

# 1 **Retinotopic organization of visual cortex in human infants**

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## 8 **Abstract**

9 Vision develops rapidly during infancy, yet how visual cortex is organized during this period is  
10 unclear. One possibility is that the retinotopic organization of visual cortex emerges gradually as  
11 perceptual abilities improve. This may result in a hierarchical maturation of visual areas from stri-  
12 ate to extrastriate cortex. Another possibility is that retinotopic organization is present from early  
13 infancy. This early maturation of area boundaries and tuning could scaffold further developmental  
14 changes. Here we test the functional maturity of infant visual cortex by performing retinotopic  
15 mapping with fMRI. Infants aged 5–23 months had retinotopic maps, with alternating preferences  
16 for vertical and horizontal meridians indicative of area boundaries from V1 to V4, and an orthog-  
17 onal gradient of preferences from high to low spatial frequencies indicative of growing receptive  
18 field sizes. Although present in the youngest infants, these retinotopic maps showed subtle age-  
19 related changes, suggesting that early maturation undergoes continued refinement.

## 20 **Introduction**

21 Vision is the dominant sense in humans, but develops slowly throughout childhood and even into  
22 adolescence (Braddick and Atkinson, 2011; Kiorpes, 2016; Lewis and Maurer, 2005). How is  
23 infant visual cortex organized and how does this organization change over early development?  
24 One hypothesis is that visual cortex develops hierarchically (Bourne and Rosa, 2006), with low-  
25 level areas (such as V1) maturing first, followed by mid-level areas (such as V2–V4), and then  
26 high-level areas (such as LO and PHC) (Bourne and Rosa, 2006; Condé, Lund, and Lewis, 1996;  
27 Distler, Bachevalier, Kennedy, Mishkin, and Ungerleider, 1996; Gomez, Natu, Jeska, Barnett, and  
28 Grill-Spector, 2018; Kiorpes, 2016; Zhang, Zheng, Watanabe, Maruko, Bi, Smith, and Chino,  
29 2005). By maturation, we consider the emergence of an organized retinotopic map of visual space  
30 that defines the tuning and boundaries of an area (i.e., arealization). According to hierarchical  
31 maturation, young infants may have mature arealization in only V1, whereas older infants may  
32 additionally show arealization in V2–V4. An alternative hypothesis is that the organization of  
33 visual cortex is established early in infancy. By this early arealization account, even young infants  
34 may have distinct retinotopic maps in areas V1–V4 with stereotyped tuning to features such as  
35 curvature and scale (Arcaro and Livingstone, 2017).

36 In support of hierarchical maturation, animal models show a sequence of cellular and macro-  
37 scopic changes across the cortical hierarchy (Condé, Lund, and Lewis, 1996; Distler, Bachevalier,  
38 Kennedy, Mishkin, and Ungerleider, 1996; Zhang and Fang, 2012). At birth, mature cells are only  
39 found in low-level visual areas, whereas in the weeks following birth, they can be found through-

40 out the visual hierarchy (Bourne and Rosa, 2006), including mid- and high-level areas. The be-  
41 havioral capacities of humans similarly suggest sequential development of visual areas (Kovács,  
42 2000; Siu and Murphy, 2018). Visual behaviors thought to rely primarily on V1, such as orienta-  
43 tion discrimination and spatial frequency discrimination (Banks, Stephens, and Hartmann, 1985;  
44 Braddick, Wattam-Bell, and Atkinson, 1986), are present in rudimentary form near birth. More  
45 complex visual behaviors thought to depend on V2–V4 and interconnectivity between visual areas  
46 (Burkhalter, Bernardo, and Charles, 1993; Kiorpes and Bassin, 2003; Zhang, Zheng, Watanabe,  
47 Maruko, Bi, Smith, and Chino, 2005), such as contour integration (Baker, Tse, Gerhardstein, and  
48 Adler, 2008; Kovacs, Kozma, Feher, and Benedek, 1999), develop up to a year later. Indeed, the  
49 receptive field properties of high-level visual areas continue to develop during childhood, whereas  
50 those of low- and mid-level visual areas do not (Gomez, Natu, Jeska, Barnett, and Grill-Spector,  
51 2018). In support of the early arealization hypothesis, arealization is present throughout the visual  
52 hierarchy in neonatal macaques (Arcaro and Livingstone, 2017). At 2 weeks old — homologous to  
53 2 months old in humans (Boothe, Dobson, and Teller, 1985; Kiorpes, 2016) — functional connec-  
54 tivity in macaque visual cortex mirrors boundaries between retinotopic areas. Although these two  
55 hypotheses about arealization are juxtaposed here, they are not necessarily mutually exclusive: the  
56 boundaries of areas may be present early in infancy with other properties, such as receptive field  
57 size, maturing at different rates across areas.

58       The question of how visual cortex is organized in human infants remains unanswered because  
59 it has not been studied directly. Current theorizing is limited because it depends upon neural data  
60 from non-human animals and behavioral data from humans. For example, evidence for early areal-

61 ization in macaques might not translate to humans. Even though the visual systems of humans and  
62 macaques are similar at maturity (Wandell, Dumoulin, and Brewer, 2007), human infancy is more  
63 protracted than macaque infancy (Boothe, Dobson, and Teller, 1985; Kiorpes, 2016). This allows  
64 for the possibility that retinotopic maps emerge in the human brain over postnatal development,  
65 consistent with hierarchical maturation. Likewise, the sequential emergence of visual behaviors in  
66 human infants could reflect hierarchical maturation of the visual areas that support these behaviors  
67 or the development of non-visual regions downstream that receive the read-out from areas showing  
68 early arealization.

69       Our approach for measuring the organization of visual cortex in human infants is to perform  
70 retinotopic mapping with functional magnetic resonance imaging (fMRI) — the gold standard for  
71 defining visual areas V1–V4 in older children and adults (Conner, Sharma, Lemieux, and Men-  
72 dola, 2004; Wandell, Dumoulin, and Brewer, 2007). Indeed, no prior study has used experimental  
73 stimuli to define the boundaries and properties of V1–V4 in infant primates — work at this age  
74 in non-human primates relied on functional connectivity rather than on more standard mapping  
75 stimuli (Arcaro and Livingstone, 2017) and the youngest evidence of retinotopy in humans so  
76 far has come from 5 year olds (Conner, Sharma, Lemieux, and Mendola, 2004; Gomez, Natu,  
77 Jeska, Barnett, and Grill-Spector, 2018). The reason why this was not previously performed in  
78 human infants is that fMRI studies in awake infants (human or non-human) present many chal-  
79 lenges. Some of these challenges are general, such as head motion and fussiness, whereas others  
80 are specifically problematic for retinotopic mapping, such as an inability to instruct or enforce eye  
81 fixation (Braddick and Atkinson, 2011; Ellis and Turk-Browne, 2018). Moreover, the organization



82 of infant visual cortex may not be detectable at the macroscopic level accessible to fMRI (Chap-  
83 man, Gödecke, and Bonhoeffer, 1999). That said, there is some reason for optimism: fMRI has  
84 revealed that infant visual cortex is functionally interconnected (Gao, Lin, Grewen, and Gilmore,  
85 2017), shows evoked responses to visual inputs (Ellis, Skalaban, Yates, Bejjanki, Córdova, and  
86 Turk-Browne, 2020a), and responds in a localized way to motion (Biagi, Crespi, Tosetti, and Mor-  
87 rone, 2015) and categories (Deen, Richardson, Dilks, Takahashi, Keil, Wald, Kanwisher, and Saxe,  
88 2017). Nonetheless, it is unknown whether infants have retinotopic maps, which has long been  
89 considered critical for grounding the study of infant vision (Braddick and Atkinson, 2011).

90 To perform retinotopic mapping, we used a new protocol that enables fMRI in awake and  
91 behaving infants (Ellis, Skalaban, Yates, Bejjanki, Córdova, and Turk-Browne, 2020a,b; Ellis,  
92 Skalaban, Yates, and Turk-Browne, 2020c). In individual infants from 5 to 23 months old, we  
93 sought to define ventral and dorsal V1, V2, and V3, dorsal V3A/B, and ventral V4. In an alternat-  
94 ing block design, we used meridian mapping (horizontal vs. vertical) to identify area boundaries  
95 between quarter-field (V1–V3) and half-field (V3A/B, V4) representations (Fox, Miezin, Allman,  
96 Van Essen, and Raichle, 1987; Schneider, Noll, and Cohen, 1993) and spatial frequency mapping  
97 (high vs. low) as a proxy for foveal and peripheral representations of eccentricity within these  
98 areas (Arcaro and Livingstone, 2017; Henriksson, Nurminen, Hyvärinen, and Vanni, 2008). We  
99 chose these stimuli because they are relatively more tolerant to inconsistent fixation than traveling  
100 wave (Engel, Rumelhart, Wandell, Lee, Glover, Chichilnisky, and Shadlen, 1994; Sereno, Dale,  
101 Reppas, Kwong, Belliveau, Brady, Rosen, and Tootell, 1995) or population receptive field (Du-  
102 moulin and Wandell, 2008) approaches (Wandell, Dumoulin, and Brewer, 2007). Namely, the

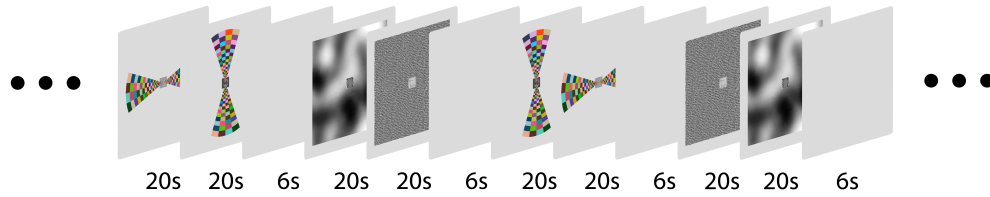


Figure 1: Experimental stimuli for retinotopic mapping. Participants viewed wide-field ( $40^\circ$  visual angle) meridian or spatial frequency stimuli on the ceiling of the scanner bore in an alternating block design. Each block contained two phases in a counterbalanced order: vertical and horizontal for meridian mapping, high and low for spatial frequency mapping. The two phases lasted 20 s each and appeared back-to-back with no break, followed by 6 s of rest. A small illustrated movie ( $1.5^\circ$ ) was played at center to encourage fixation.

103 desired stimulation was received wherever the infant fixated on the stimulus. These two measures  
104 of arealization provided independent, potentially divergent, measures of functional maturity in in-  
105 fant visual cortex. This allowed us to test whether arealization is present early in infancy, as well  
106 as how it develops over our age range.

## 107 Results

108 We showed 17 infants (5–23 months old) blocks of stimuli (Figure 1) for meridian mapping (Fox,  
109 Miezin, Allman, Van Essen, and Raichle, 1987; Schneider, Noll, and Cohen, 1993) and spatial  
110 frequency mapping (Arcaro and Livingstone, 2017; Henriksson, Nurminen, Hyvärinen, and Vanni,  
111 2008). In meridian mapping blocks, large horizontally and vertically oriented meridian bow ties  
112 were shown for 20 s each in a counterbalanced order. In spatial frequency mapping blocks, low  
113 and high spatial frequency Gaussian random fields were shown for 20 s each in a counterbalanced  
114 order. Throughout all blocks, an illustrated movie was shown at center to encourage fixation.  
115 Blocks were separated by 6 s of rest.

116 **Looking behavior** Gaze was manually coded from a video recording of the infant's face dur-  
117 ing the scan. In meridian mapping blocks, participants similarly looked at the horizontal meridian  
118 ( $M=0.92$ ) and vertical meridian ( $M=0.92$ ) for almost the entirety of the block (difference  $CI=[-0.02,$   
119  $0.02]$ ,  $p=0.866$ ). As expected, and motivating our use of task designs tolerant to eye movements,  
120 looking at the meridian did not necessarily mean fixating the movie at center. Infants often looked  
121 left or right of center on horizontal meridians (proportion  $M=0.41$ ) and above or below center on  
122 vertical meridians ( $M=0.30$ ). There was a trend toward more off-center looking for horizontal vs.  
123 vertical (difference  $CI=[0.000, 0.221]$ ,  $p=0.050$ ), which may reflect the ease of saccading in az-  
124 imuth compared to elevation (Aslin and Salapatek, 1975). In spatial frequency blocks, participants  
125 similarly looked at high spatial frequencies ( $M=0.90$ ) and low spatial frequencies ( $M=0.91$ ) for al-  
126 most the entirety of the block (difference  $CI=[-0.040, 0.014]$ ,  $p=0.310$ ). Infants infrequently looked  
127 off-center on high spatial frequencies ( $M=0.08$ ) and low spatial frequencies ( $M=0.05$ ). There was  
128 reliably more off-center looking for high vs. low (difference  $CI=[0.003, 0.070]$ ,  $p=0.033$ ), which  
129 may reflect a need to foveate high-frequency stimuli (given that the movie was shown at fixation).  
130 Overall, stimulation was uniform in the visual field the majority of the time, and the remaining  
131 time was still usable because of designs that ensured similar stimulation regardless of where the  
132 stimulus was fixated.

