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Using individual functional channels of interest to study cortical development with fNIRS

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Abstract

Functional near-infrared spectroscopy (fNIRS) is a noninvasive neuroimaging technique that could be uniquely effective for investigating cortical function in human infants. However, prior efforts have been hampered by the difficulty of aligning arrays of fNIRS optodes placed on the scalp to anatomical or functional regions of underlying cortex. This challenge can be addressed by identifying channels of interest in individual participants, and then testing the reliability of those channels' response profiles in independent data. Using this approach, cortical regions with preferential responses to faces versus scenes, and to scenes versus faces, were observed reliably in both adults and infants. By contrast, standard analysis techniques did not reliably identify significant responses to both categories in either age group. These results reveal scene-responsive regions, and confirm face-responsive regions, in preverbal infants. More generally, the analysis approach will be a robust and sensitive tool for future characterization of the early functional development of the human brain.

RESEARCH HIGHLIGHTS

- fNIRS is a promising developmental cognitive neuroscience method, but suffers from the difficulty of aligning measurement channels across participants and experiments.
- Selecting functional channels of interest in individual participants helps resolve this difficulty and increases statistical power.
- We use this method to demonstrate preferential responses to faces and scenes in infant cortex in the same regions that such responses can be observed in adult participants.

1 | INTRODUCTION

In the first year of life there is massive change in infants' ability to perceive, act on, and think about the world, driven by both maturation and experience. This cognitive development is concurrent with major structural and functional development of the brain (Johnson, 2001). For example, synaptic density, cortical glucose metabolism, and myelination are all subject to substantial change in the first year (Chugani, Phelps, & Mazziotta, 1987; Huttenlocher, 1990; Matsuzawa et al., 2001). Investigating the development of specific functional properties of the brain, and how such development relates to cognitive abilities and experience, will be crucial in understanding how brain development supports learning and cognition.

One common, noninvasive approach to studying the relationship between brain function and cognition is to measure the hemodynamic responses to neural activity, as in functional magnetic resonance imaging (fMRI). The main obstacle to applying this approach to developmental questions is a practical one: many neuroimaging methods, including fMRI, require participants to stay extremely still, and so are especially difficult to employ with awake infants. To overcome this difficulty, some developmental cognitive neuroscientists have adopted a newer noninvasive brain imaging technique, functional near-infrared spectroscopy (fNIRS). fNIRS uses absorption of near-infrared light between emitters and detectors embedded in a cap and placed against the scalp to measure hemodynamic responses to neural activity. Consequently, fNIRS can be employed with infants who sit on their parents' laps and move relatively freely while data are collected (see Lloyd-Fox, Blasi, & Elwell, 2010; Gervain et al., 2011).

Studies using fNIRS have begun to yield some information about the functional properties of the infant brain. Responses to basic visual, auditory, and somatosensory stimuli have been observed in the areas corresponding to adult primary sensory cortices in infants

between 0 and 3 months of age (Kotilahti et al., 2005; Kusaka et al., 2011; Meek et al., 1998; Taga, Asakawa, Maki, Konishi, & Koizumi, 2003; Watanabe, Homae, Nakano, & Taga, 2008). By 6 months, infants show modality-specific responses in occipital and temporal cortices to the presence or expectation of visual and auditory input, respectively (Emberson, Richards & Aslin, 2015). Other experiments have investigated the possibility that regions are specialized early for more specific or abstract functions (e.g., for face, language, or number processing) and have found some evidence for response profiles similar to those observed in adults (e.g., Hyde, Boas, Blair, & Carey, 2010; Otsuka et al., 2007; Peña et al., 2003). Repetition suppression paradigms have also been used to test the information that is encoded in infant cortex about a given stimulus or event type, demonstrating neural habituation to specific goals, face identities, and syllable patterns in different regions (e.g., Bouchon, Nazzi, & Gervain, 2015; Kobayashi et al., 2011; Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014; see Aslin, Shukla, & Emberson, 2015, for a recent review of fNIRS research).

Despite the unprecedented access to the infant brain provided by fNIRS, there are several unresolved methodological issues hampering substantial, cumulative progress. Chief among these issues is the difficulty of mapping the measurement "channels" (between each near-infrared light source and detector) to specific underlying regions of cortex, in order to align these measures meaningfully across individuals and across experiments and labs. In typical fNIRS studies a limited array of sources and detectors, embedded in a cap or headband, is placed on each participant's head according to landmarks of the 10–20 system (Gervain et al., 2011). This process introduces several sources of uncertainty in the position of measurement channels with respect to underlying cortical anatomy. First, 10–20 landmarks are a general guide to the layout of underlying cortex, but there is variability in the actual cortical anatomy underneath each landmark (Okamoto et al., 2004). For infants, in particular, the same landmark may be positioned over one of several sulci or gyri (Kabdebon et al., 2014). Second, sources and detectors are typically fixed into a rigid array, separated at specific distances to optimize both the strength of the signal between them and the depth of its penetration (Cristia et al., 2013; Gervain et al., 2011). Infants' head sizes vary substantially (e.g., average change in head circumference across the first year is over 10 cm, and for male and female infants matched in age, head circumferences within the 5th–95th percentile range differ by ~5.5 cm; CDC/NCHS, 2006a, 2006b), so this rigid array cannot cover precisely the same physiological area across participants. Finally, concerns about infants' patience and comfort mandate placing the array relatively quickly, at the potential cost of some precision.

One possible strategy is to record the final position of the fNIRS optodes on individual participants and then map the resulting channels to structural MR images of the specific participant, or of an age- and head size-matched individual, or even to an age-matched average template (Emberson et al., 2015; Lloyd-Fox et al., 2014). The results of these mappings make it clear how difficult it is to align channels with a targeted area of cortex across participants, even when positioning the same source-detector array with respect to the same 10–20 landmarks. There is substantial variability in how channels map onto anatomical locations segmented into different gyri. Indeed, channels near a major anatomical boundary (e.g., between the frontal and temporal lobe) are likely to be measuring functional activity in different *lobes* in different participants. This variability is exacerbated by the dramatic growth in head size during infancy. Even 3 months of aging produces considerable change in the anatomical region underlying a given fNIRS channel of the same array (Lloyd-Fox et al., 2014).

These sources of variability cause problems both within and across experiments. Within experiments, standard analysis approaches assume that each channel is tapping a stable anatomical (and functional) region across participants. Variability in the actual cortical location sampled by a channel across participants introduces noise in the estimate of the underlying region's response profile. Across experiments, different positioning of sources and detectors, with respect to each other and with respect to participants' physiology, make it difficult to directly compare results.

Consider neural activation during face processing. fNIRS studies with infants 5 months of age and older have found increased blood oxygenation in lateral occipital and temporal lobe regions in response to images, videos or point-light displays of upright faces when contrasted with inverted faces or other natural or mechanical objects (e.g., Lloyd-Fox, Blasi, Everdell, Elwell & Johnson, 2011; Lloyd-Fox et al., 2009; Nakato et al., 2009; Otsuka et al., 2007). Viewpoint- and size-independent repetition suppression to repeated versus varying facial identity has also been observed (Kobayashi et al., 2011; Kobayashi, Otsuka, Kanazawa, Yamaguchi, & Kakigi, 2012; for review see Otsuka, 2014). Yet the wide variety of locations in which channels were positioned and activation was observed, and the difficulty of relating these channels to specific anatomically or functionally defined brain regions, make it difficult to aggregate across these findings and build a cumulative understanding of the neural mechanisms that support infant face processing. For example, do static and dynamic presentations of faces activate the same or different regions (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011)? Is viewpoint-invariant face identity encoded in the same regions that respond preferentially to upright faces over inverted faces and other objects, or more broadly across areas that engage in domain-general encoding of shape (Freiwald & Tsao, 2010)? Future studies designed to test these hypotheses would benefit from a way to assess how new measurements align with previous findings.

