Dorsal and ventral stream activation and object recognition performance in school-age children

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ABSTRACT

We explored how developing neural artifact and animal representations in the dorsal and ventral stream play a role in children's increasingly more proficient interactions with objects. In thirty-three 6- to 10-year-old children and 11 adults, we used fMRI to track the development of (1) the cortical category preference for tools compared to animals and (2) the response to complex objects (as compared to scrambled objects) during a passive viewing task. In addition, we related a cognitive skill that improved substantially from age 6 to 10, namely the ability to recognize tools from unusual viewpoints, to the development of cortical object processing. In multiple complementary analyses we showed that those children who were better at recognizing tools from unusual viewpoints outside the scanner showed a reduced cortical response to tools and animals when viewed inside the scanner, bilaterally in intraparietal and inferotemporal cortex. In contrast, the cortical preference for tools in the dorsal and ventral visual stream did not predict object recognition performance, and was organized in an adult-like manner at six. While cortical tool preference did not change with age, the findings suggest that animal-preferring regions in the ventral visual stream may develop later, concordant with previous reports of a protracted development in similar regions for faces. We thus conclude that intraparietal and inferotemporal cortical networks that support aspects of object processing irrespective of tool or animal category, continue to develop during the school-age years and contribute to the development of object recognition skills during this period.

Introduction

Objects, and children's interactions with those objects, play a fundamental part in many theoretical frameworks of learning, instruction, and cognitive development. For example, Piaget (1952, 1954) placed object permanence squarely at the center of his theory of active learning in early development. In exploring the process of learning itself in more details, Bruner (1966) proposed three modes of representation during learning. The first (enactive representations) was action-based and was believed to bootstrap learning at all ages. The second mode (iconic representation) was image or visually based and enabled a more concrete representation of a problem or situations. Finally, the third mode (symbolic representation) was language-based and supported abstract and hypothetical reasoning. Importantly, Bruner argued that these modes of representation were co-existent, even in the most advanced learner, and only loosely sequential in that they "translate" into each other as learning unfolds. An implication of Bruner's theory is that new material is best presented in a way that fosters the progression from enactive to iconic to symbolic representation. Objects that support action— especially through fantasy and play—also hold a special role in Vygotsky's theory of development (Vygotsky, 1934, 1978). Vygotsky argued that through play and tool use the child develops abstract meaning separate from the objects in the world, thereby fostering the emergence of an abstract understanding of relations in the world.

While these ideas remain at the heart of the many theoretical frameworks that underlie current educational theories, surprisingly little is known about the development of the neural systems that support object and action processing in the developing brain. This is despite the fact that the regions involved in object processing in the adult brain are well understood, suggesting that identifying the neural mechanisms that underlie the development of object processing, and particularly tool processing, during childhood is possible.

What we do know from cognitive and behavioral studies is that the perception and recognition of complex objects such as faces and 3D shapes, continues to improve dramatically during childhood and even into adolescence. In particular the ability to recognize objects or images presented to the visual system in unconventional and hard-to-decode ways is known to develop late (Bova et al., 2007; Juttner et al., 2006; Mondloch et al., 2002, 2003, see Nishimura et al., 2009 for a detailed review). Further, it is well established that aspects of face

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processing keep on improving into adolescence (Mondloch et al., 2006, although see Crookes and McKone, 2009) and two recent studies also indicate that tool processing keeps on developing until at least well into the school-age years. For example, Bova et al. (2007) have shown that the ability to recognize tools from a non-canonical viewpoint, improves rapidly between the 6th and 12th year. In addition, Mounoud et al. (2007) reported that seeing tool action primes speeds up decisions about tools in 5–9-year-olds, but not at older ages, suggesting that the link between tool action representations and tool perception is changing during childhood.

The ventral visual pathway plays an important role when adults process aspects of objects for perception such as shape, color, texture, location- and size-constancy and to an extent orientation constancy (Grill-Spector, 2003, 2009). Another well-known characteristic of the adult object sensitive cortex in the ventral stream is its organization by category; complex objects are represented in a distributed manner across the inferotemporal cortex (ITC), but there are clustered regions with a relatively stronger BOLD response for certain object categories (Haxby et al., 2001). These regions show a highly consistent spatial organization across individuals that even emerges in the absence of visual experience with tool- and house-selective clusters are located more medially in the fusiform gyrus (FFG) compared to face-, animal- and body-part selective clusters (Hasson et al., 2003; Mahon et al., 2009). Object processing in the dorsal visual pathway is less extensively investigated. However, earlier reports from single-unit studies in macaques (Sereno and Maunsell, 1998) suggested that in the lateral intraparietal area (LIP), there is selectivity for object identity independent of location, which has been confirmed in studies in adult humans (Konen and Kastner, 2008). In addition, dorsal cortical regions thought to be human homologues of the macaque inferior parietal cortex (IPc) and anterior inferior parietal cortex (AIP), are thought to play a role in adult visuo-motor transformations for planning and execution of object manipulation (Arbib, 2005; Rizzolatti and Matelli, 2003; Valyear et al., 2007). Perhaps because of the close link between tools and specific manual actions, a preference for tools over animate objects is distributed widely across a ventral *and* dorsal stream-spanning network. Tool preference was most consistently shown in the medial frontal gyrus, AIP, IPc, the premotor cortex and an area in the medial temporal gyrus (MTG) that responds to non-biological tool movement and the earlier mentioned medial FFG. This activation pattern even persists during passive viewing tasks that do not require explicit actions or involve tool motion, which has led to suggestions that these regions may be important for representing action and motion related aspects of tools (Beauchamp et al., 2003; Chao and Martin, 2000; Johnson-Frey, 2004). However, to what extent regions with a category preference perform some special computations relevant to their specific preferred category, and what driving principles lie behind the consistent organization by category across the dorsal and ventral stream, is currently unclear (Grill-Spector, 2009). Recently, some developmental fMRI studies have shed new light on this debate by investigating how the category selectivity in the ventral stream emerges.

Most consistently, these studies have shown that the response to faces in the ventral stream keeps on developing until late in childhood. According to the Interactive Specialization view (Johnson, 2001, 2010), we need to discriminate between stimulus-*sensitive* and stimulus-*selective* (or *preferring*) tissue. For example, face-sensitive tissue is revealed by a contrast between cortical responses to faces and a baseline response to a non-object stimulus that has comparable low-level visual characteristics. Face-preferring (or selective) tissue refers to cortical regions that respond to faces considerably more than closely related stimuli such as other categories of complex visual objects. As cortical regions become better tuned to particular stimuli, the Interactive Specialization view predicts increasingly focal patterns of activation of cortical tissue sensitive to stimuli such as faces with development, alongside the emergence of face-preferring tissue.

These predictions have been confirmed for faces in several recent developmental fMRI studies. (Aylward et al., 2005; Gathers et al., 2004; Golarai et al., 2007; Joseph et al., 2010; Passarotti et al., 2003; Scherf et al., 2007 see Johnson et al., 2009 for review). These studies thus support the Interactive Specialization account and provide evidence against modular views of the brain that hypothesize that regions of the cortex that perform evolutionary important functions such as face processing are hard-wired for that purpose from birth.

The development of tool processing and object processing in the dorsal stream in general has not been systematically investigated. Because regions that will eventually show a preference for graspable objects during passive viewing are located across the whole brain, tracking the development of the cortical response to tools can provide important insights into object processing in the dorsal stream and its developmental interactions with the ventral stream. Previous developmental fMRI studies on object processing have mainly focused on category specific regions of interest (ROIs) in the ventral stream. However, object representations do not solely depend on the regions that are most specifically tuned to the category an object belongs to. In fact, substantial information about tools and other types of objects is represented in a distributed manner across the inferotemporal cortex (Haxby et al., 2001) and in dorsal regions of the brain (Barsalou, 2008; Konen and Kastner, 2008). The possibility that developmental changes take place in the object sensitive cortex outside regions with a category preference, and may not even be specific to a category but general to complex objects, has not yet been addressed.