133 **Volumetric analyses** A general linear model (GLM) was used to estimate blood oxygenation  
134 level-dependent (BOLD) responses to the four stimulus conditions. As a sanity check, infant vi-  
135 sual cortex was robustly activated when collapsing across conditions (Figure 2a). Indeed, contrasts  
136 between horizontal and vertical meridians (Figure 2b) and between low and high spatial frequen-

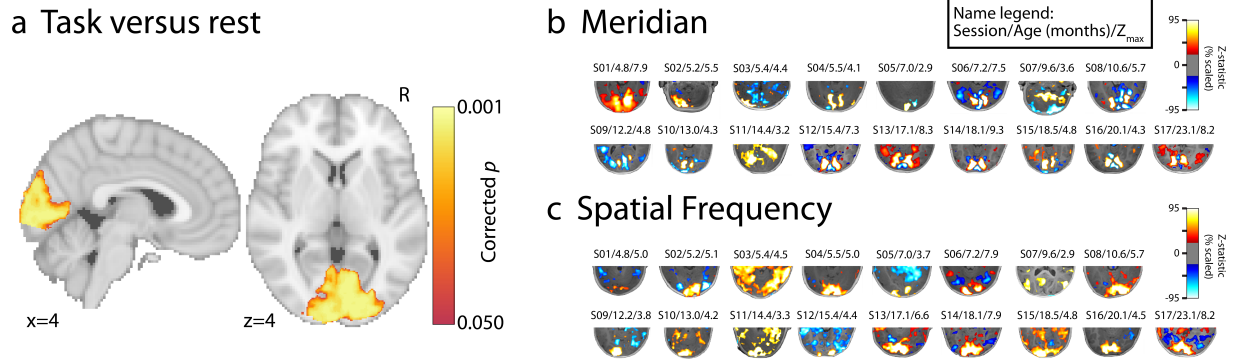


Figure 2: Statistical maps in volumetric space. (a) Significant voxels (TFCE corrected  $p < 0.05$ ) from an  $F$ -test across participants, demonstrating reliable evoked BOLD activity in standard space. (b) Contrast of horizontal greater than vertical meridians on each participant's anatomical image for the posterior portion of the brain. The minimum  $Z$ -statistic threshold is 1.96 and the maximum differs by participant, indicated by  $Z_{\max}$ . Participants are ordered youngest to oldest from top left to bottom right. The text above each volume indicates: session number/age in months/ $Z_{\max}$ . (c) Analogous contrast of high greater than low spatial frequency. Refer to Table S1 for details about the participants.

137 cies (Figure 2c) in each participant's volumetric space indicate strong differential responding to  
 138 the conditions.

139 **Evidence of arealization** To determine whether infants have retinotopic organization, we first  
 140 created surface reconstructions using iBEAT v2.0 (Li, Nie, Wang, Shi, Gilmore, Lin, and Shen,  
 141 2014; Li, Wang, Shi, Gilmore, Lin, and Shen, 2015; Li, Wang, Yap, Wang, Wu, Meng, Dong, Kim,  
 142 Shi, Rekik, et al., 2019; Wang, Li, Shi, Cao, Lian, Nie, Liu, Zhang, Li, Wu, et al., 2018) (Figure  
 143 S1). These surfaces were inflated and cut to make flatmaps. The contrast between horizontal and  
 144 vertical meridians was projected onto each participant's flatmap and used for tracing visual areas.  
 145 Areas were traced based on the alternations in sensitivity to horizontal and vertical meridians using  
 146 a suitable protocol for adults (Wandell, Dumoulin, and Brewer, 2007). For instance, the V1/V2

147 border was based on the peak in the vertical meridian representation on the gyral banks of the cal-  
148 carine and the V2/V3 border was based on the next peak in the horizontal meridian representation.  
149 Figure 3a shows this contrast for an example 5.5-month old participant. Overlaid on this surface  
150 are the manually traced areas demarcating low- and mid-level visual cortex. In this participant we  
151 traced V1, V2, and V3 in both hemispheres and in both ventral and dorsal cortex, as well as left  
152 dorsal V3A/B and bilateral ventral V4. Although there was variability across participants (Figure  
153 3b), differential sensitivity to horizontal and vertical meridians was clear enough to identify areas  
154 in 16 out of 17 infants (average of 6.6 out of 8 areas in each hemisphere).

155 To verify that there were gradients of selectivity to different meridians across the visual areas  
156 (Arcaro, McMains, Singer, and Kastner, 2009), we traced lines perpendicular to the area bound-  
157 aries, starting at the fundus of the calcarine sulcus and progressing anterior, and extracted the  
158 contrast values from points along those lines (dashed lines on Figure 3a). There were reliable  
159 oscillations in sensitivity to horizontal and vertical meridians across areas (Figure 3c). Although  
160 this analysis is not suitable for statistical analysis (the same data were used to trace the areas), it  
161 remains a useful analysis to quantify the amount of change across areas. The difference between  
162 the peaks for vertical and horizontal meridians was smaller in anterior compared to posterior areas,  
163 potentially reflecting the larger receptive fields and thus coarser retinotopic maps of these anterior  
164 areas. Furthermore, this analysis shows the consistency of these patterns across participants. In-  
165 deed, three participants under 6 months also showed this same pattern, providing evidence of early  
166 retinotopic organization.

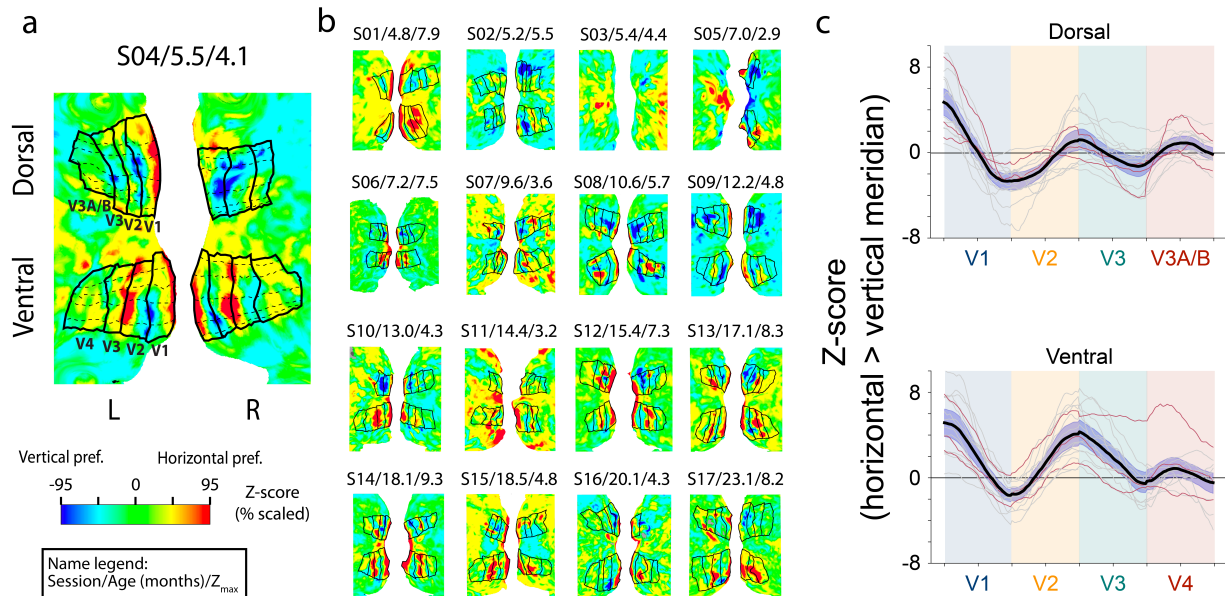


Figure 3: Arealization of infant visual cortex. (a) Example 5.5 month old participant with areas traced on the cortical surface. Labels shown for left V1, V2, V3, V3A/B and V4. Colors indicate the Z-statistic value for the contrast of horizontal greater than vertical meridian, scaled to the range of the 95th percentile of voxel Z-statistics in the occipital lobe (here, 4.1). Dashed lines drawn perpendicular to area boundaries were used to measure oscillations in sensitivity to horizontal and vertical meridians across areas. The text above each surface indicates: session number/age in months/Z<sub>max</sub>. (b) Statistical maps for all 16 other participants, ordered youngest to oldest from top left to bottom right. Refer to Table S1 for details about the participants. (c) Contrast values of horizontal greater than vertical meridian for points on lines drawn perpendicular to the area boundaries, separately for dorsal and ventral areas. The extracted values were interpolated to a normalized length across areas. The black line indicates the average of all participants, the gray lines indicate participants over 6 months, and the red lines indicate participants under 6 months. The purple shaded region around the black line is the 95% confidence interval across participants.

167 To evaluate the reliability of our manual tracings, we examined whether the resulting areas  
168 were more similar within versus between infants in the subset of four participants with two or three  
169 sessions. Participant surfaces were aligned to standard space and the similarity of the manually  
170 traced areas was computed between participants using the Dice coefficient. Similarity was higher  
171 within the same participant across sessions ( $M=0.47$ ) than between different participants yoked  
172 to have the same age difference ( $M=0.35$ ,  $CI=[0.08, 0.17]$ ,  $p<0.001$ ). In fact, when a participant  
173 was compared across sessions, they were often more similar to themselves than to almost any  
174 other participant (rank  $M=2.0$ ,  $p<0.001$ ). This was true for even the youngest participant with two  
175 sessions (S02 at 5.2 months and S05 at 7.0 months). Such reliability of the functional topographies  
176 is remarkable because the surfaces were based on anatomical scans from different ages that could  
177 vary in size and cortical folding.

178 **Spatial frequency tuning** We next examined sensitivity to eccentricity in infant visual cortex.  
179 Standard eccentricity mapping requires presenting stimuli at different distances from fixation. Be-  
180 cause we could not instruct or enforce fixation, such stimuli are not viable in infants. Instead, we  
181 used spatial frequency tuning as a proxy for eccentricity (Arcaro and Livingstone, 2017; Henriks-  
182 son, Nurminen, Hyvärinen, and Vanni, 2008; Tolhurst and Thompson, 1981): neurons sensitive to  
183 high spatial frequencies have small receptive fields that tend to process close eccentricities near  
184 the fovea and that are more prevalent in low-level visual areas; conversely, neurons sensitive to  
185 low spatial frequencies have larger receptive fields that tend to process farther eccentricities in the  
186 periphery and that are more prevalent in mid- and high-level visual areas. Thus, to assess voxel-  
187 wise sensitivity to eccentricity, we used a GLM to contrast BOLD activity for high vs. low spatial

188 frequency conditions. Figure 4a shows the spatial frequency map from a 5.5-month old participant.  
189 There is a gradient from the fovea within each area, as well as the gradient from low- to mid-level  
190 visual cortex. This pattern was observed across all participants with traced areas (Figure 4b).

191 To quantify the gradient in sensitivity to spatial frequency within areas, we traced lines with  
192 each area parallel to the area boundaries (dashed lines on Figure 4a). Importantly, these areas  
193 were drawn using the meridian mapping blocks, so the tracings were independent from the spatial  
194 frequency data. We measured the contrast of high greater than low spatial frequency along the  
195 lines, starting at the foveal boundary. Sensitivity to spatial frequency transitioned significantly  
196 from foveal (first quarter of the line) to peripheral (last quarter of the line) edges (Figure 4c),  
197 in dorsal and ventral V1 (CI=[3.18, 4.55],  $p<0.001$ ), V2 (CI=[2.53, 4.22],  $p<0.001$ ), and V3  
198 (CI=[0.96, 2.25],  $p<0.001$ ), but not V4 (CI=[-1.23, 0.05],  $p=0.081$ ) or V3A/B (CI=[-0.96, 0.61],  
199  $p=0.695$ ). This confirms a gradient in sensitivity to spatial frequency from the fovea to periphery  
200 in infant visual cortex, including in infants under 6 months. Indeed, the first vs. last quarter  
201 difference did not reliably correlate with age in V1 ( $r=0.00$ ,  $p=0.958$ ), V2 ( $r=0.04$ ,  $p=0.793$ ), V4  
202 ( $r=0.26$ ,  $p=0.258$ ), or V3A/B ( $r=0.18$ ,  $p=0.520$ ), although was stronger in older children in V3  
203 ( $r=0.52$ ,  $p=0.014$ ).

