Face processing in the infant brain after pandemic lockdown

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Abstract

The role of visual experience in the development of face processing has long been debated. We present a new angle on this question through a serendipitous study that cannot easily be repeated. Infants viewed short blocks of faces during fMRI in a repetition suppression task. The same identity was presented multiple times in half of the blocks (Repeat condition) and different identities were presented once each in the other half (Novel condition). In adults, the fusiform face area (FFA) tends to show greater neural activity for Novel vs. Repeat blocks in such designs, suggesting that it can distinguish same vs. different face identities. As part of an ongoing study, we collected data before the COVID-19 pandemic and after an initial State lockdown was lifted. The resulting sample of 12 infants (9–24 months) divided equally into pre- and post-lockdown groups with matching ages and data quantity/quality. The groups had strikingly different FFA responses: pre-lockdown infants showed repetition suppression (Novel>Repeat), whereas post-lockdown infants showed the opposite (Repeat>Novel), often referred to as repetition enhancement. These findings provide speculative evidence that altered visual experience during the lockdown, or other correlated environmental changes, may have affected face processing in the infant brain.

Keywords

face identity, face recognition, experience, neuroimaging, fMRI

Introduction

What is the role of visual experience on the development of face processing? Although some researchers have argued that infants possess innate specialization for faces (Morton and Johnson, 1991; Turati, 2004; Kanwisher, 2010; Johnson et al., 2015), early visual experience can shape at least one aspect of face pro-cessing: the ability to distinguish individual faces (Pascalis et al., 2020). In a seminal study, 6-month-olds, 9-month-olds, and adults were shown pictures of human and monkey faces. All groups looked more at a novel human face than a familiar human face during test, evidence that they could distinguish human identities (Pascalis et al., 2002). However, only the youngest infants looked longer at a novel monkey face than a familiar monkey face, hinting that perceptual abilities narrow over early development (Maurer and Werker, 2014; Pascalis et al., 2020; Werker and Tees, 1984).

Evidence that perceptual narrowing is related to experience, rather than maturation, comes from stud-ies that manipulate exposure to non-native faces (Sangrigoli and De Schonen, 2004; Pascalis et al., 2005; Anzures et al., 2012). For instance, infants exposed to monkey faces between 6 and 9 months are not only able to recognize the monkey faces to which they were exposed, but could also distinguish novel and fa-miliar monkey faces from a new set when tested at 9 months (Pascalis et al., 2005). Even past 9 months, visual experience can influence the ability to process non-native faces, with infants recovering the ability

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41 to distinguish Asian female and male faces after daily exposure to videos of Asian women (Anzures et al.,
42 2012). This period of plasticity is not indefinite: other-race (white) face recognition in Asian immigrants is
43 significantly related to when in development they moved to a majority white country (Zhou et al., 2019).
44   Cases of deprivation provide an additional angle on the critical role that early visual experience plays in
45 face identity processing. For instance, individuals with bilateral congenital cataracts at birth are impaired at
46 holistic face processing (Le Grand et al., 2001; Grand et al., 2004) and individual face memory (de Heering
47 and Maurer, 2014) even years after corrective surgery (Maurer 2017; cf. McKone et al. 2012). In another
48 study, infant monkeys deprived of faces early in life were later shown either human or monkey faces for
49 a month, prior to daily exposure to both species; immediately and one year later, monkeys could only
50 distinguish face identities for the species to which they were initially exposed (Sugita, 2008; Arcaro and
51 Livingstone, 2021).
52   It is unethical to conduct these kinds of causal tests in healthy human infants. In early 2020, however,
53 the opportunity for a natural experiment in visual plasticity arose in response to the coronavirus disease
54 2019 (COVID-19) global pandemic. Emergency lockdowns and stay-at-home orders, as well as face mask cov-
55 erings in public spaces, were used to prevent viral spread. These precautions abruptly changed daily life,
56 including the nature of face-to-face interactions. Although infant face experience is highly biased toward
57 primary caregivers (Sugden and Moulson, 2019), which continued and if anything may have expanded dur-
58 ing lockdowns, absent or altered exposure to relatives and strangers during the COVID-19 pandemic may
59 have influenced the development of face processing (Green et al., 2021; Carnevali et al., 2021). In particu-
60 lar, exposure to a more homogenous set of faces at home could alter identity processing. Indeed, smaller
61 hometowns are associated with reduced accuracy on more difficult face recognition tasks (Balas and Saville,
62 2017; Sunday et al., 2019).
63   The tragic events of the COVID-19 pandemic therefore resulted in a quasi-experiment: we had been
64 investigating neural measures of face identity processing in infants who underwent fMRI before the lock-
65 downs were put in place, and then resumed data collection after a few months of the pandemic. Although
66 the original purpose of this study was to investigate perceptual narrowing, as reflected in the design, we
67 hypothesized that there may be a difference in face processing in the brains of infants tested pre- and post-
68 lockdown. We used fMRI because it has the spatial resolution and sensitivity to resolve brain regions on the
69 ventral surface of visual cortex distant from the scalp, including face-selective regions such as the fusiform
70 face area (FFA). Recent studies established that the FFA is present in infants (Deen et al., 2017; Kosakowski
71 et al., 2021). However, it is unknown whether the infant FFA additionally distinguishes face identities, similar
72 to adult FFA, and if so, how the COVID-19 pandemic affects this processing.
73   Following a classic repetition suppression (or adaptation) design from adult fMRI (Grill-Spector et al.,
74 2006; Turk-Browne et al., 2008), we showed infants blocks of faces that were of the same or different iden-
75 tities. In adults, the FFA tends to show reduced neural activity when the identity of a face is repeated vs.
76 changed (Grill-Spector and Malach, 2001; Barron et al., 2016; Henson, 2016). We hypothesized from the start
77 of this study that (pre-lockdown) infants would show repetition suppression in FFA. To the extent that the
78 lockdown affected the development of face identity processing, we hypothesized that repetition suppres-
79 sion might be attenuated or eliminated. Specifically, if the post-lockdown infant FFA does not distinguish
80 face identities, there should be no neural difference between same vs. different identities.

