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RESEARCH ARTICLE

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 versus repeat blocks in such designs, suggesting that it can distinguish same versus different face identities. As part of an ongoing study, we collected data before the COVID-19 pandemic and after an initial local 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
experience, face identity, face recognition, fMRI, neuroimaging

1 | 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 (Johnson et al., 2015; Kanwisher, 2010; Morton & Johnson, 1991; Turati, 2004), early visual experience can shape at least one aspect of face processing: 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 & Werker, 2014; Pascalis et al., 2020; Werker & Tees, 1984).

Evidence that perceptual narrowing is related to experience, rather than maturation, comes from studies that manipulate exposure to non-native faces (Anzures et al., 2012; Pascalis et al., 2005; Sangrigoli & De Schonen, 2004). 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 familiar 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 to distinguish Asian female and male faces after daily exposure to videos of Asian women (Anzures et al., 2012). This period of plasticity is not indefinite: other-race (White) face recognition in Asian immigrants is significantly related to when in development they moved to a majority White country (Zhou et al., 2019).

Cases of deprivation provide an additional angle on the critical role that early visual experience plays in face identity processing. For instance, individuals with bilateral congenital cataracts at birth are impaired at holistic face processing (Grand et al., 2004; Le Grand et al., 2001) and individual face memory (De Heering & Maurer, 2014) even years after corrective surgery (Maurer, 2017; cf. McKone et al., 2012). In another study, infant monkeys deprived of faces early in life were later shown either human or monkey faces for a month, prior to daily exposure to both species; immediately and one year later, monkeys could only distinguish face identities for the species to which they were initially exposed (Arcaro & Livingstone, 2021; Sugita, 2008).

It is unethical to conduct these kinds of causal tests in healthy human infants. In early 2020, however, the opportunity for a natural experiment in visual plasticity arose in response to the coronavirus disease 2019 (COVID-19) global pandemic. Emergency lockdowns and stay-at-home orders, as well as face mask coverings in public spaces, were used to prevent viral spread. These precautions abruptly changed daily life, including the nature of face-to-face interactions. Although infant face experience is highly biased toward primary caregivers (Sugden & Moulson, 2019), which continued and if anything may have expanded during lockdowns, absent or altered exposure to relatives and strangers during the COVID-19 pandemic may have influenced the development of face processing (Carnevali et al., 2022; Green et al., 2021). In particular, exposure to a more homogenous set of faces at home could alter identity processing. Indeed, smaller hometowns are associated with reduced accuracy on more difficult face recognition tasks (Balas & Saville, 2017; Sunday et al., 2019).

The tragic events of the COVID-19 pandemic therefore resulted in a quasi-experiment: We had been conducting an infant fMRI study before the pandemic, paused it during the first lockdown, and then resumed data collection after 5 months. The original purpose of this study was to investigate how the infant brain represents human and non-human face identities during the period of infancy when perceptual narrowing is thought to occur, as reflected in the experimental design. However, with access to pre- versus post-lockdown infant groups, we hypothesized that the lockdown and associated changes in infant exposure to faces may have altered face processing in the infant brain. Following a classic repetition suppression (or adaptation) design from adult fMRI (Grill-Spector et al., 2006; Turk-Browne et al., 2008), we showed infants blocks of faces that were of the same or different identities. We used fMRI because it has the spatial resolution and sensitivity to resolve visual regions on the ventral surface of the brain distant from the scalp, including the fusiform face area (FFA), which was our primary region of interest (ROI). In adults, the FFA tends to show reduced neural activity when the identity of a face is repeated versus changed (Barron et al., 2016; Grill-Spector & Malach, 2001; Henson, 2016). Recent studies have established that the FFA is present in infants (Deen et al., 2017; Kosakowski et al., 2021). However, it is unknown whether the infant FFA additionally distinguishes face identities like in adults, and if so, how this may have been impacted by lockdowns. There are several possible reasons to expect such an impact, for example: limited exposure to novel faces may reduce the density of face space and broaden identities (Humphreys & Johnson, 2007; Tanaka et al., 1998), enhanced exposure to familiar faces (in this case, primary caregivers) may alter the dimensions of face space (De Haan et al., 2002; Quinn et al., 2002), and/or exposure to masked faces may disrupt holistic processing (Carnevali et al., 2022).