Throughout this report, we use the word "tools" when *only* referring to graspable utensils, the word "animals" when *only* referring to animals, and the term "objects" when referring to *both* categories of complex objects (both animals and tools). In line with the Interactive Specialization approach discussed earlier, we distinguish between the development of a cortical category *preference* and the development of cortical object *sensitivity*. More specifically, in order to get a full picture of the developmental changes in object processing across the brain during a passive viewing task in the scanner, we identify *object sensitive regions* (tools + animals − scrambled images) to explore the developing response distribution to objects irrespective of the local category preference and we identify *tool-preferring* regions (tools > scrambled minus animals > scrambled) and *animal-preferring regions* (animals > scrambled minus tools > scrambled images) to explore the development of a category preference. Additionally we relate these two types of developmental changes to an object recognition skill that is still developing between age 6 and 10, the age-range of the children in the present study.

Although it is currently unknown if mere passive viewing of tools will preferentially activate dorsal stream regions in children, we can formulate two contrasting hypotheses about the development of a dorsal and ventral category preference based on previous research. Firstly, behavioral developmental studies suggest that tool representations keep on developing during childhood (Bova et al., 2007; Mounoud et al., 2007) and it has been suggested that dorsal stream action representations may play an important role in the development of tool representations (Mahon et al., 2007, 2009). We therefore may expect protracted tuning of regions with a tool preference, similar to what has previously been reported for ventral regions with a face preference (Hypothesis 1). Secondly, three recent fMRI studies have reported that an adult-like preference for abstract sculptures, body parts and film material in which body parts, furniture and tools were intermixed is present in the ventral LOC from 5–8 years onwards (Golarai et al., 2007; Scherf et al., 2007; Pelphrey et al., 2009). Although these authors did not specifically compare the response to tools across age and restricted their analysis to the ventral stream, their findings raise the possibility that a cortical preference for non-social objects may mature before the preference for faces. We may therefore hypothesize that a preference for tools in the dorsal and ventral stream will be adult-like in childhood, contrary to what has

previously been reported for faces (Hypothesis 2). Finally, we can formulate a hypothesis with respect to the development of object sensitive cortex: to the extent that object-processing skills that keep on developing until late into childhood depend on processes that are relevant to multiple types of objects (Nishimura et al., 2009), we may expect that the response to both tools and animals in the object sensitive cortex will show a protracted development with age and increasing object experience (Hypothesis 3). Note that this third hypothesis is not mutually exclusive with either of the first two hypotheses.

To summarize, in the present study we aim to get more insight into which aspects of the BOLD response to objects (tool or animal preference and/or objects in general) in dorsal and ventral cortical regions show a protracted development during childhood. In addition, we explore which developmental changes in cortical tool and animal processing relate to performance on an independently measured object recognition task that is still improving in childhood, in order to gain a better understanding of the functional role that developing neural artifact- and animal representations in the dorsal and ventral stream play in children's day to day interactions with objects.

Materials and methods

Participants

Thirty-three 6- to 10-year-old children and eleven 21- to 34-year-old adults took part in a passive viewing task in the MRI scanner and in an object perception task that took place outside the scanner. The participants were split into an age group of fifteen 6–7-year-olds that consisted of 6 boys (average age = 6.9 years, SD = 0.7) and 9 girls (average age = 7.1 years, SD = 0.5), a group of eighteen 8–10-year-old children consisting of 8 boys (average age = 9.6 years, SD = 0.9) and 10 girls (average age = 9.4 years, SD = 0.8) and 11 adults consisting of 5 women (average age = 25.3, SD = 3.0) and 6 men (average age = 30, SD = 3.9). All participants were right-handed with normal or corrected vision and without any past or current neurological or psychiatric conditions, or structural brain abnormalities. Children were recruited through advertisements in newspapers. Adult participants were recruited via local recruitment facilities. Before testing, adult participants and caretakers signed an informed

consent form and children signed an assent form. A medical clearance questionnaire and a metal detection test were administered to each participant to ensure MR safety criteria were adhered to. The research was executed under the approved University protocols for the use of human adult and minor participants in research.
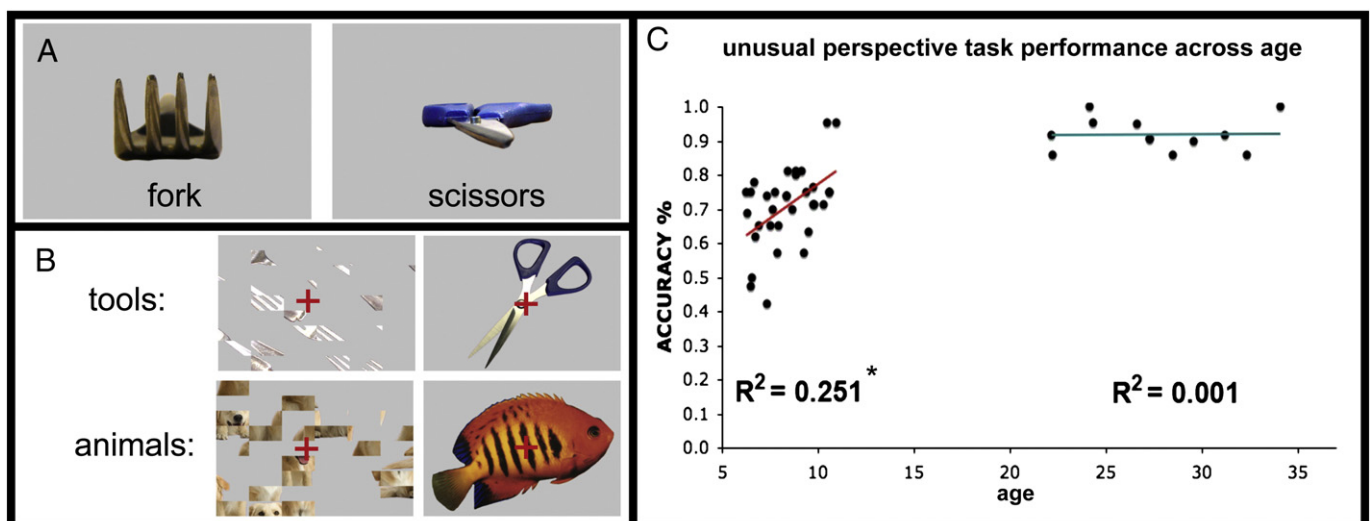
Unusual perspective task (outside the scanner)

Stimuli

All participants performed an object recognition task outside the MRI scanner. The task was based on the "unusual perspective task" developed by Bova et al. (2007). To create the stimuli, twenty-one common, graspable objects were photographed from a viewpoint in which they are typically viewed and from which they are easy to recognize. The same objects were also photographed from an unusual, more difficult to recognize, viewpoint. Objects in the original color photographs were separated from their original background using adobe Photoshop and placed on a neutral, gray background (rgb: 200×200×200, 600×800 pixel size, see Fig. 1A for examples and supplementary material for more details on the items in the task). The objects were presented on a 15.7 in. monitor with a viewing distance of ca 50 cm (37°×24.2° visual angle) using E-prime stimulus presentation software.