Methods

Participants

83 Data were collected from 12 infant fMRI sessions (9.20 – 23.80 months; M = 15.25, SD = 3.85; 9 female)
84 that met inclusion criteria for 2 blocks of each condition, and with pairs of Novel and Repeat face blocks
85 occurring in the same functional run (Table 1). Half of the sessions were collected prior to the onset of
86 pandemic restrictions (until March 2020), and the other half of sessions were collected after our State's first
87 lockdown was lifted (from August 2020 until February 2021). As part of the original study, an additional 13
88 usable sessions were collected prior to the pandemic from infants under 9 months, but infants this young
89 were not available post-lockdown for age matching purposes and so were not included in this analysis. We

excluded data from 14 infant sessions in our target age range because an insufficient number of blocks were attempted or were retained after exclusion for eye movements or head motion. In the final sample, 2 unique infants provided 2 sessions of usable data each. Following prior work (Deen et al., 2017; Ellis et al., 2020; Kosakowski et al., 2021), the data from these sessions were treated as independent because they occurred several months apart (3.9 and 4.4 months). These second sessions were matched across groups, with one of the repeat infants in each of the pre- and post-lockdown groups, respectively. These infants saw a different set of images and counter-balancing in each session. The study was approved by the local Institutional Review Board. Parents provided informed consent on behalf of their child.

	Pre-lockdown infants	Post-lockdown infants	*p*-value
N (female)	6 (6)	6 (3)	n/a
Days quarantine	n/a	237.00 (52.91)	n/a
Age in months	14.42 (3.19)	16.08 (4.25)	0.442
Number blocks total	13.33 (2.36)	13.00 (2.16)	0.732
Percent gaze reliability	95.6 (1.9)	93.3 (4.3)	0.214
Percent TRs after motion (Novel Human)	98.5 (3.3)	97.1 (4.2)	0.484
Percent TRs after motion (Repeat Human)	99.7 (0.7)	95.6 (7.8)	0.076
Percent looking during exposure phase (Novel Human)	89.5 (3.5)	86.9 (7.7)	0.524
Percent looking during exposure phase (Repeat Human)	88.4 (2.8)	87.9 (4.9)	0.860

Table 1. Comparison of pre- and post-lockdown infant groups across demographic factors and measures of data quality and quantity. We found no reliable differences, all *p*s >0.1, with the exception of a marginally larger percent of TRs retained after exclusion for head motion for Repeat human blocks in pre-lockdown compared to post-lockdown infants.

fMRI Data Acquisition

We followed validated procedures and parameters (see Figure 1A) for collecting fMRI data from awake infants (Ellis et al., 2020, 2021a,b,c; Yates et al., 2022). Data were acquired using the bottom half of a 20-channel head coil on a Siemens Prisma (3T) MRI. We collected functional images using a whole-brain T2* gradient-echo EPI sequence (TR = 2s, TE = 30ms, flip angle = 71, matrix = 64x64, slices = 34, resolution = 3mm iso, interleaved slice acquisition). For each session, we also collected anatomical images with a T1 PETRA sequence (TR1 = 3.32ms, TR2 = 2250ms, TE = 0.07ms, flip angle = 6, matrix = 320x320, slices = 320, resolution = 0.94mm iso, radial slices = 30,000).

Procedure

Prior to their first scan, experimenters met with families for a mock scanning session. Families were invited for a scan session during a time when the parent thought the infant was most likely to be compliant. Before and at the scan visit, infants and accompanying parents were extensively screened for metal. Infants received three layers of hearing protection (silicon inner ear putty, over-ear adhesive covers, ear muffs) and were placed on top of a comfortable vacuum pillow on the scanner bed. We projected stimuli directly on the ceiling of the scanner bore above the infant's face. We video recorded their face during scanning with a MRC high-resolution camera and coded their gaze offline. Procedures were identical for the pre-lockdown and post-lockdown groups, with the exception that for post-lockdown infants, all experimenters wore personal protective equipment for COVID-19 (respiratory mask, transparent face shield or goggles, and gloves), and parents wore masks throughout.

The task was presented to infants in MATLAB using Psychtoolbox (http://psychtoolbox.org/). Stimuli were human face images from the color FERET database (Phillips et al., 1998, 2000), outdoor scene images from an open dataset (http://olivalab.mit.edu/MM/sceneCategories.html; Konkle et al. 2010) and an internal database of web photos, and sheep face images (for the original perceptual narrowing study) photographed by the experimenters at a local sheep farm and supplemented through a web search. All stimuli were resized to 256 x 256 pixels. The background was cropped except for external features of the face (i.e., hair for humans, ears for sheep). Because fur color was consistent across sheep (all white/beige), we constrained the human face set to light-skinned or white human faces.

Each experimental block began with an exposure phase in which eight images were shown consecutively for two seconds each, looming from 1 to 20 visual degrees at the center of the screen (Figure 1B). An engaging attention-getter (rotating and expanding stars) was shown in the center of the screen for six seconds to encourage fixation. This was followed by a five-second visual-paired comparison (VPC) test phase, where one of the eight images from exposure was presented on one side and a novel image from the same category on the other side, separated by ten visual degrees. Each block thus lasted 27 seconds, followed by seven seconds of rest with a blank screen.