We hypothesized from the start of this study that (pre-lockdown) infants would show repetition suppression in FFA, which would indicate that the infant FFA can distinguish face identities. To the extent that the lockdown affected the development of face identity processing, we hypothesized that repetition suppression might be attenuated or eliminated. Specifically, if the post-lockdown infant FFA does not distinguish face identities, there should be no neural difference between same versus different identities.

2 | METHODS

2.1 | Participants

The study was approved by the Institutional Review Board at Yale University. Parents provided informed consent on behalf of their child. A total of 12 sessions of fMRI data from infants aged 9–24 months met inclusion criteria of at least two blocks per condition with pairs of novel and repeat face blocks occurring in the same functional run (Table 1; Table S1). The dataset divided equally into six pre-lockdown sessions (six female) collected prior to the onset of pandemic restrictions in March 2020 and six post-lockdown sessions (three female) collected after these restrictions were lifted in August 2020 (through February 2021). This sample size was determined by matching the number of post-lockdown sessions to the number of usable pre-lockdown sessions. The amount of data collected before the lockdown could not be planned prospectively, given the unexpected arrival of the pandemic. The sample size of 12 was thus fixed by external circumstances, as it was impossible to add more infants to the pre-lockdown group after the lockdown. Although this small sample is an inherent limitation of the study, it is nevertheless within the range of the seminal fMRI studies with awake infants (Biagi et al., 2015; Deen et al., 2017; Dehaene-Lambertz, 2002).

An additional 13 usable sessions were collected prior to the pandemic from infants under 9 months, but infants this young 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. Families were invited to return to the laboratory to participate in this and other ongoing fMRI experiments. In the final sample, two unique infants provided two sessions of usable data each (in other words, these participants had two or more usable pairs of novel and repeat face blocks at one fMRI session, and two or more usable pairs of novel and repeat face blocks at a later fMRI session). 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. Following prior studies (Ellis et al., 2020), the data from these sessions

TABLE 1 Comparison of pre- and pos-tlockdown infant groups across demographic factors and measures of data quality and quantity. Values reflect mean with standard deviation in parentheses

	Pre-lockdown infants	Post-lockdown infants	*p* Value
Days between start of lockdown and test date	n/a	237.00 (52.91)	n/a
Age in months	14.42 (3.19)	16.08 (4.25)	.442
Number blocks total	13.33 (2.36)	13.00 (2.16)	.732
Percent gaze reliability	95.56 (1.93)	93.26 (4.32)	.214
Percent TRs after motion (novel human)	98.53 (3.29)	97.06 (4.20)	.484
Percent TRs after motion (repeat human)	99.67 (0.73)	95.59 (7.76)	.076
Percent looking during exposure phase (novel human)	89.53 (3.46)	86.91 (7.70)	.524
Percent looking during exposure phase (repeat human)	88.41 (2.79)	87.88 (4.86)	.860

were treated as independent because they occurred several months apart (3.9 and 4.4 months between sessions, respectively). Regardless, our main neural results replicated when we restricted analysis to the first session from the 10 unique infants (Figure S1a).

We recontacted the families of all 10 unique participants in March 2022 to collect additional demographic data and information on COVID-19 experiences. One of the families could not be reached despite multiple attempts. Most parents reported the race/ethnicity of their child to be White (pre-lockdown infants: $N = 4$ White, $N = 1$ no answer; post-lockdown infants: $N = 5$ White) and non-Hispanic (pre-lockdown infants: $N = 4$ non-Hispanic, $N = 1$ no answer; post-lockdown infants: $N = 3$ non-Hispanic, $N = 2$ Hispanic). The responding parent self-identified as White (pre-lockdown parents: $N = 4$ White, $N = 1$ no answer; post-lockdown parents: $N = 5$ White) and non-Hispanic (pre-lockdown parents: $N = 4$ non-Hispanic, $N = 1$ no answer; post-lockdown infants: $N = 5$ non-Hispanic). According to the 2020 American Community Survey (https://data.census.gov/cedsci), these families tended to live in urban/suburban areas (average population size in zip code for pre-lockdown infants: 24,643; post-lockdown infants: 21,479) where the majority of residents were White (average percent in zip code for pre-lockdown infants: 90.6%; post-lockdown infants: 73.1%; note that respondents identifying as White plus one or more other races are counted separately in the survey). Finally, infants were from roughly equal household sizes (average household size for pre-lockdown infants: 3.8; post-lockdown infants: 4.0). Thus, the demographics of the groups were comparable.

