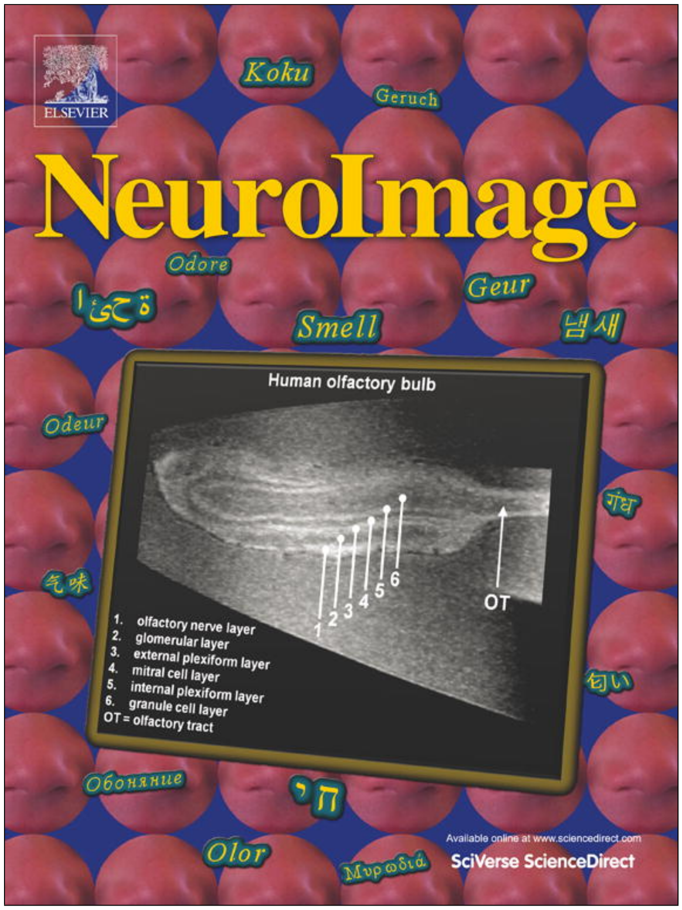
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Expert individuation of objects increases activation in the fusiform face area of children

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ABSTRACT

The role of experience in the development of brain mechanisms for face recognition is intensely debated. Experience with subordinate- and individual-level classification of faces is thought, by some, to be foundational in the development of the specialization of face recognition. Studying children with extremely intense interests (EII) provides an opportunity to examine experience-related changes in non-face object recognition in a population where face expertise is not fully developed. Here, two groups of school-aged children —one group with an EII with Pokémon cards and another group of age-matched controls — underwent fMRI while viewing faces, Pokémon characters, Pokémon objects, and Digimon characters. Pokémon objects were non-character Pokémon cards that experts do not typically individuate during game play and trading. Neither experts nor controls had previous experience with Digimon characters. As expected, experts and controls showed equivalent activation in the fusiform face area (FFA) with face stimuli. As predicted by the expertise hypothesis, experts showed greater activation than controls with Pokémon characters, and showed greater activation with Pokémon characters than Pokémon objects. Experts and controls showed equivalent activation with Digimon characters. However, heightened activation with Digimon characters in both groups suggested that there are other strong influences on the activation of the FFA beyond stimulus characteristics, experience, and classification level. By demonstrating the important role of expertise, the findings are inconsistent with a purely face-specific account of FFA function. To our knowledge, this is the first demonstration of the effects of expertise and categorization level on activation in the FFA in a group of typically developing children.

Introduction

There is considerable debate about the exact role experience has on activation patterns measured with fMRI in visual cortex during recognition of faces and other objects, but particularly on activation patterns in the fusiform face area (Bukach et al., 2006; Kanwisher and Yovel, 2006; McKone et al., 2006). The FFA is a region of the fusiform gyrus that responds more strongly with faces than with other categories of objects (Downing et al., 2006; Kanwisher et al., 1997). One account of this preference is that the FFA represents a "hardwired" cognitive module that selectively processes face-shaped objects and, after some reliance on very early developmental experience with faces, can only be "fine-tuned" by experience later in development and into adulthood (Downing et al., 2006; Kanwisher et al., 1997; McKone et al., 2006). Although there are variations of this basic domain-specific account, they generally consider that the FFA makes use of a Gestalt or global representation of faces (usually referred to as either holistic or configural) and that this representation cannot be decomposed and, importantly, cannot be used for recognition of other object categories (Farah et al., 1998). An alternative account, however, is that the FFA is one node in a distributed system of object representations and that the distribution can be changed fundamentally by experience — including, but not limited to, experience with faces — during child and adult development (Gauthier, 2000; Haxby et al., 2000; Weiner and Grill-Spector, 2012). Two variations of this basic domain-general account are, first, that the FFA may be involved in coding object features that are more useful for recognizing faces than other objects, but that are still used for recognizing other objects (Gauthier, 2000; Haxby et al., 2000, 2001; Ishai et al., 1999; Nestor et al., 2008), or second, that the FFA is involved in configural/holistic processing of objects of expertise and/or objects that are classified at the subordinate or individual level, of which faces are the most common kind (Gauthier and Tarr, 1997; Gauthier et al., 2000a,b; Schiltz and Rossion, 2006; Wong et al., 2009).

A strong prediction of the face-selective account is that the FFA cannot be co-opted for recognition of object categories other than faces. Thus, domain-general accounts — and especially "expertise" accounts — are supported by findings that experts — for instance, people with extreme levels of experience with birds or dogs —

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show preferential FFA activation with their category of expertise (Gauthier et al., 2000a,b). However, even in these experts, activation in the FFA shows a strong preference for faces over and above the preference for objects of expertise (Kanwisher and Yovel, 2006). Thus, the extant evidence does not conclusively support either the domain-specific face-selective or the domain-general expertise and classification level accounts.

A recent trend in research on the role of experience in organizing visual cortex has been to study the developmental trajectory of different functionally specialized brain regions, including the FFA, in both typical and atypical populations. In the studies of typical individuals, there is general agreement that the FFA requires longer to develop than other specialized brain regions involved in object and scene recognition (Golarai et al., 2007, 2010; Scherf et al., 2007). Individually-defined FFA clusters in children 5–8 or 7–11 years old are smaller than in children 11–14 or 12–16 years old (Golarai et al., 2007; Scherf et al., 2007) and FFA clusters in 11–14 year olds and 12–16 year olds are smaller again than clusters in young adults (Golarai et al., 2010; Scherf et al., 2007). In one study, a random-effects group analysis found a significant FFA cluster in young adults and 11–14 year olds, but not in 5–8 year olds (Scherf et al., 2007). The differences across age groups were attributed to three factors: first, that only 80% of 5–8 year olds showed individually-defined FFA clusters, which is consistent with percentages reported in another study (Golarai et al., 2010); second, that the clusters in 5–8 year olds were smaller, which allowed for less overlap across children; and third, that the location of the clusters in 5–8 year olds was more variable, again allowing for less overlap (Scherf et al., 2007). The same studies also show that other functionally specialized brain regions, specifically the object-selective lateral occipital cortex (LO) and the scene-selective parahippocampal place area (PPA), display adult-like patterns of activation in the youngest groups tested (Golarai et al., 2007; Scherf et al., 2007). The extended developmental trajectory of FFA compared to other visual regions suggests that experience plays a primary role in that development and provides some support for domain-general accounts, especially expertise accounts, of face specialization.