For the original purpose of the study, infants saw five block conditions: three were Novel blocks, in which each image was a new identity from the given category, and two were Repeat blocks, in which all eight images were the same identity. Scenes were only ever shown in Novel blocks, while human and sheep faces were shown in both Novel and Repeat blocks. Blocks were counter-balanced using a Latin-square design, with up to 25 blocks total available to participants. In a given session, we aimed to collect 2 blocks of each condition (10 total blocks = 5.7 minutes of data) but continued collecting more data if possible. Infants in the pre-lockdown group had 7.6 minutes (13.3 blocks) of usable data on average, and infants in the post-lockdown group had 7.4 minutes (13.0 blocks).
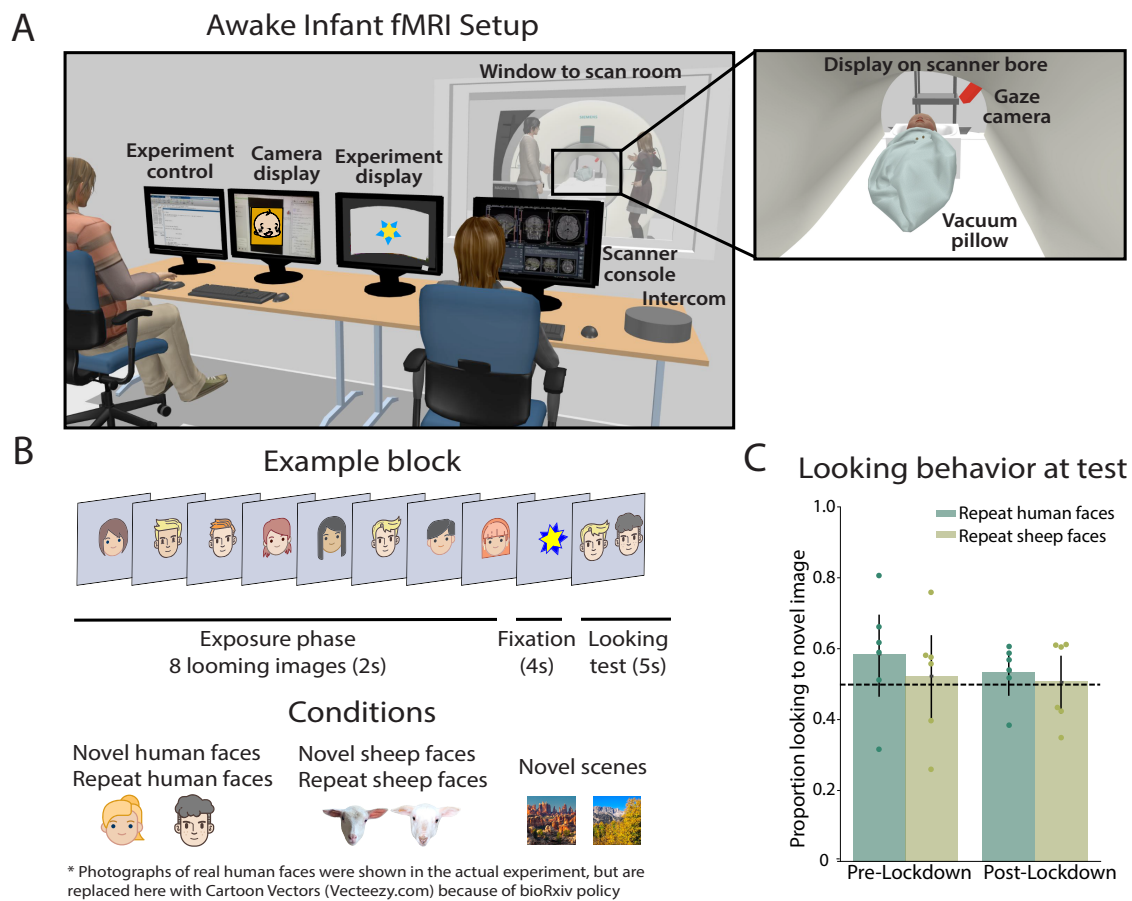

Figure 1. A. Setup for awake infant fMRI. In the control room, one experimenter monitors the infant and runs the tasks and another experimenter runs the scanner console and communicates with the experimenter in the scan room. In the scan room, an experimenter and parent stand on either side of the scanner bore. The infant is placed on a comfortable vacuum pillow at the center of the scanner bore with a panoramic view of the stimulus. A camera records the infant's face. A full description of scanning methods is available (Ellis et al., 2020). B. During an experimental block, infants viewed a series of eight looming faces or scenes, followed by a short fixation period and a VPC looking test. Example images for different block conditions are shown (bottom). C. Infant behavior during the VPC test following Repeat face blocks for pre- and post-lockdown infants. There was no reliable evidence that infants in either group looked longer to the novel vs. repeated image, for either human or sheep faces. Dots represent individual participants.

Offline Gaze Coding

Infant gaze was coded offline by 2-3 coders who determined whether their eyes were looking center, right of center, left of center, off-screen (i.e., blinking or looking away), or undetected (i.e., out of the camera's field of view). During frames from the exposure and fixation phases, the coder was instructed that the infant was "probably looking at center." This instruction was given to help calibrate coders to where the center of the screen was, but coders were allowed to indicate other responses if they believed the infant was not looking at the center. No instruction about likely looking was given for frames collected during the VPC test. Coders reported the same response code on an average of 94.4% (*SD* = 3.53%; range across participants = 83.8–97.6%) of frames. To combine across coders, we assigned each frame the modal response across coders from a moving window of five frames centered on that frame, and used the response from the previous frame in the case of ties. For a block to be included, infants needed to be looking at the screen (gaze coded as "center" during exposure and fixation phases, and either "left," "right," or "center" during VPC trials) for more than half of the frames.