One path forward is to continue improving the mapping of channels, as placed on individual participants, to the best available structural image of underlying anatomy, and to use this mapping to select channels that correspond to anatomical ROIs either in individuals or across a whole group of participants (Emberson et al., 2015). However this approach is labor intensive and provides the most accurate results when a structural MR image is available for each individual infant participant, a condition that can rarely be met by most fNIRS labs. Furthermore, using large-scale anatomical information as a guide to uniform functional hypotheses across participants neglects the fact that these landmarks do not precisely define functional properties of the brain. The size and location of specific functional regions with respect to gyral and sulcal landmarks varies across individuals, and often a specific sulcus or gyrus

contains multiple regions with differing functional and connective profiles (e.g., Allison, Puce, & McCarthy, 2000; Amunts et al., 1999; Wang et al., 2015). This means that accurately mapping a channel to a specific gyrus or sulcus is still insufficient to establish that it is measuring from a particular, functionally discrete region.

A potent solution to this problem frequently employed in fMRI research is to identify regions of interest using functional data in individual participants (Poldrack, 2007; Saxe, Brett, & Kanwisher, 2006). Identifying a functional ROI in individual participants reduces blurring with neighboring but distinct functional regions. Individually defined ROIs can be used to identify a candidate region with a particular functional profile and then test the reliability of that functional profile using left-out trials or runs of the same task (e.g., Peelen & Downing, 2005). They can also be used to identify a region with a particular functional profile and then further test the characteristics of that region, such as its responsiveness to additional categories of stimuli, its sensitivity to repetition of different stimulus characteristics, or the information that can be decoded from the pattern of responses across voxels within the ROI (e.g., Epstein & Kanwisher, 1998; Henson, Shallice, & Dolan, 2000; Kamitani & Tong, 2005; Kanwisher, McDermott, & Chun, 1997). In both cases, the ROI approach is especially helpful in increasing sensitivity to smaller effects, not only by reducing contamination from neighboring functional regions but also by limiting the number of comparisons that need to be made from the space of many voxels (or channels) to one or a few candidate regions.

This strategy could be applied to fNIRS research as well. Instead of assuming that a given source-detector channel is measuring from functionally identical regions of cortex across participants, some data could be used to identify the channel(s) of interest in each participant's data, with additional runs or trials then used to independently gauge the response in those selected channels. If the same or similar functional contrasts are used to identify channels of interest across experiments, this approach would also facilitate cumulative conclusions about the existence and properties of a particular functional region over the course of development.

Taking this individual functional channel of interest (fCOI) approach would also help to deal with another problem of collecting neuroimaging data with infants: the relatively small amount of data collected from each participant as a result of infants' limited attention spans. This relative paucity of data lowers statistical power and makes it difficult for researchers to appropriately correct for multiple comparisons without risking a high rate of false negatives. Comparing responses across conditions in selected fCOIs would make it possible to utilize a large number of channels (and thus cover a substantial cortical area) while limiting the number of comparisons needed to test each hypothesis. Moreover, the minimum amount of data necessary for fCOI analyses need not be appreciably more than thresholds often employed in standard, array-based analyses, as it is possible to identify individual fCOIs and test their responses in independent data even with a small number of trials using iterated split half or leave-one-trial-out approaches (Vul & Kanwisher, 2010).

In two experiments, we tested the utility of an individual fCOI approach for fNIRS studies of cortical function. We contrasted activation to dynamic movies featuring faces versus scenes. The fMRI literature has robustly demonstrated multiple regions of adult cortex with functional specialization for these two stimulus types. These include regions on the ventral surface of cortex (e.g., the fusiform face area and parahippocampal place area; Epstein & Kanwisher, 1998; Kanwisher et al., 1997) that are inaccessible to fNIRS measurements due to their distance from the scalp, but also include lateral cortical regions (e.g., a face selective region of the posterior superior temporal sulcus [STS] and a scene selective region of the transverse occipital sulcus [TOS]; Dilks, Julian, Paunov, & Kanwisher, 2013; Grill-Spector, 2003; Haxby, Hoffman, & Gobbini, 2000; Puce, Allison, Asgari, Gore, & McCarthy, 1996) that are readily accessible to fNIRS measurements. We thus aimed to find regions responsive to both directions of this contrast, providing a double dissociation of function by channel. Finding channels with preferential responses to both categories helps to reduce concerns that infants were generally more interested in or aroused by one stimulus category, a confound which could produce changes in blood flow to surface vasculature (Aslin, 2012). A double dissociation would also alleviate concerns that the appearance of a spatially selective response to one stimulus type actually merely reflects confounds like differences in noise across channels or difference in scalp to cortex distance (Aslin, 2012).

Finally, this contrast can contribute novel information to the existing literature on functional specialization in infant cortex. Although a number of fNIRS studies have tested for preferential responses to static or dynamic faces compared to other objects in temporal or occipital cortex (Otsuka, 2014), the specificity of these responses with respect to other classes of stimuli, including natural scenes, has not yet been determined. And no study to date has asked whether regions of the infant brain respond preferentially to scenes. Identifying a part of infant cortex that responds more to scenes than to faces would not establish the existence of the sort of highly selective "place" regions that exist in the adult brain (e.g., Dilks et al., 2013; Epstein & Kanwisher, 1998), but it would demonstrate that this sort of specialization—or a broader division between processing of animate vs. large and small inanimate entities (Konkle & Caramazza, 2013)—is beginning to develop in the first year of life, and it would establish a method of localizing such regions with functional data in a way that would allow them to be identified and investigated further in future work.

2 | EXPERIMENT 1

Before testing for preferential face and scene responses in infant cortex, we first assessed the individual fCOI approach to fNIRS data analysis in a sample of adults. This allowed us to compare the effectiveness of this method to a standard array-based analysis approach, which treats each channel as equivalent across all participants, while ensuring that our source-detector array was capable of detecting activation from known functional regions in adult cortex. We used an infant-friendly protocol that we would be able to repeat in a subsequent study of infants with minimal alterations, and tested both for

an increase in oxygenated hemoglobin (HbO2) and a decrease in deoxygenated hemoglobin (HHb) in response to the different trial types.

2.1 | Methods

2.1.1 | Participants

Twenty adults (between 18 and 40 years, 10 female) were recruited from the MIT study pool and student population. All participants had normal or corrected to normal vision and gave written informed consent in accordance with requirements of MIT's Committee on the Use of Humans as Experimental Subjects.