204 We also observed a gradient in sensitivity to spatial frequency across areas, with a greater  
205 overall response to high vs. low spatial frequency in V1 vs. V2 (CI=[0.82, 1.50],  $p<0.001$ ),  
206 V2 vs. V3 (CI=[1.21, 2.10],  $p<0.001$ ), ventral V3 vs. V4 (CI=[0.38, 1.51],  $p=0.001$ ), and dorsal  
207 V3 vs. V3A/B (CI=[0.52, 1.26],  $p<0.001$ ). This confirms differences in spatial frequency tuning



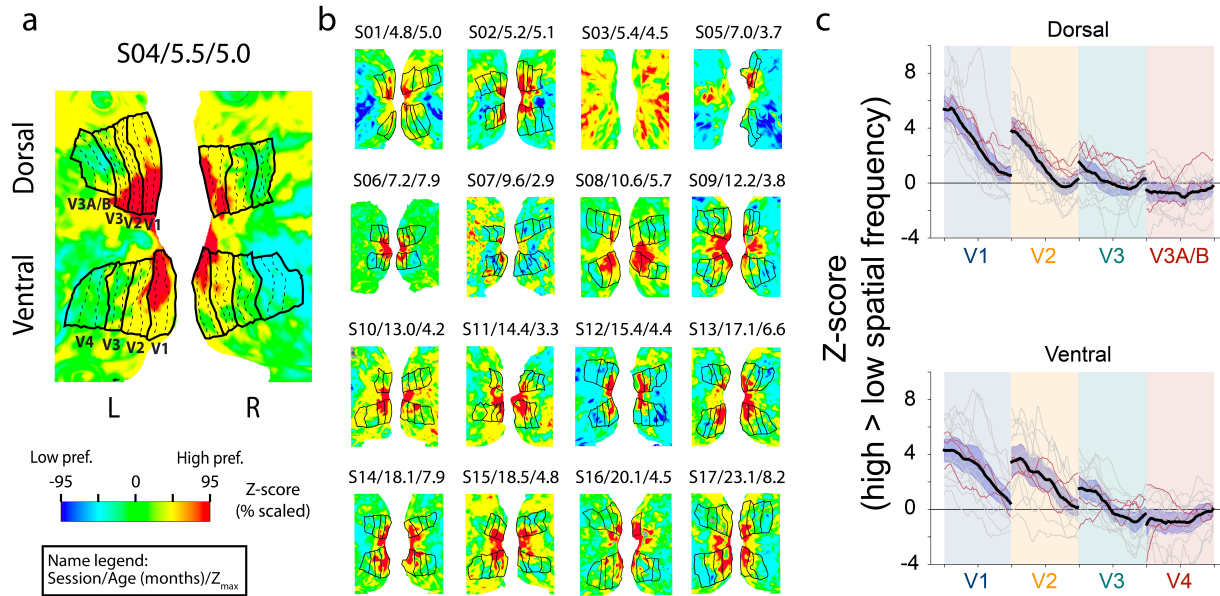


Figure 4: Spatial frequency tuning in infant visual cortex. (a) Example 5.5 month old participant with areas traced on the cortical surface. Colors indicate the Z-statistic value for the contrast of high greater than low spatial frequency, scaled to the range of the 95th percentile of voxel Z-statistics in the occipital lobe (here, 5.0). Dashed lines drawn parallel to area boundaries were used to measure gradients in sensitivity to high and low spatial frequencies across areas. The text above each surface indicates: session number/age in months/ $Z_{\max}$ . (b) Statistical maps for all 16 other participants, ordered youngest to oldest from top left to bottom right. Refer to Table S1 for details about the participants. (c) Contrast values of high greater than low spatial frequency for points on lines drawn parallel to the area boundaries, separately for dorsal and ventral areas. Each area is demarcated by a colored column. The foveal boundary of the area is on the left side of the column. The extracted values were interpolated to a normalized length across areas. The black line indicates the average of all participants, the gray lines indicate participants over 6 months, and the red lines indicate participants under 6 months. The purple shaded region around the black line is the 95% confidence interval across participants.

208 between low- and mid-level areas in infant visual cortex, as has been observed in the adult visual  
209 cortex (Henriksson, Nurminen, Hyvärinen, and Vanni, 2008). This same pattern was present in  
210 our participants under 6 months. In fact, the average difference between sensitivity to high vs.  
211 low spatial frequency did not reliably correlate with age in V1 ( $r=0.35$ ,  $p=0.162$ ), V2 ( $r=0.27$ ,  
212  $p=0.300$ ), V3 ( $r=-0.12$ ,  $p=0.571$ ) V3A/B ( $r=-0.39$ ,  $p=0.140$ ), or V4 ( $r=-0.13$ ,  $p=0.683$ ). These  
213 findings are consistent with the possibility that gradients of spatial frequency tuning within and  
214 across areas are largely stable across infancy.

215 **Area configuration and size** The results so far fit an early arealization hypothesis, in which area  
216 boundaries and spatial frequency tuning are established in infants as young as 5 months. However,  
217 this does not preclude the possibility of hierarchical maturation in other properties of these areas,  
218 including their configuration and size. To test for such age effects, we extended the Dice simi-  
219 larity analysis. Rather than compare maps within individual infants across repeat sessions, here  
220 we compare the manual tracings of areas V1–V4 in standard space across different infants (Figure  
221 5a). We first tested whether maps are more similar for participants of similar ages, which would  
222 lead to a negative correlation between age difference and Dice coefficient (closer in age = higher  
223 similarity). However, this relationship was not reliable and in fact was numerically in the wrong  
224 direction ( $r=0.11$ ,  $p=0.247$ ). We then tested another potential age effect in which older infants are  
225 more similar to each other than younger infants are to each other. This would lead to a positive  
226 correlation between the average age of the two infants whose maps are being compared and their  
227 Dice coefficient (older age = higher similarity). We excluded repeat sessions from this analysis  
228 because they occurred more often in older infants and yielded higher Dice coefficients, and thus

229 could bias the correlation. Across the remaining pairs of sessions between participants ( $N = 114$ ),  
230 we observed a robust positive correlation (Figure 5b;  $r=0.36$ ,  $p<0.001$ ). This correlation could be  
231 explained if we were better able to align older infants into standard space. However, the number of  
232 manually coded alignment errors (Thompson, Stein, Medland, Hibar, Vasquez, Renteria, Toro, Ja-  
233 hanshad, Schumann, Franke, et al., 2014) was not significantly correlated with age across sessions  
234 ( $r=-0.39$ ,  $p=0.185$ ). The alignment of visual gyri and sulci between each participant and standard  
235 space also was not significantly related to age across sessions ( $r=0.14$ ,  $p=0.609$ ).

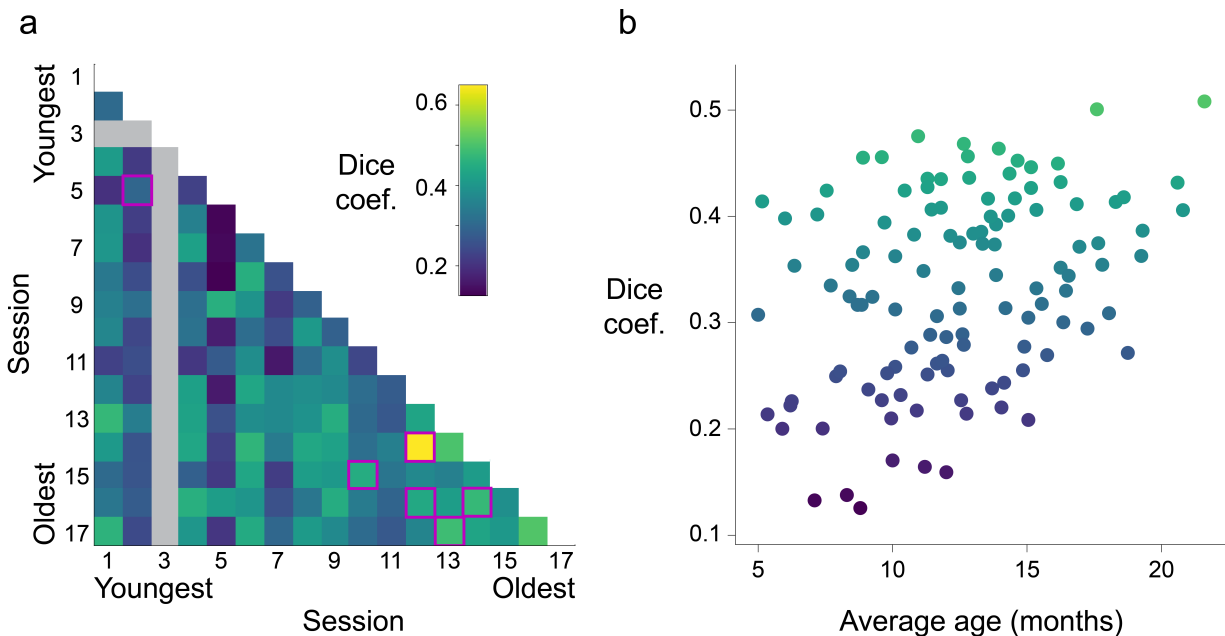


Figure 5: Overlap of retinotopic maps across infants. After alignment to standard space, the cortical locations of the manually traced visual areas were compared across pairs of sessions using the Dice coefficient. (a) Rows and columns are ordered from youngest to oldest, with each cell depicting a session pair. The purple boxes highlight repeat sessions from the same participants. The gray strip corresponds to a participant (S03) with no traced visual areas. (b) Correlation of Dice similarity with the average age (in months) of the infants in the two sessions being compared. Note that repeat sessions from the same infant are not visualized because they were excluded from the analysis to avoid biasing in favor of a correlation.

236 We interpret the increased similarity of older infants as reflecting convergence toward mature  
237 retinotopic organization. To evaluate this, we computed the Dice coefficient between the manual  
238 tracings of infant areas V1–V4 and a comprehensive atlas of adult visual areas in standard space  
239 (Wang, Mruczek, Arcaro, and Kastner, 2014). Overall, the similarity of infants to the standard  
240 adult atlas was high ( $M=0.39$ ). In fact, infants were more similar to this atlas than to other infants  
241 ( $M=0.33$ ,  $CI=[0.03, 0.08]$ ,  $p<0.001$ ). There was an overall age effect, with similarity to the adult  
242 atlas increasing as a function of infant age (Figure 6;  $r=0.41$ ,  $p=0.042$ ). This is qualified by the  
243 fact that similarity did not increase systematically within infants across repeat sessions. Indeed, the  
244 high similarity even for the youngest infants suggests that any maturation rests on a foundation of  
245 early, adult-like arealization. The high similarity is likely also an underestimate given differences  
246 in the visual extent of the stimuli between adults ( $30^\circ$  visual angle diameter) and infants ( $40^\circ$ ),  
247 and greater coverage of the fovea in the adult atlas. Moreover, different approaches to retinotopy  
248 were used for adults (traveling wave) and infants (meridian). The fact that the adult atlas still  
249 provided such a good guide to infant visual areas further helps validate the alignment of infant data  
250 to standard space, and suggests that such atlases could plausibly be used as a starting point for  
251 ROIs in future studies.

252 An alternative way to evaluate region maturation is to consider how the size of each area  
253 changes with age. The hierarchical maturation hypothesis would predict that low-level areas are  
254 mature in size by early infancy, at least relative to other areas, whereas the size of mid- and high-  
255 level areas would change over development. The most direct measure of size is surface area;  
256 however, this metric is imprecise near the foveal boundary because of the video we played at fix-

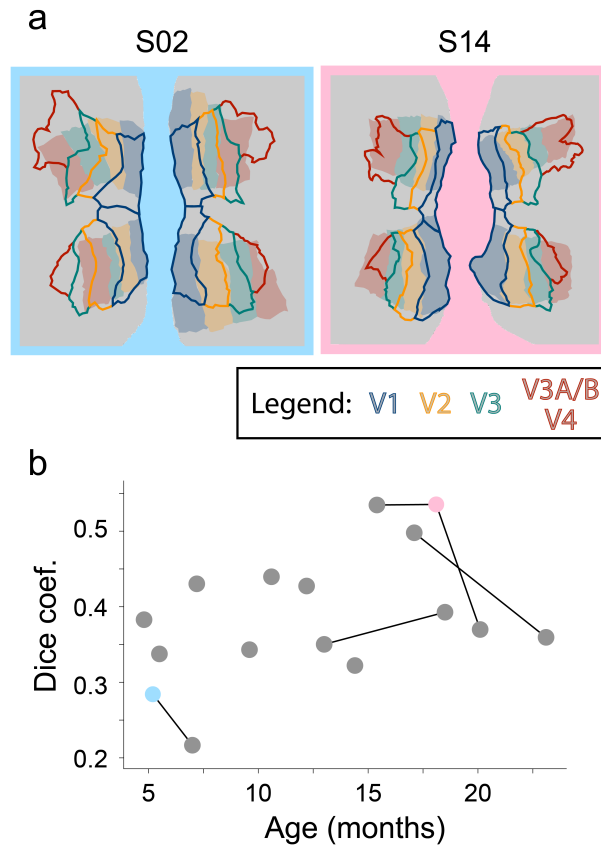


Figure 6: Overlap of infant visual areas with an adult atlas. Participants were aligned into standard space and compared to the relevant areas from an adult atlas (Wang, Mruczek, Arcaro, and Kastner, 2014). (a) Two example infants with their manually traced visual areas in shaded fill colors and the corresponding visual areas from the standard space atlas overlaid in color outlines. (b) Dice coefficient for each participant between visual areas from manual tracing in infants and standard atlas in adults. Lines connect the same participant across sessions. Cyan and pink dots correspond to participants S02 and S14, respectively.

257 ation. We therefore used the length between area boundaries (dashed lines in Figure 3a) as our  
258 measure of size (although obtained similar results for surface area; Figure S2). Figure 7 shows the  
259 relationships across the 16 participants with traceable areas. There was a significant relationship  
260 between size and age in V1 ( $r=0.78$ ,  $p<0.001$ ) and V2 ( $r=0.50$ ,  $p=0.013$ ), the relationship was  
261 marginal in V3 ( $r=0.54$ ,  $p=0.059$ ), and not significant in V3A/B ( $r=0.18$ ,  $p=0.517$ ) or V4 ( $r=0.23$ ,  
262  $p=0.398$ ). These changes in V1 and V2 size could reflect the global growth of the brain over age  
263 in our sample ( $r=0.80$ ,  $p<0.001$ ). However, the relationship between size and age persisted after  
264 controlling for global volume in V1 (partial  $r=0.57$ ,  $p=0.024$ ), though not V2 ( $r=0.29$ ,  $p=0.208$ )  
265 (Table S2). Hence, we see that only the earliest visual areas change in size across early develop-  
266 ment, counter to what would be expected from the perspective of hierarchical maturation of visual  
267 cortical areas.