We examined behavioral looking preference during the VPC test as the proportion of time looking to the novel image divided by the total time looking at either the familiar or novel image. The criteria for trials to be included in this analysis were that the infant looked at the familiar image during the earlier exposure phase (i.e., at center) and that they attended to the VPC test (i.e., at left, right, or center) for at least 500 milliseconds. We only analyzed behavior during VPC tests for Repeat blocks that were included in the fMRI analyses. We used non-parametric bootstrap resampling (Efron and Tibshirani, 1986) to test for significant preferences to the novel image. Proportion looking to the novel image was first averaged within a subject for a given condition. We then sampled average participant data from each group with replacement 1,000 times, calculating the average looking preference on each iteration. We calculated the *p*-value as the proportion of samples for which the mean was in the opposite direction from the true effect, doubled to make the test two-tailed.

fMRI Preprocessing

We preprocessed data using a pipeline that has been used in prior awake infant fMRI studies and released publicly (Ellis et al., 2020). We sometimes collected tasks for other studies in the same functional runs. When this occurred (*N* = 9), the data were separated into pseudoruns for each task. In two sessions, experimental blocks were separated by a long break within session (205 and 2,913 seconds). Otherwise, participants viewed all blocks within the same functional run.

We removed three burn-in volumes from the beginning of each run/pseudorun. The centroid volume of each run/pseudorun (i.e., the volume that minimized the Euclidean distance to all other volumes) was used as the reference volume for motion correction and anatomical alignment. Slice-timing correction was used to realign slices in each volume. We excluded timepoints with greater than 3mm of translational motion; across participants, the majority of timepoints were included after motion exclusion (*M* = 97.3%, *SD* = 3.9%; range across participants = 86.6–100%). Excluded time points were interpolated to not bias the linear detrending, and then ignored in later analyses. We also excluded blocks of data if more than 50% percent of the timepoints were excluded due to motion or infants looking away from the screen. The mask of brain vs. non-brain voxels was formed by calculating the signal-to-fluctuating-noise ratio (SFNR) (Friedman and Glover, 2006) for voxels in the centroid volume. A Gaussian kernel (5mm FWHM) was used to spatially smooth the data. Data were also linearly detrended in time, and aberrant timepoints were attenuated using AFNI's (https://afni.nimh.nih.gov) despiking algorithm.

We registered the centroid volume for each run/pseudorun to the infant's anatomical image. Alignment was initially performed using FLIRT with a normalized mutual information cost function and six degrees of freedom (DOF). After manual inspection, this automatic registration was corrected if necessary using mrAlign from mrTools (Gardner lab). Functional data were then transformed into standard adult MNI space to make comparisons across infants. First, functional data were linearly aligned to an age-specific infant template using 12 DOF. This alignment was improved with non-linear warping using diffeomorphic symmetric normalization (ANTS; Avants et al. 2011). A predefined transformation (12 DOF) between the infant template and adult standard was then used. For all analyses, we only considered voxels included in the

190   intersection of all infant brain masks.

Regions of Interest

192   Regions of interest (ROIs) were defined using Neurosynth, a meta-analytic tool that combines results from
193   published fMRI studies on different topics (Yarkoni et al., 2011). We used the search term "face" and obtained
194   a whole-brain statistical map showing z-scores from a two-way ANOVA testing the presence of activated
195   voxels associated with this term. This map indicates which regions are more consistently activated in the
196   896 studies about faces compared to all other studies in the database. The resulting map was thresholded
197   using a false discovery rate of 0.01. The coordinates for peak activation in the anatomical vicinity of the
198   right and left FFA were used as the centers of two 10mm radius spheres around these peaks of activation.
199   This bilateral FFA mask was used as the search space for our leave-one-participant-out functional ROI (fROI)
200   analysis. We also created spheres around the peak activations for other regions known to be involved in
201   face processing (Haxby et al., 2000): bilateral occipital face area (OFA), bilateral superior temporal sulcus
202   (STS), bilateral amygdala (Amyg) and right inferior frontal gyrus (rIFG). Finally, we used the same procedure
203   with search terms "primary visual cortex" and "heschl's gyrus" to obtain whole brain statistical maps for
204   defining control regions in primary visual cortex and primary auditory cortex, respectively.

Statistical analyses

206   We fit general linear models (GLMs) to preprocessed BOLD activity using FEAT in FSL. Data were split and
207   z-scored within functional runs according to three different GLM analyses: (1) a balanced number of Novel
208   human face blocks and scene blocks, (2) a balanced number of Novel and Repeat human face blocks, and (3)
209   a balanced number of Novel and Repeat sheep face blocks. In each GLM, regressors were created for the 16-
210   second exposure phases of each of the two modeled conditions, as well as for 6-second fixation periods and
211   5-second VPC tests combined across the two modeled conditions (to isolate exposure differences). Events
212   were modeled using a boxcar for their duration, convolved with a double-gamma hemodynamic response
213   function (Deen et al., 2017; Ellis et al., 2020). Motion parameters (3 translation and 3 rotation) from motion
214   correction were included in the GLM as regressors of no interest. Time points excluded for high motion
215   were scrubbed with an additional regressor for each time point.

216   The main contrast of interest for the first GLM was Novel human faces greater than scenes during the
217   exposure phase, to reveal face-selective visual responses. For the second GLM, the contrast of Novel greater
218   than Repeat human faces during the exposure phase provided an index of identity processing, with positive
219   values reflecting repetition suppression. The third GLM tested for repetition suppression of sheep faces.
220   The z-statistic volumes from these contrasts were extracted for each participant and aligned to standard
221   space.

