



Category structure guides the formation of neural representations

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Abstract

Perceptual variability is often viewed as having multiple benefits in object learning and categorization. Despite the abundant results demonstrating benefits such as increased transfer of knowledge, the neural mechanisms underlying variability as well as the developmental trajectories of how variability precipitates changes to category boundaries are unknown. By manipulating an individual's exposure to variability of novel, metrically organized categories during an fMRI-adaptation paradigm, we were able to assess the functional differences between similarity and variability in category learning and generalization across two time-points in development: adulthood ($n = 14$) and late childhood ($n = 13$). During this study, participants were repeatedly exposed to category members from different distributions. After a period of adaptation, a deviant stimulus that differed from the expected distribution was then presented. This deviant differed in either an invariant dimension (a feature that remained consistent throughout presentation was altered) or a similarity dimension (a feature that changed throughout exposure was changed in a new dimension). Our results can be summarized in three main findings: (1) Variability during exposure recruited the right fusiform gyrus to a greater extent than tight exposure. (2) Deviant items were generalized based on the exemplar distributions during exposure, although children only generalized items if provided variable exposure. (3) Variability influenced release to a greater extent in children than adults. These results are discussed in relation to the variability and category learning literature more broadly.

Keywords Variability · Category learning · Development · Neural adaptation · FMRI

Category structure guides the formation of neural representations

Category learning is a central feat of cognition. The ability to group objects into categories allows individuals to flexibly adapt and act both accurately and optimally. The internal structure of a category—the relationship among its members—is important for understanding how we create category boundaries. Across auditory, visual, and motoric domains, individuals are extremely capable of learning category boundaries by extracting commonalities among members and transferring these regularities to new instances (Dhawale et al. 2017; Fiser and Aslin 2001; Saffran et al. 1996). These processes are so inherent that individuals

extract category structure from noise without awareness (Turk-Browne et al. 2009).

Thus, the distributional information among category members is easily attainable, but how one uses this information for category formation is less clear. To effectively learn a category, a system must be able to extract critical features that define membership while ignoring irrelevant features that may occur across category boundaries (be present in multiple, different categories) (eg. Smith 1989; Sloutsky 2010). For example, color is an irrelevant feature of the category “duck”, but “bill” is a critical feature. One is better able to learn the duck category if presented with many different exemplars of varying colors, rather than only white ducks. There is mounting evidence that high variability in these irrelevant features among members within a given category may enhance the ability to extract the critical feature(s) to define membership. For instance, Perry et al. (2010) demonstrated that providing variable exemplars during novel category learning not only supports the acquisition of more immediate understandings of the relevant category, but also facilitates a broader understanding of global category

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structure. Additionally, research on object orientation has demonstrated that receiving more variably organized views in comparison to continuous object views results in faster recognition of novel objects (Harman and Humphrey 1999). Further, classifying objects (e.g., circles) into known categories that are either highly variable (pizzas) or low variability categories (quarters) results in classification into highly variable categories even if the feature (size) of the novel object is equidistant to both category exemplars given (Rips 1989). In a similar paradigm that involved learning categories that were either highly variable or had low variability among members on two feature dimensions (in this case brightness and hue) also resulted in higher classification of a target stimulus into the highly variable category (Cohen et al. 2001).

Variability among category members has been shown to also influence how learning categories proceeds during development. Self-generated variability such as rotation of objects supports learning in infancy (Slone et al. 2019) toddlers (James et al. 2014) and in adulthood (James et al. 2002). Even without self-generated action, variability facilitates young children's learning of new object categories including symbols (Li and James 2016; James 2017).

In addition, Quinn et al. (1993) demonstrated that an infant's natural categories of cats and dogs were dependent on the distributions of category members during learning. If infants saw a series of dogs, the category formed also included cats. However, if infants saw a series of cats, the category excluded dogs. Furthermore, if the variability of the dog exposure was equalized to the narrower cat category, infants no longer assimilated cats into the dog category. Therefore, it is clear that variability, as well as how the exemplars of a category are encountered, can affect category formation, demonstrating its dynamic nature.

Even though variability affects category learning in both adults and children, research has demonstrated that *how* categories are learned in childhood compared to adulthood has revealed some important differences. Past behavioral studies have demonstrated that while adults are capable of forming categories based on critical features alone, children form broader representations that often include features that are irrelevant to category membership (Deng and Sloutsky 2015, 2016; Smith and Kehler 1977; Rabi et al. 2015). Specifically, young children tend to group items together based on overall similarity instead of on a diagnostic feature (eg. Smith 1989). Both of these strategies can be influenced by variability among members. For example, variability in irrelevant features may serve to highlight the consistent features, aiding the abstraction of relevant structure and critical features (Medin et al. 1993). Variability also decreases the similarity among irrelevant features, precluding the ability to group members based on *overall* similarity (eg., Sloutsky 2010). Therefore, many researchers propose that variability

plays a substantial role in category learning through both routes (Estes and Burke 1953; Perry et al. 2010; Posner and Keele 1968; Smith and Thelen 2003).

Interestingly, there is a switch in terms of how category structure is learned during childhood. Early in development, children learn categories by grouping members together that share overall similarity (e.g., ducks and chickens). As described above, this is not an effective way of forming a category, and, therefore, young children (until about age 7–8) often form broader categories than adults (e.g., Deng and Sloutsky 2016). Ages 7–9 are considered transitional, when children begin to form categories based on diagnostic features more than overall similarity and display more accurate (adult-like) category formation. Previous work has demonstrated that variability in non-diagnostic features of category members does not facilitate younger children's (5- to 6-year-olds) category formation based on diagnostic features, but it does effect 8-year-olds category learning (Plebanek and James, under review). Although the categorization ability of 8-year old children was affected by variability, this age group did not categorize novel members by matching the diagnostic feature as much as would be expected by adults. This finding supports the assumption this age group is in a transitional stage of category learning (Deng and Sloutsky 2015, 2016; Plebanek and Sloutsky 2019; Smith and Kehler 1977; Plebanek and James, under review).

Another contributing factor to category learning in addition to category structure (degree of variability) is how the category is learned. The measurements of category learning are often limited by requiring both explicit training paradigms as well as singular, explicit categorization responses (e.g., Ashby et al. 2019; Ashby and Valentin 2017). Because many categories are learned without explicit feedback, there must be a mechanism that supports categorization with implicit exposure only. Ashby et al. (2019) have asserted that implicit category learning is no more difficult than explicit learning, but relies more on procedural learning rather than verbal working memory. Given that young children have limited working memory ability (e.g., Cowan and Alloway 1997), explicit category learning may be more difficult than implicit category learning. It is also possible that children can learn categories with either explicit learning or implicit exposure as well as adults, but response demands preclude this demonstration. That is, children can have difficulty in task understanding, in verbal response (e.g., Engle et al. 1991), and have slower reaction times and lower accuracy than adults overall (e.g., Manning et al. 2018). In addition, there is very high variability among children throughout the elementary school years in terms of working memory and response to verbal instruction (Engle et al. 1991). It is arguable that explicit categorization tasks require an understanding of verbal instruction, working memory and attention, all of which are immature in the child compared to a typical

adult (e.g., Konrad et al. 2005). Therefore, implicit learning without verbal instruction and measuring competencies without overt verbal or manual responses may allow the researcher to acquire a more accurate understanding of the learning capabilities of young children and provide an unbiased comparison of object processing in children and adults.

One way to measure object processing and category learning without the need for overt responses is through neuroimaging techniques. As described above, this is important in developmental science, given the difficulty in designing experiments that accurately reflect a child's knowledge. In isolation, however, this is rarely viewed as an appropriate reason for conducting neuroimaging studies. More importantly, neuroimaging data can provide information on *how* a given behavioral outcome is supported by neural processes and how these processes may differ depending on experimental manipulations or preexisting variables (e.g., age). Thus, we are not only concerned simply with the output of a process, but also with the process itself and how this changes with experience. Arguably, this is extremely important when studying learning, as there may be multiple routes in the brain for attaining a similar behavioral result (neural degeneracy) and these routes can change with age or experience.

In addition, neuroimaging measures are more sensitive than behavioral measures. A simple example is as follows: By a certain age (around 5), young children can recognize letters of the alphabet when they are presented in typed form or if those same letters are written by hand (e.g., Zemlock et al. 2018). We, therefore, assume from this behavioral result that typed and handwritten letters are processed in the same way by a certain age. Recent neuroimaging results, however, have shown that this is not entirely correct. The neural systems of young children process handwritten letters very differently from typed letters, but in older children and adults the processing is virtually the same (Vinci-Booher et al. 2020). Even though behavioral responses did not reveal that letters that are handwritten vs typed as processed as different categories in young children, the fMRI data allowed us to see this explicitly, and generated hypotheses about why this might be the case. Thus, neuroimaging can reveal processing differences that are missed with behavioral measures.

Furthermore, neuroimaging can reveal how certain systems process environmental stimuli, which allows one to better understand brain function itself. For example, there is a long history of fMRI work demonstrating that the VTC is highly involved with object processing (e.g., Grill-Spector et al. 2001). However, past research has also demonstrated that neural specialization for object categories in the ventral temporal cortex only emerges as a function of certain experiences (e.g., James 2010; James and Engelhardt 2012; Scherf et al. 2011). Further, that the role of certain brain systems can change through development (e.g., Vinci-Booher et al.

2020). Such work has led to insights into developmental competencies that result from neural system changes that could not be revealed with behavioral measures alone.