2.1.2 | Procedure

Participants were seated in front of a 58 cm monitor at a distance of approximately 60 cm. They viewed eight 85 s runs of dynamic face, scene, and scrambled scene stimuli (Pitcher et al., 2011; Walt Disney Productions, 2002). Each run began with a 4 s display of a rotating star, accompanied by a chiming sound, designed to attract infant attention to the screen. The remainder of the run was composed of two 15 s blocks of face and scene movies each, presented in counterbalanced order, as well as two 6 s and one 9 s block of scrambled scene movies interleaved at the beginning, middle, and end of the run. The scrambled scene movies (15 × 15 grid, with randomized element positions) served as a baseline stimulus that would retain infant attention when face and scene movies were not being displayed. For all stimulus types, blocks were composed of two to five short movie clips lasting 3 s apiece. The movie clips were accompanied by instrumental music intended for child-directed media, with song transitions occurring independent of trial transitions.

After each run the display paused until the participant initiated the next run by pressing a key on a keyboard located to her right. Participants were instructed to remain still and to focus on the screen throughout each run but were not asked to fixate on any point on the screen and could adjust their position between runs.

2.1.3 | Data acquisition

fNIRS measurements were collected with a continuous wave system (CW6, Techen, Milford, MA) using wavelengths of 690 nm and 830 nm with a sampling rate of 50 Hz. Four source optodes, each emitting light at both wavelengths, were arranged linearly at 1.5 cm intervals. Two rows of four photo-detectors each were arranged on either side of the source row, offset such that three of the four detectors were equidistant from two sources, resulting in 14 channels each with a source-detector separation of 3 cm (Figure 1a). The optodes were stabilized using a 3D-printed plastic holder and then affixed to participants' heads over the junction of the temporal, occipital and parietal lobes in the right hemisphere using custom headgear. The detector in the lower right corner of the array (terminal point of channel 3) was positioned approximately over the T4 location of the 10–20 system, and the rest of the array was aligned to extend along an anterior-posterior axis toward the P4 location (Figure 1b).

2.1.4 | Data preprocessing

Initial measurements of incident light reaching the detector for each channel were trimmed to remove excess time points from the beginning and end of data collection and were then preprocessed using the HomER NIRS processing package (Huppert, Diamond, Franceschini, & Boas, 2009). The raw data were first transformed into changes in optical density (ΔOD) relative to a normalized baseline value (function *hmrIntensity2OD*). Then channels with very high or very low optical density and channels with a low signal to noise ratio were pruned from individual participants' data sets (*enPruneChannels*). Next a principal components analysis (PCA) was used to filter out motion artifacts, which typically create large signal changes correlated across all

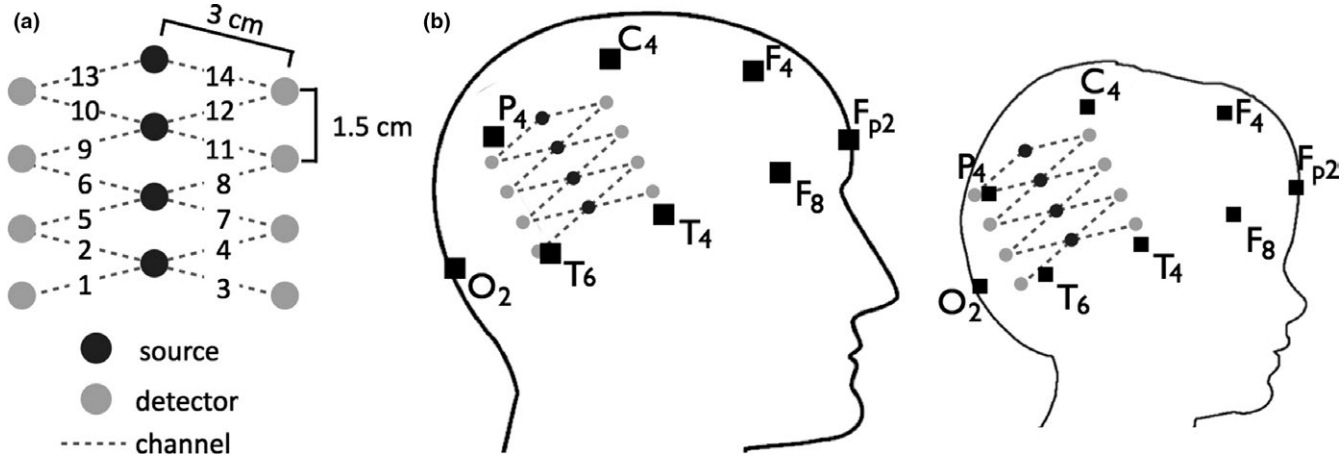

FIGURE 1 (a) Diagram of the array used for both experiments, and (b) the orientation with which it was placed on participants' heads. The bottom, rightmost detector was placed just above and slightly posterior to participants' T4 landmark, with the rest of the array extending in a posterior and superior direction toward the P4 landmark

channels in the array (Wilcox, Bortfeld, Woods, Wruck, & Boas, 2005). Based on past evaluations of this correction technique for adult data sets with small and infrequent motion artifacts, components accounting for 80% of the covariance of the data across channels were filtered out (*enPCAFilter*; Brigadoi et al., 2014). The resulting time courses were then band-pass filtered with cut-off frequencies of 0.01–0.5 Hz to remove slow drifts and high frequency and physiological noise (*hmrBandpassFilt*). Finally, the ΔOD values were transformed into changes in HbO2 and HHb concentration according to the modified Beer-Lambert law (*hmrOD2Conc*).

2.1.5 | Data analysis

For each participant in each channel, we computed the mean change in HbO2 and HHb concentration during each face and scene trial from 2 s post-stimulus onset, accounting for the lag in hemodynamic responses, until the end of the block (15 s post-onset). The differences in these responses across conditions were then analyzed according to two separate approaches.

Array-based approach

The first analysis took the conventional approach of treating channels with the same array position as equivalent sources of functional responses across participants. Each subject's mean face and scene response across trials was computed in terms of changes in both HbO2 and HHb concentration, and responses were compared within hemoglobin subtypes for each measurement channel using paired sample *t* tests. A Bonferroni correction for multiple comparisons (14 for each hemoglobin subtype) was used, resulting in a threshold of $p < .003$ for identifying reliably different responses to the two stimulus types.[1]

Individual fCOIs

Each participant's trial-by-trial HbO2 averages for the face and scene conditions were split into two equal sets per condition, matched for the trials' positions within runs and across the experiment (see Supplementary Information for details). During the selection portion of the procedure, we used independent-samples *t* tests to compare the HbO2 responses to one set of face trials against those to one set of scene trials in each channel and identified the eligible channel with the strongest *t* statistic for the contrast of faces > scenes and for that of scenes < faces. This selection process was repeated a total of four times, iteratively comparing both sets of face trials with both sets of scene trials.

During the test portion of the procedure, we then computed the participant's mean HbO2 and HHb responses to face and scene trials in each of the four selected face and scene fCOIs, using only the trials that were left out of the selection process when choosing the fCOI being queried. For each fCOI type (i.e., face-preferring or scene-preferring) and each hemoglobin type, the mean left-out face and scene responses from the four iterations were then further averaged, resulting in a single mean HbO2 and HHb response to faces and to scenes in each participant's selected face fCOI(s) and scene fCOI(s). (The channel selected as the face or scene fCOI could vary across iterations; see Supplementary Information for information on the distribution of fCOI selection within individual data sets for both Experiments 1 and 2.) We repeated this process for each participant, then compared face and scene responses across participants for each type of hemoglobin in each fCOI type with paired-samples *t* tests. As there was only one comparison testing for a preferential face response and one testing for a preferential scene response, there was no need to correct for multiple comparisons.