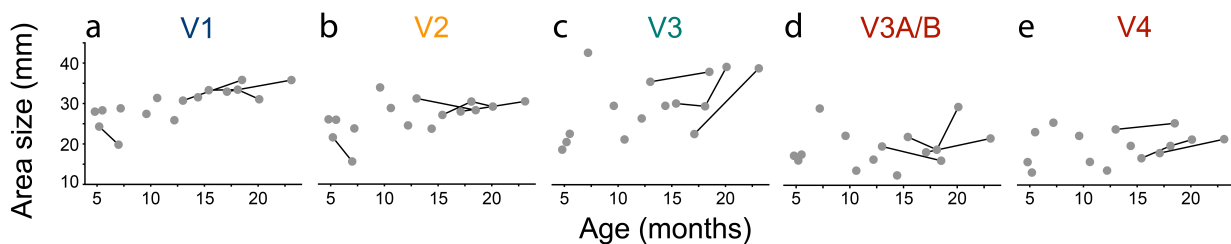


Figure 7: Relationship between the size of visual areas and infant age. Size is operationalized as the length between area boundaries averaged over hemispheres, summed over ventral and dorsal streams (for V1, V2, and V3). For a comparable analysis of surface area, see Figure S2. Lines are used to connect data from the same participant tested more than once across sessions. Raw data for each area are reported in Table S2.

## 268 **Discussion**

269 We investigated the presence of retinotopic organization in human infants as young as 5 months.  
270 We found evidence of visual areas V1–V4 even in our youngest participants and these areas were  
271 reliable within participant across sessions. Moreover, there was a gradient in sensitivity from  
272 high to low spatial frequency within visual areas as well as a gradient across areas in the hierar-  
273 chy, matching the topography of eccentricity and spatial frequency tuning in adults (Henriksson,  
274 Nurminen, Hyvärinen, and Vanni, 2008). Together, these results support the existence of a hier-  
275 archical, retinotopic organization across visual cortex early in development. Area boundaries and  
276 spatial frequency tuning did not consistently vary with age in our sample, although the size of  
277 V1 (but not the other areas) did increase with age controlling for global brain growth. The weak  
278 evidence for change in retinotopic organization over this age range suggests that the development  
279 of visual cortex from 5–23 months may reflect fine-tuning rather than reorganization.

280 We examined two properties of the visual system to evaluate the hierarchical maturation hy-  
281 pothesis that visual areas develop sequentially from low-, to mid-, to high-level areas (Bourne and  
282 Rosa, 2006; Condé, Lund, and Lewis, 1996; Distler, Bachevalier, Kennedy, Mishkin, and Unger-  
283 leider, 1996; Gomez, Natu, Jeska, Barnett, and Grill-Spector, 2018; Kiorpes, 2016; Zhang, Zheng,  
284 Watanabe, Maruko, Bi, Smith, and Chino, 2005). First, we examined the presence and develop-  
285 ment of visual areas by defining their boundaries with meridian mapping. Our evidence that visual  
286 areas exist even early in infancy is consistent with anatomical findings from non-human primates  
287 (Bourne and Rosa, 2006). However, functional confirmation of visual areas has not been previ-

288 ously reported in human infants. Even if these areas are established, the hierarchical maturation  
289 hypothesis might suggest that properties like area size would develop sequentially. Although we  
290 did observe age-related changes in the size of visual areas, they were strongest in low-level areas  
291 (V1 and V2), contrary to what this hypothesis would predict. Second, we tested for gradients in  
292 spatial frequency tuning within and across areas with spatial frequency mapping. Gradients in  
293 preference from high to low spatial frequencies are thought to reflect changes in receptive field  
294 size from smaller to larger, respectively (Arcaro and Livingstone, 2017; Henriksson, Nurminen,  
295 Hyvärinen, and Vanni, 2008). Mirroring changes that occur with eccentricity, there were spatial  
296 frequency gradients from the fovea to the periphery within visual areas and overall from low- to  
297 mid-level visual areas. There was reason to believe that gradients might develop at these levels  
298 of the hierarchy in infancy, given that the receptive field properties of high-level areas change  
299 later in childhood (Gomez, Natu, Jeska, Barnett, and Grill-Spector, 2018). However, we observed  
300 gradients in low- and mid-level areas even in our youngest participants, and the strength of these  
301 gradients was not reliably related to age.

302         Considering the two lines of evidence together, our results are consistent with an early are-  
303 alization account where arealization is present and stable in infancy for low- and mid-level visual  
304 cortex. Critically, hierarchical maturation of the visual system could be occurring in human de-  
305 velopment but outside of the age range tested here, either earlier in neonates/fetuses or later in  
306 toddlers or children. Additionally, more research is needed to explore how other components of vi-  
307 sual cortical function develop in infancy in these areas. Even so, our results suggest that important  
308 architectural features of the visual system are established early in development. One consequence



309 is that gradients in receptive field size may be available to scaffold the development of functionally  
310 selective high-level visual cortex (Arcaro, Schade, Vincent, Ponce, and Livingstone, 2017; Gomez,  
311 Barnett, and Grill-Spector, 2019; Hasson, Levy, Behrmann, Hendler, and Malach, 2002). In par-  
312 ticular, this architecture may enable high-level visual cortex to develop stereotyped localization of  
313 category-selective cortex (e.g., faces require high precision near fovea, buildings require precision  
314 in the periphery; (Hasson, Levy, Behrmann, Hendler, and Malach, 2002)). Our results also sug-  
315 gest that substantial changes in visual processing during infancy (Baker, Norcia, and Candy, 2011;  
316 Kovacs, Kozma, Feher, and Benedek, 1999; Lewis and Maurer, 2005; Patel, Maurer, and Lewis,  
317 2010; Siu and Murphy, 2018) do not hinge on the emergence of retinotopic organization in low-  
318 or mid-level visual cortex. One possibility is that improvements in visual processing over infancy  
319 and childhood could relate to improvements in downstream regions responsible for the read-out  
320 of initial visual cortical processing, like high-level visual, association, or frontal cortices (Kiorpes  
321 and Movshon, 2014).

322 The protocol we developed for drawing areas was modeled on adult retinotopy (Arcaro,  
323 McMains, Singer, and Kastner, 2009), which has been extensively validated with animal models  
324 (Wandell, Dumoulin, and Brewer, 2007). A potential limitation of our study is that these compar-  
325 isons may not be appropriate for human infants. For instance, tracing human V4 is notoriously  
326 difficult, in part because of the venous eclipse (Winawer, Horiguchi, Sayres, Amano, and Wandell,  
327 2010) and in part because it is hard to distinguish the anterior border of V4 from surrounding ar-  
328 eas like VO1. These challenges may be exacerbated in infants, for example, because their areas  
329 are smaller and their scans are poorer quality. On the other hand, area boundaries in infant visual

330 cortex, even if imprecise, were reliable within and between participants in our sample.

331 We used a block-design approach that is uncommon in adult retinotopy. Meridian mapping  
332 designs like ours have drawbacks (Wandell, Dumoulin, and Brewer, 2007), such as limited cov-  
333 erage of the visual field and potentially mislabeling voxels that are only partially responsive to a  
334 stimulus. However, our goal was to demarcate visual areas (Kastner, De Weerd, and Ungerlei-  
335 der, 2000; Schneider, Noll, and Cohen, 1993; Shipp, Watson, Frackowiak, and Zeri, 1995; Tootell,  
336 Reppas, Kwong, Malach, Born, Brady, Rosen, and Belliveau, 1995), rather than estimate the se-  
337 lectivity of individual voxels (cf. population receptive fields; (Dumoulin and Wandell, 2008)), so  
338 these drawbacks are less pertinent. Indeed, the block design we used is relatively robust because it  
339 can survive the exclusion of a small number of individual time-points if the participant looks away  
340 or moves their head excessively. This is a key advantage for infant fMRI, in which data loss is ex-  
341 pected within blocks. More critically, the traditional traveling wave approach (Engel, Rumelhart,  
342 Wandell, Lee, Glover, Chichilnisky, and Shadlen, 1994) requires central fixation throughout each  
343 block. In our experience, this is impractical in human infants. Fixation cannot be instructed or  
344 enforced, and they look away from center approximately one third of the time, even with a movie  
345 at fixation. That said, if a traveling wave approach could somehow be adapted to these constraints,  
346 this might enable tracing of high-level visual areas (Arcaro, McMains, Singer, and Kastner, 2009)  
347 that cannot be resolved with meridian mapping (Kastner, De Weerd, and Ungerleider, 2000; Shipp,  
348 Watson, Frackowiak, and Zeri, 1995; Tootell, Reppas, Kwong, Malach, Born, Brady, Rosen, and  
349 Belliveau, 1995).

350 In sum, we found robust evidence for retinotopic organization in awake behaving human  
351 infants, ranging in age from 5 to 23 months old. We identified four areas in both ventral and  
352 dorsal streams, spanning low- and mid-level visual cortex, and these areas were reliable across  
353 sessions. The receptive field properties within and across the areas mirrored what has been ob-  
354 served in adults. We found limited evidence of developmental change in retinotopic organization,  
355 other than the size of low-level areas. Together, these results suggest that the early infant visual  
356 system has the basic cortical architecture needed for low- and mid-level visual processing. These  
357 results also provide a foundation for understanding infant visual abilities, such as acuity, contrast  
358 sensitivity, and contour integration, as well as the neural basis of infant visual dysfunction in disor-  
359 ders such as amblyopia (Braddick and Atkinson, 2011). More broadly, retinotopy gave credibility  
360 to fMRI research during its earliest days by validating that architectural features of visual cortex  
361 first identified in animals could be measured in human BOLD (Engel, Rumelhart, Wandell, Lee,  
362 Glover, Chichilnisky, and Shadlen, 1994; Schneider, Noll, and Cohen, 1993; Sereno, Dale, Rep-  
363 pas, Kwong, Belliveau, Brady, Rosen, and Tootell, 1995). Likewise, the current study shows the  
364 promise of fMRI with awake behaving infants to reveal the function of the infant brain and to track  
365 changes across early postnatal development.

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374 **Author Contributions** C.T.E., M.J.A., & N.B.T-B. initially created the experiment design. C.T.E., L.J.S.,  
375 V.R.B., & N.B.T-B. did early piloting. C.T.E., T.S.Y., & N.B.T-B. collected the data. C.T.E. & T.S.Y.  
376 preprocessed the data. C.T.E. & M.J.A performed the analyses. All authors contributed to the drafting of  
377 the manuscript.

378 **Declaration of Interests** The authors declare no competing interests.

## 379 **Methods**

380 **Participants** Data from 17 sessions with infants aged 4.8 to 23.1 months ( $M=12.2$ ,  $SD=5.7$ ; 13  
381 females) met our inclusion criteria of at least one usable phase per condition. The planned sample  
382 size was to have two participants in each three-month window between 3 and 24 months. We  
383 met this criteria, except we only had one participant between 21 and 24 months. This sample  
384 size is larger than previous developmental studies of retinotopy (Conner, Sharma, Lemieux, and  
385 Mendola, 2004). Not included in the sample are data from 15 sessions with enough blocks prior to  
386 exclusions for head motion and eye gaze, or from four sessions without enough blocks even prior  
387 to exclusions. The final sample included 12 unique participants, three participants who provided  
388 two sessions of usable data, and one participant who provided three sessions. These sessions  
389 occurred at least one month apart (range=1.8–6.0) and so the data from these sessions were treated  
390 separately, similar to prior work (Deen, Richardson, Dilks, Takahashi, Keil, Wald, Kanwisher, and  
391 Saxe, 2017). Refer to Table S1 for information on each participant. Data was collected at the  
392 Brain Imaging Center (BIC) at Yale University. Parents provided informed consent on behalf of  
393 their child. The study was approved by the Human Subjects Committee at Yale University.

394 **Data acquisition** Data were acquired with a Siemens Prisma (3T) MRI with the bottom of the  
395 20-channel Siemens head coil. Anatomical images were acquired with a T1-weighted PETRA  
396 sequence ( $TR_1=3.32ms$ ,  $TR_2=2250ms$ ,  $TE=0.07ms$ , flip angle= $6^\circ$ , matrix=320x320, slices=320,  
397 resolution=0.94mm iso, radial slices=30000). For three of our younger, compliant participants,  
398 we also collected a T2-weighted SPACE sequence ( $TR=3200ms$ ,  $TE=563ms$ , flip angle= $120^\circ$ ,

399 matrix=192x192, slices=176, resolution=1mm isotropic), and these were supplied to iBEAT to  
400 support surface reconstruction. Functional images were acquired with a whole-brain T2\* gradient-  
401 echo EPI sequence (TR=2s, TE=30ms, flip angle=71°, matrix=64x64, slices=34, resolution=3mm  
402 iso, interleaved slice acquisition).