One valuable method of neuroimaging that has proven to enhance our understanding of category representation in the brain is the neural adaptation paradigm. A long history of research has shown that neurons, populations of neurons, and brain regions respond preferentially to specific environmental inputs. This ranges from the seminal work of Hubel and Wiesel in felines detecting line orientations to research examining face processing throughout the ventral temporal cortex (VTC) (Hubel and Wiesel 1959; Kanwisher et al. 1997). Neural adaptation can help us further understand such input by invoking a biological predisposition of the brain to reduce activation across repetitions of stimuli (Grill-Spector and Malach 2001). Although adaptation was originally studied through single cell recordings of non-human animals (Desimone 1996), one can use coarser measures to investigate adaptation in humans using functional magnetic resonance imaging (fMRI). For example, Grill-Spector and Weiner (2014) adapted neuronal populations to study object properties: size, position, illumination, and viewpoint, and whether they influenced representations. Interestingly for category learning, the repeated stimuli do not need to be identical for brain responses to diminish. Rather, in some regions of the VTC, neural adaptation occurs during exposure to repetitions of category members, even if they are different exemplars of the category (Grill-Spector and Malach 2001). When a subsequent stimulus belongs to a different category, relevant brain systems increase their responding, indicating a 'release from adaptation.' Thus, one can manipulate exemplar similarity during exposure to determine where a category boundary lies by observing under what conditions 'release' occurs (Folstein et al. 2012). Importantly for the present work, neural adaptation paradigms have been used successfully when comparing children of various ages to adults (e.g., Scherf et al. 2011; Kadosh et al. 2013). These past studies have established that the neural properties of adaptation do not change through development. That is, the 5-year-old brain shows neural adaptation properties just as the adult brain does. The method is especially useful for studying child populations given that there is no need for an explicit task to reveal an adaptation response from the brain. Measuring category learning through neuroimaging techniques such as neural adaptation can, therefore (a) allow the measurement of learning without overt responses, (b) reveal changes that occur in underlying mechanisms that may not be measurable in overt responses, and (c) is particularly useful for understanding category learning through adaptation paradigms in developing populations.

The purpose of the present study was to probe the potential effects that different degrees of variability have on category learning and neural processing in 8-year-olds and

adults by measuring brain adaptation and release from adaptation. We compared exposure to category members that are similar to one another (tight structure) to those that are more dissimilar (variable structure) and measured neural adaptation, and release from adaptation, in the entire brain but were most interested in responses in the Ventral Temporal Cortex (VTC). As shown by previous work, we hypothesized that exposure to variability during category learning would facilitate the extraction of diagnostic features that defined category membership (Medin et al. 1993). We predicted that with variable exposure, an object presented after category exposure would result in a release from adaptation, but only if that object differed in the diagnostic feature. This result would directly reflect behavioral findings in adults (Cohen et al. 2001). We further predicted that if 8-year-old children were using the same neural mechanisms as adults to categorize objects, then this group would show the same pattern of adaptation as the adults. However, if 8-year-olds were truly transitioning between categorizing based on similarity to categorizing based on diagnostic feature, then we may see release from adaptation both when new objects did not share the same diagnostic feature and when they differed based on the irrelevant features. We chose to focus our interpretations on the VTC, given the well-known response properties of this broad region during object processing. Research has shown that the VTC responds to objects in a similar manner in children compared to adults (Dekker et al. 2011). However, we also attended to age differences in the entire brain, given that dorsal stream processing (posterior parietal cortex in particular) has a protracted development compared to the VTC (Dekker et al. 2011). This may be important given the conjecture that implicit category learning may require more of a procedural learning mechanism rather than working memory and attention (Cohen et al. 2001). Given that working memory and attention is also immature in children, we remained agnostic to hypotheses related to the frontal systems because immaturity in these competencies could either show more activation in frontal systems (because they are not as efficient) or less activity because they are not recruited (e.g., Conklin et al. 2007). Because response properties are similar in adults and children in the VTC, we focused our conclusions on responses in this region to avoid any spurious conclusions due to maturational differences in the two populations. Specifically, we hypothesized that adults would show release from adaptation in this region to both variable and tight category structures, given the expertise with which adults can abstract critical features in category members. This release is expected to be more consistent when the deviant stimulus differs from the exposure stimuli in terms of the invariant (diagnostic) feature. However, because children are thought to be in a transitional stage in terms of how they assign members to categories, we expected that exposure to a variable structure would result in a release from

adaptation more than exposure to a tight category structure and further that release from adaptation would occur with similarity deviants as well as invariant feature deviants given the transitional nature of children's categorization strategies.

Methods

Participants

The final sample included 14 adults ($M = 22.2$ years, range = 18–28 years, seven males) and thirteen 8-year-old children ($M = 8.7$ years, range = 7.7–9.1 years, five males).¹ Two additional adults were excluded: one for equipment failure and one for experimenter error. Four additional children were excluded: three for excessive motion² and one for equipment failure.

The ages were selected for two reasons: (1) The development of category representations via a singular feature undergoes a protracted developmental trajectory maturing around approximately 8 years of age (Deng and Sloutsky 2015, 2016; Plebanek and Sloutsky 2019; Smith and Kemler 1977). (2) Behavioral data measuring implicit categorization judgments using these stimuli revealed that younger children were not sensitive to variability without task support (Plebanek and James, under review). In contrast, 7- and 8-year-old children were sensitive to variability (Plebanek and James, under review).

Adult participants were graduate or undergraduate students. Children were recruited from the local community using an in-house database. Each participant and parent provided informed consent and/or assent and were compensated \$25 per hour (\$20 gift card and a toy for children). Participants were right handed, spoke English as a primary language, and were screened for neurological trauma and MRI contraindications.

¹ Of the included children, two children only contributed data from two functional runs due to excessive motion. For all children, this useable data was for separate categories and category structures, thus every participant contributed at least 1 useable run in each exposure condition. This resulted in 48 (24 tight and 24 variable) useable runs for children compared to 56 (28 tight and 28 variable) useable runs for adults.

² To keep an equal number of variable and tight runs and an equal number of runs for each category, runs were grouped into pairs (Tight Flower and Far Alien; Tight Alien and Far Flower). Both runs in a pair were excluded if one of the runs had more than five spikes or they had a combined total of more than eight spikes. No adults had no motion spikes. Children had an average of 1.9 spikes on variable runs and an average of 1.6 spikes on tight runs.

Materials and stimuli

Apparatus

Stimuli were presented using a Mitsubishi XL30 projector that was back presented onto a screen in the MRI environment using a mirror. Instructions were given to participants via Siemens MR-compatible headphones. A Matlab program using the Psychophysics Toolbox extensions was created to dictate the presentation of stimuli (Brainard and Vision 1997; Pelli and Vision 1997). Manual responses during scanning were made on an in-house constructed 4-finger response pad placed underneath the right hand of the participants.

Stimuli

For the learning runs, the stimuli were comprised of systematically organized sets of objects called “Aliens” and “Flowers.” These stimulus sets each consisted of four dimensions that could be manipulated metrically to create 18 possible values on each dimension (Appendix 1). For the alien set, these dimensions included the length of the eye stalk, the surface area of the body, the angle of the arms, and the vertex of the hand and arm. For the flower set, dimensions included the gradient of the center, the roundness of the petals, the width of the stem, and the rotation of the symbol on the pot.

The inclusion of multiple, continuous dimensions was important for several reasons. First, it allowed us to manipulate the learning stimuli to control the similarity and structure of the category. We selected three dimensions of each set to vary continuously to create what is henceforth referred to as the “similarity space”. The fourth dimension, henceforth referred to as the “invariant feature”³, could vary to the same extent as the other dimensions, but remained constant on the central value of the dimension. Therefore, the invariant feature was more “predictive” of category membership. This structure allowed us to establish a dichotomy in our categories to mimic the rule-plus-similarity structures of categories used by other research such as Deng and Sloutsky (2015, 2016). Second, the use of a continuous similarity space allowed us to clearly define the variability of the categories to which each individual was exposed. We created two different levels of variability (tight and variable)

³ Note that in many studies using similar category designs, the invariant feature is referred to as the rule (see Deng and Sloutsky, 2015 and 2016). However, because the categories were not explicitly taught, and because the design is ultimately agnostic to whether invariant deviants do or do not belong within the category, we believe “invariant deviants” to be a more accurate description of these items in this study.

by manipulating the distribution of the similarity space (Fig. 1a). Therefore, we were able to quantify and manipulate the variability in order to alter the similarity component of our category structures (Appendix 1). Finally, because our categories consisted of two streams of information (the similarity space and the invariant feature), we further manipulated the category features to create test stimuli called “deviant stimuli.” Deviant stimuli had two classes: similarity-based and invariant feature-based. Similarity-based deviants were created by continuously manipulating a dimension from the similarity space in a manner that was inconsistent with the standard construction of the dimension. For example, in the flower set, although the gradient dimension appeared horizontally, a similarity-based deviant could rotate the gradient (Fig. 1b). Each of the three dimensions in the similarity space had two potential deviants, resulting in a total of six similarity-based deviants. Invariant feature-based deviants were constructed by introducing new values on the invariant dimension (the hand vertex in aliens or symbol rotation in flowers). Two deviants were created for each category by manipulating the invariant feature in opposite directions across its dimension. These deviants were repeated three times each, resulting in a total of six presentations of invariant-deviants per run. For both deviants, the non-deviant features were values sampled from the tight similarity space.

Design

Participants completed four functional neuroimaging runs. Each of the four functional runs followed the same adaptation design and lasted 306 s (5 min and 6 s). Runs were counterbalanced so that each participant received different categories and structures as their first two runs. The goal was to explore how individuals’ neural activation adapted to repeated presentation of category members and how this adaptation was affected (maintenance or release) in response to the deviant stimuli. To achieve this goal, we implemented a design that combined elements of blocked and event-related fMRI (Fig. 1c) for 750 ms followed by a short 250-ms black fixation cross. This resulted in blocks consisting of the adaptation stimuli lasting 16 s each.