2.2 | fMRI data acquisition

We followed validated procedures and parameters (see Figure 1a) for collecting fMRI data from awake infants (Ellis et al., 2020, 2021a, 2021b, 2021c; 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 = 30 ms, flip angle = 71, matrix = 64 × 64, slices = 34, resolution = 3 mm iso, interleaved slice acquisition). For each session, we also collected anatomical images with a T1 PETRA sequence (TR1 = 3.32 ms, TR2 = 2250 ms, TE = 0.07 ms, flip angle = 6, matrix = 320 × 320, slices = 320, resolution = 0.94 mm iso, radial slices = 30,000).

2.3 | 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 an 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 × 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. Note that the families who responded to our retrospective demographic survey were White, making White faces a same-race category for them.

Each experimental block began with an exposure phase in which eight images were shown consecutively for 2 s each, looming from 1

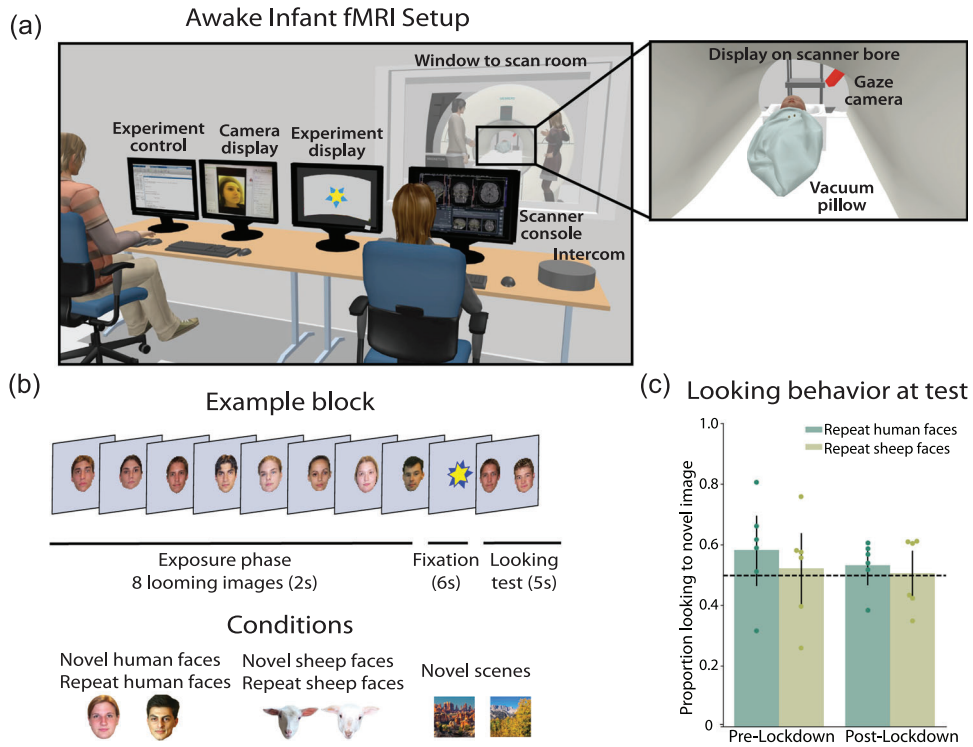

FIGURE 1 (a) Setup for awake infant fMRI. In the control room, one experimenter monitors the infant and runs the tasks and another experimenter runs the scanner console and communicates with the experimenter in the scan room. In the scan room, an experimenter and parent stand on either side of the scanner 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 versus repeated image, for either human or sheep faces. Dots represent individual participants.

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 6 s to encourage fixation. This was followed by a 5-s 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 10 visual degrees. Each block thus lasted 27 s, followed by 7 s 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 two blocks of each condition (10 total blocks = 5.7 min of data) but continued collecting more data if possible. Infants had 7.5 min (13.3 blocks) and 7.0 min (13.0 blocks) of usable data on average in the pre-lockdown and post-lockdown groups, respectively, not including TRs excluded for motion. Although less data than typical adult fMRI studies, these numbers compare favorably with other awake infant fMRI studies (2.5–6.7 min; Biagi et al., 2015; Deen et al., 2017; Ellis et al., 2020, 2021a, 2021b, 2021c; Kosakowski et al., 2021).

2.4 | Offline gaze coding

Infant gaze was coded offline by two to three 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). Coders were blind to block and condition information. 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 ms. We only analyzed behavior during VPC tests for repeat blocks that were included in the fMRI analyses. We used nonparametric bootstrap resampling (Efron & 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 1000 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.