Studies of atypical development of face recognition have frequently targeted high-functioning children with autism spectrum disorders (ASD), a developmental disorder for which a primary characteristic is social motivational impairment, including impaired face recognition (Dekowska et al., 2008; Golarai et al., 2006). Consistent with their impaired behavior with faces and with the specialized role of the FFA in face processing, several studies have found evidence for hypo-activation of the fusiform gyrus in children with ASD (Dekowska et al., 2008; Golarai et al., 2006; Schultz et al., 2000). However, these results do little to separate domain-specific from domain-general accounts of face specialization. Social motivational impairment — for instance, avoiding looking at faces — is observed early in development with ASD, but it is difficult to disentangle whether this atypical behavior causes atypical development of the FFA or congenital impairment of the FFA causes the atypical behavior.

One case study of a child with ASD is unique in that the child had an intense interest with Digimon characters and was tested with pictures of Digimon characters in addition to faces (Grelotti et al., 2005). In this child, activation in the FFA was greater when viewing Digimon characters than when viewing faces, in contrast to a typical child in whom the pattern was reversed. On the one hand, this study suggests that the FFA can be co-opted for recognition of non-face objects with enough experience (Grelotti et al., 2005), however, on the other hand, it is difficult to estimate how much hypo-activation of the FFA with faces in the child with ASD contributed to the demonstration of differences in activation between Digimon characters and faces. In sum, there has been some evidence for the notion that the FFA can be co-opted for expert recognition of non-face object categories, but the data are not overwhelming.

A limitation of previous studies of adult expertise is that it is almost impossible to match the amount of experience with faces to the amount of experience with other objects of expertise, especially those learned as an adult. In this regard, studying children — and perhaps especially studying children with extremely intense interests (EII) — may provide a rare and interesting opportunity to explore the influence of experience on development of object and face processing. It has been documented that approximately 30% of preschool children have an extremely intense interest with a non-face object category, with 75% of these being boys (Alexander et al., 2008; DeLoache et al., 2007). Children are classified as having an EII if they have a passionate, bordering on obsessive, interest in a category of objects, with the interest being cross-situational and usually lasting longer than six months (Alexander et al., 2008; DeLoache et al., 2007; Johnson et al., 2004). Categories of objects that children find extremely interesting are not random; studies report a dominance of categories such as dinosaurs and vehicles for younger children (DeLoache et al., 2007; Johnson et al., 2004) and trading card game characters, such as Pokémon and Digimon, for older children (Johnson et al., 2004). Children with EIIs spend most of their free time playing with, collecting, studying, and learning about objects in their category of EII (Johnson et al., 2004). Thus, these children have considerable experience with objects in their category of EII, verging on the level knowledge and single-minded focus attributed to adult experts (Johnson et al., 2004).

The current study was designed to study children with EIIs for two reasons: 1) because they have less experience with faces than adults, and 2) because they have a more extreme amount of experience with a non-face object category than other children. The combination of these factors makes it possible that differences in activation patterns between children with EIIs and controls may be greater than differences in activation patterns previously seen between adult experts and controls. If the FFA is domain-general and its development is dependent on experience with non-face objects, then children with EIIs may be a case where category-selectivity in the FFA can be influenced more potently by experience with a non-face category. Here, we chose to focus on children who had an EII with Pokémon for four reasons: first, Pokémon collecting cards provide a rich set of test stimuli, second, we wanted to test elementary school age children and this tends to be the age at which interest in Pokémon cards peaks, and third, the local community where the study was conducted supports an extremely active Pokémon club that aided with recruitment.

Determination of the specific stimulus conditions was based on an observational pilot study of Pokémon experts engaged in game play and trading conducted by the authors at the local gaming club. Tallies were collected of basic-, subordinate-, and superordinate-level labels used to describe character and non-character (object) Pokémon cards. Experts used subordinate and individual labels almost exclusively for characters (>90%). For example, experts identified a character as "Pikachu" or "Typhlosion" rather than as a "Pokémon" or even as a "lightning-type Pokémon" and a "fire-type Pokémon". For objects (non-characters), experts used a mixture of the three classification levels, but the subordinate level was used only rarely (<20%). For example, when building a deck, experts often expressed the need to add "energy" or "trainer" cards rather than being more specific, such as "fire energy" or "ball trainer" or "luxury ball trainer" cards. It was also clear from observation that most of the Pokémon experts had a specific interest in Pokémon cards; they were familiar with other kinds of trading cards, such as Digimon, Yugi Oh, and so forth, but did not have an intense interest in these other kinds of cards.

Based on these observations the current study was designed to test Pokémon experts and age-matched non-experts with images of child faces, Pokémon characters, Pokémon objects (non-characters), and Digimon characters while undergoing fMRI. Pokémon characters are usually fantastical animals with anthropomorphized faces and bodies. During typical game play and trading activities, experts usually verbally classify Pokémon characters at the subordinate level. Pokémon objects were included as control stimuli, because they usually depict fantastical inanimate objects that do not have faces. Also, during typical game play and trading activities, experts usually verbally classify Pokémon objects at the basic level ("energy", "ball", "stadium") or super-ordinate level ("trainer", "supporter"). For some examples of Pokémon objects used in the study, including energies, ball trainers, and stadiums, see Supplemental Fig. 1. Digimon characters were included as control stimuli, because they are similar looking to Pokémon characters and, like Pokémon characters, contain anthropomorphized faces, but neither Pokémon experts nor non-experts had much experience with them.

Consideration of these characteristics of the stimulus types led to the following hypotheses (Fig. 1) based on extant theories of FFA function (Gauthier et al., 2000b; Rhodes et al., 2004). First, if activation in the FFA is domain specific to faces (face specificity), there should be no differences between experts and controls. Also, Pokémon characters and Digimon characters should show slightly more activation than Pokémon objects, because of their anthropomorphized faces. Second, if activation in the FFA is domain general and driven by expert individuation, then differences in activation across groups and stimulus types will be driven by the amount of experience with individuation of the specific stimulus type. Thus, there should be differences between experts and controls with Pokémon characters, but not with the other stimulus types. Also, experts should show more activation with Pokémon characters than Pokémon objects or Digimon characters, but controls should show no differences among stimulus types. Third, if activation in the FFA is domain general and driven by *separate* effects of experience and classification level (Gauthier et al., 1997), then differences in activation across groups and stimulus types will be driven independently by the amount of experience with the stimulus type and the level at which the stimuli are classified during scanning. Differences in experience should produce differences between experts and controls with Pokémon characters *and* Pokémon objects. Differences in classification level should produce greater activation with Pokémon characters than Pokémon objects in experts, but controls should show no differences among stimulus types.

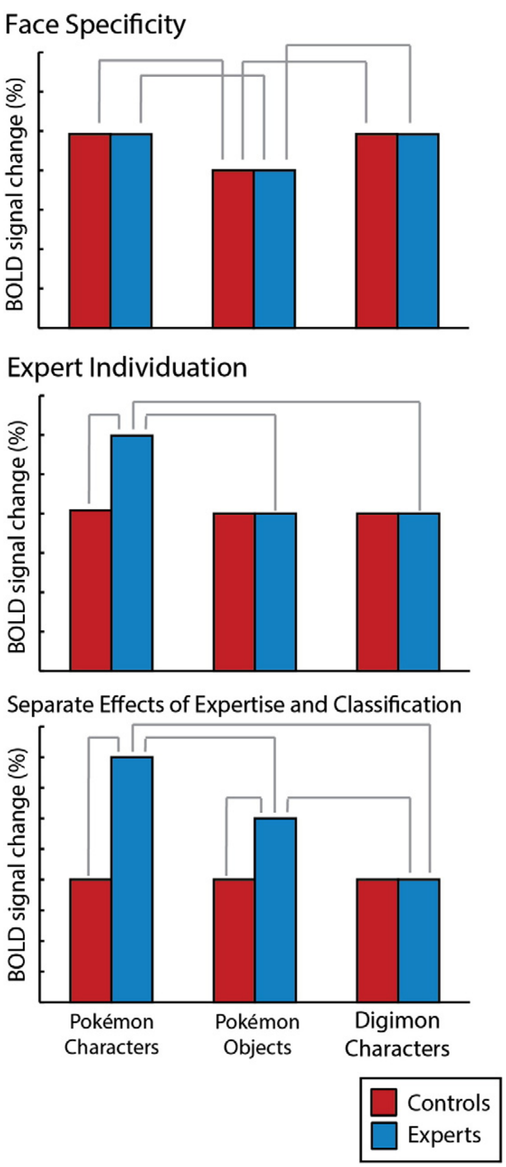

Fig. 1. Hypotheses based on extant theories of FFA specialization.