A deviant stimulus (either similarity or invariant, presented in a randomized order) then appeared for 2 s. Deviant stimuli always appeared in the center of the display. After 2 s, the deviant stimulus was removed from the screen and replaced with a fixation cross for a jittered interval (2, 4, or 6 s). Each of these runs consisted of 12 blocks followed by a deviant. Each run contained six invariant and six similarity deviants. This type of design has been used successfully in neural adaptation studies comparing children to adults (e.g., Kadosh et al. 2013).

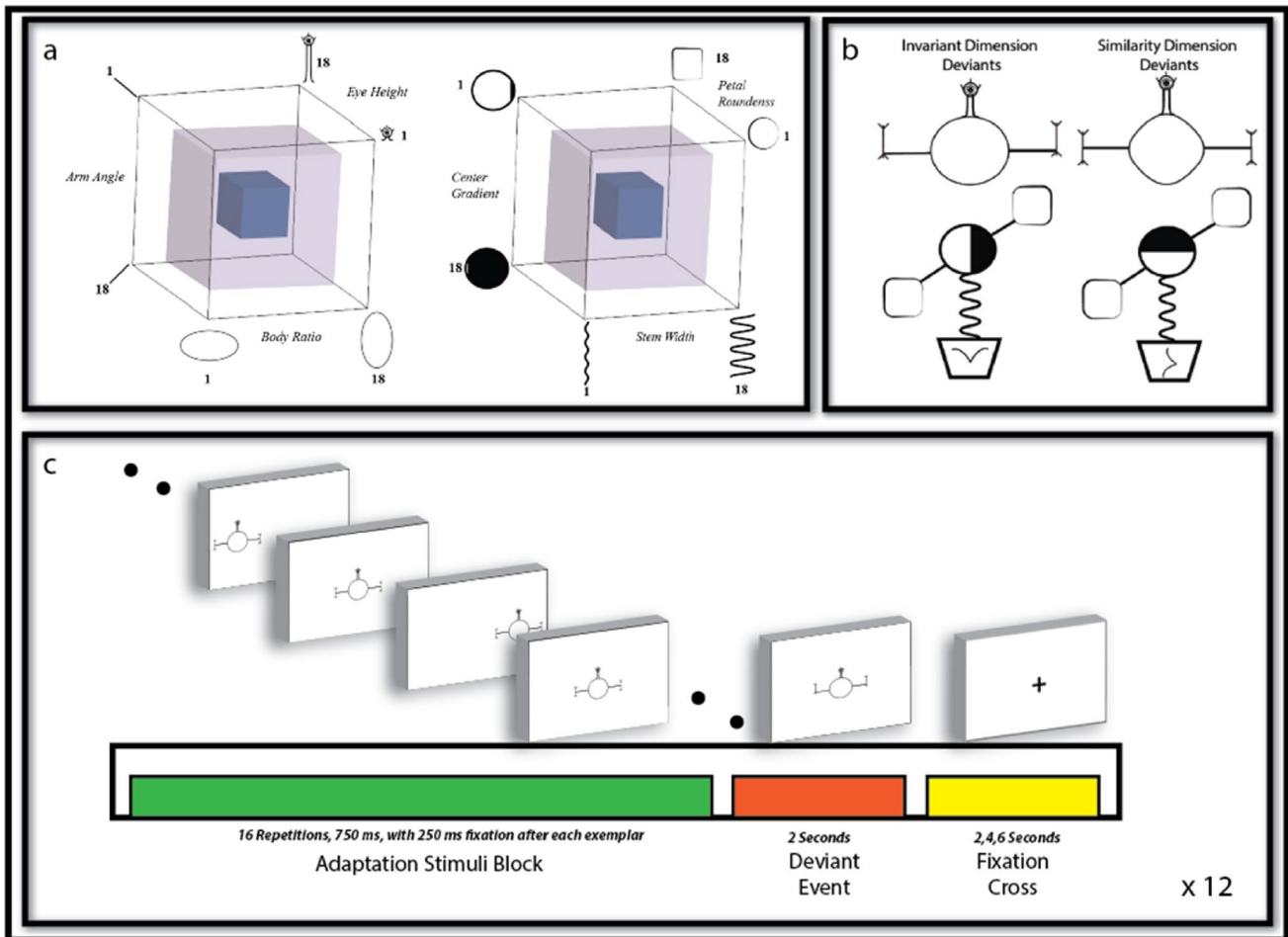


Fig. 1 Depiction of the stimuli and procedure in the experiment. **a** presents the alien and flower similarity space. Present are the three continuous dimensions ranging from value 1 to 18 that comprised the similarity space. Each number across this range corresponds to a specific quantity for a given dimension (e.g., eye height). Every increase in value corresponds to a specific quantitative change (e.g., an increase in eye height). The blue cube represents the narrow sam-

pling of the tight similarity space comprising only values 8–10. The light gray cube represents the more diverse sampling of the variable similarity space comprising of values 4–14. **b** presents examples of deviant stimuli. **c** presents the fMRI protocol used for adaptation runs. During the blocks (green portion) individuals saw the 16 repetitions of category members, during the deviant event (red portion) participants were shown either an invariant or a similarity deviant

Procedure

Imaging procedure

After providing informed consent, participants were escorted to the imaging facility. Children completed a brief training session in a MRI simulator to acclimate to the scanning environment. This session lasted approximately 15 min, during which children watched short videos and were taught to remain still during the scan. They did not see experimental stimuli during this time. Adults did not complete this session. At the start of the actual scan, participants underwent an anatomical scan, during which they watched a video (children) or rested (adults). Participants then began the functional runs. During the runs, participants were told to track the items as they appeared on the screen, and when

items were presented in the center of the screen to press the button on the response pad with their right index finger. When items were presented off-center, to press a button on the response pad with their right middle finger. Participants were given the response pad and shown the screen prior to entering the bore of the scanner and practiced button pressing to ensure they understood the task. This task was implemented only to enhance attention to the stimuli (category exposure was implicit) and response accuracy was not measured, due to the blocked design. However, compliance with the task was noted by the experimenter in the scanning room with the participants. Our previous behavioral study found that children as young as 5 years of age perform at ceiling level in this task (Plebanek and James, under review). All participants performed the task with ease. Scanning sessions lasted between 30 and 45 min.

Scanning parameters

Neuroimaging was conducted at the Indiana University Imaging Research Facility, using a Siemens Magnetom Prisma 3-T whole-body MRI system. High-resolution T1-weighted anatomical volumes were acquired using a MPRAGE sequence: TI = 900 ms, TE = 2.98 ms, TR = 2300 ms, flip angle = 9°, with 176 sagittal slices of 1.0 mm thickness, a field of view of 256 ×

248 mm, and an isometric voxel size of 1.0 mm³. For functional images, the field of view was 220 × 220 mm, with an in-plane resolution of 110 × 110 pixels and 72 axial slices of 2.0 mm thickness per volume with 0% slice gap, producing an isometric voxel size of 2.0 mm³. Functional images were acquired using a gradient echo EPI sequence with interleaved slice order: TE = 30 ms, TR = 2000 ms, flip angle = 52° for blood-oxygen-level-dependent (BOLD) imaging.

Neuroimaging preprocessing

All neuroimaging analyses were conducted using Brain Voyager, Version 20 (Brain Innovation, Maastricht, Netherlands). Anatomical volumes for each individual were normalized to the adult template in Talairach space (Talairach and Tournoux 1988). The functional preprocessing pipeline included slice scan time correction, 3-D motion correction using trilinear/sinc interpolation, and 3D Gaussian spatial smoothing with at 6 mm. During normalization, functional data were resampled to 3 mm³ isometric voxels. Coregistration of functional volumes to anatomical volumes was performed using a rigid body transformation. Rigid body parameters were included in the study design matrix as predictors of no interest to account for head motion (Bullmore et al. 1999).

Statistical analyses

The data were analyzed using a random-effects general linear model (GLM) using Brain Voyager's multi-subject GLM module with one predictor of interest for each condition and seven predictors of no interest that were included only for motion correction. The analyses were split into two mixed model, whole-brain ANOVAs. The first ANOVA examined group differences in learning the structures during the 16 s learning blocks using betas as our dependent measure: 2 (Structure: Variable vs. Tight) by 2 (Age: Adults vs. Children). The second analysis examined generalization, 2 (Structure: Variable vs. Tight) by 2 (Deviant: Invariant vs. Similarity) by 2 (Age: Adults vs. Children), using release as the dependent measure. Release was calculated by measuring the difference in neural response between the deviant stimulus and the last three seconds of the adapted

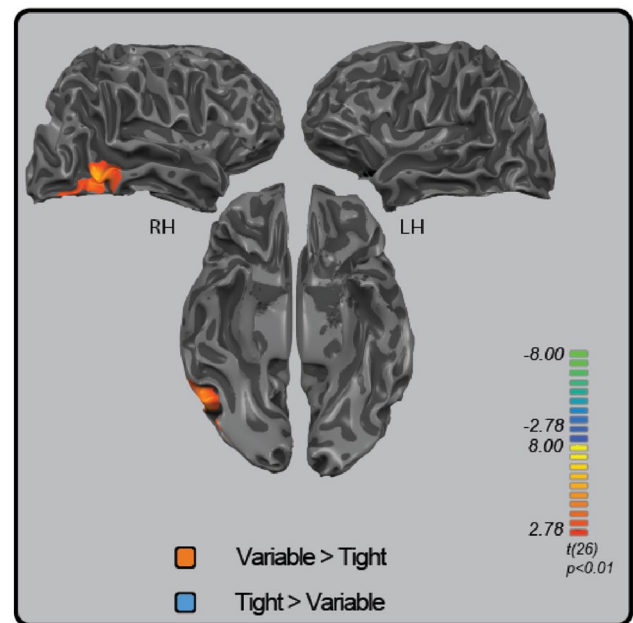


Fig. 2 Analysis of learning blocks examining difference in variable and tight learning across repetitions using contrast, variable > tight across the entire 16 s learning block, voxelwise threshold, $p < 0.01$, cluster corrected to $p < 0.01$

stimuli. Resulting F and t -maps were corrected for multiple comparisons by analyses using a voxel-wise threshold of $p_{\text{voxel}} < 0.01$, and cluster corrected to $p_{\text{cluster}} < 0.01$ using Brain Voyager's cluster-threshold estimator plug-in. We then examined the interactions through a series of planned comparisons.