Procedure

The unusual perspective task took place in a testing room separate from the scanner suite. In this self-paced task, participants first identified graspable objects that appeared consecutively on the screen from an unusual viewpoint. Next, they identified the same objects, but now presented from their typical viewpoint. This second part of the task ensured that participants could recognize the objects in typical view. All participants were instructed to look carefully at each object presented on the screen and to press the spacebar as soon as they were ready to guess what the object was. After each press, a buzzer sounded and the object was replaced with a blank screen with a central fixation cross. After the participant had made a guess and refocused attention to the cross, the experimenter initiated the next trial. The same procedure was followed for objects that were presented from an unusual and from a typical viewpoint. As this was a recognition test and not a naming or language test, descriptions

Fig. 1. A: Examples of items viewed from an unusual perspective from the object recognition task that participants performed outside the scanner. B: Examples of the stimuli participants were presented with in the scanner during the passive viewing task while they fixated on the central cross. C: Accuracy scores on the unusual perspective task (based on a similar task by Bova et al., 2007) are plotted against age. Answers were considered to be correct if participants correctly named or described the object from an unusual viewpoint as well as from a typical viewpoint and incorrect if only the typical viewpoint was recognized. Items that were not correctly recognized in their typical view were excluded from the analysis. The graph shows that performance on this task increases substantially with age from childhood to adulthood (Pearson r = 0.7, p < 0.000, R^2 = 0.49; F (1,43) = 40.33, p < 0.000), however, performance only increases with age from 6 to 10 (R^2 = 0.251, F (1,32) = 10.406, p = 0.003) and no longer improves after the 22nd year of life, F = 1.23, p = n.s.).

of the object or indications regarding their use (e.g., instead of saying "*nailclipper*", saying: a thing to cut your nails) were accepted as correct answers. An item was considered as not recognized when the answer given referred to a different object (e.g., "*fork*": rake, "*lightbulb*": plug). See Bova et al. (2007) for similar scoring criteria. Items were excluded from the analysis if the usual perspective was not recognized correctly or if the unusual perspective was recognized incorrectly but the answer was plausible (instead of saying "*mobile phone*", saying: remote control). See Supplement 1 for more information about the items.

Passive viewing task (inside the scanner)

Stimuli

Fifteen types of highly familiar animals and tools were selected for the passive viewing task in the MRI scanner. A single color photograph was selected for each of these 30 types of objects and the animal or tool on the photo was placed on a neutral gray background using Adobe Photoshop (background: $200 \times 200 \times 200$ rgb, stimulus size: 600×450 pixels). A scrambled version of each picture was created in Matlab, by applying a 6×9 grid to the object stimuli and shuffling the grid cells (grid cell size 100×50 pixels). Object details were still visible in these scrambled stimuli but the overall object shape was grossly distorted. A red fixation cross with a black outline (30 pixels height and width) was displayed in the center, on top of all stimuli and during inter-stimulus intervals when no objects were presented (see Fig. 1B for examples of the stimuli). Images were projected onto a back projection screen ($23° \times 14°$ visual angle, screen resolution 800×600) attached to the bore of the scanner. Participants saw this screen through a mirror that was mounted on the radiofrequency coil that surrounded their head. Stimuli were presented using Matlab 6.0 (Mathworks) and Cogent 2000 extensions (www.vislab.ucl.ac.uk/cogent.php).

Procedure and task

In the scanner, we asked all subjects to look at the screen while fixating a cross in the center throughout the run. This task has two important benefits. Firstly, task demands are very low, so participants of a wide range of ages can do the same task with minimal confounding influences of developmental differences in performance. Secondly, because all participants looked at the same location on the screen, developmental differences in eye-movements, which can mask the BOLD response to objects in the retinotopic regions that make up about 50% of the brain, including the fusiform gyrus, regions in the parietal and frontal cortex (Saygin and Sereno, 2008) are minimized.

Animals, tools and scrambled objects were presented in 16 blocks of 15 s (4 animal blocks, 4 tool blocks and 8 scrambled object baseline blocks). During a block, 15 items from one of the three stimulus conditions were each presented for 800 ms, followed by a 200 ms fixation screen. The order of the blocks was randomized, as was the order of the stimuli, with the constraint that no stimulus occurred more than once during a block. The total duration of a run was $16 \times 15 = 240$ s. Each stimulus was repeated four times during a run. Two runs were acquired for each participant. The runs were separated by a structural scan to limit stimulus adaptation effects and to prevent young children from getting bored with the task.

Children were trained to lie still in the scanner before the experimental runs began. Each time an MR-compatible video camera recorded excessive movement during the training, the scanner operator stopped a cartoon that the child was watching and explained that the movement he/she was making would harm the image quality. This training continued until the child was lying sufficiently still for a few minutes. Children were monitored with the camera and via an intercom throughout the session to ensure that they remained still, that they were fixating the central cross on the screen, and that they were comfortable during scanning. All participants held an alarm button in their left hand so that they could notify the scanner operator at any time they chose to, in case they wanted to stop the experiment.

MR data acquisition and preprocessing

MR data were collected with a Siemens TIM Avanto 1.5 T MRI scanner using a 12-channel receive-only head coil. A high ($1 \times 1 \times 1$ mm) resolution T1-weighted 3D MPRAGE anatomical sequence (magnetization prepared low angle spoiled gradient echo) was performed to acquire high-resolution images of the brain structure of each participant (image matrix = 224×256, 160 partitions, TR: 2730, TE: 3.57, effective TI 1000 ms, flip angle: 7°). Functional data were collected using an echo planar 2D imaging sequence with image-based prospective acquisition correction for head motion (Thesen et al., 2000). Per run, we collected one hundred volumes that covered the whole brain and consisted of thirty-two slices, acquired in the axial plane in interleaved ascending order (bandwidth = 1906 Hz/pix, TR: 2.5, TE: 39, flip angle: 90, voxel size: $3.5 \times 3.5 \times 3.5$ cm, matrix 64×64).

All functional data were converted to NIFTI format and analyzed using FSL (http://www.fmrib.ox.ac.uk/fsl). First, the images were flipped into the standard FSL orientation and the non-brain structures in the co-planar high-resolution T2-weighted EPI volume and the T1-weighted MPRAGE volume were removed with FMRIB's Brain Extraction Tool (Smith, 2002). Before statistical estimation, the following preprocessing steps were undertaken: the first 4 volumes of functional data from each run were discarded, brain volumes were motion corrected to the middle volume using the Oxford Centre for Functional Magnetic Resonance Imaging of the Brain (FMRIB) Linear Image Registration Tool (MCFLIRT) (Jenkinson et al., 2002). Spatial smoothing was applied using a Gaussian-weighted kernel of 5 mm at full-width half-maximum, and data were high-pass filtered to remove linear trends. Estimates of the degrees of freedom in the statistical model were corrected for autocorrelation in the data by using the FSL pre-whitening technique (Woolrich et al., 2001). Only runs with less than 2 mm maximal absolute movements were included (53 child runs and 21 adult runs). To deal with remaining noise due to excessive subject movement not dealt with by correction for head motion (Diedrichsen and Shadmehr, 2005), the mean absolute deviation from the median was calculated for each volume using Afni (3DToutcount, http://afni.nimh.nih.gov/afni/). In each run, the volumes with the fifteen most extreme values were identified and modeled in the design matrix as regressors of no interest. Delays and undershoots in the hemodynamic response were accounted for by convolving the model with a double-gamma basis function. Functional images were registered to the high-resolution T1 weighted 3D MPRAGE using the low resolution 3D MPRAGE acquired in the same plane as the functional images. The high-resolution structural T1-weighted EPI volume was registered to the Montreal Neurological Institute Talairach compatible MR atlas averaging 152 normal subjects using FMRIB's Linear Image Registration Tool (FLIRT). Child brain normalization is an accepted method in developmental fMRI studies since total cerebral volume does not change significantly with age after 5 years of age to adulthood (Klingberg et al., 2002; Passarotti et al., 2007; Reiss et al., 1996) and from 6 years of age, standard normalization procedures do not lead to artifacts (Kang et al., 2003; Muzik et al., 2000). Therefore data from 6- to 10-year-olds and adults can be effectively transformed into the same stereotactic space.

fMRI analyses

Animal and tool blocks were modeled as regressors of interest in the design matrix with respect to a scrambled image baseline. Each functional run for a given subject was modeled separately at the first

level. Statistics for the contrasts of interest, averaging across the runs of each subject, were estimated using fixed effects modeling. At the group level, random-effects components of mixed effects variance were modeled and estimated for each contrast of interest using FLAME1 (Beckmann et al., 2003). To identify significant clusters of activation, all Z-statistic images (Gaussianized T/F) were first thresholded at an uncorrected voxel threshold of $z = 2.3$, $p = 0.01$. Correction for multiple comparisons was performed at the cluster level by applying a cluster size probability threshold of $p < 0.05$ to the Z-statistic images. We only report clusters that survived this cluster corrected threshold.