Materials and methods

Subjects

Participants were children aged 8 years 3 months to 12 years, 5 months (see Table 1 for demographics). Pokémon experts were recruited through flyers posted at game stores and on the Indiana University Bloomington campus and controls were recruited through an Indiana University Bloomington child-participant database. Parents reported that their children had normal or corrected-to-normal visual acuity, no history of brain trauma, and no record of learning disabilities. Participants were rewarded for their time and inconvenience with gift certificates. Separate gift cards were rewarded for the fMRI scan session and the WISC test session. All children/parents provided informed assent/consent. Recruitment and testing were approved by the Indiana University Institutional Review Board.

Pokémon/Digimon tests

Membership in either the Pokémon expert or control group was determined based on a 37-question test about Pokémon characters. All children were also administered a 14-question test about Digimon characters as a basis for excluding from the study any children who were Digimon experts. The tests were developed by an adult who was both a Pokémon and Digimon expert and the questions on the tests were matched for difficulty. Children were considered Pokémon experts if they scored better than 67% correct on the Pokémon test and were considered controls if they scored less than 33% correct.

Table 1
Demographic and questionnaire variables by group.

Variable	Group	
	Pokémon Experts	Controls
N	10	11
Age, years (SD)	10.3 (1.4)	10.3 (1.2)
Sex, F–M	3–7	2–9
Handedness, L–R	3–7	2–9
Pokémon Test/37 (SD)	28.6 (5.3)	5.3 (4.1)
Digimon Test/14 (SD)	0.0 (n/a)	0.2 (0.6)
CAST/31 (SD)	5.6 (2.3)	6.2 (4.4)
Empathy quotient/54 (SD)	35 (10.4)	37 (9.1)
Systemizing quotient/56 (SD)	23 (8.8)	31 (6.7)
N	7	7
WISC verbal comprehension (SD)	129 (16.9)	104 (7.3)
WISC perceptual reasoning (SD)	126 (7.7)	109 (10.2)
WISC working memory (SD)	123 (14.8)	104 (15.4)
WISC processing speed (SD)	116 (19.6)	106 (17.0)
WISC full-scale (SD)	130 (13.7)	108 (7.5)

Of the 23 children tested, 10 were considered Pokémon experts (3 females) and 13 were considered controls (2 females). All of the children scored in either the expert range or the control range on the Pokémon test, thus no children were excluded based on an ambiguous score (i.e., 34–66%). All children scored uniformly poorly on the Digimon test, thus no children were excluded as possible Digimon experts. One control subject was excluded after determining the signal-to-noise ratio of the fMRI data was considerably lower than that of the other children's scans. Another control subject was excluded from the study due to motion artifacts in the fMRI data that exceeded 5 mm in every functional run. Removing these two control subjects produced a final sample size of 21, with 10 experts (3 females) and 11 controls (2 females).

Behavioral testing

Several pencil-and-paper tests were given to the children and/or their parents prior to scanning.

SQ-EQ test

The Systemizing Quotient — Empathizing Quotient test. Parents completed this form while children completed the Pokémon/Digimon tests. The EQ-SQ test was designed by Baron-Cohen et al. (2003) to determine the degree to which an individual is an 'empathizer' — the ability to recognize emotion and infer mental states in others — or a 'systemizer' — the drive to analyze or construct a system (Baron-Cohen et al., 2003). In general, individuals with ASD score lower on the EQ and higher on the SQ than typical individuals (Auyeung et al., 2009). It has 55 questions with a 4-point rating scale.

CAST

The Child Aspergers Spectrum Test (Allison et al., 2007), subsequently renamed the Childhood Autism Spectrum Test. Parents completed this form while children were completing the Pokémon/Digimon tests. This questionnaire was designed to determine whether or not a child exhibits behaviors associated with the Autism Spectrum Scale. In addition, it also determines if the child has been diagnosed with any learning disabilities. It has 39 yes/no questions.

WISC IV

The Wechsler Intelligence Scale for Children. This set of tests was administered to children by an experimenter on a testing day separate from, and after, the fMRI scan session. Seven children from each group returned to the lab to complete this testing.

fMRI testing

Stimuli

All stimuli were presented as color images that subtended 9 degrees of visual angle vertically. Images of Pokémon characters, Pokémon objects (non-characters), and Digimon characters were scanned from Pokémon and Digimon cards and cropped to include only the character or object and none of the surrounding information on the card. Most Pokémon and Digimon characters resemble fantastical animals with anthropomorphized faces and bodies. Characters that did not have faces were purposely excluded from the stimulus sets. Some Pokémon objects also have anthropomorphized faces and these examples were purposely omitted from the stimulus set. Thus, all Pokémon and Digimon characters had anthropomorphized faces and all Pokémon objects had no face.

Child face stimuli were images downloaded from the internet and morphed slightly to disguise their identity using Morph Age Express software (Supplemental Fig. 2 displays all of the images). Although the range of colors, shapes, and other object properties was much greater in the non-face stimulus types, to keep the children maximally engaged with the experiment, there was no attempt made to limit the complexity of the other stimulus types to equate them with the child faces.

Previous studies in children using intact objects as control stimuli for localizing the FFA produced a success rate of about 80% of cases. Work in adults suggests that the difference in activation (effect size) between scrambled images and faces is more robust than the difference between objects and faces (Berman et al., 2010); therefore, scrambled images were included as a stimulus type. Scrambled images were made from Pokémon characters and Pokémon objects. Scrambled images were created by dividing the original image into squares in a 20×30 grid and randomly exchanging the squares. Scrambled Pokémon objects and scrambled Pokémon characters were both included to complete the full-factorial $2 \times 2 \times 2$ experimental design of group (controls versus experts) by Pokémon stimulus type (characters versus objects) by image type (intact versus scrambled). Ultimately, examining the data with this model did not produce greater insight into the function of the FFA. Thus, for all of the analyses presented here, the two types of scrambled images were analyzed together as a scrambled images stimulus type. Examples of the five stimulus types are shown in Fig. 2. There were 49 unique images for each of the stimulus types, such that children viewed each stimulus only once during scanning.

Scanning procedures

Prior to scanning, before children were taken to the MRI suite, they were pre-tested for comfort level by having them watch a cartoon (not a Pokémon cartoon) in a MRI simulator (for more details on the acclimation method, see James, 2010). If the child felt comfortable in the simulator and was able to lie still, they were taken (with consent) directly to the MRI suite for scanning. Children lay supine in the MRI bore with their head secured in the head coil by foam padding. They viewed stimuli through a mirror that was mounted above the head coil on a rear-projection screen (40.2×30.3 cm) placed behind the child in the bore. Stimuli were projected onto the screen with a Mitsubishi LCD projector (model XL30U).

The stimuli were presented in blocks of 12 trials of the same stimulus type. On a trial, children viewed the stimulus passively for 1 s, followed by a variable inter-stimulus interval with mean time 667 ms. A run was made up of six 20 s blocks, interleaved with inter-block intervals of 8 s or 10 s, to make up a run of 184 s (92 volumes; ~3 minutes). Each child completed four runs. Each run contained one block from each of the six stimulus types (the two scrambled types were presented separately). The order of the stimulus types was randomized across runs. SuperLab 4 (www.cedrus.com) was used to present the stimuli during the scanning session.