As is common in fMRI experiments that employ individual functional regions of interest (Downing, Jiang, Shuman, & Kanwisher, 2001; Kanwisher et al., 1997; Nieto-Castanon, Ghosh, Tourville, & Guenther, 2003), we applied an anatomical constraint to restrict the selection of individual fCOIs to channels likely to be covering the targeted regions, specifically the STS face region and TOS scene region previously identified in the fMRI literature (Kanwisher, 2010). The shape and placement of the array were designed such that the more anterior and inferior portion of the array would cover STS and the more posterior and superior portion would cover TOS, and thus we restricted the selection of face and scene fCOIs to these respective halves of the array (Figure 1b). Note that this constraint limited where we could find preferential responses of each type but did not mandate that we would observe reliably preferential channels in either location; if none of the eligible channels were measuring from cortex with the desired response profile (i.e., faces > scenes or scenes > faces), then channel selection would simply be operating on noise in the selection data sets and we would not expect to see a reliable difference in face and scene responses in the independent data. (See Supplementary Information for results of face and scene fCOI analyses in the anatomically non-preferred sections of the array, as well as results of analyses conducted with an alternative anatomical constraint and with no constraint on the selected channels.)

2.2 | Results

The criteria for channel rejection during preprocessing resulted in the exclusion of four channels for one participant and two for a second participant. Data from the remaining channels for these two participants, as well as all 14 channels for the remaining 18 participants, were included in the subsequent analyses.

2.2.1 | Array-based approach

HbO2 results

None of the channels exhibited significantly higher HbO2 concentration during face compared to scene trials, or the reverse, at the significance threshold corrected for multiple comparisons. At a relaxed threshold of $p < .05$ there was one channel in the anterior portion of the array that responded more strongly to face stimuli than scene stimuli (Channel 4: average face response = 0.032 μmol/vol, average scene response = −0.014 μmol/vol, $t(19) = 2.46$, $p < .05$; Figure 2a & b) and one channel in the posterior portion that responded more strongly to scene stimuli than face stimuli (Channel 13: average face response = −0.004 μmol/vol, average scene response = 0.030 μmol/vol, $t(18)$

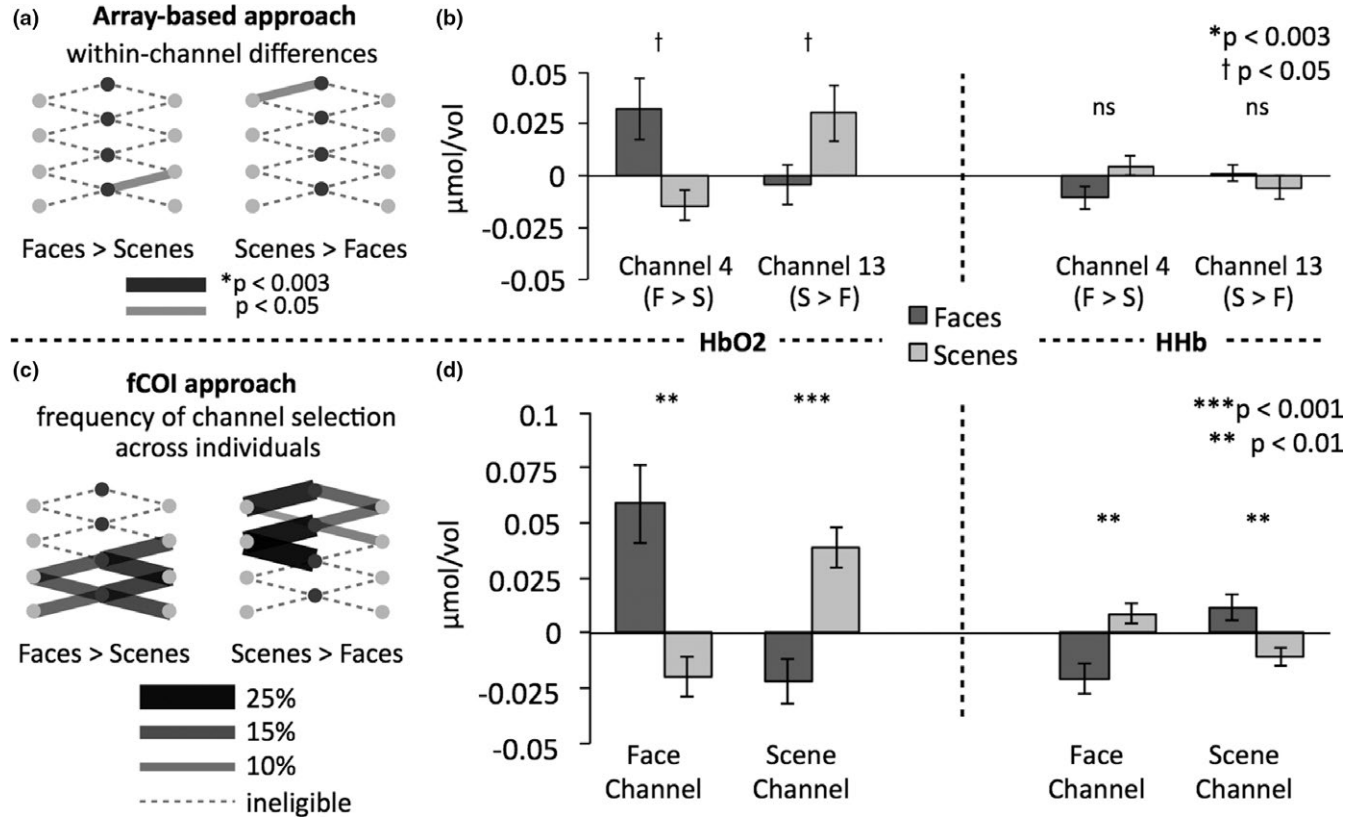

FIGURE 2 Results from Experiment 1 (adult participants). (a) Channels in the array (depicted vertically, not as aligned on participants' heads—see Figure 1) that recorded significantly ($p < .003$, threshold corrected for multiple comparisons) or marginally ($p < .05$) higher HbO2 responses to one stimulus condition than the other. Channel 4 displayed marginally higher responses to faces than to scenes, and Channel 13 displayed marginally higher responses to scenes than to faces. (b) Mean HbO2 and HHb concentrations during face and scene blocks for the two marginally selective array-based channels. Error bars represent SEM. (c) The frequency with which each channel was selected as the face- or scene-preferring fCOI based on HbO2 responses and the application of fixed anatomical constraints on selection. Variability in channel selection reflects variation in both the position of the array and the position of functionally distinct regions with respect to individuals' cortical anatomy. (d) Mean HbO2 and HHb responses to the left-out face and scene blocks in the selected fCOIs

= 2.20, $p < .05$; Figure 2a & b). The HbO2 responses to scrambled scenes in each of the selected channels were low (Channel 4: −0.012 µmol/vol; Channel 13: −0.022 µmol/vol), and at the relaxed threshold differed from face responses in Channel 4 ($t(18) = 2.37$, $p < .05$) and scene responses in Channel 13 ($t(18) = 2.43$, $p < .05$). The locations of these channels are consistent with fMRI evidence of face and scene selective brain regions in the STS and TOS, respectively (Dilks et al., 2013; Grill-Spector, 2003; Haxby et al., 2000; Puce et al., 1996), and thus may reflect true functional differences despite the low protection against type I errors provided by the relaxed threshold necessary to identify these channels.