We included adults in our study as a mature benchmark for development, but a number of changes that are not of interest when studying the development of cortical object processing, such as eye-movements and cognitive strategies that are unrelated to object processing, motion, respiration differences, and cardiac activity, can affect the magnitude or extension of the BOLD response. Each of these factors has the potential to lead to artifactual differences between age groups. We dealt with these common challenges of developmental fMRI by using a robust blocked design, by minimizing eye-movements, and by applying stringent corrections for motion artifacts (see previous section). In addition, we performed multiple, complementary types of analyses in which we tracked changes in activation from 6 years of age to adulthood and investigated changes that occurred during childhood separately from the adult group.

We identified *object sensitive regions* (tools + animals > scrambled images), *tool-preferring regions* (tools > scrambled – versus animals > scrambled) and *animal-preferring regions* (animals > scrambled – tools > scrambled) in each age group. We explored where the object sensitive and category-selective BOLD response varied with age in whole brain correlation analyses as well as in a-priori, structurally defined regions in which we expected developmental changes in object processing to take place based on both developmental and adult literature on tool and object processing (Chao and Martin, 2000; Golarai et al., 2007; Grill-Spector, 2003; Konen and Kastner, 2008; Rizzolatti and Matelli, 2003; Sereno and Maunsell, 1998; Valyear et al., 2007). These structural ROIs encompassed the fusiform gyrus, the parietal cortex, the inferior lateral occipital cortex and the superior lateral occipital cortex/posterior parietal cortex. Because normalization from age six onwards does not lead to artifacts (Muzik et al., 2000) we did not manually draw the borders of anatomical ROIs in each individual anatomical scan but defined them in standard space after normalization was performed, as has been done in several other developmental fMRI studies (Passarotti et al., 2003, 2007; Nelson et al., 2003). The four structurally defined ROIs consisted of (1) the combined occipital and temporal fusiform cortex atlas region masks, (2) the combined superior parietal cortex and supra-marginal gyrus, anterior division atlas region masks (3) the inferior LOC atlas region mask and (4) the superior LOC atlas region mask derived from the probabilistic Harvard–Oxford Cortical Structural Atlas (probabilistic masks were converted to binary masks).

To further investigate the development of category-selective regions in the dorsal and ventral object sensitive cortex, we compared the animal and tool preference of 6- to 7-year-old children, 8- to 10-year-old children, and adults in independently defined functional regions of interests. Finally, we explored where in the brain and in the earlier described a-priori defined structural ROIs, individual differences in (1) tool and animal preference and (2) object sensitivity, correlated with age and with individual scores on an independent tool recognition task between age 6 to 10.

Results

The behavioral results acquired from the same subjects that were subsequently scanned are presented first, followed by fMRI results.

The unusual perspective task

The percentage of graspable objects that were correctly recognized from an unusual viewpoint is plotted against age in Fig. 1C. The graph shows that accuracy increased overall with age from 6 years to 34 years of age ($R^2 = 0.49$, F $(1,43) = 40.33$, $p < 0.001$). A regression analyses showed that recognition of graspable objects from an unusual perspective improved markedly during childhood, between age 6 and 10 ($R^2 = 0.25$, F $(1,32) = 10.406$, $p = 0.003$) but did not improve further in the group of adults ($R^2 = 0.032$, F $(1,10) = 0.009$, $p < 0.92$). The high adult scores on this task, which was specifically designed for children, may reflect a ceiling effect rather than stabilization of the ability to recognize graspable objects from unusual viewpoints in adulthood.

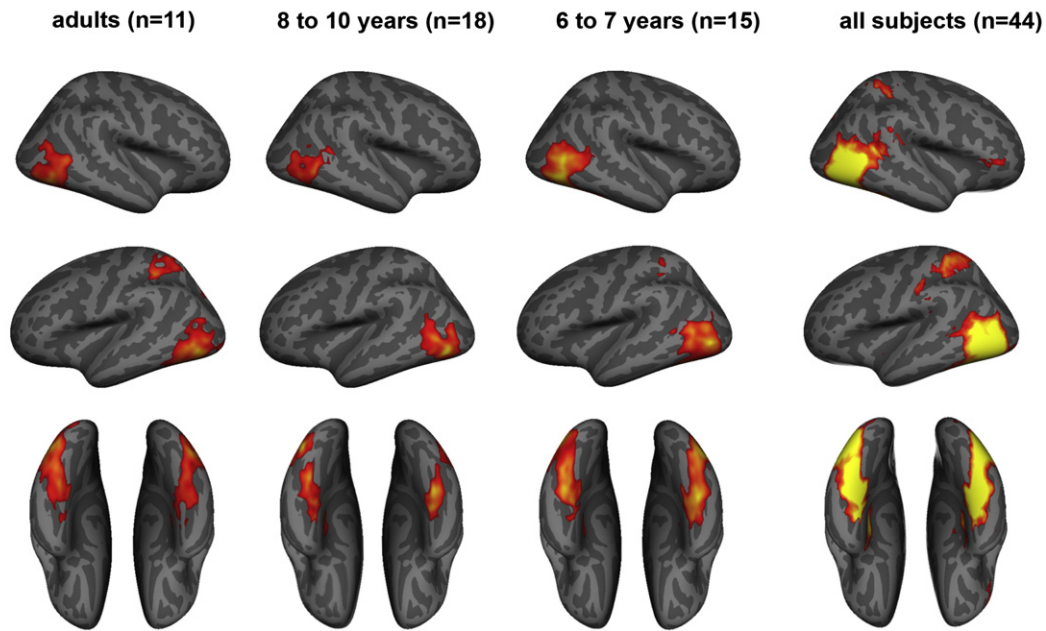### The development of object sensitive cortex

We explored how the distribution of object sensitive cortex, irrespective of its category preference, changes between age 6 and adulthood (contrasting tools + animals with scrambled images). Collapsing across all forty-four participants, we obtained a map of object sensitive cortex that extended from the occipital cortex into the fusiform gyrus and into the lateral occipital- and medial temporal cortex and dorsally into the left superior parietal cortex extending to the anterior intraparietal sulcus (right panel of Fig. 2A). Object sensitive regions are displayed separately for 6- to 7-year-olds, 8- to 10-year-olds and adults in the left three panels of Fig. 2A.