2.5 | 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 2913 s). 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 time points with greater than 3 mm of translational motion; across participants, the majority of time points 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 time points were excluded due to motion or infants looking away from the screen. The mask of brain versus nonbrain voxels was formed by calculating the signal-to-fluctuating-noise ratio (Friedman & Glover, 2006) for voxels in the centroid volume. A Gaussian kernel (5 mm FWHM) was used to spatially smooth the data. Data were also linearly detrended in time, and aberrant time points 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 nonlinear 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 intersection of all infant brain masks.

2.6 | Regions of interest

ROIs were defined with help from Neurosynth, a meta-analytic tool that combines results from published fMRI studies (Yarkoni et al., 2011). Most of these studies were conducted in adults, whose neural selectivity may differ from infants. Thus, we used Neurosynth only as a rough guide to define a search space within which we could identify face-selective voxels from infants alone in a data-driven and cross-validated manner, resulting in infant-specific functional ROIs (fROIs). We used the search term "face" and obtained a whole-brain statistical map showing *z*-scores from a two-way ANOVA testing the presence of activated voxels associated with this term. This map indicates which regions are more consistently activated in the 896 studies about faces compared with all other studies in the database. The resulting map was thresholded using a false discovery rate of .01. The coordinates for peak activation in the anatomical vicinity of the right and left FFA were used as the centers of two 10 mm radius spheres around these peaks of activation. This bilateral FFA mask was used as the search space for our leave-one-participant-out fROI analysis, described below. We also created spheres around the peak activations for other regions known to be involved in face processing (Haxby et al., 2000): bilateral occipital face area (OFA), bilateral superior temporal sulcus (STS), bilateral amygdala (Amyg), and right inferior frontal gyrus (rIFG). Finally, we used the same procedure with search terms "primary visual cortex" and "Heschl's gyrus" to obtain whole brain statistical maps for defining control regions in primary visual cortex and primary auditory cortex, respectively.

2.7 | Statistical analyses

We fit general linear models (GLMs) to preprocessed BOLD activity using FEAT in FSL. Data were split and *z*-scored within functional runs according to three different GLM analyses: (1) a balanced number of novel human face blocks and scene blocks, (2) a balanced number of novel and repeat human face blocks, and (3) a balanced number of novel and repeat sheep face blocks. In each GLM, regressors were created for the 16-s exposure phases of each of the two modeled conditions, as well as for 6-s fixation periods and 5-s VPC tests combined across the two modeled conditions (to isolate exposure differences). Events were modeled using a boxcar for their duration, convolved with

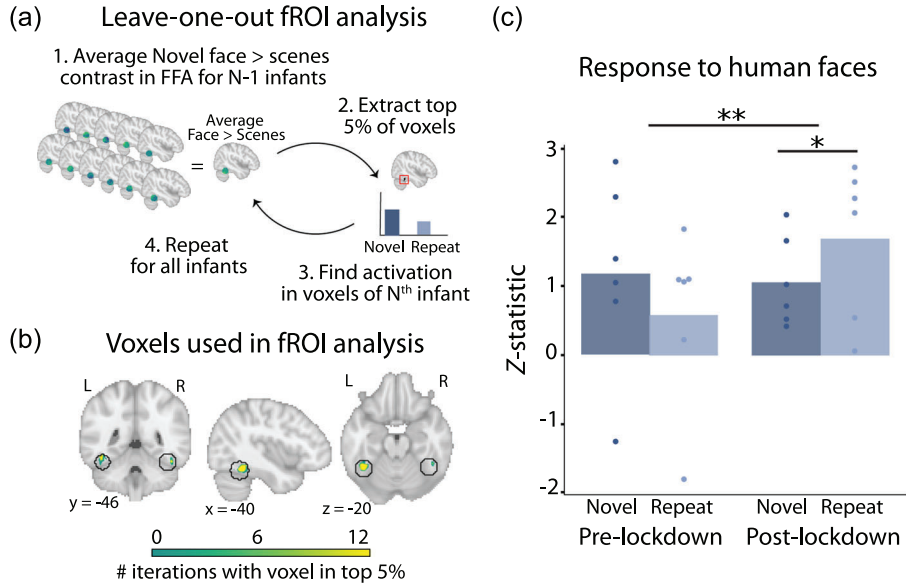

FIGURE 2 (a) Leave-one-out fROI analysis. First, we averaged the *z*-statistics for the contrast of novel human face blocks greater than scene blocks in *N* minus one infants. We selected the voxels with the top 5% of average values as being the most face-selective to define an fROI independently of 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 versus 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. $^{**}p < .01$, $^{*}p < .05$.

a double-gamma hemodynamic response function (Deen et al., 2017; Ellis et al., 2020). Motion parameters (three translation and three rotation) from motion correction were included in the GLM as regressors of no interest. Time points excluded for high motion were scrubbed with an additional regressor for each time point.