HHb results

Again, no channels showed a significantly larger decrease in HHb in response to one stimulus type compared to the other. Average HHb values for the channels showing marginal HbO2 responses were in the predicted direction (i.e., lower HHb concentration in response to the stimulus type evoking higher HbO2 concentration; see Figure 2b), but did not reach even a relaxed threshold for significance in either channel (Channel 4: average face response = −0.011 µmol/vol, average scene response = 0.003 µmol/vol, $t(19) = 1.77$, $p = .09$; Channel 13: average face response = 0.001 µmol/vol, average scene response = −0.006 µmol/vol, $t(18) = 0.98$, $p > .3$). At a relaxed threshold, scene trials did elicit significantly lower concentrations of HHb compared to face trials in Channel 9 (average face response = 0.003 µmol/vol, average scene response = −0.008 µmol/vol, $t(19) = 2.27$, $p < .05$), although this was not a channel that reliably differentiated the trial types on the basis of HbO2 response.

2.2.2 | Individual fCOIs

HbO2 results

The distribution of anterior channels with the strongest *t* statistic values when comparing faces to scenes is displayed in Figure 2c. The mean HbO2 response in the left-out data for the selected face fCOIs was significantly higher for face trials (0.059 µmol/vol) than scene trials (−0.020 µmol/vol; $t(19) = 3.14$, $p < .01$; Figure 2d), confirming a reliable functional preference. The responses to left-out face trials were also significantly higher than those to scrambled scenes (−0.020 µmol/vol; $t(19) = 3.25$, $p < .005$).

In posterior channels selected as scene fCOIs (see Figure 2c), the average HbO2 response for left-out scene trials (0.039 μmol/vol) was significantly higher than that for left-out face trials (−0.022 μmol/vol; $t(19) = 4.12$, $p < .001$; Figure 2d), again confirming a reliably specialized response profile in the fCOIs. The response to the left-out scene trials was also significantly higher than the average response to scrambled scenes (−0.031 μmol/vol; $t(19) = 4.18$, $p < .001$).

HHb results

In contrast to the array-based approach, which failed to find evidence of decreases in HHb accompanying the marginal increases in HbO2, the individual fCOI approach revealed small but reliable changes in HHb concentration in channels selected based on differential HbO2 responses (Figure 2d). The face-responsive fCOIs showed significantly lower HHb concentrations during face trials (−0.021 μmol/vol) than during either scene trials (0.009 μmol/vol, $t(19) = 2.92$, $p < .01$) or scrambled scene trials (0.006 μmol/vol, $t(19) = 2.56$, $p < .05$). Conversely, the scene-responsive fCOIs showed significantly lower HHb concentrations during scene trials (−0.011 μmol/vol) than during either face trials (0.012 μmol/vol, $t(19) = 2.87$, $p < .01$) or scrambled scene trials (0.013 μmol/vol, $t(19) = 3.84$, $p = .001$).

2.3 | Discussion

The goal of Experiment 1 was to assess the feasibility of detecting known functional regions that respond preferentially to faces and to scenes using fNIRS, and to compare the effectiveness of an individual fCOI approach to identifying these regions against the standard, array-based approach. The results demonstrate that fNIRS can detect these functional regions in adult participants, and that the individual fCOI approach provides greater sensitivity for this detection relative to array-based comparisons. The utility of identifying fCOIs for reducing the number of comparisons was made evident by the fact that while the array-based approach did identify channels that displayed higher responses to faces than to scenes and vice versa in plausible locations, the differences between face and scene responses in these channels did not survive suitable corrections for multiple comparisons.

The individual fCOI approach also likely increased sensitivity through the effective selection of the specific channels placed over the functional regions being investigated in each individual participant, and the exclusion of channels over neighboring regions with different functional profiles. For contrasts of both faces over scenes and the reverse, the effect size of condition on HbO2 response was larger in individually selected fCOIs than in even the most selective array-based channels. Moreover, the individual fROI approach was able to detect condition-related differences in HHb concentration whereas the array-based approach was not. Even examining only the array-based channels that showed uncorrected differences in HbO2 response to the two conditions (i.e., Channels 4 and 13), essentially using the HbO2 data to identify group-level channels of interest and eliminating the need to correct for multiple comparisons, there was still no evidence of reduced HHb in response to preferred stimulus types for either channel. This likely reflects the fact that HHb differences tend to be small and could easily be averaged out by blurring with adjacent functional regions (Jasdzewski et al., 2003). In contrast, when we examined HHb concentrations in channels selected based on their HbO2 response profiles for individual participants, we found small but highly reliable decreases in HHb concentration in response to the preferred stimuli for each channel type, consistent with past research on the nature of the hemodynamic response in adults.

3 | EXPERIMENT 2

Experiment 2 asked whether the same face- and scene-preferring regions identified in adults in Experiment 1 could be observed in infants under 1 year of age using fNIRS, again comparing an array-based analysis to the approach of identifying fCOIs in individual participants. Although the specific contrast of faces versus scenes has not previously been reported in the infant cognitive neuroscience literature, we expected to find a region that responded preferentially to faces in temporal or ventral occipital cortex based on past fNIRS research comparing face stimuli to other natural and mechanical objects (Lloyd-Fox et al., 2009; Lloyd-Fox et al., 2011; Otsuka et al., 2007). There are no existing reports of cortical regions specialized for scene processing in the infant brain.

3.1 | Methods

3.1.1 | Participants

Sixteen full-term (born at 37 weeks or later) infants between 3 and 12 months of age (mean: 7 months 3 days; range: 3 months 10 days–11 months 5 days; 7 female) were recruited from the greater Boston area. One additional infant was excluded for failing to watch a sufficient number of trials (see below). A parent or guardian gave written informed consent for each participant in accordance with requirements of MIT's Committee on the Use of Humans as Experimental Subjects.

3.1.2 | Procedure

The stimuli were the same as in Experiment 1. The procedure was similar except that infant participants sat on their parents' laps while viewing the display, and the experiment was discontinued, either during or between runs, if the participant became fussy or highly inattentive or if the parent indicated he or she wished to end the experiment.

3.1.3 | Data acquisition

The NIRS measurements were acquired with the same system in the same manner as in Experiment 1. A padded version of the same 14-channel optode array was affixed to participants' heads using a smaller version of the same custom headgear, again anchored on the T4 10–20 landmark and extending toward the P4 landmark.