We used a whole brain correlation analysis to determine if the cortical BOLD response to objects varied linearly with age in any region. Clusters where object sensitivity changed from the 6th year of life to adulthood were located in the bilateral insular cortex, posterior cingulate and visual cortex. In the insular, the response to objects increased with age; children showed a preference for scrambled images vs objects and adults a preference for objects vs the scrambled image baseline. Conversely, in the posterior cingulate the response to objects reduced with age, with a preference for objects over scrambled images in childhood but a stronger response during the baseline in adulthood (Fig. 2B, left). Finally, at all ages there was a preference for the baseline in the occipital pole and the lingual gyrus, but this preference reduced with age (Fig. 2B, right). The posterior cingulate cortex and the insular gyrus are often linked to the regulation of cognitive resources and the default-network (Augustine, 1996; Fransson and Marrelec, 2008; Hayden et al., 2008) we therefore suggest that the patterns of response in these regions reflect age-related differences in cognitive strategies during the task. For example, the reducing response in the posterior cingulate may reflect the allocation of fewer resources to scrambled images vs objects in adults than in children, presumably because adults were more efficient at the passive viewing task, i.e., they engaged less with the stimuli. Likewise, the activation differences in or near primary visual cortex may have reflected slight differences in fixation strategies. Thus, we have identified several regions where the response to objects correlated linearly with age. In later discussions of age-related differences in the response to objects in childhood alone, we explore age differences in object processing with a more complex developmental pattern.
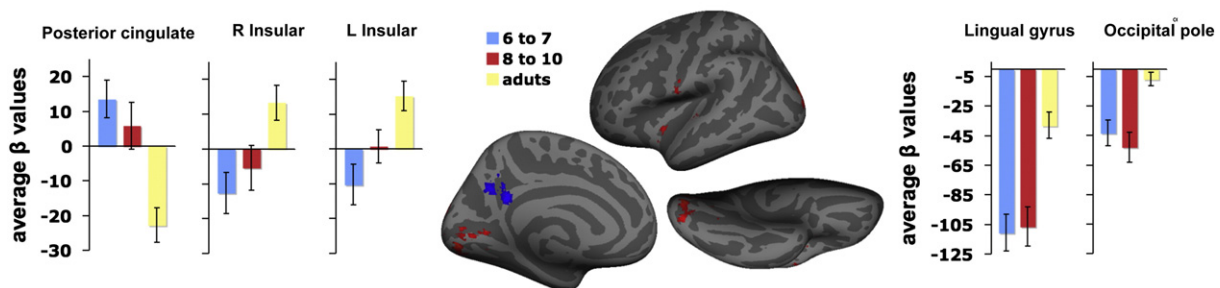
The development of a cortical preference for tools and animals

We next performed multiple complementary analyses to investigate how cortical patterns of the preference for tools and animals in the dorsal and ventral stream change from the 6th year of life (contrasting tools > scrambled – animals > scrambled to obtain tool-preferring regions and animals > scrambled – tools > scrambled to obtain animal-preferring regions). Collapsing across all participants we obtained an average map of cortex with a tool preference. As can

A object response (tools + animals > scrambled) across age

adults (n=11)   **8 to 10 years (n=18)**   **6 to 7 years (n=15)**   **all subjects (n=44)**

B object response increases (red) and decreases (blue) from age 6 to adulthood

Posterior cingulate   R Insular   L Insular

■ 6 to 7
■ 8 to 10
□ aduts

average β values

Lingual gyrus   Occipital pole

average β values

Fig. 2. Only clusters exceeding a threshold of z = 2.3, p = 0.01, with a cluster size probability of p > 0.05 are depicted. A: Object sensitive regions that respond more to tools and animals than scrambled pictures are displayed separately in red/yellow on the Freesurfer average surface for 6- and 7-year-olds, 8- to 10-year-olds and adults in the left three panels. In the right panel all object sensitive regions averaged over all 44 subjects is displayed. Regions that showed sensitivity to objects compared to scrambled pictures were located in the bilateral fusiform gyrus, the lateral occipitotemporal cortex, the medial temporal cortex and in the left and right inferior parietal cortex and the left inferior frontal gyrus. Note that the three left surfaces indicate a complex developmental trend with a decreasing response to objects vs scrambled stimuli during childhood and a subsequent increasing response in adulthood in the posterior parietal cortex and the FFG. This pattern is further discussed in the Results section "The neural correlates of age and developing tool recognition during childhood" and the supplementary material. B: Clusters that correlated significantly with age in 44 subjects, ranging from 6 to 34 years of age after are displayed on the left Freesurfer average surface hemisphere. The response in the posterior cingulate decreased with age (depicted in blue) while the response in the left and right insular cortex increased with age (note that the insular cluster spreads out when registered and painted onto the average inflated Freesurfer surface). There were also age-related differences in the V1 response.

be seen in the right panel of Fig. 3, dorsal tool-selective regions were located in the bilateral dorsal occipital and parietal cortex, extending into LIP, VIP, AIP, the bilateral precentral sulcus near the frontal eye fields, the right inferior frontal gyrus, pars opercularis and triangularis and the frontal pole. Ventral tool-selective regions were located in the left and right LOC adjacent to the medial temporal gyrus and in the more medial aspects of the bilateral FFG. Animal selective cortex extended from V1 into the fusiform gyrus. On the right, this extension encompassed regions in the LOC and FGG that are reported to be selective to faces as well (Grill-Spector, 2003).

Adult dorsal and ventral tool-selective regions were already unmistakably present in 6- and 7-year-old children, and showed a similar spatial organization in each age group. Cortical regions that showed tool or animal selectivity during passive viewing are depicted separately for 6- to 7-year-old children, 8- to 10-year-old children and adults in the left panels of Fig. 3. Although at first glance there appear to be some developmental changes in tool preference, for example in

medial FFG and posterior parietal lobe, we identified no regions where tool or animal selectivity varied with age in a whole brain correlation analyses. Even when limiting the analyses to a-priori defined structural ROIs that encompassed all visualized regions with a tool preference, namely, parietal cortex, the fusiform gyrus and the inferior and superior LOC we found no regions where the BOLD response correlated with age. We thus found no evidence for developmental changes in the distribution of category-selective cortex in the dorsal or ventral visual stream in correlation analysis of the whole brain or within structurally defined ROIs at thresholds adjusted for smaller volumes (see Materials and methods). Comparing functionally defined ROIs across groups (Scherf et al., 2007; Mahon et al., 2009; Golarai et al., 2007) is considerably more powerful than a whole brain analysis, or than analyses that are restricted to relatively large structurally defined ROIs and thus may be able to pick up on subtle developmental differences, or more complex developmental patterns than linear activation decreases or increases with age.

category preference for tools (red/yellow) and animals (blue) across age

adults (n=11)   **8 to 10 years (n=18)**   **6 to 7 years (n=15)**   **all subjects (n=44)**
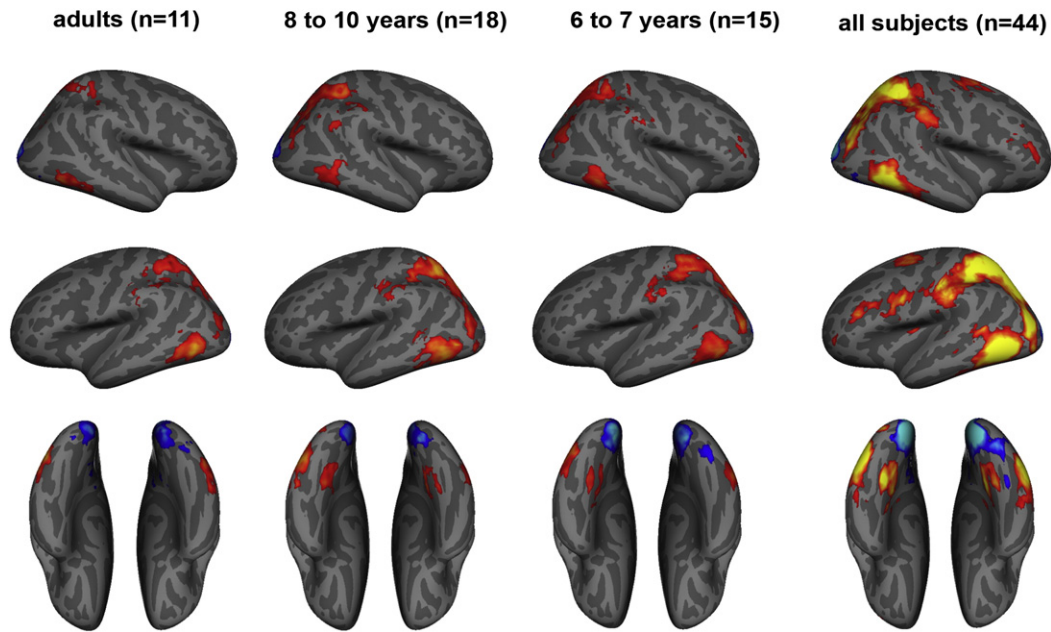
Fig. 3. Only clusters exceeding z = 2.3, p = 0.01 with a cluster size probability of p>0.05 are depicted. Regions with a tool preference are depicted in red/yellow (resulting from the contrast tools>scrambled − animals>scrambled) and regions with an animal preference are depicted in blue (resulting from the contrast animals>scrambled − tools>scrambled). Group average maps are displayed for 6- to 7-year-olds, 8- to 10-year-olds and adults separately in the left three panels and for all 44 participants together on the right. Regions with a tool preference in the omnibus analysis were located dorsally in the bilateral superior parietal cortex and extended into the anterior inferior parietal cortex, the bilateral precentral sulcus in the frontal eye fields and the right inferior frontal gyrus, pars opercularis and triangularis and frontal pole. More ventrally, clusters with a tool preference were located in the left and right lateral fusiform gyrus (FFG) and lateral occipital cortex (LOC) adjacent to the medial temporal gyrus (MTG) and in the more medial aspects of the bilateral fusiform gyrus (FFG). A large cluster with a preference for animals over tools was located in V1, extending into the fusiform gyrus. Most prominently on the right, the cortical preference for animals in V1, extended into the LOC and FGG. The blue animal-preferring region located between two tool-preferring clusters on the right inferior view and the small blue animal-preferring region on the right lateral view are located in the "fusiform face area" (FFA) and the occipital face area (OFA) (Grill-Spector, 2003). There were no regions where the preference for tools or animals correlated with age in a whole brain analysis and correlation analyses restricted to a-priori defined structural ROIs in FFG, inferior and superior LOC and the Parietal cortex.