403 **Data and code availability** The code for running the retinotopy task can be found at: [https:](https://github.com/ntblab/experiment_menu/tree/retinotopy/)  
404 [//github.com/ntblab/experiment\\_menu/tree/retinotopy/](https://github.com/ntblab/experiment_menu/tree/retinotopy/). The code for per-  
405 forming the analyses can be found at: [https://github.com/ntblab/infant\\_neuropipe/](https://github.com/ntblab/infant_neuropipe/tree/Retinotopy/)  
406 [tree/Retinotopy/](https://github.com/ntblab/infant_neuropipe/tree/Retinotopy/). The data, including anonymized anatomical images, surface reconstruc-  
407 tions, manually traced areas, and both raw and preprocessed functional images can be found at: (to  
408 be shared on Dryad when published).

409 **Procedures** There are many challenges when conducting fMRI research with awake infants. We  
410 have described and validated our approach in a separate methods paper (Ellis, Skalaban, Yates,  
411 Bejjanki, Córdova, and Turk-Browne, 2020a). In brief, families visited the lab before their first  
412 scanning session for an orientation session. The aim of this was to acclimate the infant and parent to  
413 the scanning environment. Scanning sessions were scheduled for a time when the parents thought  
414 that the infant would be calm. The infant and parent were extensively screened for any metal on  
415 or in their body. Hearing protection for the infant consisted of three layers: silicon inner ear putty,  
416 over-ear adhesive covers, and ear muffs. The infant was positioned on the scanner bed, on top of  
417 a vacuum pillow that reduced movement. The top half of the head coil was not used because the  
418 bottom elements provided sufficient coverage of the smaller infant head. This allowed for sufficient

419 visibility to monitor the infant's comfort and allowed us to project stimuli onto the ceiling of the  
420 bore directly above the infant's face using a custom mirror system. A video camera (MRC high-  
421 resolution camera) allowed us to record the infant's face during scanning for monitoring and offline  
422 eye gaze coding.

423       When the infant was focused, stimuli were shown in MATLAB using Psychtoolbox ([http:](http://psychtoolbox.org)  
424 [//psychtoolbox.org](http://psychtoolbox.org)), against a gray background. For the meridian mapping blocks, a bow  
425 tie cut-out of a pastel-colored checkerboard was presented in either a vertical or horizontal ori-  
426 entation (Tootell, Reppas, Kwong, Malach, Born, Brady, Rosen, and Belliveau, 1995). The arcs  
427 of the bow ties were  $45^\circ$  and their diameter spanned 40 visual degrees. The checkerboard spac-  
428 ing increased logarithmically out from the fovea, approximating the cortical magnification factor  
429 (Tootell, Reppas, Kwong, Malach, Born, Brady, Rosen, and Belliveau, 1995). The color of the  
430 checkerboard alternated every 125ms between the original color pattern and its negative. For the  
431 spatial frequency mapping blocks, the stimuli were grayscale Gaussian random fields of high (1.5  
432 cycles per visual degree) or low (0.05 cycles per visual degree) spatial frequency (Arcaro and Liv-  
433 ington, 2017). The difference between these spatial frequencies should be detectable to 3-month  
434 old infants (Banks, Stephens, and Hartmann, 1985), although spatial frequency discrimination de-  
435 velops into adolescence (Patel, Maurer, and Lewis, 2010; van den Boomen and Peters, 2017).  
436 These patterns were shown as squares spanning  $40^\circ$  on each edge. There were five images for each  
437 spatial frequency, one of which was shown every 500 ms. Meridian and spatial frequency blocks  
438 contained two phases of stimulation. The first phase consisted of one of the conditions (e.g., hori-  
439 zontal or high) for 20s, followed immediately by the second phase with the other condition of the

440 same block type (e.g., vertical or low, respectively) for 20s. The order of conditions was counter-  
441 balanced across blocks. At the end of each block there was at least 6s rest before the start of the  
442 next block. Participants alternated between blocks of the spatial frequency and meridian mapping  
443 tasks, with the goal of acquiring 8 blocks total.

444 To facilitate attention to the center of the stimulus, a movie was played in a small window  
445 (1.5° in diameter) at that location. For spatial frequency blocks this was overlaid on top of the  
446 stimulus, for meridian mapping blocks the bow tie was overlaid on the movie. The movie showed  
447 grayscale shapes moving in unpredictable patterns, including jittering, looming, and smooth mo-  
448 tion. The movie was saturated in order to minimize the amount of high contrast changes.

449 **Gaze coding** Infant gaze was coded offline by two or three coders ( $M=2.12$ ) blind to condition.  
450 The coders determined whether the eyes were oriented left, right, up, down, center, off-screen (i.e.,  
451 blinking or looking away), or were undetected (i.e., out of the camera's field of view). Codes for  
452 the directional gazes (i.e., left, right, up, and down) were only applied if the coder believed the  
453 infants were still looking at the screen. For instance, if the participant was looking left but off the  
454 screen then that frame was coded as off-screen. For the spatial frequency blocks, the gaze was  
455 considered acceptable if it was coded as center or any of the four directions. For the meridian  
456 mapping blocks, gaze directions perpendicular to the bow tie orientation were treated as equivalent  
457 to off-screen in preprocessing. For example, if the infant was viewing a horizontal bow tie, looking  
458 to the left, center, or right was considered acceptable.

459 The frame rate and resolution varied across participants, but the minimum rate was 16Hz and



460 we always had sufficient resolution to identify the eye. The label for each frame was determined as  
461 the mode of a moving window of five frames centered on that frame across all coder reports. In case  
462 of a tie, we used modal response from the previous frame. The coders were highly reliable: when  
463 coding the same frame, coders reported the same response on 79% (range across participants=71–  
464 86%) of frames. Phases were excluded if the participant was coded as looking away from the  
465 stimulus for more than 25% of the time, computed separately for the two phases within each block.  
466 This was a stricter criterion than our other infant fMRI studies (Ellis, Skalaban, Yates, Bejjanki,  
467 Córdova, and Turk-Browne, 2020a,b; Ellis, Skalaban, Yates, and Turk-Browne, 2020c) because of  
468 the importance of eye position for retinotopy. Across all included phases, participants looked at  
469 the stimulus 91% of the time on average (range across participants=87–95%).

470 To determine whether there were differences in the looking behavior across the conditions,  
471 we computed each participant's average proportion of looking time for every manual code that  
472 was allowable in that phase (e.g., left, center, or right for horizontal meridian). We quantified  
473 the difference in mean looking for horizontal and vertical conditions using bootstrap resampling.  
474 We also compared the mean looking time away from center per condition (e.g., left or right for  
475 horizontal meridian) with bootstrap resampling.

476 **Preprocessing** Individual runs were preprocessed using FEAT in FSL ([https://fsl.fmrib.](https://fsl.fmrib.ox.ac.uk/fsl)  
477 [ox.ac.uk/fsl](https://fsl.fmrib.ox.ac.uk/fsl)), with optimizations for infant fMRI data. We discarded three volumes from  
478 the beginning of each run, along with the volumes automatically discarded by the EPI sequence.  
479 Blocks were stripped of any excess burn-in or burn-out volumes beyond the 3 TRs (6s) that were

480 planned. Some runs contained other experiments not discussed here (N=15 sessions). In such  
481 cases, pseudo runs were created containing only the data of interest. Blocks were sometimes sep-  
482 arated by long pauses (>30s) within a session because of a break, an anatomical scan, or an inter-  
483 vening experiment (N=5;  $M=556.5$ s break; range=107.9–1183.4s). We used the ‘centroid’ volume  
484 (i.e., with the minimal Euclidean distance from all other volumes) for alignment and motion cor-  
485 rection. Slice-time correction was applied to realign the slices in each volume. Time-points were  
486 excluded if the head motion between time-points exceeded 3mm (average in blocks with at least  
487 one usable phase:  $M=1.9\%$ , range=0.0–7.0%), and phases were excluded if more than 50% of TRs  
488 exceeded this threshold. We interpolated rather than removed these time-points in order to avoid  
489 biasing the linear detrending (in later analyses these time-points were removed). To make the mask  
490 of brain voxels, we thresholded the signal-to-fluctuating-noise ratio (SFNR) of each voxel in the  
491 centroid volume at the trough in the histogram of values. The data were smoothed with a Gaussian  
492 kernel (5mm FWHM) and linearly detrended. AFNI’s despiking algorithm attenuated aberrant  
493 time-points within voxels. To account for differences across runs in intensity and variance, the  
494 blocks that were considered usable were normalized over time using Z-scoring, prior to the runs  
495 being concatenated for further analyses. For further explanation and justification of this prepro-  
496 cessing procedure, please refer to (Ellis, Skalaban, Yates, Bejjanki, Córdova, and Turk-Browne,  
497 2020a).

498 Participants were excluded if they did not have at least 1 usable phase from each of the four  
499 conditions. After these criteria were applied, participants (coincidentally) had a similar number  
500 of phases of each condition on average: 3.53 (SD=1.33, range: 1–6) high spatial frequency, 3.47

501 (SD=1.72, range: 1–6) low spatial frequency, 3.47 (SD=1.46, range: 1–6) horizontal meridian, and  
502 3.47 (SD=1.46, range: 1–6) vertical meridian.

503 Each run's centroid volume was registered to the infant's anatomical scan from the same  
504 session. FLIRT with a normalized mutual information cost function was used for initial alignment.  
505 Additional manual registration was performed using mrAlign from mrTools (Gardner lab) to fix  
506 deficiencies of automatic registration. The preprocessed functional data were aligned into anatomical  
507 space with their original spatial resolution (3mm iso). This aligned data were mapped on to  
508 surface space, as described below. Whole-brain voxelwise analyses required further alignment of  
509 functional data into a standard space. For alignment to standard, the anatomical scan from each  
510 participant was automatically (FLIRT) and manually (Freeview) aligned to an age-specific MNI  
511 infant template (Fonov, Evans, Botteron, Almli, McKinstry, and Collins, 2011) and then aligned to  
512 the adult MNI template (MNI152). The functional data were transformed into standard space for  
513 the task vs. rest contrast. To determine which voxels to consider at the group level, the intersection  
514 of brain voxels from all infant participants in standard space was used as a whole-brain mask.

515 For surface reconstruction, we used iBEAT v2.0 to acquire the surfaces (Li, Nie, Wang, Shi,  
516 Gilmore, Lin, and Shen, 2014; Li, Wang, Shi, Gilmore, Lin, and Shen, 2015; Li, Wang, Yap,  
517 Wang, Wu, Meng, Dong, Kim, Shi, Rekik, et al., 2019; Wang, Li, Shi, Cao, Lian, Nie, Liu, Zhang,  
518 Li, Wu, et al., 2018). The output of the iBEAT pipeline is the inner and outer surfaces, as well  
519 as the volumetric segmentation of gray-matter and white-matter. Figure S1 shows the surface re-  
520 constructions overlaid on a slice of the anatomical data for each participant. These were then

521 inserted into a FreeSurfer-style pipeline (a walkthrough is provided in the codebase). As part of  
522 the pipeline, these surfaces were inflated into spheres and aligned to the Buckner40 template (Dale,  
523 Fischl, and Sereno, 1999). To investigate the quality of the surfaces and the alignment to standard  
524 space, we used the ENIGMA consortium quality control procedure (Thompson, Stein, Medland,  
525 Hibar, Vasquez, Renteria, Toro, Jahanshad, Schumann, Franke, et al., 2014), in which we evalu-  
526 ated defects in the projection of the Desikan-Killany atlas onto the individual data. In particular,  
527 we quantified how many errors there were in each hemisphere for the following regions (atlas  
528 labels) that are known to be prone to poor segmentation: bankssts, precentral, postcentral, peri-  
529 calcarine, parahippocampal, entorhinal, rostralanteriorcingulate, insula. The infant data showed  
530 typical amounts of errors compared to what is reported for adult data. The data were then resam-  
531 pled in SUMA, using an icosahedral shape, into standard space with a constant number of nodes  
532 (Argall, Saad, and Beauchamp, 2006). To generate flatmaps, a convexity map (based on the po-  
533 sition of gyri and sulci) was computed using AFNI (Cox, 1996) and inflated brains were cut and  
534 flattened using the FreeSurfer procedure. Once flattened, statistics maps were projected on to the  
535 surface for evaluation.

536 **GLM analysis** For the main analyses, a GLM was fit to the BOLD activity in each voxel using  
537 FEAT in FSL. Two separate GLMs were performed, one containing the horizontal and vertical  
538 meridian regressors, and the other containing the high and low spatial frequency regressors. Each  
539 regressor modeled phases with a boxcar lasting 20s, convolved with a double-gamma hemody-  
540 namic response function. The six translation and rotation parameters from motion correction were  
541 included in the GLM as nuisance regressors. TRs that were excluded (i.e., had translational mo-

542 tion greater than 3mm) were scrubbed by including an additional regressor for each to-be-excluded  
543 time-point (Siegel, Power, Dubis, Vogel, Church, Schlaggar, and Petersen, 2014). The condition  
544 regressors were then contrasted to find the differential evoked response. The voxelwise  $Z$ -statistic  
545 volumes for these contrasts were extracted for each participant. For visualization purposes, we  
546 set the maximum value of these maps to be the 95th percentile of the  $Z$ -statistic value for each  
547 participant in a large, anatomically defined occipital mask.