222   Our first objective was to determine whether an infant-defined FFA showed repetition suppression to
223   Novel vs. Repeat human face blocks, and whether this differed across the pre- and post-lockdown groups.
224   To accomplish this, we extract neural responses using an fROI approach (Figure 2A). From the first GLM and
225   collapsing across pre- and post-lockdown groups (to increase power and avoid bias), we averaged the con-
226   trast of Novel human faces greater than scenes in standard space from all but one (held-out) infant. Using
227   the meta-analysis FFA sphere as a mask, we located the top 5% of voxels that showed the greatest average
228   contrast value (i.e., face selectivity; Figure 2B). Retaining these voxels, we then extracted the activation to
229   Novel and Repeat human face blocks from the second GLM of the held-out infant, and averaged across
230   voxels within condition. This procedure was iterated such that each infant was held out once. Critically, the
231   fROI was defined independently of the data from the held-out infant to prevent circularity.

232   We used non-parametric bootstrap resampling to test for the statistical significance of the extracted
233   fROI data. For each infant group and condition, we resampled z-statistic values for the contrast of Novel vs.
234   Repeat blocks (our measure of repetition suppression) with replacement 1,000 times and recalculated the
235   average for each iteration. The p-value was then the proportion of resamples that were of the opposite sign
236   as the original effect, doubled for a two-tailed test. We similarly quantified group differences in the contrast
237   of Novel vs. Repeat by performing 1,000 resamples of z-statistic contrast values for the pre-lockdown and
238   post-lockdown groups. On each iteration, we recalculated the mean value for each group and then sub-

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239 tracted the post-lockdown mean from the pre-lockdown mean. Again, the *p*-value was the proportion of
240 resamples that were of the opposite sign as the original effect, doubled for a two-tailed test.
241   We next assessed whether our results generalized beyond this fROI approach by extracting the *z*-statistic
242 values for Novel and Repeat human face blocks in all voxels from the meta-analysis FFA sphere (i.e., not just
243 the top 5%) and averaged within condition. We also measured responses in the other meta-analysis face
244 ROIs and control ROIs to test specificity to the FFA.
245   Finally, we assessed whether group differences were specific to human faces, or might apply more
246 broadly to identity processing of other types of faces by repeating these analyses for the sheep data.

Code and data availability

248 The code for the task is available at: https://github.com/ntblab/experiment_menu/tree/RepetitionNarrowing.
249 The code for the analyses is available at: https://github.com/ntblab/infant_neuropipe/tree/RepetitionNarrowing.
250 Raw and preprocessed functional and anatomical images will be released publicly upon acceptance

Results

Behavioral looking time to novel images

253 We first asked whether the pre- and post-lockdown infants differed in their amount of looking to novel
254 vs. familiar faces. We focused on VPC tests that followed Repeat blocks because these blocks contained
255 repetitions that might habituate infants to a face identity, allowing them to make a discrimination between
256 the novel and familiar test items. There was no group difference in novelty preferences for human faces (*M*
257 = 0.050, bootstrap *p* = 0.466; Figure 1C), with neither group showing a reliable preference relative to baseline
258 (pre-lockdown: proportion looking to novel *M* = 0.584, CI = [0.465, 0.697], vs. 0.5 *p* = 0.162; post-lockdown:
259 *M* = 0.534, CI = [0.468, 0.584], *p* = 0.278). This may in part reflect the relatively short habituation time and the
260 use of multiple identities and blocks across the study. Likewise, there was no group difference in novelty
261 preferences for sheep faces (*M* = 0.016, *p* = 0.848), and again neither group showed a reliable preference
262 relative to baseline (pre-lockdown: *M* = 0.522, CI = [0.396, 0.639], *p* = 0.726; post-lockdown: *M* = 0.506, CI
263 = [0.419, 0.581], *p* = 0.890). This is more expected given research showing a decline in discrimination of
264 other-species faces after 9 months (Pascalis et al., 2002; Simpson et al., 2011).

Neural responses to human face identity in infant FFA

266 We next asked whether the pre- and post-lockdown infants differed in their neural responses to human
267 faces. There was a significant group difference in the FFA fROI for the contrast of Novel vs. Repeat hu-
268 man face blocks (z-score *M* = 1.499, bootstrap *p* = 0.006; Figure 2C). In the pre-lockdown group, there was
269 marginally greater activation in the FFA fROI for Novel blocks (z-score *M* = 1.185) than Repeat blocks (*M* =
270 0.588; difference *M* = 0.749, CI = [-0.096, 1.648], *p* = 0.088), consistent with the repetition suppression hy-
271 pothesized for this group. In the post-lockdown group, however, there was *less* FFA fROI activation in Novel
272 blocks (*M* = 1.067) than Repeat blocks (*M* = 1.705; difference *M* = -0.749, CI = [-1.617, 0.016], *p* = 0.033). This
273 significant repetition *enhancement* effect implies that infants in the post-lockdown group were still able to
274 neurally distinguish face identities, but responded differently to the repetitions.
275   The group difference in the contrast of Novel vs. Repeat human face blocks remained significant when
276 considering the entire spherical FFA ROI from the meta-analysis of adult studies, rather than constraining
277 it to face-selective voxels from (other) infants (*M* = 1.325, *p* = 0.004; Figure 3B). In pre-lockdown infants, the
278 pattern was similar to the FFA fROI (Novel >Repeat) but not significant (*M* = 0.574, CI = [-0.136, 1.282], *p* =
279 0.124). In post-lockdown infants, the difference observed with the fROI approach (Repeat >Novel) remained
280 significant (*M* = -0.751, CI = [-1.337, -0.207], *p* = 0.004). Thus, our findings were fairly robust to the number
281 and selectivity of voxels contained in the FFA.