In the next section we therefore adopt a functionally defined ROI approach to further explore the response patterns in object sensitive cortical regions with a category preference.

### ROI analysis of the category preference in object sensitive cortex

Within the object sensitive cortex, we selected ROIs that were organized by category at ages 6 to 7, ages 8 to 10 and in adulthood. We then investigated if there were age-related changes in the response patterns of these functionally defined ROIs. This approach allowed us to define voxels with a category preference using a separate age group (e.g., a region with a tool preference in the adult group) from the one used to test the experimental hypothesis (e.g. whether a group of 6- to 7- and a group of 8- to 10-year-old children display a tool preference in this adult region). Specifically, we contrasted tools with animals and vice versa (tools>scrambled − animals>scrambled and animal-scrambled − tools>scrambled) for each age group separately, within a functionally defined mask of the omnibus object sensitive cortex. The omnibus object sensitive mask is depicted in Fig. 2A, right panel and was obtained by contrasting animals + tools − scrambled images, averaging across all forty-four subjects. We identified all resulting clusters with a tool and animal preference for each age group and then extracted from these clusters the average BOLD response to animals and tools (both compared to a scrambled picture baseline) for each individual. For example, in a tool-preferring region in the adult left parietal cortex, we extracted the response to tools and animals for all subjects, including all children. Subsequently, we tested if the same region preferred tools to animals in 6- to 7- and 8- to 10-year-old children using sets of ANOVA's.

In Fig. 4, the responses to tools and animals in each ROI are displayed for all age groups. As can be seen in the graphs, all participants showed a tool preference in each ROI, even if the ROI from which the response was extracted was defined in a different age group. A tool preference was already present in what will later become an adult tool-specific region in both groups of children. Likewise, ROIs that had a preference for tools in 6- to 7-year-olds and 8- to 10-year-olds showed a preference for tools in adults. In addition, ANOVA's showed that there were no stimulus-by-age interactions in any of the ROIs (all F's are smaller than 1.809, p = 0.177). We thereby show that no significant developmental changes such as an increasing focalization of tool-preferring response were taking place outside the functionally defined adult regions.

An animal selective region in the object sensitive cortex surpassed the statistical threshold only in adults. In accordance with previous reports (Mahon et al., 2009), this region was located in the lateral occipital fusiform gyrus, somewhat anterior to what has been reported as the functional occipital face area (OFA) (Grill-Spector et al., 2004). In the groups of children, the average BOLD response in this region (see Fig. 3A, right bottom graph) did not show a preference for animals. To further explore the emergence of animal selectivity, we compared the average BOLD response of 6- to 7-year-olds, 8- to 10-year-olds and adults in the cluster with an animal preference that we identified in the medial FFG in the omnibus analysis of all 44 subjects (see Fig. 3, right-most panel, the medial and most anterior blue region in the inferior view of the right hemisphere). The region showed a preference for animals in adults (F (1,10) = 12.190, p = 0.006) but not in children (F (1,14) = 0.131, p = 0.131, F (1,17) = 0.751, p = 0.398). There were no significant age × stimulus interactions in the group average fusiform

ROI analysis of object sensitive cortex with a category preference for tools (red) and animals (blue)
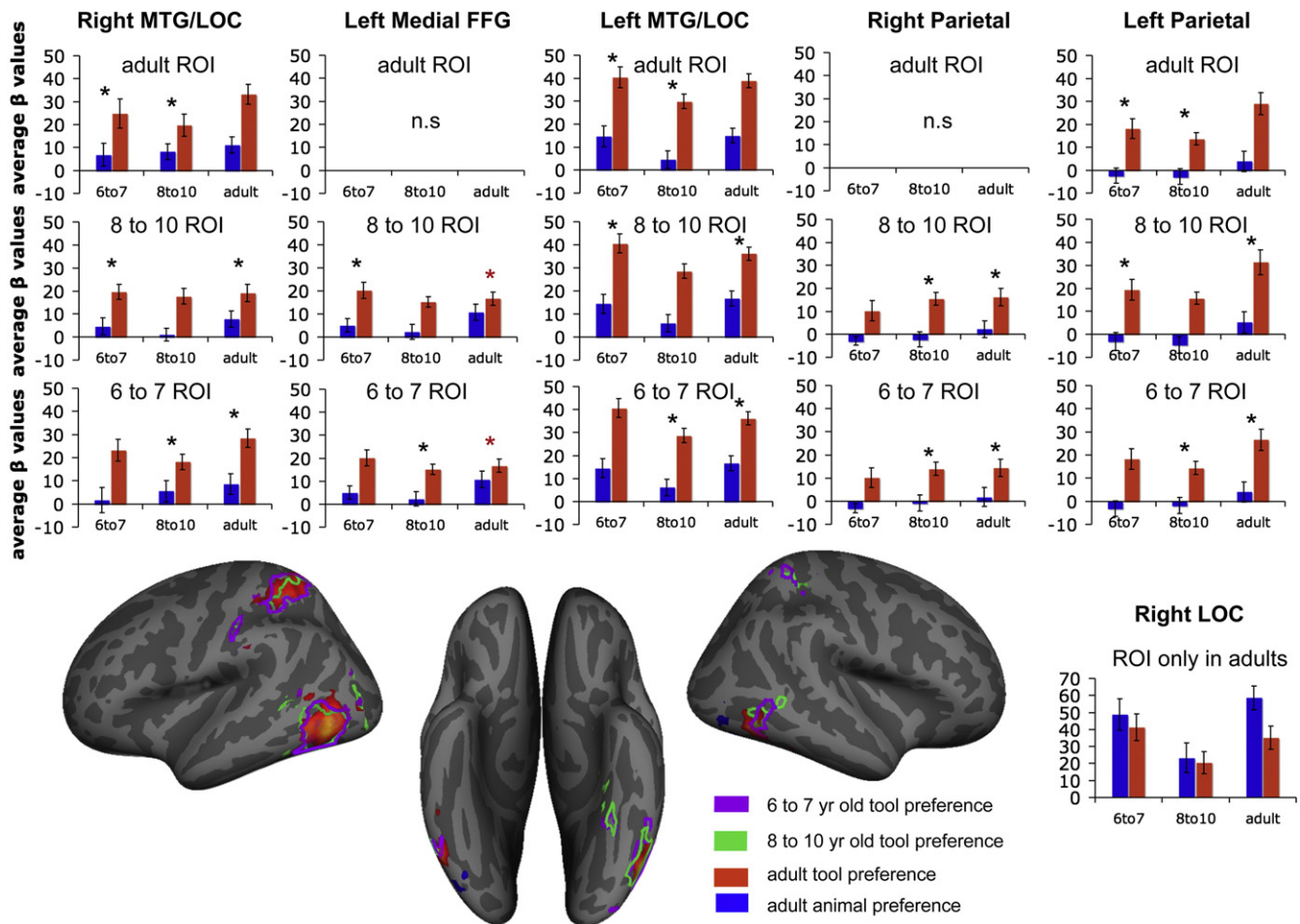
Fig. 4. Clusters located in object sensitive cortex (functionally defined by contrasting tools + animals − scrambled pictures in all 44 subjects, see Fig. 2A right panel for mask) with a preference for tools or animals were identified separately in adults, 8- to 10-year-olds and 6- to 7-year-olds, at a thresholded of z = 2.3, p = 0.01, $p_{cluster} < 0.05$. In all age groups, we located object sensitive regions with a tool preference in the left parietal cortex and the left and right MTG/LOC. In both groups of children there were additional clusters in the left medial FFG. The adult group showed a cluster with a significant animal preference in the right LOC. Adult regions of interest with a tool preference are depicted on the Freesurfer average inflated cortex in orange, and regions with an animal preference are depicted in blue. In the adult maps, the edges of the corresponding regions of interests in the group 8- to 10-year-olds are depicted in green and those of the 6- to 7-year-olds are depicted in purple. In the graphs, the average beta-values to animals and tools are displayed separately for each group, for each region of interest. Black stars indicate a significant category preference (all F's > 5.6, all p's < 0.03). The two red stars in the medial FFG indicate a marginally significant category preference (top graph: F (1,10) = 4.308, p < 0.065, bottom graph F (1,10) = 4.318, p < 0.064). Note that no statistical comparisons of the animal vs tool response were made for the group in which the region was defined, because they differ significantly per definition. ANOVA's showed that there were no stimulus-by-age interactions in any of the ROIs (All F's are smaller than 1.809, p = 0.177). The graphs show that from six years onwards, the tool preference in the dorsal and ventral object sensitive cortex is strikingly consistent. Conversely, in the region with an animal preference that is only present in the adult group, neither of the child age groups showed a significant preference for animals compared to tools.