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

Our first objective was to determine whether an infant-defined FFA showed repetition suppression to novel versus repeat human face blocks, and whether this differed across the pre- and post-lockdown groups. To accomplish this, we extracted neural responses using an fROI approach (Figure 2a). From the first GLM and collapsing across pre- and post-lockdown groups (to increase power and avoid bias), we averaged the contrast of novel human faces greater than scenes in standard space from all but one (held-out) infant. Using the meta-analysis FFA sphere as a mask, we located the top 5% of voxels that showed the greatest average contrast value (i.e., face selectivity; Figure 2b). Retaining these voxels, we then extracted the activation to novel and repeat human face blocks from the second GLM of the held-out infant and averaged across voxels within condition. This procedure was iterated such that each infant was held out once. Critically, the fROI was defined independently of the data from the held-out infant to prevent circularity. We also explored whether our results were consistent if we instead held out two infants (one from each group) when determining the top voxels (Figure S1b) and when varying the percent of top voxels we used (Figure S2).

We used nonparametric bootstrap resampling to test for the statistical significance of the extracted fROI data (Efron & Tibshirani, 1986). Bootstrapping requires fewer assumptions than parametric tests and has been shown to increase power while maintaining a low type I error rate in small samples (Dwivedi et al., 2017). Nonetheless, our main FFA results persist when we instead used a parametric independent samples *t*-test or a nonparametric randomization test (*p*s < .05). For each infant group and condition, we resampled *z*-statistic values for the contrast of novel versus repeat blocks (our measure of repetition suppression) with replacement 1000 times and recalculated the average for each iteration. The *p* value was then the proportion of resamples that were of the opposite sign as the original effect, doubled for a two-tailed test. We similarly quantified group differences in the contrast of novel versus repeat by performing 1000 resamples of *z*-statistic contrast values for the pre-lockdown and post-lockdown groups. On each iteration, we recalculated the mean value for each group and then subtracted the post-lockdown mean from the pre-lockdown mean. Again, the *p* value was the proportion of resamples that were of the opposite sign as the original effect, doubled for a two-tailed test.

We next assessed whether our results generalized beyond this fROI approach by extracting the *z*-statistic values for novel and repeat human face blocks in all voxels from the meta-analysis FFA sphere

(i.e., not just the top 5%) and averaged within condition. We also measured responses in the other meta-analysis face ROIs and control ROIs to test specificity to the FFA.

Finally, we assessed whether group differences were specific to human faces or might apply more broadly to identity processing of other types of faces by repeating these analyses for the sheep data.

2.8 | Data availability

The code for the task is available at: https://github.com/ntblab/experiment_menu/tree/RepetitionNarrowing. The code for the analyses is available at: https://github.com/ntblab/infant_neuropipe/tree/RepetitionNarrowing. Raw and preprocessed functional and anatomical images are available on DataDryad: https://doi.org/10.5061/dryad.tb2rbp045.

3 | RESULTS

3.1 | Parental report on the COVID-19 pandemic experience

To better understand infants' experiences with faces around the time of their session, we collected self-reported data from the nine (of 10) unique families who responded to our survey (Table S2; no response from one pre-lockdown family). Parents answered questions including "On average, how often did your child spend time in daycare or school?" and "On average, how often did your child spend time in a public space where they might see people outside of their household (e.g., park, library, restaurant)?" on a scale from "Never" to "Daily." All parents answered the same set of questions for the time periods prior to the pandemic (before March 2020), at the start of the pandemic (between March 2020 and February 2021), and more recently (February 2021 to present). Parents were also given free-form space to elaborate on their COVID-19 experiences, although only a subset of parents provided additional information (Table S3). Here, we summarize the time periods immediately prior to data collection, namely the pre-pandemic period for pre-lockdown infants and the pandemic start period for the post-lockdown infants. Overall, at the time of their scan, many of the pre- and post-lockdown infants never went to daycare/school or spent time with a nanny (Table S2). Infants in both groups saw family members outside of the home environment infrequently, between once a month to a few times a week. The most noticeable difference between the groups was the time spent in public spaces: Although pre-lockdown infants tended to spend time in public several times a week, post-lockdown infants tended to spend time in public only once a month. This very coarse measure of exposure to faces outside of the immediate or extended family fits with our supposition that the COVID-19 lockdown may have reduced infant exposure to novel faces. Additionally, post-lockdown infants seemed to have had increased exposure to faces of familiar others, with at least one caregiver working from home in four of five post-lockdown families (Table S3). Finally, there was variability in the amount of time post-lockdown infants saw people wearing face masks, whereas pre-lockdown infants had no face mask exposure at the time of their scans. Thus, although limited, our survey data suggest that some aspects of infant face experience differed between groups.