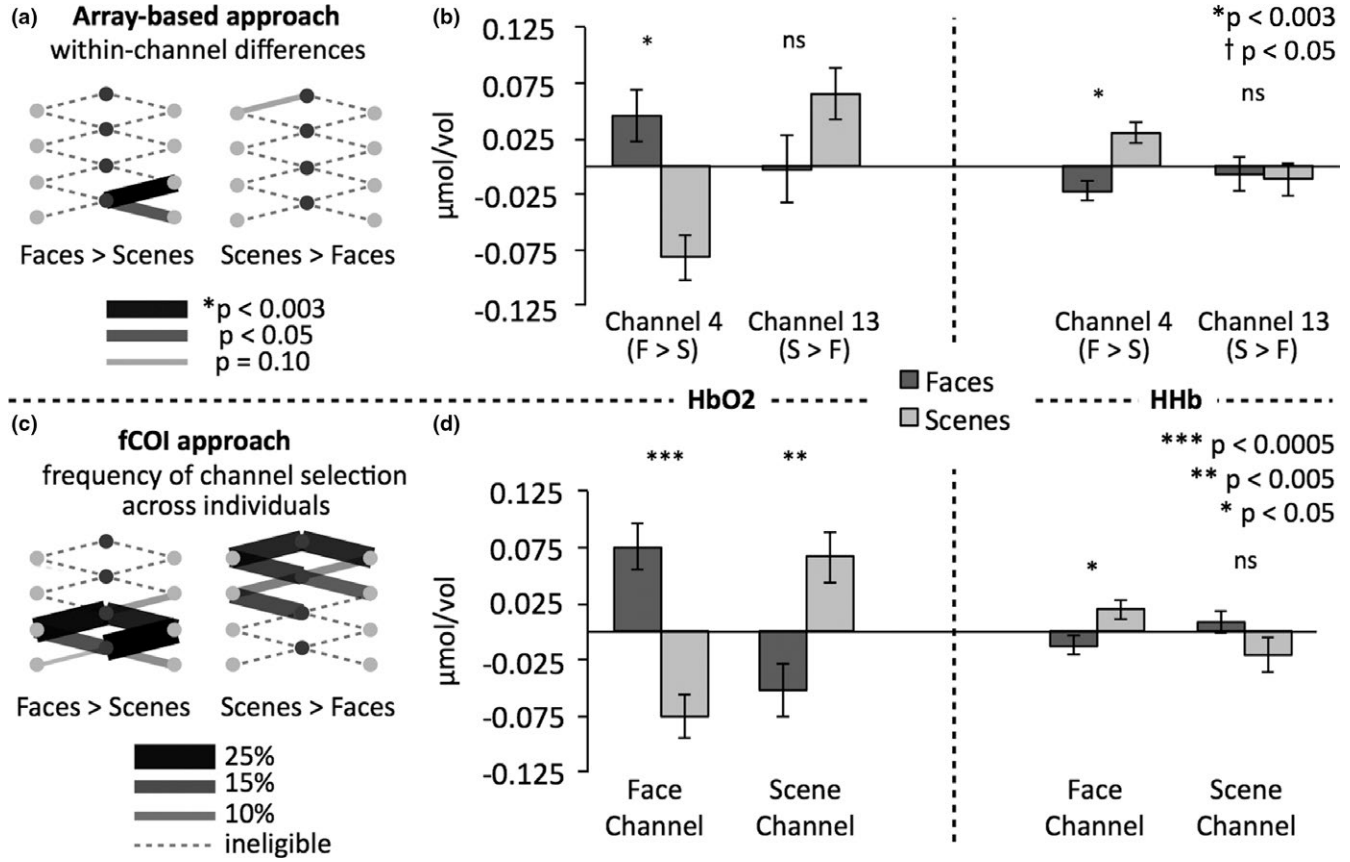

FIGURE 3 Results from Experiment 2 (infant participants). (a) Channels in the array for which HbO2 responses to face and scene blocks differed significantly or marginally. Channel 4 displayed significantly higher HbO2 responses to faces than scenes ($p < .003$), and marginal differences were found in Channels 3 (faces > scenes, $p < .05$) and Channel 13 (scenes > faces, $p < .1$). (b) Mean HbO2 and HHb responses to face and scene blocks in the channels with the highest t values for the contrast of faces > scenes (Channel 4) and scenes > faces (Channel 13). Error bars represent SEM. (c) The frequency with which each channel was selected as the face- or scene-preferring fCOI based on HbO2 responses and the application of fixed anatomical constraints on selection. (d) Mean HbO2 and HHb responses to the left-out face and scene blocks in the selected fCOIs

3.1.4 | Data preprocessing

Fourteen of the 16 participants were filmed during data collection. Subsequently, an offline coder marked time points in each run where a participant looked away from the display. Trials were excluded from subsequent analysis when infants looked away for more than one-third (5 s) of the trial duration. Scene trials were also excluded when infants turned around and looked at their parent's face, even if the duration of this look was less than 5 s. For the two remaining participants, no video was recorded but both of the experimenters present during data collection tracked the infants' attention to the display, and agreed that the infants had attended to all trials presented to them before the experiment was terminated between stimulus runs.

The experiment ended several seconds after the end of the last valid face or scene trial to which the infant attended, and any excess measurements from the beginning or end of data collection were removed. Data were then preprocessed in the same manner as Experiment 1, with the exception of the strength of the PCA filter (*enPCAFilter*). Given the greater frequency and magnitude of the motion artifacts present in the infant data, we filtered out 97% of the covariance across channels, a parameter value previously found to optimize the simultaneous reduction of noise and maintenance of the underlying hemodynamic response function when correcting for large motion artifacts (Cooper et al., 2012). No additional motion correction or artifact removal was employed, although nearly all remaining artifacts occurred during trials already excluded for inattentiveness.

3.1.5 | Data analysis

Mean concentration changes of HbO2 and HHb during face and scene trials were calculated on a trial-by-trial basis in each channel for each participant as in Experiment 1, with the exception that the time period contributing to each trial average began 6 s post-stimulus onset and extended until 2 s post-offset. This choice of time period was made in advance of data collection, and reflects both research on the shape of the hemodynamic response function (HRF) in full-term infants (Arichi et al., 2012) and the extension of the HRF lag time that has been assumed in infant NIRS research (ranging from no

difference from the adult HRF, e.g., Kobayashi et al., 2011, to 5 s post onset, e.g., Emberson et al., 2015, to 10 s post onset, e.g., Lloyd-Fox et al., 2009). Due to the extension of the presumed HRF lag and to the shorter duration of the scrambled scene periods (6–9 s), we did not compute average HbO2 or HHb responses to these periods for the infant data set.

Both the array-based and individual fCOI approaches to identifying face and scene selective regions were employed as in Experiment 1. Although infants watched a variable number of trials of each condition, sometimes at irregular intervals throughout the experiment, the trials assigned to split halves for each condition were again matched as best as possible for position within runs and across the experiment (see Supplementary Information). Infants were required to watch a minimum of six trials of each condition—resulting in a minimum of three trials per split half—in order to be included in the data set. This resulted in the exclusion of one infant who watched only five scene trials.

3.2 | Results

The criteria for channel rejection during preprocessing resulted in the exclusion of three channels for one participant, two channels for another, and one channel each for three additional participants. For infants included in the sample, the average numbers of included trials were 10.4 face movies and 9.1 scene movies. These values differed significantly across participants ($t(15) = 3.18$, $p < .01$), which is consistent with previous research on infants' enhanced interest in faces compared to inanimate stimuli. Although testing for a double dissociation in different regions' responses to the two trial types helps to rule out the possibility that any observed increases in HbO2 in response to faces is merely the result of a spatially non-specific effect of attention, we also conducted a supplementary analysis on a matched subset of face and scene trials to further rule out this account of any findings (see Supplementary Information).

3.2.1 | Array-based approach

HbO2 results

At the Bonferroni-corrected threshold, Channel 4 showed a significantly higher HbO2 response to faces versus scenes across participants (average face response: 0.046 μmol/vol, average scene response = −0.081 μmol/vol, $t(15) = 3.70$, $p < .003$; see Figure 3a, b). At a relaxed threshold of $p < .05$, Channel 3 also showed a higher response to faces than to scenes (average face response = 0.025 μmol/vol, average scene response = −0.062 μmol/vol, $t(15) = 2.54$, $p < .05$). Both of these channels were located in the anterior, inferior portion of the array near T4, and thus were likely positioned over STS (Kabdebon et al., 2014).