animal area (F (2,41) = 1.058, p = 0.357) or the occipital "animal" region detected in adults (F (2,41) = 1.763, p = 0.184). However, the animal preference was distinctly less consistent across age (in right FFG and LOC) than the tool preference, which was adult-like from six years onwards.

The neural correlates of age and developing tool recognition during childhood

In the previous analyses we already established that there were regions in which the response to objects correlated linearly with age. However, these analyses were not sensitive to more complex, non-linear patterns of development from childhood to adulthood. In a final set of analyses we therefore explored changes in the object sensitive cortical response in the group of 33 children alone.

When we explored how the response to objects, irrespective of its category preference (contrasting tools + animals with scrambled images), varies with age across the whole brain during childhood, we

identified a cluster in the left posterior lateral sulcus. When the analysis was performed at a lower threshold within a-priori defined structural ROIs that encompassed regions where we expected developmental differences in object processing to take place based on previous reports (see Materials and methods; namely the fusiform gyrus, the parietal cortex and the inferior and superior lateral occipital cortex) we identified a cluster in the right medial fusiform gyrus. As can be seen in Figs. 5A and B, the response to objects in the posterior lateral sulcus increased with age during passive object viewing, and the response was also positively correlated with performance on the unusual viewpoint task. The response in the medial right fusiform gyrus, in contrast, decreased with age, and in this region a reduced response to objects correlated with better performance on the independent object recognition task. We performed partial correlation analyses to disentangle the unique contribution of age and object recognition to the BOLD response to objects vs scrambled stimuli in rFFG and the posterior lateral sulcus. Activity in both rFFG and posterior lateral sulcus was correlated with age after correcting for recognition performance
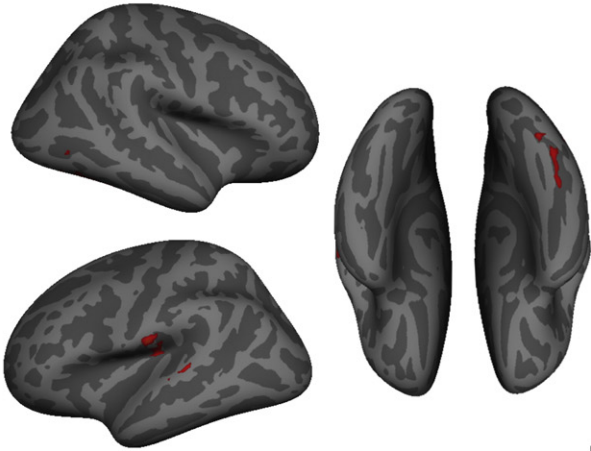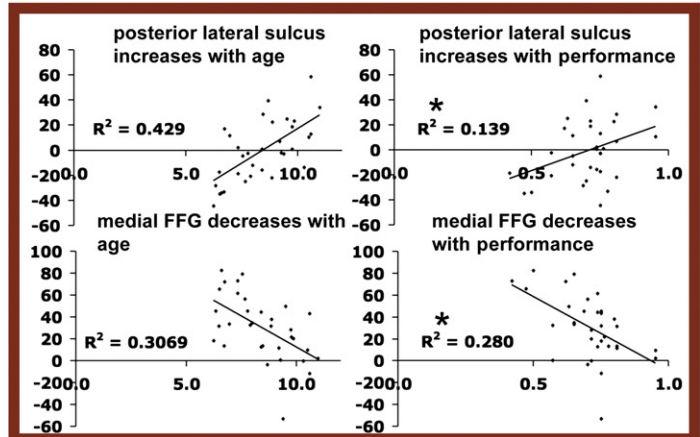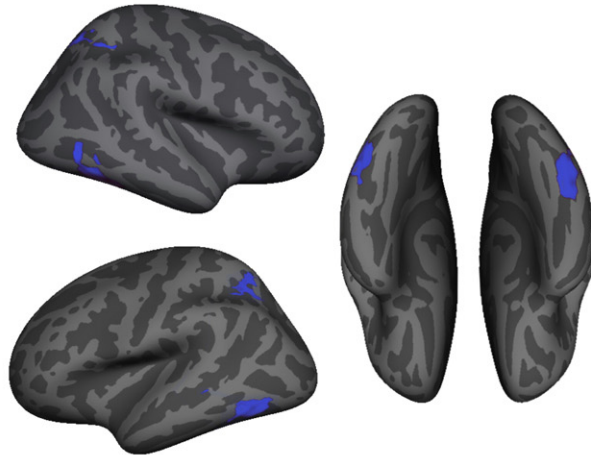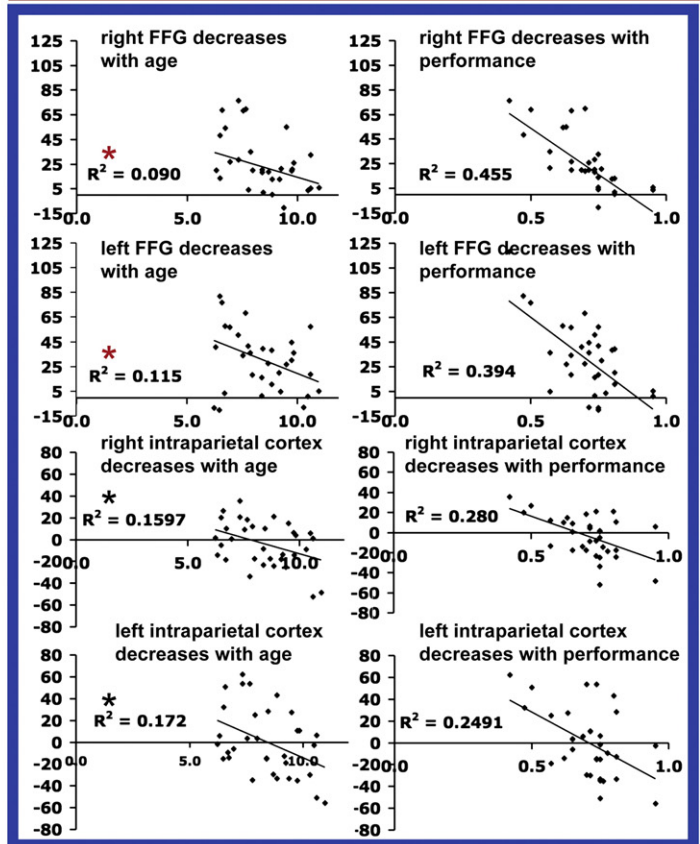
Fig. 5. A: In a whole brain correlation analysis of the BOLD response to objects (passively viewed animals + tools) and age in the group of 33 children, activation in a cluster in the left posterior lateral sulcus correlated positively with age. We located a cluster in the right medial FFG that correlated negatively with age when restricting the analysis to the FFG. Both regions are depicted on an average Freesurfer Surface. B: Average individual responses to objects versus scrambled objects in the clusters depicted in panel A are plotted against age (left) and performance on the unusual perspective task (right). Regression analyses show that the BOLD response in both regions explains a significant part of the variance in performance on the unusual perspective task that participants performed outside the scanner (posterior lateral sulcus gyrus: $R^2 = 0.139$, $F(1,31) = 4.99$, $p = 0.033$; medial FFG: $R^2 = 0.279$, $F(1,31) = 12,01$, $p = 0.002$; note that the correlation between age and the BOLD response in these regions is significant per definition). However, in contrast to the response in the rFFG, the left posterior lateral sulcus cluster no longer correlated with performance after correcting for age. C: Two bilateral inferotemporal regions and two bilateral intraparietal regions in which the BOLD response to objects correlated negatively with accuracy on the unusual perspective task in 33 children are displayed on the Freesurfer average surface. D: The average individual response to objects in the regions in panel C is plotted against age and performance. In the ventral inferotemporal regions, there was a trend towards an age-related decrease in response (right $R^2 = 0.09$, $F(1,31) = 3.05$, $p = 0.09$; left $R^2 = 0.112$, $F(1,31) = 3.90$, $p < 0.057$, trend indicated by red star) and there was a significant age-related decrease in the intraparietal regions (right $R^2 = 0.160$, $F(1,31) = 5.90$, $p = 0.021$; left $R^2 = 0.712$, $F(1,31) = 6.46$, $p = 0.01$). Note that the correlations between performance and the BOLD response in these four regions are significant by definition. Partial correlations confirmed that after correcting for age these four regions still correlated with performance on the usual perspective task. Age did not explain significant additional variance over and above performance.