Imaging parameters and analysis

Imaging data were acquired with a Siemens Magnetom TIM TRIO 3-T whole-body MRI and a 12-channel phased-array head coil. For functional images, the field of view was 192×192 mm, with an in-plane resolution of 64×64 pixels and 33 axial slices of 3.8 mm thickness per volume. These parameters produced voxels that were $3.0 \times 3.0 \times 3.8$ mm. Functional images were acquired using a gradient echo EPI sequence with interleaved slice order: TE = 30 ms, TR = 2,000 ms, flip angle = 70°. Parallel imaging was not used. High-resolution T1-weighted anatomical volumes were acquired using a Turbo-flash 3-D sequence: TI = 900 ms, TE = 2.67 ms, TR = 1500 ms, flip angle = 9°, with 120 sagittal slices of 1.5 mm thickness, a field of view of 192×192 mm, and an isometric voxel size of 1.5 mm^3.

Imaging data were analyzed using BrainVoyager™ QX 2.2. Individual anatomical volumes were transformed into a common stereotactic space based on the reference of the Talairach atlas using an eight-parameter affine transformation. Functional volumes for each run were re-aligned to the first functional volume in that run using an intensity-based motion-correction algorithm. Functional volumes also underwent slice scan-time correction, 3-D spatial Gaussian filtering

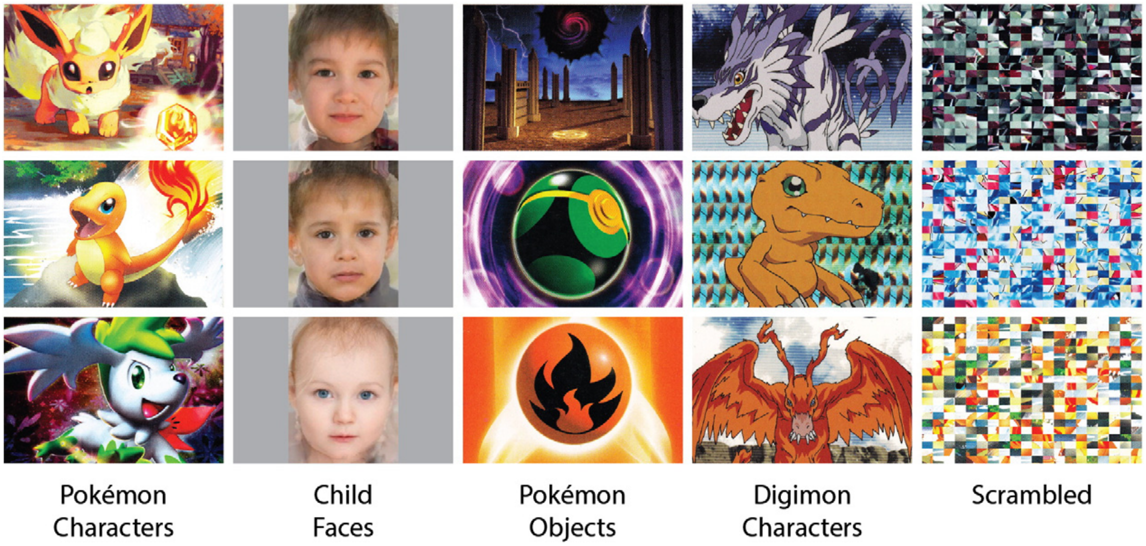

Fig. 2. Three examples of each stimulus type. More examples of Pokémon objects are illustrated in Supplemental Fig. 1.

(FWHM 6 mm), and linear trend removal. Each functional volume was co-registered to the anatomical volume using an intensity-based matching algorithm and normalized to the common stereotactic space using an eight-parameter affine transformation. During normalization, functional data were re-sampled to 3 mm^3 isometric voxels.

Whole-brain statistical parametric maps were calculated using random-effects general linear models with predictors based on the timing protocol of the blocked stimulus presentation, convolved with a two-gamma hemodynamic response function. Motion estimates were included in the model as predictors of no interest. For the group-defined ROI analysis, face-preferring functional ROIs were localized from a contrast of child faces versus scrambled images. Previous work in adults suggests that contrasts with scrambled images and faces are more robust than contrasts with faces and other control images (Berman et al., 2010). Other work in children has used generic objects as control stimuli, but, although we considered the Pokémon objects to be analogous to generic objects, the difference in familiarity of those objects between groups would make them a less than ideal choice for the localizer contrast. For the group-defined ROI analysis, estimates of BOLD signal change (beta weights) were extracted for each stimulus type for each subject using the BrainVoyager ROI/VOI-ANCOVA table tool and the GLM model described above.

Whole-brain statistical parametric maps were also calculated for each individual using fixed-effects GLMs. These individual maps were thresholded using the false discovery rate method. These maps were used for two purposes. First, they were used to localize individually-defined FFA ROIs and from those ROIs, BOLD time courses were extracted using event-related averaging. BOLD signal change was calculated from the extracted time courses as the area under the curve between 4 s and 20 s post-stimulus onset converted to percent using the mean stimulus onset value as a baseline. Differences in stimulus onset values across groups were normalized before conversion to percent signal change. Second, the individual maps were also used to generate a probability map, indicating at each voxel the number of individuals that showed a significant face preference.

Statistical hypothesis testing on BOLD signal change values extracted from ROIs (either as beta weights or through event-related averaging) was performed using repeated measures ANOVAs in SPSS. All planned and post hoc tests were performed using the within-subjects mean squared error from the highest order interaction term.

Results

Because of the link between ASD and atypical functioning of the FFA (Dekowska et al., 2008; Golarai et al., 2006), children or their parents completed questionnaires about behaviors that have been linked to ASD, including the systemizing quotient (SQ), which is higher for ASD individuals, the empathy quotient (EQ), which is lower for ASD individuals, and the Childhood Autism Spectrum Test (CAST). In general, Pokémon experts and controls scored similarly on these variables, with no significant differences between groups except that the Pokémon experts scored significantly *lower* on the systemizing quotient (SQ) than controls ($t_{(19)}=2.25$, $p=.05$). Wechsler Intelligence Scale for Children (WISC) measures were also collected on seven children from each group. Pokémon experts had significantly greater full-scale, verbal comprehension, perceptual reasoning, and working memory scores (all $t_{(19)}>2.88$, $p<.01$), with no difference between processing speed scores. Descriptive statistics for these measures, as well as demographic measures, are shown in Table 1.

Definition of regions of interest

To perform a group region of interest (ROI) analysis, the FFA was functionally localized by contrasting child faces and scrambled images across all children in both groups ($N=21$). We chose to use a group-average-defined ROI such that the location and extent of the ROI were not different for the two groups and such that the data from every child in each group would be included in the subsequent analyses. Using a false discovery rate (FDR) correction for multiple tests ($q=.05$; $t_{(20)}=3.52$) produced the map shown in Fig. 3A, which contained a cluster of 57 significant voxels (1539 mm^3) at the location of the FFA. Because it has been suggested that defining the FFA too liberally (i.e., including too many voxels) may diffuse its specialized activation profile (Kanwisher and Yovel, 2006) and because the FDR-threshold-defined cluster was somewhat larger than what has been previously reported for this age group (Golarai et al., 2007; Scherf et al., 2007), a second, smaller cluster was also defined using a stricter arbitrary threshold ($t_{(20)}=4.00$) so as to analyze only the most statistically significant voxels. This threshold produced the map shown in Fig. 3B, which contained a cluster of 21 significant voxels (567 mm^3) at the location of the FFA. The coordinates of the