Even at the relaxed threshold of $p < .05$, no channel responded significantly more to scenes than to faces. The most selective profile of this type was observed in Channel 13 (average face response = −0.003 μmol/vol, average scene response = 0.066 μmol/vol, $t(13) = 1.72$, $p = .11$), which was located in the most posterior and superior portion of the array, positioned to cover TOS.

HHb results

Channel 4, which showed a higher HbO2 response to faces than scenes, also showed a significant reduction in HHb during face trials relative to scene trials (average face response = −0.022 μmol/vol, average scene response = 0.030 μmol/vol, $t(15) = 3.57$, $p < .003$; Figure 3b). No other channels showed a differential HHb response during face and scene trials, even at a relaxed threshold of $p < .05$, and decreases in HHb concentration for faces in Channel 3 and scenes in Channel 13 did not approach significance.

3.2.2 | Individual fCOI approach

HbO2 results

The average responses in the left-out data for the face fCOIs, selected from the anterior portion of the array, were significantly higher for face trials (0.075 μmol/vol) than for scene trials (−0.075 μmol/vol, $t(15) = 4.80$, $p < .001$, Figure 3d). In the scene fCOIs selected in the posterior portion of the array, the average left-out responses were significantly higher for scene trials (0.066 μmol/vol) than for face trials (−0.052 μmol/vol, $t(15) = 3.38$, $p < .005$). The fCOI analysis thus confirmed the existence of a region in infant cortex that reliably responds more to faces than to scenes and, in contrast to the standard array-based analysis, provided evidence of a region that responds more to scenes than to faces. Moreover, these preferential response profiles were observed in the same approximate anatomical locations where they were observed in adults. (No reliably face- or scene-preferring fCOIs were observed in the non-targeted portions of the array; see Supplementary Information.)

HHb results

The face fCOIs showed a significant decrease in HHb concentration during face trials (−0.012 μmol/vol) relative to scene trials (0.020 μmol/vol, $t(15) = 2.64$, $p < .05$, Figure 3d). The scene fCOIs had lower HHb concentrations during scene trials (−0.021 μmol/vol) than during face trials (0.008 μmol/vol), although this difference was not significant $t(15) = 1.33$, $p = .20$).[2]

3.3 | Discussion

Experiment 2 demonstrates that infants under 1 year of age have cortical regions that respond preferentially to faces relative to scenes and to scenes relative to faces. In addition to providing the first evidence that infants under a year of age possess cortical regions that respond preferentially to scenes, these data strengthen the evidence for spatially specific preferential responses to faces in infants by demonstrating these responses in the presence of another region with a contrasting functional profile. This dissociation rules out the possibility that what seem to be spatially specific responses to faces merely reflect channels in which signal gain is particularly sensitive to differences in infants' arousal or attention to faces compared to less engaging baseline or contrast stimuli (Aslin, 2012).

Both face- and scene-preferring channels were found within independent anatomical regions of interest based on the location of

matching functional profiles observed in adults, suggesting some spatial continuity for each type of selectivity. Moreover, in analyses of both infants and adults, we failed to find any evidence of a preferential scene response in the anterior portion of the array (see Supplementary Information). Data from adults, but not infants, showed a preferential face response in the posterior portion of the array (Supplementary Information). These results, combined with an examination of the distribution of selected face fCOIs (Figures 2c and 3c), suggest that preferential face responses extend farther into the posterior portion of the array for adults than for infants. This could reflect growth in brain size, expansion of face selective cortex with age, the development of additional functional regions specialized for face processing, or some combination of the three. Nonetheless, the results of Experiments 1 and 2 support the conclusion that there is some degree of continuity in the spatial organization of cortical functions across the lifespan.

As in Experiment 1, we found that the individual fCOI approach was a more sensitive detector of these functional differences than the standard, array-based approach to analyzing fNIRS data. This is not to say that the array-based approach could not have provided evidence for the same functional regions given a larger sample size and thus more power to pass a corrected threshold and overcome the noise introduced by differences in array-to-cortex alignment. Still, in every comparison reported above for both HbO2 and HHb, the contrast based on independent data from individually selected fCOIs had substantially greater power to detect the difference between conditions than the analogous array-based contrast. This was particularly true for the scene-preferring channels in the superior and posterior corner of the array, which were farthest from the T4 10–20 landmark used to guide array placement and thus perhaps most subject to differences in alignment introduced by variation in head size and shape. Overall, the results demonstrate that, like individual fROI approaches developed for fMRI data analysis, the individual fCOI approach to analyzing fNIRS data provides a clearer, less noisy estimate of the response profile for functionally defined regions of cortex.

4 | GENERAL DISCUSSION

These two experiments demonstrate the effectiveness of an individual fCOI approach for analyzing fNIRS data. We implemented this approach by using some of each participant's data to identify the channels with the highest test statistics for the contrasts of interest and then characterizing the response profile of those channels in the left-out data, avoiding the problem of non-independence between channel selection and response estimation (Vul & Kanwisher, 2010). By eliminating the need for comparisons between conditions of interest in every channel and by using functional data to solve difficulties in aligning measurements across participants, this approach reduced noise from the blurring of the functional regions under investigation with neighboring regions and increased the sensitivity of our tests to differences between conditions while keeping the risk of Type I errors low. Moreover, the selection and test of individual fCOIs proved to be robust even when executed with the variable and often small number of trials attended to by infant participants.

The particular choices made here—the selection of a peak channel within predefined anatomical ROIs—were aimed at optimizing the detection of particular regions given highly constrained hypotheses about where those regions would be and what their response profiles would look like. There are a variety of other ways, however, that functional data can be used to define or align data of interest depending on the goal of the investigation. Rather than choosing a peak channel, one could define fCOIs by selecting all channels (or all contiguous channels) that pass a particular threshold. This could be a useful approach for addressing hypotheses about how the extent or selectivity of a functional region changes with experience or development (although the selectivity of peak channels may differ from that of a broader, threshold-defined region), or to obtain patterns of activation across an ROI to ask what information is encoded within the region (e.g., Kamitani & Tong, 2005, Norman, Polyn, Detre, & Haxby, 2006). The functional profiles of one or more channels could also be used to realign data either in array space or in a space defined by the channels' response patterns, as in the fMRI method of hyperalignment (Haxby et al., 2011). Following this alignment, one could ask additional questions about the spatial distribution of responses to similar or novel stimulus conditions.

Individual fCOI approaches may not always successfully identify the same functional region of interest across participants. If the contrast used to identify fCOIs is sufficiently non-specific (e.g., objects vs. scrambled images) such that multiple functional regions with different overall profiles distinguish between the conditions, then the specific functional regions measured by the selected fCOIs could vary substantially across participants and experiments. Particular care should be taken with respect to this concern when comparing the response profiles of fCOIs across groups (e.g., age groups), as differences could reflect differences in the selection rate of distinct functional regions across the two groups, rather than developmental change. Approaches to minimizing this issue include restricting the anatomical region of interest to effectively exclude competing functional regions with similar responses to the localizer contrast, and using increasingly specific contrasts that ought to differentiate the particular functional region of interest when selecting fCOIs.