3.2 | Behavioral looking time to novel images

We first asked whether the pre- and post-lockdown infants differed in their amount of looking to novel versus familiar faces. We focused on VPC tests that followed repeat blocks because these blocks contained repetitions that might habituate infants to a face identity, allowing them to make a discrimination between the novel and familiar test items. There was no group difference in novelty preferences for human faces (M = .050, bootstrap p = .466; Figure 1c), with neither group showing a reliable preference relative to baseline (pre-lockdown: proportion looking to novel M = .584, CI = [.465, .697], vs. .5 p = .162; post-lockdown: M = .534, CI = [.468, .584], p = .278). This may in part reflect the relatively short habituation time and the use of multiple identities and blocks across the study. Likewise, there was no group difference in novelty preferences for sheep faces (M = .016, p = .848), and again neither group showed a reliable preference relative to baseline (pre-lockdown: M = .522, CI = [.396, .639], p = .726; post-lockdown: M = .506, CI = [.419, .581], p = .890). This is more expected given research showing a decline in discrimination of other-species faces after 9 months (Pascalis et al., 2002; Simpson et al., 2011).

3.3 | Neural responses to human face identity in infant FFA

We next asked whether the pre- and post-lockdown infants differed in their neural responses to human faces. There was a significant group difference in the FFA fROI for the contrast of novel versus repeat human face blocks (z-score M = 1.499, bootstrap p = .006; Figure 2c). In the pre-lockdown group, there was marginally greater activation in the FFA fROI for novel blocks (z-score M = 1.185) than repeat blocks (M = 0.588; difference M = 0.749, CI = [−0.096, 1.648], p = .088), consistent with the repetition suppression hypothesized for this group. In the post-lockdown group, there was *less* FFA fROI activation in novel blocks (M = 1.067) than repeat blocks (M = 1.705; difference M = −0.749, CI = [−1.617, 0.016], p = .033). This significant repetition *enhancement* effect implies that infants in the post-lockdown group were still able to neurally distinguish face identities, but responded differently to the repetitions. This pattern of results was also found when we considered only unique participants (Figure S1a) and when we used a leave-two-out procedure (Figure S1b).

The group difference in the contrast of novel versus repeat human face blocks remained significant when considering the entire spherical FFA ROI from the meta-analysis of adult studies, rather than constraining it to face-selective voxels from (other) infants (M = 1.325, p = .004; Figure 3b). In pre-lockdown infants, the numerical pattern was similar