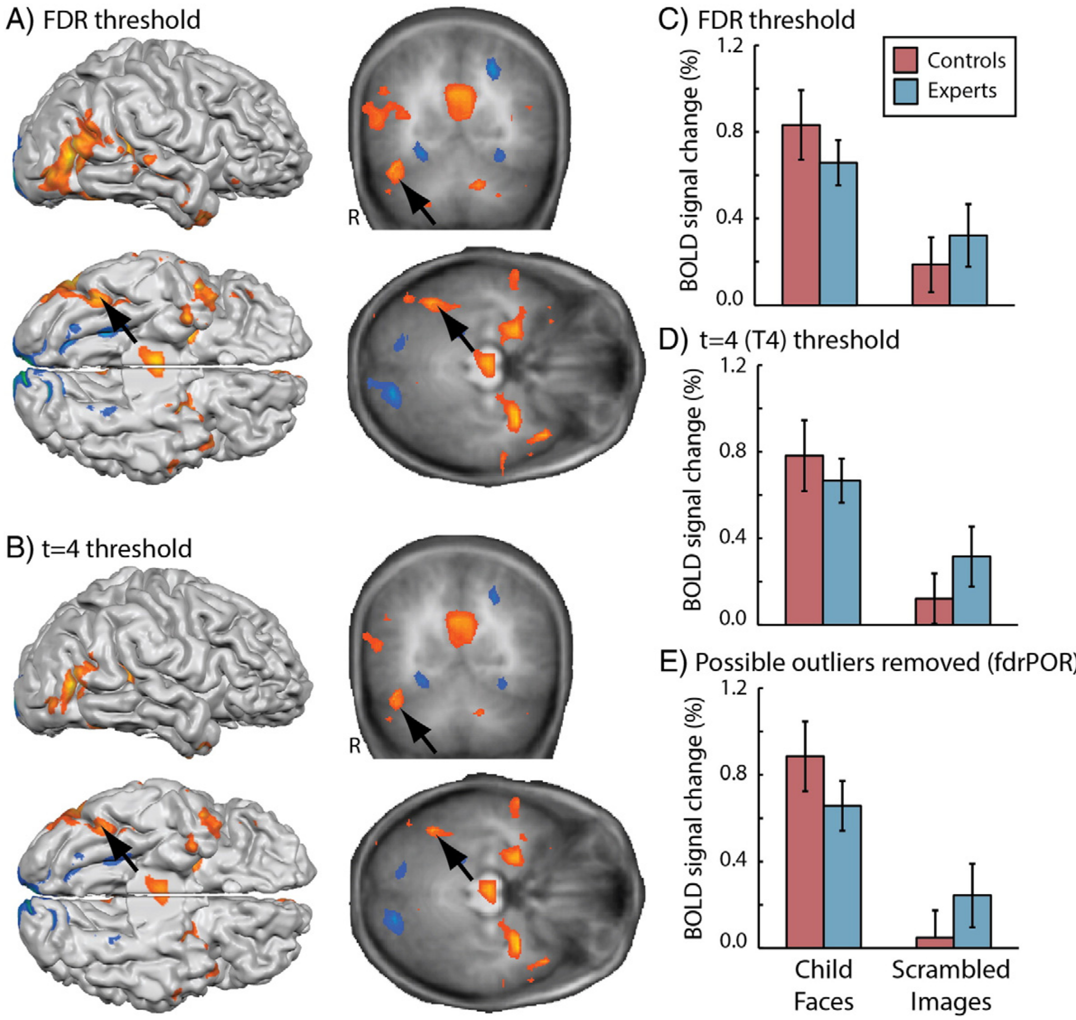

Fig. 3. Functional localization of the group FFA ROI. Maps of the contrast Child Faces versus Scrambled Images across both groups ($N=21$) are shown thresholded using FDR (A) and with an arbitrary $t=4$ (B). Top left image is a lateral view, bottom left is a ventral view, top right is a coronal slice ($Y=-55$) and bottom right is an axial slice ($Z=-18$). Black arrows point to the location of the right FFA. BOLD signal change (beta weights) in the right FFA as a function of group and stimulus type are shown for the FDR-defined ROI (C), the arbitrary $t=4$ (T4) threshold (D), and for the FDR-defined threshold with possible outliers excluded (E). Possible outliers were individuals who did not show a face preference in the group FFA ROI ($N=4$). Error bars are SEM.

center of mass of the two clusters were similar (FDR: $X=-40$, $Y=-56$, $Z=-19$; $t=4$: $X=-40$, $Y=-55$, $Z=-20$; Talairach reference); it was only the extent of the two clusters that varied. Estimates of BOLD signal change (beta weights) were extracted from the FFA clusters for each stimulus type and for each subject.

To assess individual differences in face preference at the location of the group FFA ROI, subject-by-subject *t*-tests comparing child faces and scrambled images were performed. Note: a separate localizer scan was not performed; therefore, these tests were biased toward positive face preference due to non-independence with the ROI selection contrast (Kriegeskorte et al., 2009). Of the 21 individuals (10 experts and 11 controls), 17 of them (81%; 8 experts and 9 controls) showed preferential activation for faces in the FDR-defined group FFA ROI. In subsequent analyses, these four individuals were considered possible outliers and analyses were performed with them both included and excluded.

In addition to analyses on data from the FDR- and $t=4$ (T4)-defined group ROIs, analyses were also performed on the set of 21 individually-defined ROIs. Individual ROI analyses have the benefit of selecting the most significant voxels in each individual, rather than the most significant voxels in the group (Poldrack, 2007; Saxe et al., 2006). Significant clusters were found in the location of the FFA in 16 of 21 individuals (9 controls and 7 experts), thus the individually-defined ROI analysis had a reduced sample size relative to the group-defined analysis.

Fig. 3C shows BOLD signal change in the FDR-defined group FFA ROI as a function of group for child faces and scrambled images ($N=21$). Fig. 3 also shows activation for the T4-defined group FFA ROI (Fig. 3D; $N=21$) and also for the FDR-defined group FFA ROI, but with the possible outliers removed (Fig. 3E; $N=17$). Planned contrasts showed no significant differences between groups for either child faces or scrambled images, regardless of how the ROI was defined or the inclusion/exclusion of possible outliers.

The overlap of face preferring voxels across individuals is illustrated in the probability map in Fig. 4. Note: due to correction for multiple tests of the individual maps that were used to generate the probability map and because of the lack of circularity, this test of overlap is stricter than the group ROI analysis reported above and the maximum overlap found in the FFA was between 15 individuals (71%) as opposed to 17 (81%). Besides the FFA, other clusters that showed high overlap were