Results

Variability during learning

We averaged the total activation during the adaptation portion of the experiment to determine whether neural adaptation was occurring and whether this changed depending on age and category structure. Lower mean activation across this block would imply that the system considers the stimuli to be very similar (belonging to the same category), whereas higher activation would imply that there are differences among the stimuli for neural systems.

We first performed a 2 (Structure: Variable vs. Tight) × 2 (Age: Adults vs. Children) mixed model ANOVA ($p_{\text{voxel}} < 0.01$, $p_{\text{cluster}} < 0.01$) on the adaptation portion of the runs. There was a main effect of Structure ($F(1, 25) = 30.82$, $h^2 = 0.552$) associated with the right fusiform gyrus that demonstrated higher activation for variable compared to tight blocks. No clusters demonstrated the reverse pattern (Fig. 2; Table 1). Thus, because the right fusiform gyrus is

Table 1 Effects from analysis 1

Effect	Contrast	Cluster size (voxels)	Talairach coordinates			Peak stat	Average <i>p</i> value	Anatomical location
			Peak <i>x</i>	Peak <i>y</i>	Peak <i>z</i>			
Main structure	Tight > variable	–	–	–	–	–	–	–
	Variable > tight	7825	51	– 58	– 11	5.77	0.003	Right fusiform gyrus
Main group	Adults > children	2290	24	– 46	– 25	4.58	0.007	Right fusiform gyrus
		Children > adults	933	12	29	– 11	3.86	0.006
	1700	24	23	– 5	4.84	0.005		
	1797	39	– 58	– 2	5.46	0.004	Right middle temporal gyrus	
	6551	54	10	4	5.42	0.004	Right superior temporal gyrus	
	17,313	– 48	23	4	4.91	0.004	Left frontal gyri	
	8545	– 48	2	9	4.95	0.004	Left superior frontal gyrus	
	3535	– 27	7	14	4.42	0.004	Left hippocampus	
	3507	25	1	17	5.22	0.004	Right Hippocampus	
	1214	6	– 34	40	4.39	0.005	Right posterior cingulate gyrus	
Structure	–	2370	45	11	52	4.22	0.005	Right middle frontal gyrus
		10,236	21	49	58	5.30	0.003	Right inferior parietal lobule
		528	– 57	– 19	25	11.21	0.003	Left post central gyrus
		Age	–	462	6	32	52	17.71

adapting (lowering activation) to tightly structured categories but not variable structure, we can assume that it processes each stimulus as different when exposed to variable exemplars.

There were several regions associated with a main effect of Group ($p_{\text{voxel}} < 0.01$, $p_{\text{cluster}} < 0.01$). One cluster in the right fusiform gyrus demonstrated greater activation overall for adults compared to children ($F(1, 25) = 16.98$, $h^2 = 0.404$), implying that the stimuli were processed as different in adults more than children in this region. In contrast, children demonstrated higher activation than adults associated with the left ($F(1, 25) = 16.86$, $h^2 = 0.403$) and right hippocampus ($F(1, 25) = 20.05$, $h^2 = 0.445$), the left superior temporal gyrus ($F(1, 25) = 27.38$, $h^2 = 0.523$), the right middle ($F(1, 25) = 32.61$, $h^2 = 0.566$), and superior temporal gyri ($F(1, 25) = 29.29$, $h^2 = 0.540$), the right inferior parietal lobule ($F(1, 25) = 25.36$, $h^2 = 0.504$), the left frontal gyri ($F(1, 25) > 14.45$, $h^2 > 0.367$) the right middle frontal gyrus ($F(1, 25) = 17.93$, $h^2 = 0.418$), the right posterior cingulate gyrus ($F(1, 25) = 14.19$, $h^2 = 0.362$), and the anterior cingulate ($F(1, 25) > 16.50$, $h^2 > 0.395$) (Table 1). Thus, children appear to have a more distributed system that is not adapting to the stimulus presentations, but is sensitive to object perception.

However, these main effects should be interpreted with caution, given the significant interaction between Structure and Group associated with the left postcentral gyrus ($F(1, 25) = 11.09$, $h^2 = 0.307$) and the right superior frontal gyrus ($F(1, 25) = 14.52$, $h^2 = 0.368$) ($p_{\text{voxel}} < 0.01$, $p_{\text{cluster}} < 0.01$; Fig. 3; Table 1). We performed planned comparisons to examine differences in each region between tight and

variable structures within each age group. Planned comparisons revealed that within both regions, children had higher activation for variable compared to tight structures (postcentral gyrus: $t(12) = 2.33$, $p = 0.038$, $d = 0.649$, superior frontal gyrus: $t(13) = 3.16$, $p = 0.008$, $d = 0.844$) whereas adults demonstrated higher activation for tight structure in the superior frontal gyrus ($t(13) = 2.49$, $p = 0.029$, $d = 0.685$) and no difference in the postcentral gyrus ($p = 0.06$, $d = 0.562$). Therefore, children showed less adaptation during viewing variably structured categories compared with tightly structured categories. In contrast, adults adapted to variable category structure either to the same degree, or more than tightly structured categories. The implications here are that children formed categories only after exposure to tight category structure, whereas adults formed categories from either type of exposure or from only variably organized category structure. Interestingly these effects were only seen in the frontal cortex.

The impact of category structure on generalization

We also examined the influence of development and variability on the degree to which new exemplars were assimilated into, or differentiated from, the learned categories. Release from adaptation indicated that the new (deviant) exemplar did not fit into the category, whereas no release (the same or less activation to the new exemplar) indicated that it was processed as belonging to the same category. Release was calculated as (Deviant Beta—Last 3 s Beta). A positive difference suggested that the deviant stimulus was different from the adapted category, a negative difference

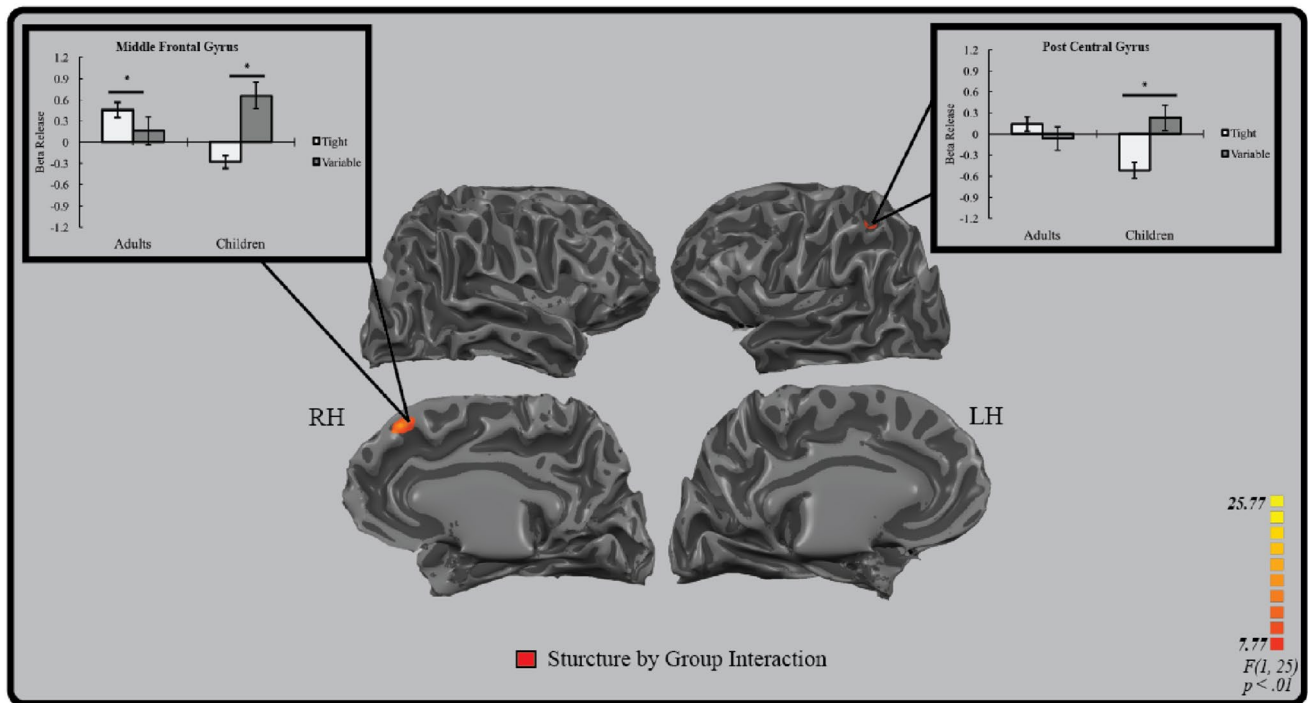


Fig. 3 Results from a 2 (Structure) by 2 (Age) repeated measures, whole-brain ANOVA, $p < 0.01$, $p_{\text{cor}} < 0.01$. Asterisks represent results ($p < 0.05$) of paired-samples t tests comparing betas during the entire

learning block for tight and variable structures within each age group. Error bars are standard error of the mean

suggested continued adaptation, indicating that it was processed as the same as the adapted category.