Specificity of findings to FFA

283 We next investigated the specificity of the key group difference in facial identity processing to the FFA by
284 considering spherical ROIs in the broader face processing network (OFA, STS, amygdala, rIFG; Figure 3A). The
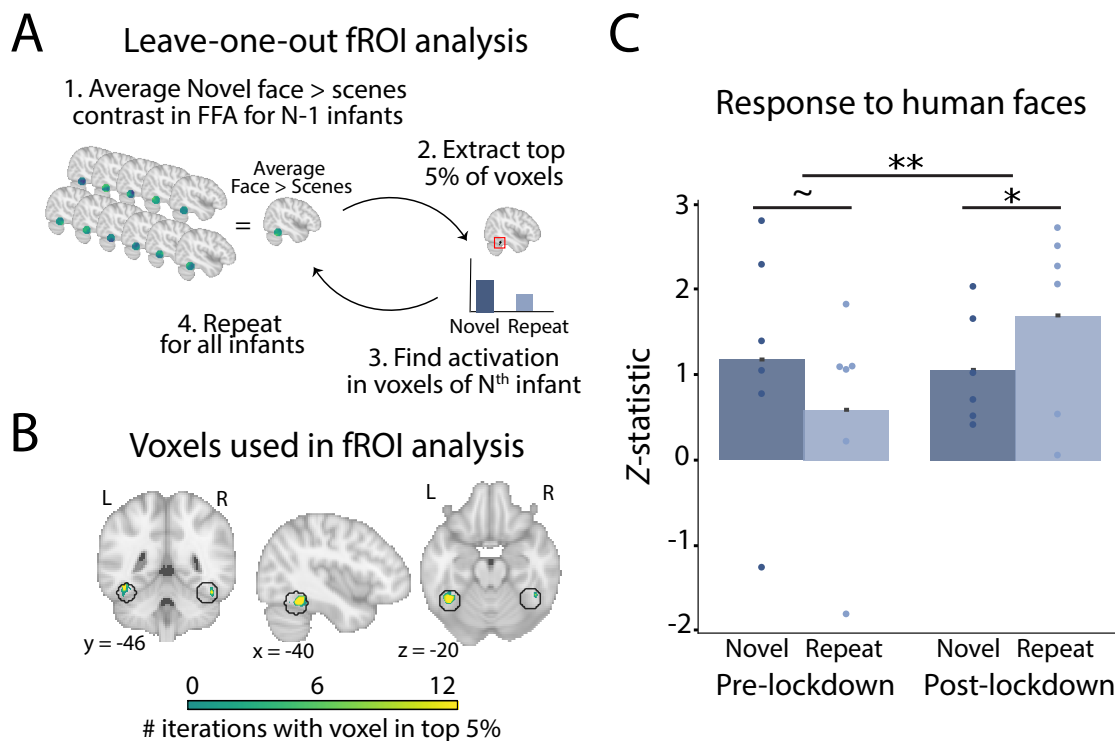
Figure 2. A. Leave-one-out fROI analysis. First, we averaged the *z*-statistics for the contrast of Novel human face blocks greater than scene blocks in *N* minus one infants. We selected the voxels with the top 5% of average values as being the most face-selective to define an fROI independently of the remaining infant. We then extracted the average *z*-statistics for Novel and Repeat human face blocks from these voxels in this held-out infant. We repeated the procedure 12 times so that each infant was held-out once. B. Voxels used in the fROI analysis. The circles outline the spherical FFA search space from the meta-analysis. Each voxel is colored by the number of iterations (of 12) in which it was among the top 5%. C. There was a robust group difference in the contrast of Novel vs. Repeat human face blocks: the neural response was marginally greater for Novel than Repeat human face blocks in pre-lockdown infants (repetition suppression), and significantly greater for Repeat than Novel in post-lockdown infants (repetition enhancement). Dots are individual participants. ** *p* < 0.01, * *p* < 0.05, ~*p* < 0.10.

group difference between pre- and post-lockdown infants in the Novel vs. Repeat contrast was significant in the STS (*M* = 1.251, *p* = 0.018) and marginal in OFA (*M* = 0.946, *p* = 0.058) and rIFG (*M* = 1.089, *p* = 0.083), but not in amygdala (*M* = 0.670, *p* = 0.157; 3B). This effect extended to a spherical ROI in primary visual cortex (*M* = 1.372, *p* = 0.009) but not primary auditory cortex (*M* = 0.839, *p* = 0.218; Figure 3C). If correcting for multiple comparisons across all seven spherical ROIs, only the FFA survives (Bonferroni *p* = 0.007). These results indicate relative specificity of the group effect to the FFA.