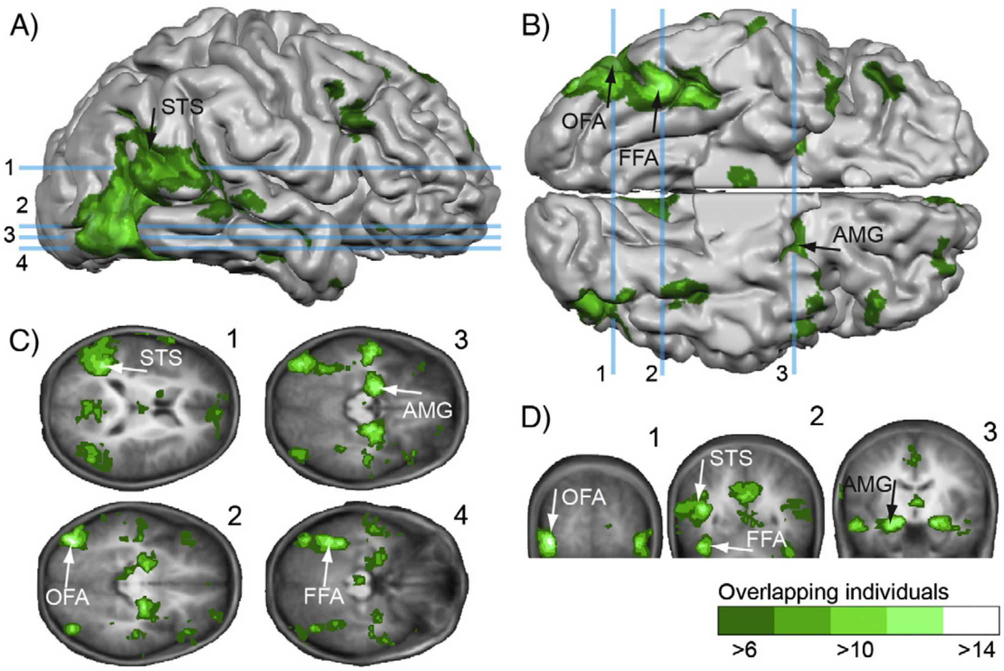

Fig. 4. Probability map for faces minus scrambled. Individual maps of the contrast Child Faces versus Scrambled Images were combined after thresholding with FDR. The color scale indicates the number of thresholded individual maps that overlapped at each voxel. The probability map is thresholded at a minimum overlap of 6 of 21 individuals. The map is shown on a rendered lateral view (A) and a ventral view (B). Blue lines on the rendered images indicate the slice planes of the axial slices (C) and coronal slices (D). The mapping of lines to slices is indicated by the numbers. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the occipital face area (OFA), the posterior aspect of the superior temporal sulcus (STS), and the amygdala (AMG).

Region of interest analyses

The effect of expertise was assessed in the ROIs by examining BOLD signal change across the Pokémon character, Pokémon Object, and Digimon character stimulus types. Fig. 5A shows BOLD signal change in the FFA as a function of group and stimulus type for the FDR-defined FFA ROI. Although Fig. 5 shows data from only the FDR-defined ROI, the analyses were also performed on an additional four data sets to ensure generalizability across ROI selection criteria (see Supplemental Fig. 3). These four other data sets were derived from 1) only the voxels in the T4-defined FFA ROI, 2) the voxels in the FDR-defined FFA ROI, but with the possible outliers removed (fdrPOR), 3) only the voxels in the T4-defined FFA ROI, but with the possible outliers removed (t4POR), and 4) only the voxels in the individually-defined ROIs (IND). Three planned contrasts were performed to assess group differences in activation with Pokémon characters, Pokémon objects, and Digimon characters. These differences are shown explicitly in Fig. 5B. Experts showed greater activation with Pokémon characters than controls (FDR: $t_{(19)}=2.28$, $p=.017$; T4: $t_{(19)}=2.67$, $p=.008$; fdrPOR: $t_{(15)}=2.48$, $p=.013$; t4POR: $t_{(15)}=2.54$, $p=.011$; IND: $t_{(14)}=2.85$, $p=.006$). There were no group differences with Pokémon objects or Digimon characters (there was one exception among the effects with Pokémon objects, IND: $t_{(15)}=2.28$; $p=.034$, with experts showing more activation than controls).

A 2×3 ANOVA was performed with BOLD signal change as the dependent variable and with group and stimulus type as between-subject factors. There was a significant main effect of stimulus type (FDR: $F_{(2,18)}=4.45$, $p=.027$; T4: $F_{(2,18)}=3.87$, $p=.040$; fdrPOR: $F_{(2,14)}=4.32$, $p=.035$; t4POR: $F_{(2,14)}=3.76$, $p=.05$; IND: $F_{(2,13)}=3.05$, $p=.08$). These effects are explicitly shown in Fig. 5C, where the effect of stimulus type is shown collapsed across groups. Post hoc tests performed on these values revealed that Pokémon characters showed more activation than Pokémon objects (FDR: $t_{(10)}=2.41$, $p=.037$; T4: $t_{(10)}=2.47$, $p=.033$; fdrPOR: $t_{(8)}=3.17$, $p=.010$; t4POR: $t_{(8)}=2.48$, $p=.038$; IND: $t_{(8)}=3.26$, $p=.014$) and Digimon characters showed more activation than Pokémon objects (FDR: $t_{(10)}=3.52$, $p=.006$; T4: $t_{(10)}=3.48$, $p=.006$; fdrPOR: $t_{(8)}=3.75$, $p=.004$; t4POR: $t_{(8)}=3.39$, $p=.010$; IND: $t_{(8)}=3.24$, $p=.014$).

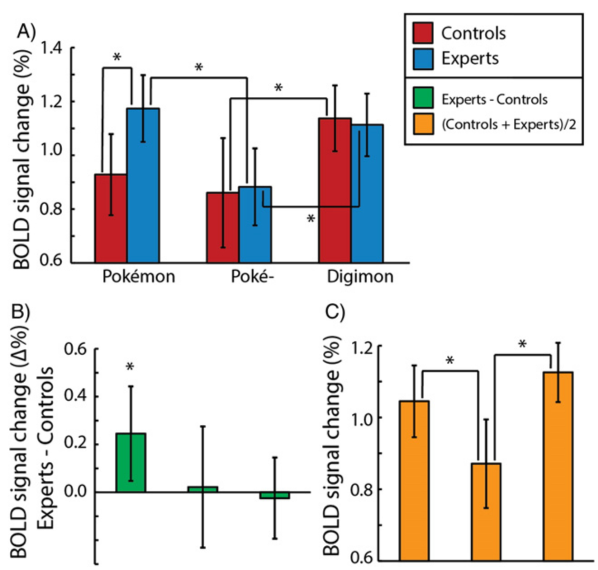

Fig. 5. Bold signal change from the group FFA ROI. BOLD signal change (beta weights) is shown as a function of stimulus type and group (A). The difference in BOLD signal change between experts and controls is shown as a function of stimulus type (B). BOLD signal change is shown as a function of stimulus type, collapsed across group (C). An * indicates significance of a planned comparison or post hoc test.

Post hoc tests were also carried out between stimulus types within each group (Fig. 5A). In Pokémon experts, Pokémon characters showed more activation than Pokémon objects (FDR: $t_{(10)}=2.41$, $p=.037$; T4: $t_{(10)}=2.47$, $p=.033$; fdrPOR: $t_{(8)}=3.17$, $p=.010$; t4POR: $t_{(8)}=2.48$, $p=.038$; IND: $t_{(8)}=3.26$, $p=.014$). There were no other significant stimulus type effects in experts (there was one exception among these effects, FDR: $t_{(10)}=2.25$, $p=.05$, with Digimon showing more activation than Pokémon objects). In controls, Digimon characters showed more activation than Pokémon objects (FDR: $t_{(10)}=2.70$, $p=.022$; T4: $t_{(10)}=2.72$, $p=.022$; fdrPOR: $t_{(8)}=3.00$, $p=.017$; t4POR: $t_{(8)}=2.95$, $p=.019$; IND: $t_{(8)}=3.34$, $p=.013$). There were no other significant stimulus type effects in controls.

The OFA, STS, and AMG ROIs from Fig. 4 were analyzed in the same manner as the right FFA, however, these regions did not show significant group differences for any of the stimulus types.

Whole-brain analysis of Digimon character stimuli

Lastly, because of the unexpectedly high activation found with Digimon characters — 8 of 11 controls showed greater activation with Digimon than Pokémon characters, which was not a prediction of either extant theory — whole-brain group contrasts were performed among the other stimulus types, with an emphasis on contrasts with Digimon character stimuli. Several of these contrasts produced informative results and are shown in Fig. 6 along with a duplication of the contrast of child faces versus scrambled images. All maps were thresholded using the FDR method. The location of the parahippocampal clusters in the faces versus scrambled map are highlighted by the white circles and superimposed on all maps. The location of the FFA cluster is likewise highlighted with a hollow circle.