548 To test for visual-evoked activity, an  $F$ -test was performed in FSL using each phase type  
549 (i.e., horizontal and vertical meridians, high and low spatial frequencies) as regressors in a GLM to  
550 identify which voxels respond to any visual stimulation. As a conservative test to evaluate where  
551 the brain was most activated across participants, we  $Z$ -scored the resulting  $F$ -values within each  
552 participant. Hence, any mean differences in  $F$ -values across participants are mitigated. Instead,  
553 what matters is whether the  $F$ -values are high, relative to other voxels in that participant, in the  
554 same voxels across participants. The resulting statistic map was volumetrically aligned to standard  
555 space and then merged across all participants. We used threshold free cluster enhancement through  
556 the randomise function in FSL, resulting in voxel clusters  $p < .05$  corrected.

557 **Visual area and gradient tracing** The contrast maps for horizontal greater than vertical were  
558 transformed onto the flat surface map and used for tracing (Argall, Saad, and Beauchamp, 2006).  
559 Traditional tracing guidelines for adult humans were followed (Wandell, Dumoulin, and Brewer,  
560 2007). The areas traced were ventral V1, V2, V3 (also known as VP), and V4 (also known as  
561 hV4), and dorsal V1, V2, V3 and V3A/B. The border between V1 and V2 was defined by the peak

562 in the vertical meridian, the border between V2 and V3 was defined by the peak in the horizontal  
563 meridian, the border between V3 and ventral V4 or dorsal V3A/B was defined by the peak in the  
564 vertical meridian, and the terminal border of ventral V4 and dorsal V3A/B was defined by the peak  
565 of the vertical meridian after a half cycle. It is typical to trace only these areas using a merid-  
566 ian mapping paradigm (Kastner, De Weerd, and Ungerleider, 2000; Shipp, Watson, Frackowiak,  
567 and Zeri, 1995; Tootell, Reppas, Kwong, Malach, Born, Brady, Rosen, and Belliveau, 1995), as  
568 well as early traveling wave studies (Serenio, Dale, Reppas, Kwong, Belliveau, Brady, Rosen, and  
569 Tootell, 1995). This procedure is likely to lead to imprecision between the V4 boundary and the  
570 VO1 boundary, and did not provide sufficient resolution to demarcate V3A and V3B. When the  
571 distinctions between areas were not clear, the maximum range of the colormap was varied. If this  
572 did not resolve the ambiguity then the evoked response to just the vertical meridian (rather than the  
573 contrast between horizontal and vertical) was checked. If these additional steps did not clarify the  
574 boundary between areas, the area was not drawn. The peripheral extent of the area was estimated  
575 by the horizontal greater than vertical contrast and the *F*-test for each participant. Because of the  
576 movie shown at fixation, the foveal response was expected to be contaminated, hence the areas  
577 were not traced to the foveal confluence. To test how the foveal confluence varied with age, we  
578 also traced the areas that bridged between the ventral and dorsal areas of V1, V2, and V3 for each  
579 hemisphere.

580 To quantify alternations in sensitivity to horizontal vs. vertical meridians across visual areas  
581 (Figure 3c), we traced additional lines of interest in the visual cortex using SUMA (Figure 3a;  
582 (Arcaro, McMains, Singer, and Kastner, 2009)). These lines were drawn perpendicular to the area

583 boundaries, posterior to anterior, for areas that were traced. Five lines, spaced equally along the  
584 width of the areas, were drawn for each hemisphere and the dorsal and ventral areas. These lines  
585 were drawn using only the areal boundaries for guidance, making the coder unaware of the local  
586 intensity changes within areas. Nodes in surface space on those lines were indexed for their values  
587 of the horizontal greater than vertical meridian contrast. The number of nodes along each line  
588 varied between areas and participants. In order to standardize the size of these lines for the sake of  
589 comparison, we interpolated the values along each line to contain 50 values within each area (up  
590 to 200 total).

591 The gradients in sensitivity from high to low spatial frequency (Figure 4c) were quantified by  
592 tracing lines within each area, parallel to the areal boundaries (Figure 4a). Two lines were traced  
593 from the foveal to the peripheral boundary of each area and were used to index the values of the  
594 high greater than low spatial frequency contrast. The indexed values along these lines were also  
595 interpolated to include 50 values.

596 To statistically test the gradients in sensitivity from high to low spatial frequency within area,  
597 we divided the lines running parallel to the area boundary into quartiles, with the first quartile con-  
598 taining the section of the line closest to the foveal confluence. The contrasts for ventral and dorsal  
599 areas were averaged for lines in V1, V2, and V3. We averaged the contrast of high greater than  
600 low spatial frequency for the first quartile and compared it to the fourth quartile using bootstrap  
601 resampling (Efron and Tibshirani, 1986). Namely, we sampled, with replacement, the difference  
602 in contrast values from all participants 10,000 times, averaging across participants on each itera-

603 tion to generate a sampling distribution. Confidence intervals reflect the 2.5 and 97.5 percentiles  
604 of this distribution. For null hypothesis testing, we calculated the  $p$ -value as the proportion of  
605 samples whose mean was in the opposite direction from the true effect, doubled to make the test  
606 two-tailed. To test whether the difference in contrast between quartiles varied with age, we used  
607 bootstrap resampling of the correlation, randomly sampling bivariate data from 17 participants  
608 with replacement and calculating the Pearson correlation on each of 10,000 iterations. We calcu-  
609 lated the  $p$ -value as the proportion of samples resulting in a correlation with the opposite sign from  
610 the true correlation, doubled to make the test two-tailed.

611 To statistically test the gradient of spatial frequency tuning across (rather than within) areas,  
612 we averaged the contrast values along the whole lines and compared adjacent areas (i.e., V1 vs. V2,  
613 V2 vs. V3, etc.) using bootstrap resampling. Areas were averaged across dorsal and ventral, except  
614 when comparing ventral V3 with V4 and dorsal V3 with V3A/B. We used bootstrap resampling of  
615 the correlation to test the relationship between age and the averaged contrast within area.

616 **Comparing visual areas** The consistency of the traced visual areas across participants was quan-  
617 tified using the Dice coefficient (Dice, 1945). This was computed by finding every node in the  
618 surface that was labeled as belonging to a visual area and comparing whether those nodes had the  
619 same label across participants. The Dice coefficient is a fraction where the number of matching  
620 nodes, multiplied by 2, is the numerator, and the total number of nodes with a label in either partic-  
621 ipant is the denominator. For a given pair of sessions, the Dice coefficient was quantified for each  
622 hemisphere separately and averaged. Only areas that were traced in both participants were consid-



623 ered. This means the denominator of the Dice coefficient is not inflated by labels that could not  
624 possibly match between participants. The Dice coefficient was calculated for all pairwise compar-  
625 isons between sessions. Comparisons of the same participant across multiple sessions are used to  
626 determine whether there is greater reliability over time within vs. between participants. To approx-  
627 imately match the ages of the participants being compared, we started with one of the participants  
628 with repeat sessions and calculated the age differential; we then found another participant with the  
629 most similar age difference to one of these sessions (mean difference in age between the repeat  
630 session and the matched participant = 0.97 months). For example, consider the participant who  
631 was 5.2 months at their first session (S02) and 7.0 months at their next session (S05). To provide a  
632 between-participant control, we found the participant (S06) who was closest in age to the second  
633 session (7.2 months). We then compared the Dice coefficient of S02 and S05 with the Dice coeffi-  
634 cient of S02 and S06. To evaluate this statistically, we used bootstrap resampling of the difference  
635 in Dice coefficients between the within- and between-participant pairs. The Dice coefficient com-  
636 paring a participant to themselves across sessions was ranked against the Dice coefficients from  
637 relating that participant to all other participants. To evaluate significance of this rank, for each  
638 participant with a repeat session we generated a random rank in the possible range of values for  
639 that participant and averaged across the group. We did this 10,000 times to get a distribution of  
640 permuted ranks. We then compared the observed average rank to this permuted distribution to find  
641 the likelihood of finding a ranking as extreme as the one we observed.

642 To test how similarity between participants varied with age, we compared the ages of the  
643 participants to their Dice coefficient. We first tested whether similarity in age predicted the Dice

644 coefficient. To do this, we subtracted the ages of participants and related the absolute value of this  
645 difference to the Dice coefficient. We next tested if the overall age of the participants predicted  
646 the Dice coefficient. To do this, we compared the average age of each pair of participants with  
647 the Dice coefficient for each pair. Bootstrap resampling was used to evaluate the significance  
648 of these correlations. In both of these analyses, comparisons using the same participant across  
649 multiple sessions were ignored because the sampling of these participants was skewed to older  
650 ages. Because within-participant Dice coefficients were higher, this skew would have biased the  
651 correlations to be positive.

652 To measure the quality of alignment to the standard template, we used two complemen-  
653 tary metrics. First, we quantified the number of defects in the projection of the Desikan-Killany  
654 atlas, as described above. Second, we correlated the convexity map of individual participants  
655 with the convexity map from standard space (from fsaverage (Dale, Fischl, and Sereno, 1999)).  
656 The convexity maps of the individual and standard surface were masked according to the relevant  
657 regions (V1–V4) that were labelled in the atlas of visual cortex (Wang, Mruczek, Arcaro, and  
658 Kastner, 2014). The correlation between the convexity map and standard space was computed for  
659 each hemisphere separately. This correlation was Fisher transformed and then averaged between  
660 hemispheres. Bootstrap resampling of the correlation was used to quantify the significance of the  
661 relationship between age and the measure of alignment.

662 To determine the degree to which the visual areas have adult-like localization, the Dice co-  
663 efficient was calculated between the traced areas in each infant and those same areas as defined

664 in an atlas of the visual hierarchy (Wang, Mruczek, Arcaro, and Kastner, 2014). All of the areas  
665 we traced were available for comparison in the atlas except for V3A/B, which is separated in the  
666 atlas but was combined here. The maximum probability surface was used so that each node was  
667 uniquely assigned to a specific area, if at all.

668 The Dice coefficient to the standard atlas was computed for each individual and related to  
669 their age to determine whether the similarity to adults changes across early development. The  
670 significance of this correlation was computed using bootstrap resampling. We also tested whether  
671 the Dice coefficient was higher between two participants than between one participant and the  
672 atlas. The Dice coefficients comparing each participant with the other participants (excluding  
673 comparisons across sessions from the same participant) were averaged and subtracted from the  
674 Dice coefficient from that participant and the atlas. This difference for each participant was then  
675 tested for significance with bootstrap resampling.

676 Our main measure of the visual area size was the length of each traced area. This length  
677 was computed on surfaces in native space by taking all pairwise distances of nodes along the  
678 lines traced running perpendicular to the area boundaries and averaging them (Figure 3a). That is,  
679 length corresponds to the distance between boundaries. Length was chosen as the primary metric  
680 over other measurements like surface area because it is less sensitive to challenges in drawing the  
681 foveal border. Nevertheless, a similar pattern of results was obtained with surface area, computed  
682 by averaging the extent of the white matter and pial surface for all nodes labeled as belonging to  
683 an area. For V1, V2, and V3, we first averaged the lengths across hemispheres and then added

684 these averages for the ventral and dorsal areas. This was still possible if an area was traced in only  
685 the left or right hemisphere, but if either the ventral or dorsal areas had not been traced in both  
686 the left and right hemisphere then the length of this area was not estimated. The average length  
687 of the remaining participants was related to their age using bootstrap resampling. To observe size  
688 changes independent of overall brain size, a partial correlation was computed where overall brain  
689 size (as measured based on the skullstripped volume from iBEAT v2.0) was used as a covariate.  
690 Analyses using gray matter volume as a covariate produced similar results. This partial correlation  
691 was also evaluated statistically using bootstrap resampling. To test whether the foveal confluence  
692 varied in size with age, the area of each foveal area was divided by the area of the sum of dorsal  
693 and ventral area for that area, and then correlated with age using bootstrap resampling.

694 **Supplementary Information**

695 Retinotopic organization of visual cortex in human infants

696 Ellis, C. T., Yates, T. S., Skalaban, L. J., Bejjanki, V. R., Arcaro, M. J., & Turk-Browne, N. B.

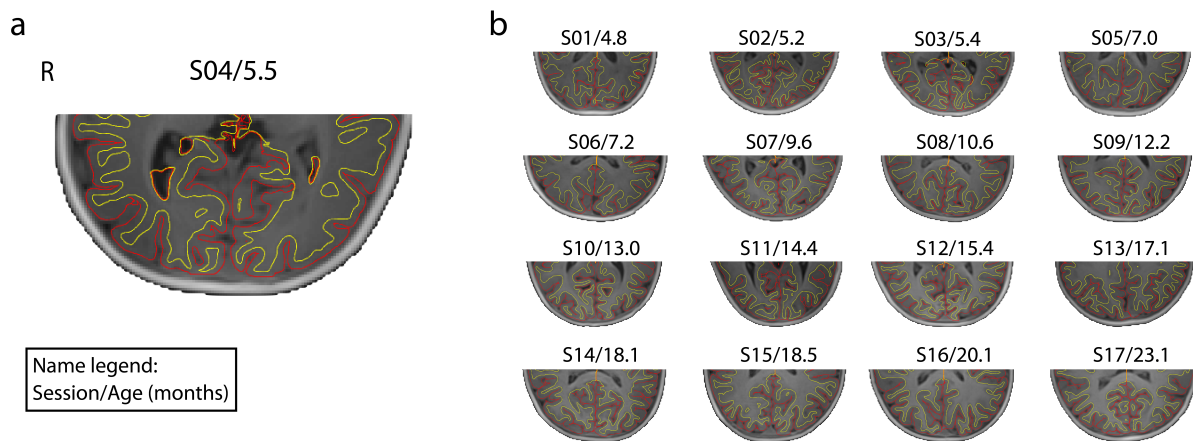


Figure S1: Pial and white matter surfaces from iBEAT v2.0. The posterior portion of anatomical images with surfaces outlined for (a) an example 5.5-month old participant, and (b) all other participants. The yellow line is the white matter surface and the red line is the pial surface. The text above each volume indicates: session number/age in months. No editing was performed on any of these surfaces before they were inflated.