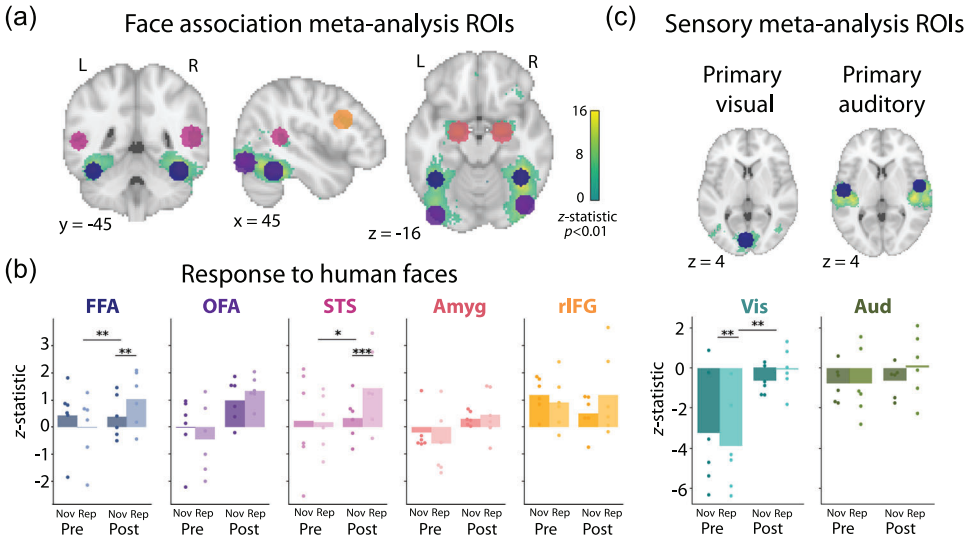

FIGURE 3 (a) Spherical ROIs derived from an adult meta-analysis for the term "face" (Yarkoni et al., 2011). The voxel with the peak *z*-statistic value was assigned the center of a 10 mm radius sphere. (b) The spherical ROI containing all FFA voxels largely mirrored the results from the FFA fROI limited to the most face-selective voxels. A similar group difference in the novel versus 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. $^{***}p < .001$, $^{**}p < .01$, $^{*}p < .05$, uncorrected. 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).

to the FFA fROI (novel > repeat: $M = 0.574$, CI = [−0.136, 1.282], $p = .124$). In post-lockdown infants, the difference observed with the fROI approach (repeat > novel) remained significant ($M = -0.751$, CI = [−1.337, −0.207], $p = .004$). Furthermore, group differences persisted across a range of top voxel percentages between 1 and 100 (Figure S2). Thus, our findings were fairly robust to the number and selectivity of voxels contained in the FFA.

3.4 | Specificity of findings to FFA

We next investigated the specificity of the key group difference in facial identity processing to the FFA by considering spherical ROIs in the broader face processing network (OFA, STS, amygdala, rIFG; Figure 3a). The group difference between pre- and post-lockdown infants in the novel versus repeat contrast was significant in the STS ($M = 1.251$, $p = .018$) and marginal in OFA ($M = 0.946$, $p = .058$) and rIFG ($M = 1.089$, $p = .083$), but not in amygdala ($M = 0.670$, $p = .157$; Figure 3b). This effect extended to a spherical ROI in primary visual cortex ($M = 1.372$, $p = .009$) but not primary auditory cortex ($M = 0.839$, $p = .218$; Figure 3c). If correcting for multiple comparisons across all seven spherical ROIs, only the FFA survives (Bonferroni $p = .007$). These results indicate relative specificity of the group effect to the FFA.

3.5 | Specificity of findings to human faces

We examined the specificity of the FFA results to human faces by repeating the analyses above for sheep face blocks (Figure S3). 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. Considering all voxels in the spherical ROI for FFA, there was a marginal group difference in the contrast of novel versus repeat sheep face blocks ($M = 1.067$, $p = .054$), 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], $p < .001$) but no difference in post-lockdown infants ($M = 0.052$, CI = [−0.702, 1.013], $p = .962$). The lack of repetition enhancement in post-lockdown infants indicates the specificity of that effect to human faces.

4 | DISCUSSION

We investigated face identity processing in the brains of infants tested before and after the initial COVID-19 lockdown in Connecticut. The neural responses of these groups to human faces differed: pre-lockdown infants showed some evidence of repetition suppression (novel > repeat) for human faces in the FFA, similar to what is

seen in adults (Grill-Spector & Malach, 2001) and older children (Natu et al., 2016); post-lockdown infants showed the opposite, repetition *enhancement* (repeat > novel). This group difference was most robust in the FFA compared with other brain regions and for human faces compared with sheep faces.

To our knowledge, this is the first study to show that the infant FFA can perform similar perceptual functions as adults, beyond its general responsivity to faces compared with scenes and objects (Deen et al., 2017; Kosakowski et al., 2021). That is, both groups of infants showed evidence of a difference in the contrast of novel versus repeat human face blocks, albeit in opposite directions, indicating that the infant FFA is sensitive to face identity. This finding is consistent with previous functional near-infrared spectroscopy (fNIRS) work that showed repetition suppression to face identities in 5- to 8-month-old infants (Kobayashi et al., 2011), though fNIRS cannot localize the FFA. Interestingly, in that study, repetition suppression for face identity was viewpoint-invariant only in older infants. In the current study, we were unable to distinguish sensitivity to low-level pixel changes from human face identity processing per se, although the weaker results for sheep faces could be seen as supportive of the latter interpretation. Future research in a larger sample of infants will be needed to better characterize the functional similarities and differences of the infant and adult FFA.