We first performed a contrast, Deviant > Last 3 s, to determine whether our deviants caused release at all (could a difference be detected) in both adults and children collapsed across other factors. In adults, significant release was associated with the right superior temporal gyrus, the left insula extending to the middle temporal gyrus, the left middle occipital gyrus extending through the right middle occipital gyrus, parahippocampal and lingual gyri, and precuneus, the right superior parietal lobule, the left inferior frontal gyrus extending through the frontal gyri, the right middle frontal gyrus, the left and right anterior cingulate, and the cingulate gyrus. Therefore, many brain regions played a role in detecting a deviant stimulus. Continued adaptation occurred in the left and right inferior occipital gyri extending to the fusiform gyri, suggesting that these regions assimilated the new stimulus into the existing category. In children, release occurred within the right inferior and superior frontal gyri. In contrast, continued adaptation occurred within the right and left middle occipital gyri (Fig. 4; Table 2). Thus, in both populations, if we do not account for our manipulations of category structure and deviant type, the occipital and VTC regions grouped the deviant stimuli with the category. It is of note that when comparing release between the two age groups, there were no areas where children showed

greater release than adults. Adults showed greater release than children ($p_{\text{voxel}} < 0.01$, $p_{\text{cluster}} < 0.01$), in the left pre- and post-central gyri, the left inferior frontal gyrus and the left temporal pole.

We then performed a 2 (Structure: Tight vs. Variable) \times 2 (Deviant: Invariant vs. Similarity) by 2 (Age: Adults vs. Children) mixed model ANOVA. The analysis revealed a main effect of group ($p_{\text{voxel}} < 0.01$, $p_{\text{cluster}} < 0.01$). Adults demonstrated significantly greater release than children associated with the right fusiform gyrus ($F(1, 25) = 16.56$, $h^2 = 0.398$). However, children demonstrated greater release than adults throughout the left frontal gyri ($F(1, 25) = 25.41$, $h^2 = 0.504$), the right superior frontal gyrus ($F(1, 25) = 13.65$, $h^2 = 0.353$), the left ($F(1, 25) = 18.47$, $h^2 = 0.425$), and right ($F(1, 25) = 21.43$, $h^2 = 0.462$) superior temporal gyri, the left ($F(1, 25) = 23.15$, $h^2 = 0.481$), and right ($F(1, 25) = 37.32$, $h^2 = 0.599$) insula, the right superior parietal lobule ($F(1, 25) = 20.53$, $h^2 = 0.451$) (Table 3). There were no main effects of Structure or Deviant at our threshold ($p_{\text{voxel}} < 0.01$, $p_{\text{cluster}} < 0.01$). Therefore adults processed the deviant as different from the category in the right fusiform, whereas children did so in the superior temporal, parietal and frontal regions.

No region demonstrated a significant three-way interaction at our threshold, ($p_{\text{voxel}} < 0.01$, $p_{\text{cluster}} < 0.01$). However, the component two-way interactions were significant

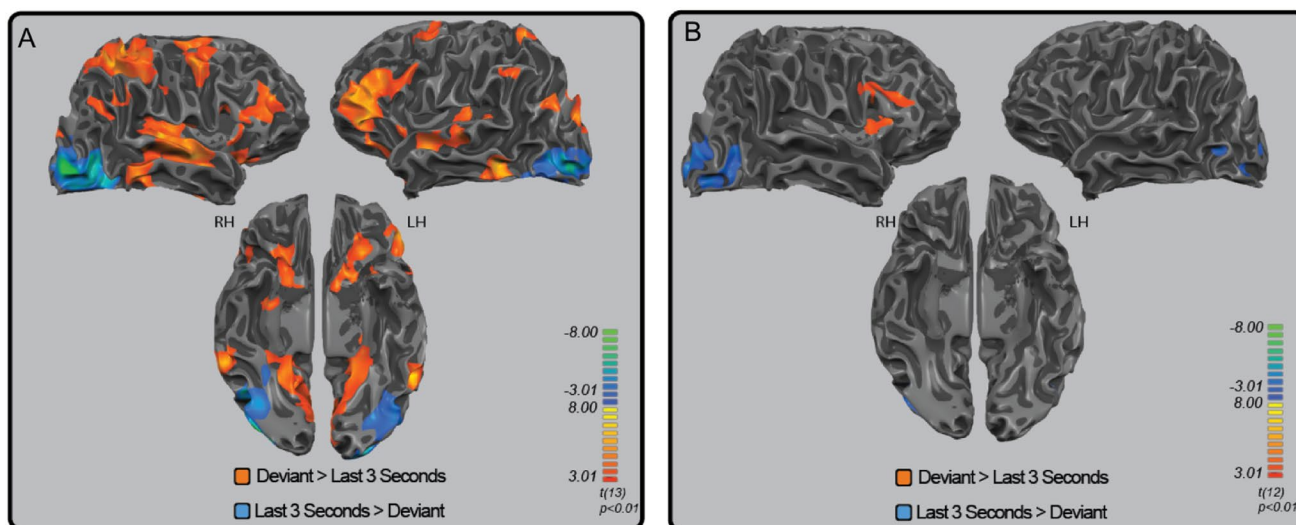


Fig. 4 Results for release from adaptation collapsed across structure and deviants conducted using the contrast Deviant > Last 3 s, voxel-wise $p < 0.01$, cluster corrected $p_{\text{cor}} < 0.01$. Red regions signify a significant release from adaptation, suggesting that the stimulus differed

in terms of previously formed representations of the object category. Blue regions signify continued adaptation. **a** Presents adults. **b** Presents children

Table 2 Release from adaptation

Group	Contrast	Cluster size (voxels)	Talairach coordinates			Peak t	Average p value	Anatomical location
			Peak x	Peak y	Peak z			
Adult	Deviant > last 3 s	25,245	39	-1	-11	9.65	0.003	Right superior temporal gyrus
		2348	21	21	-11	5.00	0.005	Right anterior cingulate
		2875	-24	26	-5	4.94	0.005	Left anterior cingulate
		8028	-36	-37	10	8.04	0.004	Left insula extending to middle temporal gyrus
		2889	0	11	31	6.70	0.004	Cingulate gyrus
	Last 3 s > deviant	12,828	9	-37	34	6.93	0.003	
		10,944	35	59	40	7.10	0.004	Right middle frontal gyrus
		20,594	21	-58	52	6.93	0.003	Right superior parietal lobule
		12,747	-27	-88	-17	9.05	0.003	Left inferior occipital gyrus extending to fusiform gyrus
		25,017	30	-88	-11	13.73	0.002	Right inferior occipital gyrus extending to fusiform gyrus
Children	Deviant > last 3 s	12,254	-45	29	10	6.99	0.003	Left inferior frontal gyrus extending through frontal gyrus
		47,971	-6	-79	10	6.69	0.004	Left middle occipital gyrus extending to right middle occipital gyrus, bilateral lingual gyrus, bilateral parahippocampal gyrus, and precunes
	Last 3 s > deviant	2336	54	32	20	4.13	0.006	Right superior frontal gyrus
		2594	42	8	13	5.46	0.004	Right inferior frontal gyrus
	Last 3 s > deviant	9220	24	-76	-26	6.92	0.004	Right middle occipital gyrus
		1915	-42	-70	-8	5.11	0.005	Left middle occipital gyrus

across several regions. First, the 2 (Structure: Tight vs. Variable) \times 2 (Deviant: Invariant vs. Similarity) interaction was associated with both the left anterior ($F(1, 25) = 15.42$, $h^2 = 0.372$) and posterior fusiform gyrus ($F(1, 25) = 11.03$,

$h^2 = 0.298$), the left lingual gyrus ($F(1, 25) = 12.78$, $h^2 = 0.329$), the left inferior parietal lobule extending to the precuneus ($F(1, 25) = 13.07$, $h^2 = 0.344$) (Fig. 5; Table 3). Given that we hypothesized that variability would lead to