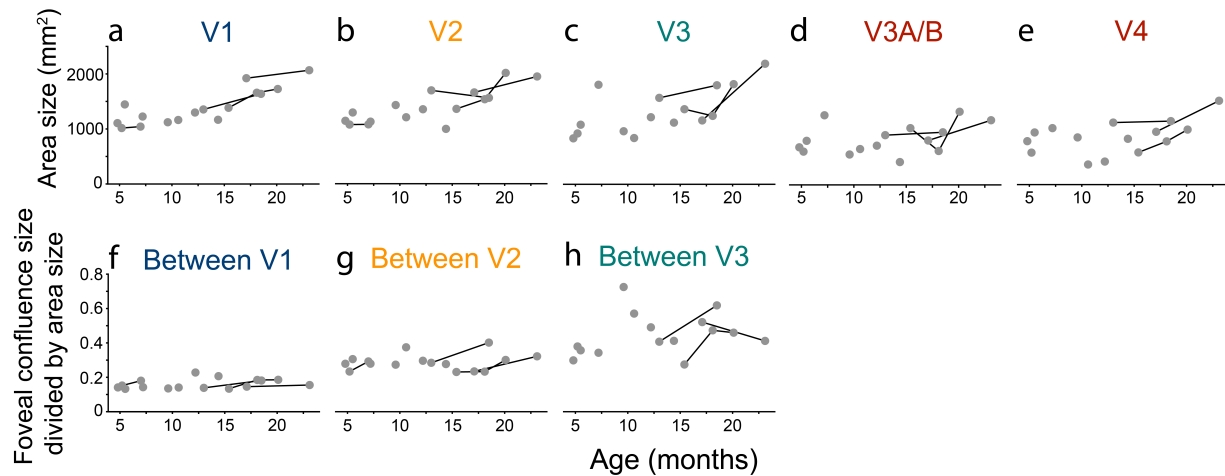


Figure S2: Relationship between surface area and the participant's age, akin to Figure 7. The size was first averaged across hemispheres. For V1, V2, and V3, ventral and dorsal areas were summed. Lines connect the same participant across sessions. Raw data for each area are reported in Table S3. There were strong positive correlations with age in V1 ( $r=0.84$ ,  $p=0.001$ ), V2 ( $r=0.79$ ,  $p<0.001$ ), and V3 ( $r=0.66$ ,  $p=0.016$ ), but not V3A/B ( $r=0.39$ ,  $p=0.170$ ) or V4 ( $r=0.46$ ,  $p=0.088$ ). Controlling for whole-brain volume, the partial correlation of area size and age remained reliable in V1 ( $r=0.79$ ,  $p=0.014$ ) and V2 ( $r=0.66$ ,  $p=0.021$ ), but not in V3 ( $r=0.36$ ,  $p=0.476$ ), V3A/B ( $r=0.24$ ,  $p=0.432$ ), or V4 ( $r=0.26$ ,  $p=0.610$ ). Moreover, imprecision in mapping area boundaries near the fovea (potentially caused by poor fixation) did not seem to confound the tests of age-related changes in area size: the surface area of the unmapped visual cortex around the fovea, relative to the area of the mapped dorsal and ventral areas, showed a marginal effect in V1 ( $r=0.32$ ,  $p=0.054$ ), but did not change with age in V2 ( $r=0.15$ ,  $p=0.559$ ) or V3 ( $r=0.24$ ,  $p=0.282$ ).

Table S1: Participant information for included participants. ‘Session num.’ is the session number used in figures to designate participants. ‘ID’ is a unique infant identifier (i.e., sXXXX\_Y\_Z), with the first four digits (XXXX) indicating the family, the fifth digit (Y) the child number within family, and the sixth digit (Z) the session number with that child. This is used in the data release for labelling participants. ‘Age’ is recorded in months. ‘Sex’ is female or male. ‘Vert. phases’ is the number of vertical meridian phases included. ‘Hori. phases’ is the number of horizontal meridian phases included. ‘Low phases’ is the number of low spatial frequency phases included. ‘High phases’ is the number of high spatial frequency phases included. ‘Prop. incl. TRs’ is the proportion of usable TRs from the included blocks. ‘Prop. incl. eye’ is the proportion of usable eye data from the included phases. ‘IRR’ is the inter-rater reliability for the gaze coding.

Session num.	ID	Age	Sex	Vert. phases	Hori. phases	Low phases	High phases	Prop. incl. TRs	Prop. incl. eye	IRR
S01	s2077_1.1	4.8	M	5	4	1	3	1.00	0.92	0.76
S02	s2097_1.1	5.2	M	4	4	4	4	1.00	0.95	0.83
S03	s8047_1.1	5.4	F	2	3	1	2	0.97	0.93	0.80
S04	s4047_1.1	5.5	F	3	3	4	4	1.00	0.95	0.82
S05	s2097_1.2	7.0	M	1	1	4	2	0.99	0.94	0.81
S06	s7017_1.3	7.2	F	6	6	6	6	1.00	0.95	0.78
S07	s7047_1.1	9.6	F	1	1	1	1	1.00	0.91	0.77
S08	s7067_1.4	10.6	F	3	3	2	3	1.00	0.89	0.78
S09	s8037_1.2	12.2	F	2	2	1	3	0.90	0.89	0.75
S10	s4607_1.4	13.0	F	5	5	4	6	0.93	0.87	0.72
S11	s1607_1.4	14.4	M	3	2	3	4	0.94	0.89	0.79
S12	s6687_1.4	15.4	F	5	6	6	4	1.00	0.91	0.84
S13	s8687_1.5	17.1	F	4	4	4	2	0.98	0.89	0.86
S14	s6687_1.5	18.1	F	5	4	6	5	1.00	0.89	0.84
S15	s4607_1.7	18.5	F	2	3	3	4	1.00	0.92	0.71
S16	s6687_1.6	20.1	F	4	3	4	4	0.97	0.92	0.83
S17	s8687_1.8	23.1	F	4	5	5	3	0.98	0.91	0.76
Av.	.	12.19	.	3.47	3.47	3.47	3.53	0.98	0.91	0.79



Table S2: Length of visual areas per participant. ‘Session num.’ is the session number used in figures to designate participants. ‘ID’ is a unique infant identifier. ‘v’ before an area name denotes ventral. ‘d’ before an area name denotes dorsal. Length is measured in mm and is averaged across the left and right hemispheres, when available. The ‘V1’, ‘V2’ and ‘V3’ columns sum across the ventral and dorsal areas. ‘Volume’ is the size of the whole-brain mask in mm<sup>3</sup>.

Session num.	ID	vV1	vV2	vV3	V4	dV1	dV2	dV3	V3A/B	V1	V2	V3	Volume
S01	s2077_1_1	9.1	11.9	7.8	15.7	18.9	14.1	10.8	17.3	28.0	26.0	18.7	619858
S02	s2097_1_1	12.1	11.6	10.2	13.1	12.2	9.9	10.4	16.1	24.3	21.6	20.5	784387
S03	s8047_1_1	nan	nan	nan	nan	nan	nan	nan	nan	nan	nan	nan	739231
S04	s4047_1_1	13.9	14.0	12.6	23.1	14.4	11.9	9.9	17.6	28.3	25.9	22.6	797135
S05	s2097_1_2	8.4	10.5	nan	nan	11.5	5.1	nan	nan	19.8	15.6	nan	760968
S06	s7017_1_3	14.3	12.8	25.2	25.4	14.6	11.0	17.5	29.0	28.8	23.8	42.6	828623
S07	s7047_1_1	10.7	12.6	15.7	22.1	16.8	21.3	13.8	22.2	27.4	33.9	29.5	867040
S08	s7067_1_4	17.1	15.2	12.6	15.7	14.3	13.6	8.6	13.6	31.4	28.8	21.2	771459
S09	s8037_1_2	14.6	13.7	12.9	13.6	11.3	10.8	13.4	16.4	25.9	24.5	26.4	834345
S10	s4607_1_4	15.6	15.7	22.4	23.7	15.2	15.5	13.1	19.6	30.7	31.2	35.4	959789
S11	s1607_1_4	18.4	13.8	13.7	19.7	13.1	9.9	15.8	12.4	31.5	23.7	29.5	940908
S12	s6687_1_4	16.1	14.1	15.4	16.6	17.2	13.0	14.6	22.0	33.3	27.1	30.1	951723
S13	s8687_1_5	16.4	14.3	12.8	17.9	16.5	13.7	9.7	18.2	32.9	28.0	22.5	863904
S14	s6687_1_5	18.2	15.1	14.5	19.7	15.2	15.3	14.9	18.8	33.4	30.4	29.4	952569
S15	s4607_1_7	16.0	15.3	22.5	25.3	19.8	12.9	15.4	16.1	35.8	28.3	37.9	1045534
S16	s6687_1_6	14.5	18.4	16.7	21.2	16.6	10.3	22.4	29.4	31.0	28.8	39.1	978040
S17	s8687_1_8	20.2	15.2	21.4	21.3	15.6	15.3	17.4	21.6	35.8	30.5	38.8	913503
Av.	.	14.72	14.01	15.76	19.60	15.18	12.74	13.85	19.35	29.91	26.74	29.61	859354

Table S3: Surface area of visual areas per participant. ‘Session num.’ is the session number used in figures to designate participants. ‘ID’ is a unique infant identifier. ‘v’ before an area name denotes ventral. ‘d’ before an area name denotes dorsal. Area is measured in mm<sup>2</sup> and is averaged across the left and right hemispheres, when available. The ‘V1’, ‘V2’ and ‘V3’ columns sum across the ventral and dorsal areas. ‘Volume’ is the size of the whole-brain mask in mm<sup>3</sup>.

Session num.	ID	vV1	vV2	vV3	V4	dV1	dV2	dV3	V3A/B	V1	V2	V3	Volume
S01	s2077_1_1	431	582	484	789	675	562	351	682	1106	1144	835	619858
S02	s2097_1_1	540	577	470	581	476	498	454	604	1016	1075	924	784387
S03	s8047_1_1	nan	nan	nan	nan	nan	nan	nan	nan	nan	nan	nan	739231
S04	s4047_1_1	681	711	609	948	765	584	474	800	1446	1294	1083	797135
S05	s2097_1_2	511	654	nan	nan	532	425	nan	nan	1043	1079	nan	760968
S06	s7017_1_3	592	557	937	1026	634	571	872	1264	1226	1128	1809	828623
S07	s7047_1_1	539	587	569	857	583	843	395	552	1122	1430	964	867040
S08	s7067_1_4	656	645	415	365	507	562	426	651	1163	1208	841	771459
S09	s8037_1_2	779	753	630	419	519	600	589	712	1299	1353	1219	834345
S10	s4607_1_4	705	864	1024	1127	650	833	547	903	1354	1697	1571	959789
S11	s1607_1_4	739	572	503	832	427	425	618	414	1167	997	1121	940908
S12	s6687_1_4	748	688	660	585	636	672	705	1031	1384	1360	1365	951723
S13	s8687_1_5	998	902	718	959	925	757	442	806	1922	1659	1161	863904
S14	s6687_1_5	1030	856	646	786	628	679	597	615	1658	1535	1243	952569
S15	s4607_1_7	841	820	1058	1154	796	740	741	955	1638	1561	1800	1045534
S16	s6687_1_6	1017	1272	856	1000	709	742	965	1329	1726	2014	1820	978040
S17	s8687_1_8	1043	930	1211	1524	1023	1019	980	1174	2067	1949	2191	913503
Av.	.	740.69	748.12	719.30	863.46	655.32	656.97	610.36	832.78	1396.02	1405.10	1329.67	859354

697 **References**

- 698 Arcaro, M. J., and Livingstone, M. S. (2017). A hierarchical, retinotopic proto-organization of the  
700 primate visual system at birth. *Elife*, 6:e26196.
- 701 Arcaro, M. J., McMains, S. A., Singer, B. D., and Kastner, S. (2009). Retinotopic organization of  
702 human ventral visual cortex. *Journal of Neuroscience*, 29(34):10638–10652.
- 703 Arcaro, M. J., Schade, P. F., Vincent, J. L., Ponce, C. R., and Livingstone M. S. (2017). Seeing  
704 faces is necessary for face-domain formation. *Nature Neuroscience*, 20(10):1404–1412.
- 705 Argall, B. D., Saad, Z. S., and Beauchamp, M. S. (2006). Simplified intersubject averaging on the  
706 cortical surface using SUMA. *Human Brain Mapping*, 27(1):14–27.
- 707 Aslin, R. N., and Salapatek, P. (1975). Saccadic localization of visual targets by the very young  
708 human infant. *Attention, Perception, & Psychophysics*, 17(3):293–302.
- 709 Baker, T. J., Tse, J. , Gerhardstein, P. , and Adler, S. A. (2008). Contour integration by 6-month-old  
710 infants: discrimination of distinct contour shapes. *Vision Research*, 48(1):136–148.
- 711 Baker, T. J., Norcia, A. M., and Candy T. R. (2011). Orientation tuning in the visual cortex of  
712 3-month-old human infants. *Vision Research*, 51(5):470–478.
- 713 Banks, M. S., Stephens, B. R., and Hartmann E. E. (1985). The development of basic mechanisms  
714 of pattern vision: Spatial frequency channels. *Journal of Experimental Child Psychology*, 40(3):  
715 501–527.