The identification of fCOIs that tap a particular functional region may also be prevented by the problem of limited and non-continuous coverage common to nearly all fNIRS experiments. In addition to the fact that the NIRS arrays used in typical experiments cover only a limited portion of cortex, high-quality data reflecting cortical blood flow are not collected from the entire area under the array. To measure cortical blood flow, the near-infrared light providing the signal must penetrate the head to a depth of at least ~1.5 cm, and only does so at the center of its curved path between the emitter and detector (Gervain et al., 2011). Thus, standard NIRS arrays likely fail to provide any information about hemodynamic responses in cortex directly beneath the emitters and detectors. If the functional region under investigation is sufficiently small or variable in its location, then it may end up in a blind spot or outside the extent of the array, and would thus not be reflected in data from any channel. The future development of arrays with overlapping

channels would help to solve this issue of coverage and would increase the spatial resolution at which signal could be resolved as well.

These experiments also provide evidence that some functional organization of the cortex for processing distinct categories of visual stimuli develops in the first year of life and that this organization seems to be stable across the lifespan. One limitation of the current data is that they do not provide a detailed picture of how specialized the regions tapped by the selected channels are in either infants or adults. In addition to highly selective regions that respond specifically to faces and to scenes relative to many other types of stimuli, fMRI studies of adults have also identified larger swaths of cortex that respond preferentially to a broad array of animate stimuli or to large objects and spatial layouts (Konkle & Caramazza, 2013). The higher relative activation to faces in some channels and to scenes in others observed here is consistent with either type of response profile.

This limitation highlights the continued value of mapping optode locations onto structural images of underlying cortex when possible. In the current research, for example, such mapping may have allowed us to determine whether the selected fCOIs were clustered over STS or were measuring from a broader region of cortex. Mapping channel position to cortex, either in individuals or for the intended array position and average head size, could also help researchers define a narrow anatomical region of interest within which to search for fCOIs, limiting the risk of selecting channels measuring from non-target functional regions. Nonetheless, the current results demonstrate that this type of individual mapping procedure is not the only possible approach to identifying the channels likely to be tapping the candidate functional region under investigation.

Fully understanding the functional profile of any brain region also requires measuring its response to more than two types of stimuli. Future research should test the responses of these regions to other categories of stimuli to ask if infant cortex contains regions as highly specialized as those observed in adults, and whether such specialization develops in a hierarchical fashion (i.e., a region initially responds to all animate stimuli and then becomes specialized for a subcategory, such as faces or bodies, over the course of development). The use of a standardized approach to identifying the same candidate fCOIs in individual participants, which can then be interrogated with respect to their response profile across a variety of stimulus types and participant age groups, is a critical tool in developing this kind of cumulative developmental cognitive neuroscience.

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ENDNOTES

[1] Bonferroni corrections are an appropriate way to control Type I errors amongst multiple tests, each of which could independently provide support for a stated hypothesis. However, we also conducted a non-parametric permutation analysis of the data from each experiment, to get the empirical distribution of maximal *t* statistics across channels in these data under the null hypothesis (no difference between conditions). Using the thresholds derived from these bootstrap analyses, there were no array-based channels in either experiment where face and scene responses were significantly different.

[2] When excluding one participant whose differential HHb response to scene vs. face trials in the scene fCOIs was more than 2.5 standard deviations above the mean, the average responses to scene trials (-0.031 μmol/vol) were significantly lower than those to face trials (0.013 μmol/vol; $t(15) = 2.67$, $p < .05$).

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SUPPORTING INFORMATION

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Graphical Abstract

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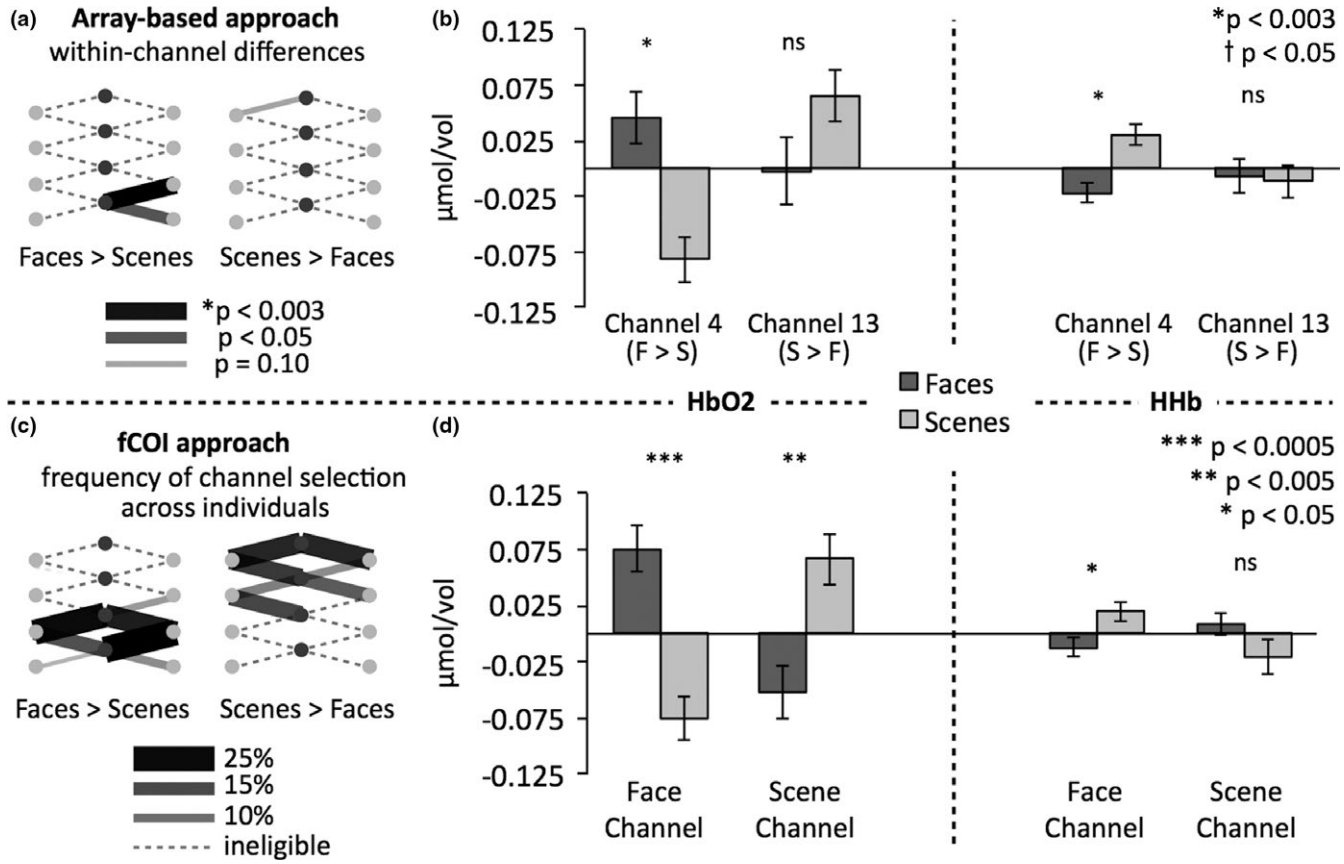

Two experiments demonstrate that the analysis of functional near infrared spectroscopy (fNIRS) data is substantially improved by the identification of individual functional channels of interest (fCOIs). Using this method, we identified regions of temporal and occipital cortex with reliable preferences for both faces and scenes in infants under 1 year of age.