The opposite response to novel versus repeat human face blocks in pre- and post-lockdown infants is reminiscent of the debate over novelty versus familiarity preferences in infant behavior (e.g., reduced vs. increased looking at repeated stimuli). Familiarity preferences are more likely in younger infants, for more complex stimuli, after shorter exposure, and for more difficult tasks (Hunter & Ames, 1988; Roder et al., 2000; Rose et al., 1982). Likewise, the adult brain shows increased processing of repeated stimuli when the stimuli are unfamiliar or briefly exposed (Henson et al., 2000; Segaert et al., 2013; Turk-Browne et al., 2007). By this account, human faces could be considered a more familiar category to pre-lockdown infants, with exposure to a greater number of unique faces building a more robust face space (Humphreys & Johnson, 2007), than to post-lockdown infants with more restricted face experiences. In particular, the pandemic presumably reduced exposure to faces that would have been experienced infrequently (e.g., relatives and strangers). This lends credence to the possibility that even limited exposure to different face exemplars can impact face processing (Spangler et al., 2013).

The current study focused on older infants (aged 9–24 months), with post-lockdown infants having on average 7.9 months of experience in the pandemic, starting at 2.6–16.7 months of age. Unfortunately, we did not collect any data from younger post-lockdown infants. Thus, the results we report may be specific to older infants. We may expect that younger infants would be less impacted by COVID-19 lockdowns, given their limited exposure to novel faces even under normal circumstances (Sugden & Moulson, 2019). At the same time, infants decrease in looking toward faces over development (Fausey et al., 2016; though see Kadooka & Franchak, 2020), which could suggest the opposite—that younger infants may be even more impacted by differential face exposure from the COVID-19 pandemic. Nonetheless, younger infants, by definition, would have spent less time in lockdown, and our data do not allow us to separate the age at onset of lockdown and duration spent in lockdown.

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

It is tempting to interpret these data in relation to how pandemic precautions such as social distancing and face masks altered early face experience, especially given the strict local guidelines that were imposed. However, this link is speculative in our study because we did not measure daily exposure to faces in the pre- or post-lockdown group; indeed, this study was designed and partially completed prior to the pandemic. We collected retrospective reports from our families, but even then, we only got a coarse snapshot of experiences that may be related to face experience. Additionally, we could not disentangle three related factors (less exposure to novel faces, more exposure to familiar faces, and more exposure to masked faces) that may have contributed to differential face experiences. Thus, we cannot conclude definitively that our results are related to altered visual experience with faces. The pandemic had many other impacts on daily life that could explain neural differences. Perhaps most relevant to face processing is an increase in maternal fear and anxiety (Cameron et al., 2020; Davenport et al., 2020) that may have affected how mothers interacted with their infants (Nicol-Harper et al., 2007) and how infants process faces (Bowman et al., 2021). Indeed, recent work has shown that prenatal stress during the COVID-19 pandemic was related to structural and functional connectivity between the amygdala and prefrontal cortex in infants (Manning et al., 2022). Although the causal mechanism remains unclear, this is a unique and likely one-time dataset that could contribute to our understanding of how face identity processing changes in early development.

Our study has a number of other limitations. First, the sample size per group was small and spanned a wide age range. Our initial intention was to use this age variability to study perceptual narrowing. We combined data across ages to increase statistical power, knowing that face processing changes over this time (Pascalis et al., 2020) and recognizing that analyses relating neural and behavioral effects to age would be underpowered. Additionally, although the groups were roughly matched (fortuitously) on key variables such as infant age,

number of usable blocks, head motion, and eye gaze, the biological sex of the infants was not matched. There was an equal number of male and female infants post-lockdown, but all pre-lockdown infants were born female. The small sample size precludes any examination of sex differences. Although there are some advantages in face processing for female infants (Gluckman & Johnson, 2013), the evidence is mixed (Maylott et al., 2021; Simpson et al., 2020). Finally, although most data collection procedures were identical across groups, there was one key difference: whether the experimenters and parents wore face masks. It is possible that exposure to normal versus obscured faces immediately prior to the experiment affected how infants processed faces. The serendipitous and opportunistic nature of this project means that we are saddled with these limitations, yet we believe the data remain valuable to report and may inform debates on the role of experience in the early development of face processing.

AUTHOR CONTRIBUTION

Conceptualization, data collection, formal analysis, writing—original draft, and writing—review and editing: T. S. Y. *Conceptualization, data collection, writing—original draft, and writing—review and editing*: C. T. E. *Conceptualization, data collection, writing—original draft, writing—review and editing, supervision, funding acquisition*: N. B. T.-B.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in https://doi.org/10.5061/dryad.tb2rbp045 at http://datadryad.org/.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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