Specificity of findings to human faces

Finally, we examined the specificity of the results to human faces by repeating the analyses above for sheep face blocks (Figure 4). We did not use the FFA fROI because the voxels in the fROI were chosen based on responses to human face blocks, which might introduce a bias in favor of specificity to human faces. However, considering all voxels in the spherical ROI for FFA, there was a marginal group difference in the contrast of Novel vs. Repeat sheep face blocks (*M* = 1.067, *p* = 0.054), which did not survive correction for multiple comparisons. There was a greater neural response for Novel than Repeat sheep face blocks in pre-lockdown infants (*M* = 1.120, CI = [0.622, 1.625], *p* <0.001) but no effect in either direction in post-lockdown infants (*M* = 0.052, CI = [-0.702 , 1.013], *p* = 0.962). Thus, FFA results for sheep faces were similar to human faces, with a weaker group difference driven by the lack of sensitivity to sheep face identity in post-lockdown infants who had shown strong repetition enhancement for human face identity.
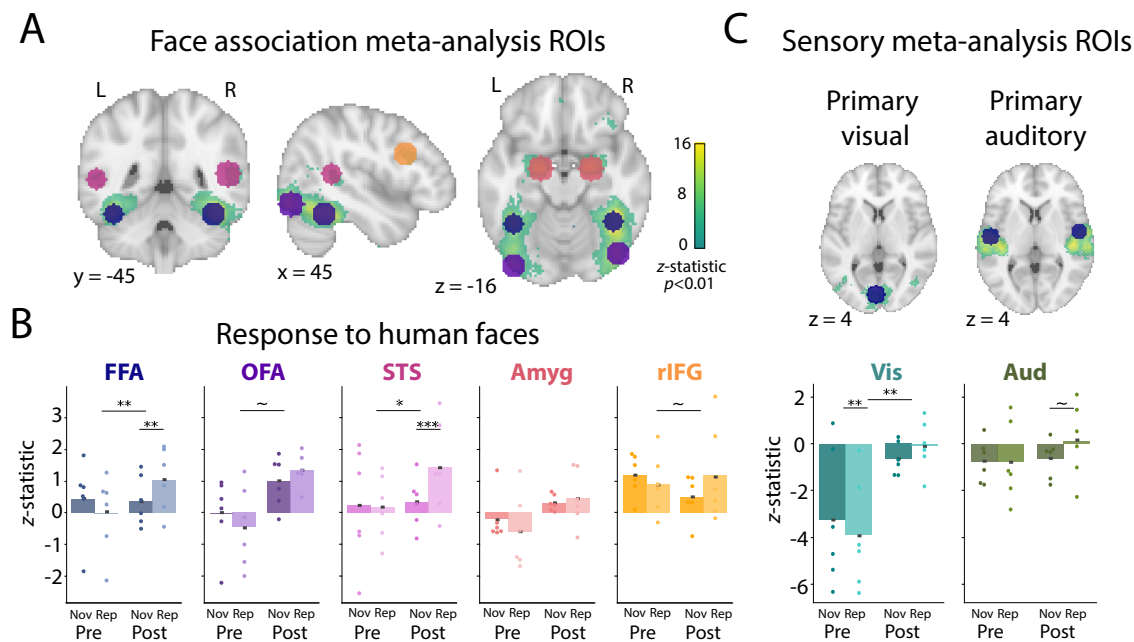
Figure 3. A. Spherical ROIs derived from an adult meta-analysis for the term "face" (Yarkoni et al., 2011). The voxel with the peak *z*-statistic value was assigned the center of a 10mm radius sphere. B. The spherical ROI containing all FFA voxels largely mirrored the results from the FFA fROI limited to the most face-selective voxels. A similar group difference in the Novel vs. Repeated contrast was found in the spherical ROI for STS and marginally for OFA and rIFG, but not for amygdala. C. The spherical ROI in primary visual cortex but not primary auditory cortex showed a similar group difference. The overall negative activity in primary visual cortex may reflect the inclusion of voxels responsive to the periphery of the visual field that did not contain stimuli. Dots are individual participants. *** *p* < 0.001, ** *p* < 0.01, * *p* < 0.05, ~*p* < 0.10. ROIs: fusiform face area (FFA), occipital face area (OFA), superior temporal sulcus (STS), amygdala (Amyg) right inferior frontal gyrus (rIFG), primary visual cortex (Vis), and primary auditory cortex (Aud)

302   When considering sheep face blocks in the broader set of spherical ROIs for face and sensory processing,
303   we again focused on the key group difference in the contrast of Novel vs. Repeat. Only the OFA showed a
304   significant group difference (*M* = 0.751, *p* = 0.049, which did not survive multiple comparisons correction).
305   The other spherical ROIs did not show a reliable group difference: STS (*M* = -0.098, *p* = 0.837), amygdala (*M*
306   = -0.154, *p* = 0.695), rIFG (*M* = -0.125, *p* = 0.836), primary visual cortex (*M* = 0.195, *p* = 0.699), and primary
307   auditory cortex (*M* = -0.733, *p* = 0.138).

Discussion

309   We investigated face identity processing in the brains of infants tested before and after the initial COVID-19
310   lockdown in our State. The neural responses of these groups to human faces differed: pre-lockdown infants
311   showed some evidence of repetition suppression (Novel >Repeat) for human faces in the FFA, similar to what
312   is seen in adults (Grill-Spector and Malach, 2001) and older children (Natu et al., 2016); post-lockdown infants
313   showed the opposite, repetition *enhancement* (Repeat >Novel). This group difference was most robust in
314   the FFA compared to other brain regions and for human faces compared to sheep faces.
315   This pattern of results is reminiscent of the debate over novelty vs. familiarity preferences in infant be-
316   havior (e.g., reduced vs. increased looking at repeated stimuli). Familiarity preferences are more likely in
317   younger infants, for more complex stimuli, after shorter exposure, and for more difficult tasks (Rose et al.,
318   1982; Hunter and Ames, 1988; Roder et al., 2000). Likewise, the adult brain shows increased processing of
319   repeated stimuli when the stimuli are unfamiliar or briefly exposed (Henson et al., 2000; Turk-Browne et al.,
320   2007; Segaert et al., 2013). By this account, human faces could be considered a more familiar category to
321   pre-lockdown infants, with exposure to a greater number of unique faces building a more robust face space
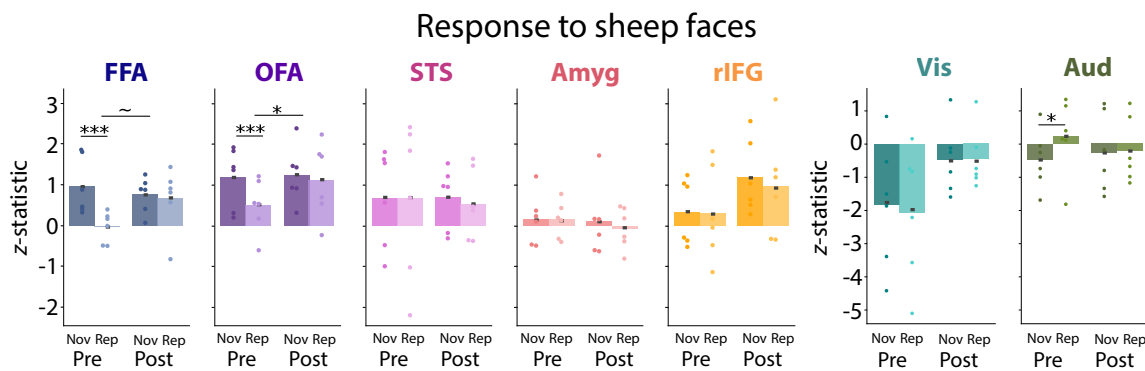
Figure 4. There was a group difference in the Novel vs. Repeat contrast for sheep faces in the spherical ROI for OFA and marginally for FFA, but was not for STS, amygdala, rIFG, primary visual cortex, or primary auditory cortex. Dots represent individual participants. *** $p < 0.001$, * $p < 0.05$, ~$p < 0.10$.