Table 3 Structure by deviant by age mixed ANOVA analysis

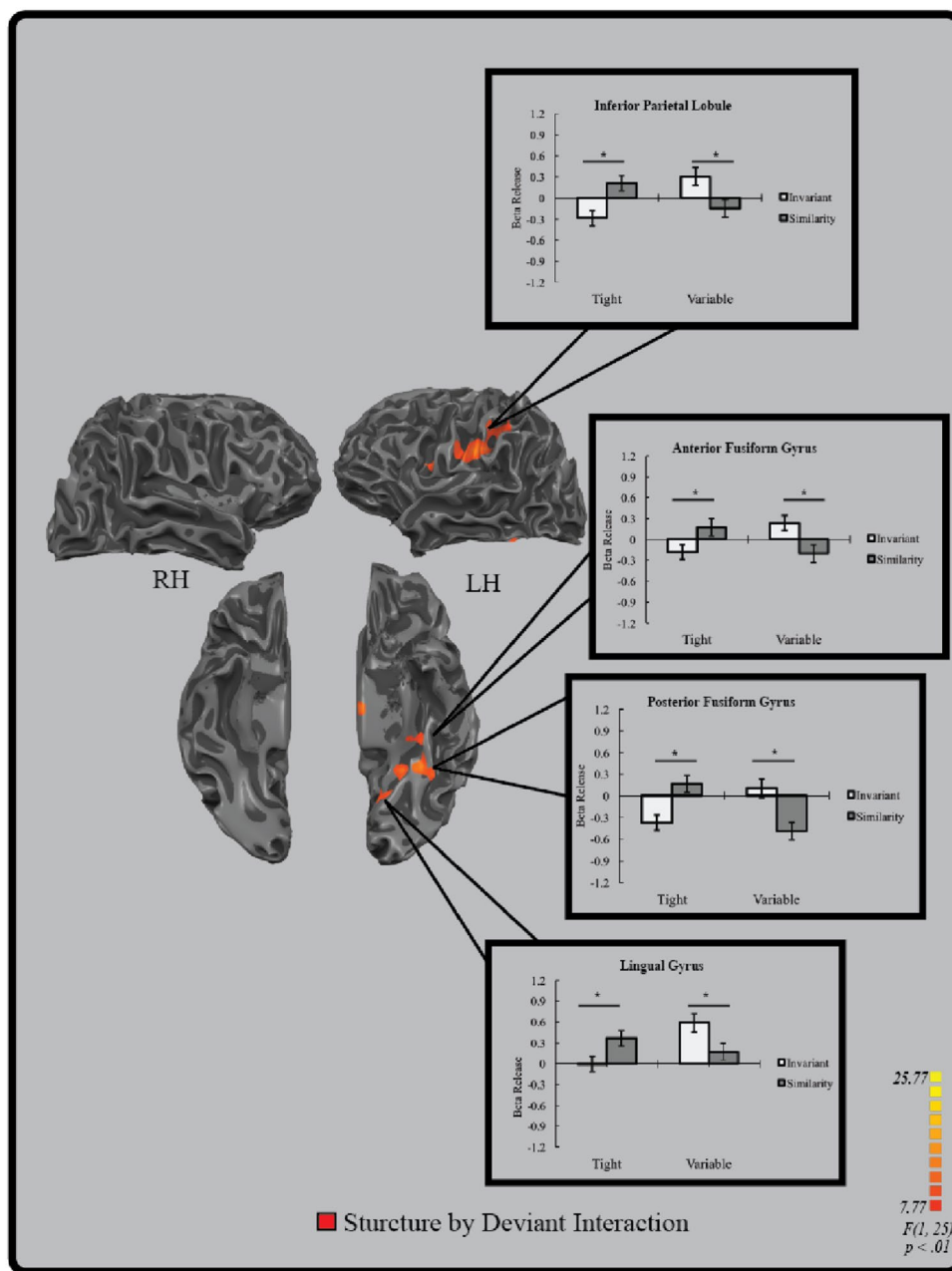
Effect	Contrast	Cluster size (voxels)	Talairach coordinates			Peak stat	Average <i>p</i> value	Anatomical location	
			Peak x	Peak y	Peak z				
Main group	Adults > children	1552	39	- 49	- 29	4.61	0.005	Right fusiform gyrus	
	Children > adults	1490	- 39	- 1	- 19	- 3.88	0.006	Left superior temporal gyrus	
		2558	24	8	- 19	- 4.90	0.005	Right superior temporal gyrus	
		2074	39	- 19	4	- 4.29	0.005	Right insula	
		1447	- 40	- 24	19	- 3.98	0.005	Left insula	
		10281	- 45	32	28	- 4.87	0.004	Left middle frontal gyrus extending throughout frontal gyri	
		1501	30	- 1	61	- 4.05	0.005	Right superior frontal gyrus	
		2655	27	- 40	61	- 4.66	0.005	Right superior parietal lobule	
	Structure × deviant -		366	- 24	- 70	- 14	11.18	0.008	Left fusiform gyrus
			1017	- 42	- 34	- 17	12.44	0.007	
		1026	- 18	- 79	- 8	15.16	0.006	Left lingual gyrus	
		2422	- 36	- 40	25	18.89	0.006	Left inferior parietal lobule extending to precuneus	
Structure × group -			1194	36	- 25	- 23	15.89	0.006	Right fusiform gyrus
		712	- 33	- 22	- 17	15.08	0.007	Left parahippocampal gyrus	
		1882	54	26	16	18.41	0.005	Right middle frontal gyrus	
		650	48	- 13	31	13.39	0.006	Right precentral gyrus	
		2045	- 51	- 31	31	14.39	0.005	Left superior parietal lobule	
Deviant × group -		1992	- 14	- 64	28	29.12	0.004	Left cingulate gyrus	
		1223	12	- 55	13	19.81	0.005	Right cingulate gyrus	

invariant-feature defined categories, we then performed a priori paired *t* tests comparing release for similarity and invariant deviants within each level of structure. For tight structure, release was greater for similarity over invariant-feature deviants in all significant regions, (L. anterior fusiform: $t(26)=2.39, p=0.024, d=0.47$, L. posterior fusiform: $t(26)=2.50, p=0.019, d=0.48$, L. lingual: $t(26)=2.96, p=0.007, d=0.57$, L. parietal lobule: $t(26)=2.46, p=0.021, d=0.47$). For variable exposure, all regions demonstrated significantly greater release for invariant-feature deviants, (L. anterior fusiform: $t(26)=2.64, p=0.014, d=0.51$, L. posterior fusiform: $t(26)=2.17, p=0.039, d=0.44$, L. lingual: $t(26)=2.38, p=0.025, d=0.46$, L. parietal lobule: $t(26)=2.74, p=0.011, d=0.52$). These findings suggested that detection of a change in the invariant feature resulted from variable exposure and was processed by ventral temporal and parietal sub regions.

We then examined the additional 2 (Structure: Tight vs. Variable) × 2 (Age: Adults vs. Children) interaction ($p_{\text{voxel}} < 0.01, p_{\text{cluster}} < 0.01$). The anterior right fusiform gyrus ($F(1, 25)=15.75, h^2=0.387$), left parahippocampal gyrus ($F(1, 25)=20.57, h^2=0.451$), left superior parietal lobule ($F(1, 25)=13.42, h^2=0.341$), right middle frontal gyrus ($F(1, 25)=19.11, h^2=0.433$), and the right precentral gyrus were significant ($F(1, 25)=12.70, h^2=0.337$) (Fig. 6;

Table 3). We then performed planned comparisons to examine the patterns of generalization for different structures within and across age groups. Planned comparisons revealed that children demonstrated significantly greater release after variable compared to tight exposure in all regions, (right fusiform gyrus: $t(12)=3.13, p=0.009, d=0.875$, left parahippocampal gyrus, $t(13)=4.37, p=0.001, d=1.21$, left superior parietal $t(12)=3.32, p=0.006, d=0.931$, right middle frontal gyrus $t(12)=3.51, p=0.004, d=0.981$, right precentral gyrus $t(12)=3.04, p=0.01, d=0.842$). Adults demonstrated significantly greater release for tight exposure in the right fusiform gyrus ($t(13)=3.16, p=0.008, d=0.884$) and the right middle frontal gyrus ($t(13)=2.65, p=0.02, d=0.712$), but no differences in the parahippocampal gyrus, the left superior lobule, and the right precentral gyrus ($ps > 0.10, ds < 0.50$). Independent-samples *t* tests revealed that within the right fusiform gyrus ($t(25)=3.64, p=0.001, d=1.46$), and the right middle frontal gyrus ($t(25)=2.90, p=0.008, d=1.40$) children demonstrated significantly greater release than adults after variable exposure, whereas adults demonstrated greater release after tight exposure, (right fusiform gyrus: $t(25)=2.18, p=0.039, d=0.868$, right middle frontal gyrus: $t(25)=2.97, p=0.007, d=1.06$). Within the left parahippocampal gyrus ($t(25)=3.35, p=0.003, d=1.34$), the left superior parietal

Fig. 5 Results from a 2 (Structure) by 2 (Deviant) interaction using release as the dependent measure, $p < 0.01$, cluster corrected $p_{\text{cor}} < 0.01$. Y-axis provides Beta Release calculated by (Beta Deviant – Beta Last 3 s). Positive values signify release while negative and zero values signify maintenance. Asterisks represent results ($p < 0.05$) of paired-samples t tests comparing release for deviants within tight and variable structures. Error bars are standard error of the mean



lobule ($t(25) = 3.64$, $p = 0.001$, $d = 1.45$), and the right precentral gyrus ($t(25) = 3.48$, $p = 0.002$, $d = 1.39$), adults still demonstrated greater release than children after tight exposure. However, there were no differences after variable exposure ($ps > 0.095$, $ds < 0.685$). These findings suggest that neural systems may be tuned to different category structures at different points in development.

Finally, we examined the significant 2 (Deviant: Invariant vs. Similarity) \times 2 (Age: Adults vs. Children) interaction ($p_{\text{voxel}} < 0.01$, $p_{\text{cluster}} < 0.01$). This interaction was associated with the left ($F(1, 25) = 19.29$, $h^2 = 0.436$) and right cingulate gyrus ($F(1, 25) = 25.08$, $h^2 = 0.520$) (Fig. 7; Table 3). In both regions, children demonstrated greater release for

invariant deviants (left: $t(12) = 4.42$, $p = 0.001$, $d = 1.24$, right: $t(13) = 6.55$, $p < 0.001$, $d = 1.82$). Adults demonstrated no differences between deviant types ($ps > 0.390$, $ds < 0.25$). We then performed planned comparisons examining developmental differences in processing deviant types via independent samples t tests. Within the right cingulate gyrus, there were no differences between adults and children across either deviant type ($ps > 0.065$, $ds < 0.75$). Within the left cingulate gyrus, children demonstrated greater release than adults for invariant-feature deviants ($t(25) = 2.80$, $p = 0.01$, $d = 1.11$) and no differences for similarity deviants ($p = 0.15$, $d = 0.59$). These results suggest differences in how category exceptions are processed across development.