- 716 Biagi, L. , Crespi, S. A., Tosetti, M. , and Morrone, M. C. (2015). BOLD response selective to  
717 flow-motion in very young infants. *PLoS Biology*, 13(9):e1002260.
- 718 Boothe, R. G., Dobson, V. , and Teller, D. Y. (1985). Postnatal development of vision in human  
719 and nonhuman primates. *Annual Review of Neuroscience*, 8(1):495–545.
- 720 Bourne, J. A., and Rosa, M. G. (2006). Hierarchical development of the primate visual cortex,  
721 as revealed by neurofilament immunoreactivity: early maturation of the middle temporal area  
722 (MT). *Cerebral Cortex*, 16(3):405–414.
- 723 Braddick, O. , and Atkinson, J. . (2011). Development of human visual function. *Vision Research*,  
724 51(13):1588–1609.
- 725 Braddick, O. , Wattam-Bell, J. , and Atkinson, J. (1986). Orientation-specific cortical responses  
726 develop in early infancy. *Nature*, 320(6063):617–619.
- 727 Burkhalter, A. , Bernardo, K. L., and Charles, V. . (1993). Development of local circuits in human  
728 visual cortex. *Journal of Neuroscience*, 13(5):1916–1931.
- 729 Chapman, B. , Gödecke, I. , and Bonhoeffer, T. (1999). Development of orientation preference in  
730 the mammalian visual cortex. *Journal of Neurobiology*, 41(1):18–24.
- 731 Condé, F. , Lund, J. S., and Lewis, D. A. (1996). The hierarchical development of monkey visual  
732 cortical regions as revealed by the maturation of parvalbumin-immunoreactive neurons. *Devel-*  
733 *opmental Brain Research*, 96(1-2):261–276.

- 734 Conner, I. P., Sharma, S. , Lemieux, S. K., and Mendola, J. D. (2004). Retinotopic organization in  
735 children measured with fMRI. *Journal of Vision*, 4(6):509–523.
- 736 Cox, R. W. (1996). AFNI: software for analysis and visualization of functional magnetic resonance  
737 neuroimages. *Computers and Biomedical Research*, 29(3):162–173.
- 738 Dale, A. M., Fischl, B. , and Sereno, M. I. (1999). Cortical surface-based analysis: I. segmentation  
739 and surface reconstruction. *NeuroImage*, 9(2):179–194.
- 740 Deen, B. , Richardson, H. , Dilks, D. D., Takahashi, A. , Keil, B. , Wald, L. L., Kanwisher,  
741 N. , and Saxe, R. (2017). Organization of high-level visual cortex in human infants. *Nature*  
742 *Communications*, 8:13995.
- 743 Dice, L. R. (1945). Measures of the amount of ecologic association between species. *Ecology*, 26  
744 (3):297–302.
- 745 Distler, C. , Bachevalier, J. , Kennedy, C. , Mishkin, M. , and Ungerleider, L. (1996). Functional  
746 development of the corticocortical pathway for motion analysis in the macaque monkey: a 14c-  
747 2-deoxyglucose study. *Cerebral Cortex*, 6(2):184–195.
- 748 Dumoulin, S. O., and Wandell, B. A. (2008). Population receptive field estimates in human visual  
749 cortex. *NeuroImage*, 39(2):647–660.
- 750 Efron, B. , and Tibshirani, R. (1986). Bootstrap methods for standard errors, confidence intervals,  
751 and other measures of statistical accuracy. *Statistical Science*, 54–75.

- 752 Ellis, C. T., and Turk-Browne, N. B. (2018). Infant fMRI: A model system for cognitive neuro-  
753 science. *Trends in Cognitive Sciences*, 22(5):375–387.
- 754 Ellis, C. T., Skalaban, L. J., Yates, T. S., Bejjanki, V. R., Córdova, N. I., and Turk-Browne, N. B.  
755 (2020a). Re-imagining fMRI for awake behaving infants. *Nature Communications*, 11(4523).
- 756 Ellis, C. T., Skalaban, L. J., Yates, T. S., Bejjanki, V. R., Córdova, N. I., and Turk-Browne, N. B.  
757 (2020b). Evidence of hippocampal learning in human infants. *bioRxiv*.
- 758 Ellis, C. T., Skalaban, L. J., Yates, T. S., and Turk-Browne, N. B. (2020c) Attention recruits frontal  
759 cortex in human infants. *bioRxiv*.
- 760 Engel, S. A., Rumelhart, D. E., Wandell, B. A., Lee, A. T., Glover, G. H., Chichilnisky, E.-J., and  
761 Shadlen, M. N. (1994). fMRI of human visual cortex. *Nature*, 369:525.
- 762 Fonov, V. , Evans, A. C., Botteron, K. , Almli, C. R., McKinstry, R. C., and Collins, D. L. (2011).  
763 Unbiased average age-appropriate atlases for pediatric studies. *NeuroImage*, 54(1):313–327.
- 764 Fox, P. T., Miezin, F. M., Allman, J. M., Van Essen, D. C., and Raichle, M. E. (1987). Retinotopic  
765 organization of human visual cortex mapped with positron-emission tomography. *Journal of*  
766 *Neuroscience*, 7(3):913–922.
- 767 Gao, W. , Lin, W. , Grewen, K. , and Gilmore, J. H. (2017). Functional connectivity of the infant  
768 human brain: plastic and modifiable. *The Neuroscientist*, 23(2):169–184.
- 769 Gomez, J. , Natu, V. , Jeska, B. , Barnett, M. , and Grill-Spector, K. (2018). Development differen-

- 770 tially sculpts receptive fields across early and high-level human visual cortex. *Nature Commu-*  
771 *nications*, 9(1):1–12.
- 772 Gomez, J. , Barnett, M. , and Grill-Spector, K. (2019). Extensive childhood experience with  
773 pokémon suggests eccentricity drives organization of visual cortex. *Nature Human Behaviour*,  
774 3(6):611–624.
- 775 Hasson, U. , Levy, I. , Behrmann, M. , Hendler, T. , and Malach, R. (2002). Eccentricity bias as an  
776 organizing principle for human high-order object areas. *Neuron*, 34(3):479–490.
- 777 Henriksson, L. , Nurminen, L. , Hyvärinen, A. , and Vanni, S. (2008). Spatial frequency tuning in  
778 human retinotopic visual areas. *Journal of Vision*, 8(10):1–13.
- 779 Kastner, S. , De Weerd, P. , and Ungerleider, L. G. (2000). Texture segregation in the human visual  
780 cortex: A functional MRI study. *Journal of Neurophysiology*, 83(4):2453–2457.
- 781 Kiorpes, L. (2016). The puzzle of visual development: behavior and neural limits. *Journal of*  
782 *Neuroscience*, 36(45):11384–11393.
- 783 Kiorpes, L. , and Bassin, S. A. (2003). Development of contour integration in macaque monkeys.  
784 *Visual Neuroscience*, 20(5):567.
- 785 Kiorpes, L. , and Movshon, J. (2014). Neural limitations on visual development in primates:  
786 Beyond striate cortex. In *The Visual Neurosciences, 2nd edition*. MIT Press.
- 787 Kovács, I. (2000). Human development of perceptual organization. *Vision Research*, 40(10-12):  
788 1301–1310.

- 789 Kovacs, I. , Kozma, P. , Feher, A. , and Benedek, G. (1999). Late maturation of visual spatial  
790 integration in humans. *Proceedings of the National Academy of Sciences*, 96(21):12204–12209.
- 791 Lewis, T. L., and Maurer, D. (2005). Multiple sensitive periods in human visual development:  
792 evidence from visually deprived children. *Developmental Psychobiology*, 46(3):163–183.
- 793 Li, G. , Nie, J. , Wang, L. , Shi, F. , Gilmore, J. H., Lin, W. , and Shen, D. (2014). Measuring the  
794 dynamic longitudinal cortex development in infants by reconstruction of temporally consistent  
795 cortical surfaces. *NeuroImage*, 90:266–279.
- 796 Li, G. , Wang, L. , Shi, F. , Gilmore, J. H., Lin, W. , and Shen, D. (2015). Construction of 4D  
797 high-definition cortical surface atlases of infants: Methods and applications. *Medical Image*  
798 *Analysis*, 25(1):22–36.
- 799 Li, G. , Wang, L. , Yap, P.-T., Wang, F. , Wu, Z. , Meng, Y. , Dong, P. , Kim, J. , Shi, F. , Reikik,  
800 I. , et al. (2019). Computational neuroanatomy of baby brains: A review. *NeuroImage*, 185:  
801 906–925.
- 802 Patel, A. , Maurer, D. , and Lewis, T. L. (2010). The development of spatial frequency discrimina-  
803 tion. *Journal of Vision*, 10(14):1–10.
- 804 Schneider, W. , Noll, D. C., and Cohen, J. D. (1993). Functional topographic mapping of the  
805 cortical ribbon in human vision with conventional MRI scanners. *Nature*, 365(6442):150–153.
- 806 Sereno, M. I., Dale, A. , Reppas, J. , Kwong, K. , Belliveau, J. , Brady, T. , Rosen, B. , and  
807 Tootell, R. (1995). Borders of multiple visual areas in humans revealed by functional magnetic  
808 resonance imaging. *Science*, 268(5212):889–893.



- 809 Shipp, S. , Watson, J. , Frackowiak, R. , and Zeki, S. (1995). Retinotopic maps in human prestriate  
810 visual cortex: the demarcation of areas V2 and V3. *NeuroImage*, 2(2):125–132.
- 811 Siegel, J. S., Power, J. D., Dubis, J. W., Vogel, A. C., Church, J. A., Schlaggar, B. L., and Petersen,  
812 S. E. (2014). Statistical improvements in functional magnetic resonance imaging analyses pro-  
813 duced by censoring high-motion data points. *Human Brain Mapping*, 35(5):1981–1996.
- 814 Siu, C. R., and Murphy, K. M. (2018). The development of human visual cortex and clinical  
815 implications. *Eye and Brain*, 10:25.
- 816 Thompson, P. M., Stein, J. L., Medland, S. E., Hibar, D. P., Vasquez, A. A., Renteria, M. E., Toro,  
817 R. , Jahanshad, N. , Schumann, G. , Franke, B. , et al. (2014). The ENIGMA consortium: large-  
818 scale collaborative analyses of neuroimaging and genetic data. *Brain Imaging and Behavior*, 8  
819 (2):153–182.
- 820 Tolhurst, D. , and Thompson, I. (1981). On the variety of spatial frequency selectivities shown by  
821 neurons in area 17 of the cat. *Proceedings of the Royal Society of London. Series B. Biological*  
822 *Sciences*, 213(1191):183–199.
- 823 Tootell, R. , Reppas, J. B., Kwong, K. K., Malach, R. , Born, R. T., Brady, T. J., Rosen, B. R.,  
824 and Belliveau, J. W. (1995). Functional analysis of human MT and related visual cortical areas  
825 using magnetic resonance imaging. *Journal of Neuroscience*, 15(4):3215–3230.
- 826 van den Boomen, C. , and Peters, J. C. (2017). Spatial frequency discrimination: Effects of age,  
827 reward, and practice. *PloS One*, 12(1):e0169800.

- 828 Wandell, B. A., Dumoulin, S. O., and Brewer, A. A. (2007). Visual field maps in human cortex.  
829 *Neuron*, 56(2):366–383.
- 830 Wang, L. , Mruczek, R. E., Arcaro, M. J., and Kastner, S. (2014). Probabilistic maps of visual  
831 topography in human cortex. *Cerebral Cortex*, 25(10):3911–3931.
- 832 Wang, L. , Li, G. , Shi, F. , Cao, X. , Lian, C. , Nie, D. , Liu, M. , Zhang, H. , Li, G. , Wu, Z. ,  
833 et al. (2018). Volume-based analysis of 6-month-old infant brain MRI for autism biomarker  
834 identification and early diagnosis. In *International Conference on Medical Image Computing*  
835 *and Computer-Assisted Intervention*, pages 411–419. Springer.
- 836 Winawer, J. , Horiguchi, H. , Sayres, R. A., Amano, K. , and Wandell, B. A. (2010). Mapping hV4  
837 and ventral occipital cortex: the venous eclipse. *Journal of Vision*, 10(5):1–22.
- 838 Zhang, B. , Zheng, J. , Watanabe, I. , Maruko, I. , Bi, H. , Smith, E. L., and Chino, Y. (2005).  
839 Delayed maturation of receptive field center/surround mechanisms in V2. *Proceedings of the*  
840 *National Academy of Sciences*, 102(16):5862–5867.
- 841 Zhang, X. , and Fang, F. (2012). Object-based attention guided by an invisible object. *Experimental*  
842 *Brain Research*, 223(3):397–404.