322 (Humphreys and Johnson, 2007), than to post-lockdown infants with more restricted face experiences. In
323 particular, the pandemic presumably reduced exposure to faces that would have been experienced infre-
324 quently (e.g., relatives and strangers). This lends credence to the possibility that even limited exposure to
325 different face exemplars can impact face processing (Spangler et al., 2013).

326 Notably, our behavioral measure in the scanner did not mirror the neural measure, as might have been
327 expected (Snyder and Keil, 2008; Turk-Browne et al., 2008; Nordt et al., 2016). We interpret these null be-
328 havioral results with caution given the difficulty of collecting reliable behavior in the scanner even in adults
329 and the possibility of different sensitivity and noise for neural and behavioral measures. Nevertheless, adult
330 fMRI studies have shown that repetition suppression and enhancement can occur in the absence of (Segaert
331 et al., 2013), and be dissociated from (Xu et al., 2007), behavioral measures of priming. Moreover, the similar
332 pattern of looking behavior between groups during exposure and test phases is inconsistent with an atten-
333 tional explanation of the group difference in neural responses, whereby the strength of neural responses
334 might be an artifact of the amount of stimulus viewing. We believe that our findings illustrate the benefit of
335 using multiple measures to study infant cognition (LoBue et al., 2020) and the potential of brain imaging to
336 disentangle cognitive processes (Yates et al., 2021).

337 It is tempting to interpret these data in relation to how pandemic precautions such as social distancing
338 and face masks altered early face experience, especially given the strict local guidelines that were imposed.
339 However, this link is speculative in our study because we did not measure daily exposure to faces in the pre-
340 or post-lockdown group; indeed, this study was designed and partially completed prior to the pandemic.
341 Thus, we cannot conclude definitively that our results are related to altered visual experience with faces.
342 The pandemic had many other impacts on daily life that could explain neural differences. Perhaps most
343 relevant to face processing is an increase in maternal fear and anxiety (Cameron et al., 2020; Davenport
344 et al., 2020) that may have affected how mothers interacted with their infants (Nicol-Harper et al., 2007)
345 and how infants process faces (Bowman et al., 2021). Although the causal mechanism remains unclear,
346 this is a unique and likely one-time dataset that could contribute to our understanding of how face identity
347 processing changes in early development.

348 Our study has a number of other limitations. First, the sample size per group was small and spanned
349 a wide age range. Our initial intention was to use this age variability to study perceptual narrowing. We
350 combined data across ages to increase statistical power, knowing that face processing changes over this
351 time (Pascalis et al., 2020). Additionally, although the groups were roughly matched (fortuitously) on key
352 variables such as infant age, number of usable blocks, head motion, and eye gaze, the biological sex of the
353 infants was not matched. There was an equal number of male and female infants post-lockdown, but all pre-
354 lockdown infants were born female. The small sample size precludes any examination of sex differences.
355 Although there are some advantages in face processing for female infants (Gluckman and Johnson, 2013),
356 the evidence is mixed (Simpson et al., 2020; Maylott et al., 2021). Finally, although most data collection

357 procedures were identical across groups, there was one key difference: whether the experimenters and
358 parents wore face masks. It is possible that exposure to normal vs. obscured faces immediately prior to
359 the experiment affected how infants processed faces. The serendipitous and opportunistic nature of this
360 project means that we are saddled with these limitations, yet we believe the data remain valuable to report
361 and may inform debates on the role of experience in the early development of face processing.

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Conflict of interest

371
372 No conflict of interest.

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517 **Appendix**

ID	Age	Sex	TR prop	Total blocks	Eye IRR	Days quarantine
s8687_1_5	17.1	F	1.000	15	0.976	n/a
s6687_1_5	18.1	F	1.000	15	0.974	n/a
s4607_1_4	13.0	F	0.982	10	0.929	n/a
s4607_1_6	16.9	F	1.000	10	0.971	n/a
s8037_1_2	12.2	F	0.976	15	0.934	n/a
s7067_1_3	9.2	F	1.000	15	0.949	n/a
s8687_2_1	10.7	F	0.975	14	0.935	244
s6057_1_6	23.8	M	1.000	10	0.961	213
s7047_1_2	17.6	F	1.000	15	0.958	216
s3097_1_4	13.4	F	0.866	14	0.838	185
s5477_1_1	13.3	M	0.933	15	0.956	215
s5477_1_2	17.7	M	0.947	10	0.948	349

Table A1. Demographic information. The first six infants are the pre-lockdown group and the next six infants are the post-lockdown group. '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. 'Age' is recorded in months. 'Sex' is female or male. 'TR prop' is the proportion of TRs included from all usable blocks. 'Total blocks' is the number of blocks across all five conditions that were usable after motion and gaze exclusion. 'Eye IRR' is the proportion of frames coded the same way across gaze coders. 'Days quarantine' is the number of days between the start of the first lockdown in our State (March 15, 2020) and the day of the scan.