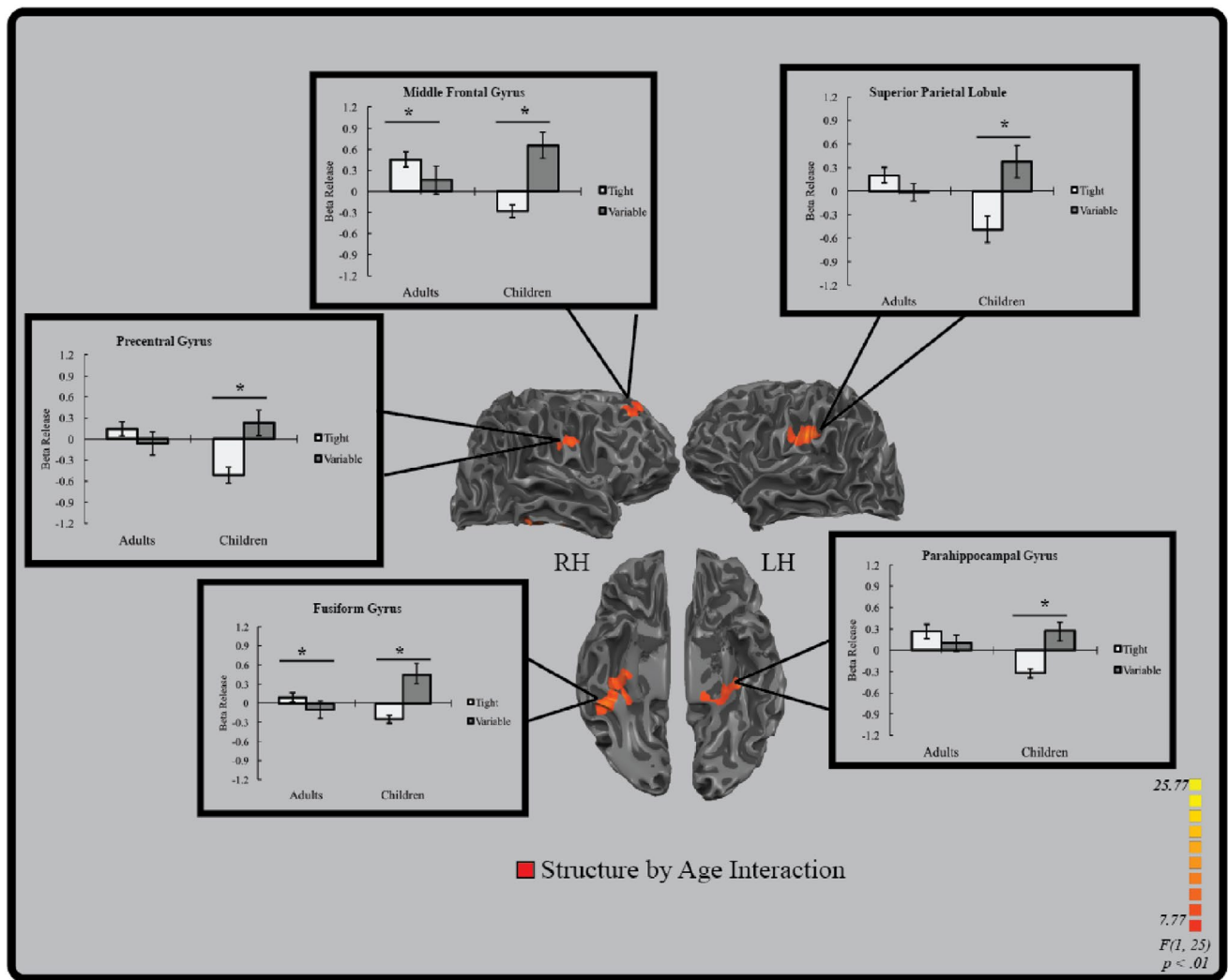


Fig. 6 Results from a 2 (Structure) by 2 (Age) interaction using release as the dependent measure, $p < 0.01$, cluster corrected $p_{cor} < 0.01$. Y-axis provides Beta Release calculated by (Beta Deviant – Beta Last 3 s). Positive values signify release while negative and

zero values signify maintenance. Asterisks represent results ($p < 0.05$) of paired-samples t tests comparing release for deviants within tight and variable structures. Error bars are standard error of the mean

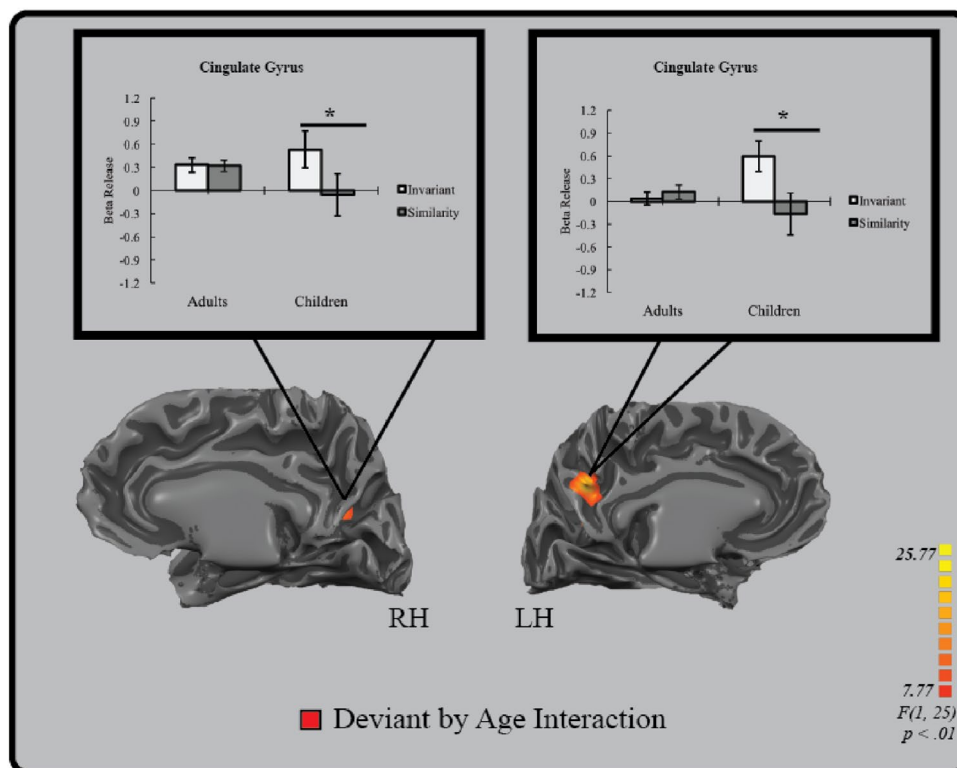
Discussion

Our results suggest that there are differences in the systems recruited by children and adults in learning categories as well as how they categorize new exemplars after implicit exposure to category members. Our findings produce three broad contributions: (1) The brain (and specifically the VTC) is sensitive to category structure (2) Generalization (measured by release) is dependent on the individual’s experience with the underlying category structure and (3) Children and adults recruit different systems to process variability and generalize category membership.

In general, our results suggested that exposure to variable category structure recruits the right fusiform gyrus to a larger extent than tight structure. In examining generalization,

variability among category members evokes greater generalization in children whereas adults demonstrated more equivalent release from category structures. Furthermore, children demonstrated more widespread release patterns compared to adults who only demonstrated greater release than children in one region—the right fusiform gyrus. This finding support the theory of interactive specialization (Johnson 2001) that asserts that during development, the acquisition of new behavioral competencies will result in a widespread recruitment of brain networks compared to adults that rely on a smaller number of interconnected regions for the same skill. Given the implicit nature of the exposure to category and that the actual task (center/off center detection) did not require working memory and had low attentional demands, we interpret this greater network of activation in children

Fig. 7 Results from a 2 (Deviant) by 2 (Age) interaction using release as the dependent measure, $p < 0.01$, cluster corrected $p < 0.01$. Y-axis provides Beta Release calculated by (Beta Deviant – Beta Last 3 s). Positive values signify release while negative and zero values signify maintenance. Asterisks represent results ($p < 0.05$) of paired-samples t tests comparing release for deviants within invariant and similarity deviants. Error bars are standard error of the mean



as reflecting a difference in how the brain is processing the category members and deviant stimuli. Behavioral work has found that children 7–8 years of age are transitioning from forming categories based on similarity among members to forming categories based more on diagnostic features. The interactive specialization account would therefore predict that children of this age would recruit a more extensive network of neural regions when learning categories than would adults.

Behaviorally, we know that during this same type of exposure and task, children are able to subsequently group the category members together but do so in a way that is different from adults (Plebanek and James, under review). Therefore, the difference in extent of neural activation is interpreted as reflecting the tendency for the developing brain to recruit extensive networks while acquiring a new skill that only reduce to a more specialized system once the skill is fully acquired (e.g., Johnson 2001).

Category structure and learning

In the present paradigm, we measure neural activation during a block of stimulus presentations that are either tightly organized or variably organized. We interpret neural activation through degree of adaptation during this block as a reflection of implicit learning. Adaptation during implicit exposure to our stimuli indicates that each stimulus is processed as similar to the other stimuli in the block

(suppression of neural signal through stimulus repetition). In the following, we split our interpretations of the results into the primary brain region of focus, the VTC, and other regions that we consider to be more exploratory in nature.