Discussion

There is considerable debate about the influence of experience during development on activation patterns produced by faces and other objects in the fusiform gyrus and particularly in the FFA (Bukach et al., 2006; Gauthier, 2000; Golarai et al., 2007; Kanwisher and Yovel, 2006; McKone et al., 2006; Scherf et al., 2007). Here, we investigated the influence of extreme amounts of experience with a non-face category during childhood on FFA activation by studying children with an EII with Pokémon cards. The results suggest that this type of relatively early experience has a dramatic effect on activation in the FFA. Pokémon experts showed greater activation in the FFA with Pokémon characters than did controls and also showed greater activation in the FFA with Pokémon characters than with Pokémon objects (non-characters). To our knowledge, this is the first demonstration of an expertise-related increase in FFA activation in a group of typically developing children. The results support the important role of experience and classification level in the functional specialization of the FFA and, specifically, the role of expert individuation.

One unexpected finding that was not consistent with the face specificity, expert individuation, and Separate Effects of Experience and Categorization level (SEEC) accounts was the surprisingly high level of activation produced by Digimon characters. Digimon characters were included because they are similar-looking to Pokémon characters, have anthropomorphized faces and bodies like Pokémon characters, but neither the Pokémon experts not the controls had much experience with Digimon characters. Because Digimon characters are similar-looking to Pokémon characters, a possible reason for heightened activation in experts may be generalization of expert individuation across related categories. However, this reasoning would not explain the heightened activation seen in controls. Another possibility is that Digimon characters were more visually complex. Examining the stimulus types suggests that visual complexity of Digimon and Pokémon characters — and even Pokémon objects — is greater than the child faces. No attempt was made to modify the visual complexity of the stimuli, because modification could have had a differential effect on experts and controls, because modification (in particular, lowering the visual complexity to match the child faces) could have interfered with the overall level of engagement with the stimuli of both groups, and because child faces were included as a localizer stimulus and were not intended to be directly compared to the other stimulus types. Regardless, the differences in visual complexity may explain the stronger response of most of the ventral occipito-temporal cortex, including fusiform and parahippocampal cortex, with Pokémon and Digimon stimulus types over child faces seen in Fig. 6. However, because Pokémon and Digimon stimuli were closely matched in visual complexity, it cannot explain the somewhat heightened activation observed with Digimon characters over Pokémon characters in controls in the FFA.

A more likely possibility is that Digimon characters may have been more "arousing" for both Pokémon experts *and* controls than the other stimulus types. There is considerable evidence that activation in the fusiform gyrus is influenced by the emotional arousal evoked by a stimulus, even when it is not a face stimulus (Sabatinelli et al., 2011). Ratings of emotional arousal were not acquired from the children during testing. However, examination of the Pokémon and Digimon characters by the experimenters led to two clear conclusions: first, that the Digimon characters had "fiercer" expressions and body postures than Pokémon characters, and second, that most Digimon characters were showing teeth, whereas most Pokémon characters were not. This suggests the possibility that Digimon characters evoked a subtle but measureable threat response in the children. Because the heightened activation with Digimon characters was unexpected, children were not specifically debriefed about the possibility of differences in emotional arousal evoked by Pokémon and Digimon characters. The few responses provided as part of the standard debriefing that were relevant to this question suggested that children considered the Digimon characters to be "for older children" than the Pokémon characters and that Digimon characters seemed more "cool". If the heightened activation with Digimon characters can be explained by increased emotional arousal, then the pattern of results clearly supports the expertise framework and is inconsistent with the face specificity account. It also suggests that the level of activation in the FFA is driven as much by social factors, such as expression or posture, as it is by the factors of main interest here, which were expertise and classification level.

We chose to use passive viewing of the stimuli, because our experience with previous perceptual studies with children in this age group suggested that forcing them to perform a cognitively or attentionally demanding task makes them more likely to withdraw early, less likely to stay on task if they do not withdraw, and more likely to produce head and body movements that translate into motion artifacts in the data. In addition, with this particular experiment, we did not want to bias the way in which experts and controls chose to differentially interact with the different stimulus types by forcing them into a specific cognitive set with task instructions. However, the choice of passive viewing and allowing the two groups to possibly engage differently with the stimuli, especially the Pokémon stimuli, raises the question of whether or not the current results can be explained by confounds of preferential attention or increased arousal with more familiar or personally salient stimuli.

Regarding familiarity, experts had more experience with Pokémon characters than controls. Thus, differences in familiarity could refute one of the key findings in favor of the expert individuation and SEEC accounts: that experts showed more activation with Pokémon characters than controls. However, there are other important effects that are inconsistent with a refutation based on differences in familiarity. For instance, experts were equally familiar with Pokémon characters and objects, yet showed greater activation with characters. This finding was consistent across the five different data sets and is one of the compelling pieces of evidence for the importance of expertise and

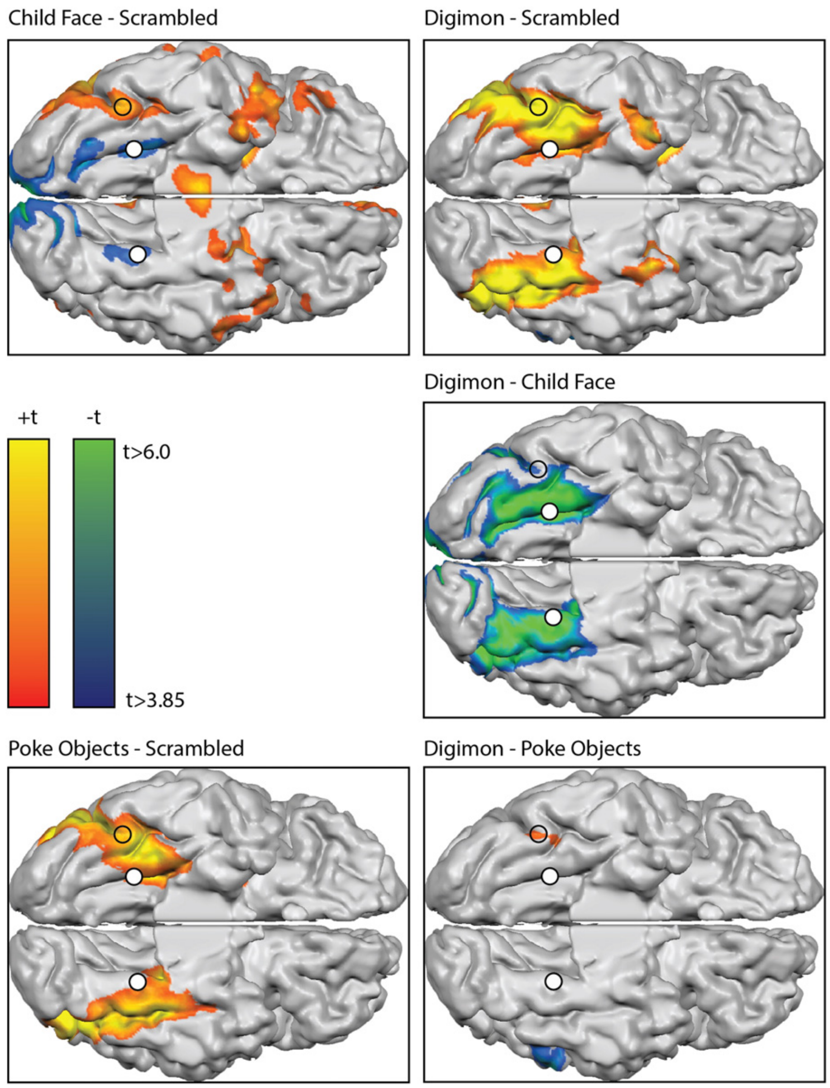

Fig. 6. Whole-brain analysis of Digimon characters. Contrasts were carried out on the groups collapsed ($N=21$). All maps are shown rendered from a ventral view. White circles indicate the location of the parahippocampus, which shows more activation with scrambled images than child faces. The hollow circle indicates the location of the FFA. Maps are thresholded using FDR, except for the Child Face versus Scrambled Images map, which used a more liberal threshold.

categorization level in the development of functional specialization in the FFA.

