reared with no exposure to faces. Proceedings of the National Academy of Sciences, 105(1), 394–398.

- Treisman, A. M. (1969). Strategies and models of selective attention. Psychological Review, 76(3), 282–299. DOI: 10.1037/h0027242.
- Walther, D., & Koch, C. (2006). Modeling attention to salient proto-objects. Neural Networks, 19(9), 1395–1407. DOI: 10.1016/j.neunet.2006.10.001.
- Whyte, E. M., Behrmann, M., Minshew, N. J., Garcia, N. V., & Scherf, K. S. (2015). Animal, but not human, faces engage the distributed face network in adolescents with autism. Developmental Science. Advance Online Publication., DOI: 10.1111/desc.12305.

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