Adaptation in the ventral temporal cortex (VTC)

Our results demonstrate that across repetitions of exemplars, the right fusiform gyrus was more active while processing variable as opposed to tight categories. In the current paradigm, this implies that exposure to variability among category members results in the right fusiform processing each stimulus as different, *not* combining them into a single category. The engagement of the VTC in object perception is very well-documented. Interpretations from results of prior work ranges from accounts supporting specialization for discrete categories of objects to generalized processing mechanisms leading to greater regional activation (Kanwisher et al. 1997; Gauthier et al. 1999). Recent work has proposed an additional role of the VTC in responding to *how* stimuli are presented (the structure of the presentation). Turk-Browne et al. (2009) presented participants with blocks of either predictive symbol triplets or randomly organized symbols. Participants demonstrated little explicit awareness for this presentation structure, but there was significant neural activity associated with ventral temporal brain regions for predictive compared to random blocks. Similarly, work on letter perception have suggested that the VTC may play

a role in how individuals process variability in visual cues that are associated with letter production (Vinci-Booher et al. 2020). Although these studies are helpful in building a neural profile of variability, they were not designed to test effects of variability on learning. By directly testing category member variability in the present work, we found that variability leads to individuation of category members in the right VTC rather than perceiving all stimuli as similar, forming a category.

Furthermore, we found that this individuation of stimuli was more pronounced in adults compared with children in the right fusiform gyrus, indicated by higher activation in this region during adaptation in adults compared with children. Therefore, children are not processing individual stimuli as different to the same degree as adults. This developmental difference in object processing in the VTC is a novel finding. Previous work comparing children to adults has demonstrated that *degree* of activation to objects in the VTC is similar in adults and children, even though the *extent* of activation is greater in children (e.g., Golarai et al. 2007; Dekker et al. 2011; Passarotti et al. 2003; Nishimura et al. 2009). However, much of this previous body of research has used familiar object stimuli that are highly distinguishable and belong to different categories (e.g., chairs, tools, fruits etc.). Our findings suggest that individuation of within-category exemplars by the VTC is still immature around eight years of age. This novel finding supports neuroimaging work that finds that individuation of members of the category of faces displays a protracted development relative to between-category object processing (e.g., Haist et al. 2013; Joseph et al. 2015; Scherf et al. 2014).

Adaptation in other brain regions

The interaction between age and category structure during the implicit exposure phase of this experiment revealed that there were two other regions that were sensitive to category structure and differed between the two ages: the left post-central gyrus (somatosensory cortex/anterior intraparietal sulcus) and the right superior frontal gyrus. Specifically, we found that children perceived the category members as distinct with variable exposure in both regions (they showed less adaptation), whereas adults did not. This finding implies that children processed exemplars with high variability as different from one another in these regions. Interestingly, these two regions have been implicated in controlling voluntary saccadic eye movements (e.g., Connolly et al. 2002; Vernet et al. 2014). We, therefore, interpret our finding as reflecting task effects (recall the task was deciding whether a stimulus was central or peripheral in the display) that were more apparent in children than adults. Saccadic eye-movements are different in children compared with adults (Yang

et al. 2002) but why they would occur more with variable exposure than tight exposure in children remains elusive.

Category structure and generalization of novel stimuli

A long-posed advantage of variability is the potential to highlight invariant features among category members (Smith 1989). Thus, variability may be useful in overcoming competing category representations to create invariant-feature based (as opposed to similarity-based) categories (Deng and Sloutsky 2016). That is, variability may distill category membership down to diagnostic features of members. Neural adaptation methods allow the researcher to determine category boundaries, that is, whether a novel stimulus that is presented after adaptation will be processed as being in the same category (continued adaptation) or in a different category (release from adaptation). We hypothesized that exposure to a variably structured category would facilitate the extraction of the critical, invariant feature that defined the category. If this were the case, then participants would demonstrate a release from adaptation when the novel stimulus contained a different critical feature from the learned category. Therefore, we would observe greater release to the invariant-feature deviant compared with the similarity based deviant. This result would be revealed by the Structure \times Deviant interaction.

In the left VTC, we found overall greater release from adaptation for invariant-feature based deviants than for similarity-based deviants after variable exposure to category members. Past research has demonstrated that during explicit category learning with feedback, the anterior fusiform gyrus and the extrastriate cortex became sensitive to small perceptual changes that crossed category boundaries (Folstein et al. 2012). Our results purport variability as another mechanism akin to explicit category training or feedback to engage the VTC in learning category boundaries. Thus, variability may help assimilate members within a category *and* extract a category's invariant features.

Neural differences based on category structure were found during the adaptation portion of the experiment in the right VTC. As reviewed above, we found that the R. VTC in both children and adults did not display adaptation after variable exposure compared with tight exposure. We suggested that the right VTC, therefore, individuates category members after variable exposure instead of grouping them together into a category. In our analyses of the release from adaptation, we found that it was the *left* VTC that was sensitive to invariant-feature deviants after variable exposure. Therefore, both left and right VTC were sensitive to category learning but in different ways. Although we cannot interpret a lack of difference, this potential hemispheric difference may be an important avenue to explore in future work. For instance, it

could be that the left VTC did not reveal a different degree of adaptation reliant on category structure simply because it adapted to both types of exposure. It did however, show a release from adaptation after variable exposure when deviants were invariant, suggesting an important role of the left VTC in using variability to construct categories based on invariant features.

Furthermore, there was also greater release after variable exposure to categories when viewing an invariant-feature based deviant in the parietal cortex (inferior parietal lobule). We are unable to discern from this study if this activation is due to greater attentional demands required when viewing invariant-based vs similarity-based deviants that may recruit parietal regions (Sloutsky 2010). However, given the implicit nature of exposure to categories, we assume that attentional demands should not play a role.

Last, we identified developmental differences in deviant processing due to specific category structures. Although there was not a 3-way interaction among our variables, there was a developmental difference in release from adaptation as a function of category structure. In the right VTC (specifically the right fusiform gyrus), children demonstrated greater release from adaptation after exposure to *variable* members of a category, whereas adults demonstrated greater release after exposure to tight structure in this same region. This finding suggests that in children, variability among category members enhances the ability to discriminate previously seen stimuli from a stimulus that deviates from prior exposure. In contrast, adults only detect deviants after exposure to tightly organized categories.

In children, these results support the idea that the right fusiform gyrus plays a crucial role in category formation (Tarr and Gauthier 2000; see Grill-Spector et al. (2004) for contrasting views), but extends past findings by showing that this formation is sensitive to category structure. Specifically, the immature fusiform responds to variability among exemplars to form a category. These results support the history of work suggesting that variability aids learning from infancy throughout childhood, and that sensitivity to variability may be impacted by development (Li and James 2016; Perry et al. 2010; Twomey et al. 2014; Perone et al. 2015, 2019). In adults, the lack of greater release for variable categories is somewhat surprising. Even adults have shown increased category subdivision, generalization, and recognition due to variability in the behavioral literature (Eidsvag et al. 2015; Harman and Humphrey 1999; Cohen et al. 2001). However, neuroimaging work has suggested that the VTC of young children is more sensitive to variability than the adult VTC (Vinci-Booher et al. 2020). In that work, children aged 5–7 showed VTC sensitivity to variability in symbols, whereas older children (mean aged 9) and adults did not (Vinci-Booher et al. 2020). One possible explanation for the difference in the behavioral work in adults and

activation of the VTC is that variability among exemplars is processed in a region other than the VTC in older children and adults. Although we did not find any region that released more after variable exposure in the adults, we did find regions that released equally after variable and tight exposure (parahippocampal gyrus, the left superior lobule, and the right precentral gyrus). This result can be interpreted as suggesting that the adult brain groups stimuli together after both tight and variable exposure.

Conclusions

Many findings have demonstrated that increasing the variability among category members facilitates learning, retention, or transfer despite adding seemingly extraneous information to the learning context. Here, we have demonstrated how the internal structure of object-categories is purposeful in guiding the learner to form specific representations without explicit training. Furthermore, we provided evidence that the formation of these representations recruits regions of the VTC differently across development. These findings may have significant implications in category formation as well as generalization.

Appendix 1

The metric changes were as follows: Within the alien similarity space, the metric changes were as follows: the eyestalk changed 0.08 inches per step, the surface area changed by adjusting the width of the body approximately 0.08 inches and the height approximately 0.07 inches, the arms changed 5° per step. Within the flower similarity space, the stems changed the zigzag function in adobe illustrator 5%, the petals were rounded 5°, the gradient of the center changed 5%. The metric nature of our categories resulted in numerical differences in our exposure types. The tight variability consisted of a similarity space that could only vary a maximum of one value per each of the three dimensions in the similarity space. Thus, potential values included only values 8 through 10 on each of the 3 dimensions. The tight exposure included a distribution of stimuli that varied from the central stimulus (stimulus 9-9-9) an average of 2.05 steps, with the average of each dimension in the similarity space being (9.01, 8.89, 9.06). For the variable space, the similarity space could vary a maximum of five values per each of the three dimensions in the similarity space. Therefore, potential values included 4–14 on each dimension. This distribution varied from the central stimulus an average of 8.25 steps, and the average of the stimulus space was (8.17, 8.52, 8.96).

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Data availability Data, stimuli, and other materials are available upon reasonable request from the authors. Interested parties can e-mail requests to the corresponding author.

Code availability Code pertaining to the experimental protocol is also available upon reasonable request from the authors.

Declarations

Conflicts of interest The authors have no conflicts of interest to report.

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