Regarding personal salience, experts were recruited because of their EII with Pokémon cards, thus Pokémon characters were no doubt more personally salient to experts than controls. An argument could also be made that, because of the different type of experience that experts have with Pokémon characters and objects, experts develop greater personal salience for Pokémon characters than Pokémon objects. Thus, differences in personal salience could refute two of the key findings in favor of the expert individuation or SEEC accounts, that experts showed more activation with Pokémon characters than controls and that experts showed more activation with Pokémon characters than Pokémon objects. However, an equally strong (or perhaps stronger) argument could be made that the personal salience of Pokémon cards in general (characters and objects) is higher for experts than controls, not just that the personal salience of Pokémon characters is greater. This counter-argument would make an explanation based on personal salience inconsistent with the results. Also, like explanations based on familiarity, explanations based on personal salience cannot account for the heightened activation shown with Digimon characters. Neither the experts nor controls had an interest in Digimon characters, so personal salience of Digimon characters was either equally low for both experts and controls or, one could argue, that personal salience of Digimon characters would be low in controls, but higher in experts, because of their similarity to Pokémon. However, neither of these situations successfully accounts for the results. Thus, refutation of the expert individuation or SEEC accounts based on differences in personal salience could account for some, but not all, of the effects, and only if specific assumptions about levels of personal salience across groups and stimulus types were made.

To summarize the discussion of familiarity and personal salience, the use of a passive viewing task makes it important to assess the possible influence of differences in attention or arousal caused by differences in familiarity or personal salience across groups. It is our opinion that the influences of familiarity or personal salience do not explain the pattern of results when considered alone or when combined with the hypothetical activation pattern for either the face specificity, the expert individuation, or the SEEC accounts. Although differences in familiarity and personal salience can explain some isolated differences in FFA activation, they fail to explain the entire pattern of differences across stimulus types and groups. The results with Digimon characters were unexpected and did not support or refute any of the extant theories. We speculate that the heightened activation with Digimon characters can best be explained as a stimulus-based increase in emotional arousal due to threat. Further research is needed to assess how different object features produce different levels of emotional arousal and how this interacts with other stimulus characteristics (such as visual complexity and the presence of a face), with experience, and with subordinate classification.

The findings of greater activation with Pokémon characters in experts than controls and greater activation with Pokémon characters than Pokémon objects in experts are consistent with both the expert individuation and SEEC accounts. It is the comparison of Pokémon objects between experts and controls that distinguishes the two expertise accounts and this is one of the few comparisons where the results differed based on ROI definition. Three of the four data sets defined with group ROIs (Supplemental Fig. 3) clearly showed no difference between experts and controls with Pokémon objects. This finding suggests that experience had little influence on stimulus types that were not classified solely at the subordinate level during the acquisition of expertise. This conclusion is more consistent with the expert individuation than the SEEC account. When the FFA was localized individually (IND), rather than on the group, a significant difference was found between experts and controls with Pokémon objects, a result that supports the SEEC account. The fourth group data set (t4POR) did not show a significant difference between experts and controls with Pokémon objects, but this data set had a reduced sample size after elimination of possible outliers, so the results in that data set remain unclear. Both the expert individuation and SEEC accounts acknowledge the importance of experience and categorization level in the development of functional specialization in the FFA, it is the details of the interaction between experience and categorization level that differ between them.

Research surrounding the debate about the function of the FFA has focused largely on perceptual mechanisms by manipulating stimulus characteristics of faces and objects. Thus, previous research on experience and its effect on activation in the FFA has tended to investigate the effect of *perceptual* expertise, rather than other types of expertise. However, even with laboratory training experiments where trainees learn to individuate novel objects with only perceptual cues to individuate them, it is known that the trainees spontaneously develop their own elaborate sets of non-perceptual or semantic features that are associated with each object (personal communication, Isabel Gauthier). It is not known whether this semantic elaboration is an epiphenomenon or a necessary component of "perceptual" expertise. What is known, however, is that experimentally manipulating the type of semantic knowledge that is associated with object categories, either through training paradigms or in extant experts, has measureable effects on both behavior and patterns of brain activation (James and Cree, 2010; James and Gauthier, 2003, 2004). Pokémon cards contain much more information than the image of the character or object and this information was purposefully cropped from the stimuli, because the aim of the current experiment was to examine the brain regions that respond to images of the characters and objects. Pokémon experts, however, spend hours associating the other information with the images and the names of the characters and objects and, during game play and trading, that information would often be used by experts to individuate the Pokémon characters. Thus, to label the effects seen in the present experiment perceptual expertise with the connotation that the mechanisms underlying it are purely sensory would be a misnomer. It is interesting to note that one of the reasons Pokémon experts gave during debriefing for preferring Pokémon cards over Digimon cards was that the complexity of the other information or knowledge was greater for Pokémon cards than Digimon. Thus, even though several of the experts considered the images of Digimon characters to be more "cool," they were not interested in becoming experts with them, and a possible reason was the less well developed network of semantic knowledge provided by the Digimon universe. More research is definitely needed to fully understand the interaction of perceptual and non-perceptual learning in the development of expertise through individuation and its effects on patterns of brain activation.

Previously, heightened activation in the FG with Digimon characters was reported in a case study of a child with ASD who had an intense interest in Digimon characters (Grelotti et al., 2005). This seminal study was the first to report greater activation in the fusiform gyrus with a non-face category than with faces, however, it was difficult to determine whether the effect was caused by an experience-driven increase in activation with Digimon characters or simply by hypo-activation with faces, as is commonly found in ASD (Dekowska et al., 2008; Golarai et al., 2006; Schultz et al., 2000). Here, children in the Pokémon expert group resembled children with ASD in that children with ASD often also develop EIIs with non-face objects. However, it was not the case in the current study that the effects of stimulus type and group were driven by hypo-activation of the FFA in Pokémon experts. The level of FFA activation with faces in Pokémon experts was not significantly different from controls and was clearly well above what would be considered "ASD-like" hypo-activation. Individually-defined FFA ROIs were found in the same proportion of Pokémon experts as controls and, in the group FFA ROI, the same proportion of Pokémon experts as controls showed a face preference. In addition, all Pokémon experts scored in the normal range on EQ-SQ and CAST and, as a group, Pokémon experts did not differ significantly from controls on these tests (except that Pokémon experts actually scored *lower* on SQ). Thus, the current results cannot be explained on the basis that the Pokémon expert group was made up solely or even partially of children with ASD. Although EIIs are often found in children with ASD, the current findings show that EIIs also commonly manifest in non-systemizing children who without ASD.

Children with EIIs often excel at early cognitive skills, come from homes that stress educational activities (Johnson et al., 2004), and that are highly verbal (Alexander et al., 2008), but, until now, full-scale IQ measures had not been reported in children with EIIs. Our finding of a significant difference in full-scale IQ in children with EIIs compared to controls is novel, but not one that we would expect to affect activation in the FFA.

In conclusion, children with an EII with Pokémon cards showed greater activation in the FFA with Pokémon characters than controls and greater activation with Pokémon characters than Pokémon objects. These results are more consistent with domain general accounts (expert individuation and Separate Effects of Experience and Classification level) than with domain specific accounts (face specificity). The results cannot be accounted for by disordered activation of the FFA in Pokémon experts, as is sometimes observed in children with ASD with face stimuli. Although Pokémon characters were more familiar and personally salient to experts than controls, familiarity and personal salience did not account for the pattern of results across stimulus types and groups. Heightened activation with Digimon characters suggested that there are other strong influences on the activation of the FFA beyond stimulus characteristics, experience, and classification level.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2012.11.007.

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