(correlation$_{partial}$ with rFFG response $= -0.394$, $p = 0.026$ and with posterior lateral sulcus response $= 0.583$, $p = 0.001$), but only the rFFG was correlated with recognition performance after variance due to age differences was partialled out (correlation$_{partial}$ performance with rFFG response $= -0.348$, $p = 0.051$ and with posterior lateral sulcus response $= 0.067$, $p = 0.714$). From this, we conclude that protracted

development of complex object processing during passive viewing, with a decreasing response to objects in the right fusiform gyrus and an increasing response to objects in posterior lateral sulcus, is correlated with age and the development of object recognition from unusual viewpoints that occurs between the 6th and 10th year of life. However, because object recognition performance explained no variance in the

activation of the posterior lateral sulcus over and above age, it is possible that the developmental changes in this region reflect more generic cortical changes between 6 and 10 years, and is not necessarily directly related to object recognition. In line with the functional ROI analysis in the previous section, we found no regions where a tool- or animal preference in the BOLD response correlated with age during childhood in a whole brain or structurally defined ROI analysis.

Finally, we investigated where in the brain, the response to objects correlated with performance on the unusual perspective task between the 6th and 10th year of life. In a whole brain analysis, we identified four regions where the BOLD response decreased significantly with improving performance. Two were located in the left and right ventral fusiform region and two in the left and right intraparietal sulcus (see Figs. 5C and D). There was a strong trend towards a decrease with age in the left and right fusiform response, and the response to objects in the left and right intraparietal cortex decreased significantly between 6 and 10 years of age (trends are indicated by red stars in Fig. 5D). Object recognition skills explained a substantial amount of variance in the response in these regions over and above age (partial correlation were between −0.369 (left intraparietal) and −0.636 (right lFFG) with p values smaller than 0.04). This suggests that the decreasing response in these regions may not simply reflect generic developmental effects but is indeed relevant to improving object-processing ability. Age no longer correlated significantly with the responses in these regions after correcting for object recognition performance (all partial correlations were smaller than −0.220 with p values larger than 0.226). A regression model that combined the average response to animals + tools − scrambled in all four regions explained 50% of the variance in performance on the unusual perspective task ($R^2 = 0.495$), while only 25% of the variation in scores was accounted for by increasing age ($R^2 = 0.251$). We conclude that children who performed better on the unusual perspective task outside the scanner processed the passively viewed stimuli in the scanner differently, which expressed itself as a lower BOLD response to objects in intraparietal and inferotemporal cortex.

There were no sex differences in the average response in any of the clusters reported in Fig. 5. We also found no age × stimulus interactions in the four dorsal and ventral regions that correlated with performance on the unusual perspective task (all four F's $(2,42) < 0.596$, $p > 0.523$). Moreover, in a whole brain correlation analysis we did not identify any regions where a tool (or animal) preference in the BOLD response was correlated with performance on the unusual perspective task during childhood. We thus show that the BOLD response to passively viewed tools *and* animals predict performance on the unusual perspective task and age of the child and in a similar way. This suggests that the cortical processes that underlie the development of this object-processing skill between age 6 and 10, are not specific to tools but are more object-general.

Contrary to what we found with children, adult performance on the object recognition task was not related to the bold-response in the inferotemporal and intraparietal regions in Fig. 5C (Pearson's r < 0.47, p < 0.145) and the decreasing response to objects that we reported between 6 and 10 years of age did not persist into adulthood either. Instead, the response to passively viewed objects compared to scrambled pictures increased again, resulting in a U-shaped developmental trajectory (see Supplement 1). This pattern is visualized in the left three panels of Fig. 2A, where the response to objects vs scrambled images is depicted separately for each age group. There is a visible decrease in response in the intraparietal cortex and fusiform regions from the younger to older groups of children, and a subsequent increase in response in adults. It is highly unlikely that this pattern is simply due to motion differences for two reasons. Firstly we would expect motion artifacts to not only appear in regions that are typically associated with object processing, and secondly because in children the response in these regions is highly predictive of performance on a completely independent object-processing task that participants performed outside the scanner.

Discussion

In the present study we explored which aspects of the BOLD response to objects (tool or animal-preferring and/or object-general) in dorsal and ventral cortical regions showed protracted development during childhood. In addition, we explored which developmental changes in cortical object processing related to the developing ability to recognize objects from unusual viewpoints.

We first replicated Bova et al.'s finding (2007) that the ability to recognize graspable objects from an unusual perspective improves rapidly from the 6th until after the 10th year of life and we showed that the ability has improved even more by the early twenties. Performance did not improve after the 20th year of life, suggesting that the ability to recognize familiar graspable objects from an unusual viewpoint stabilizes sometime during the second decade. However, it remains possible that the adults performed at ceiling with these test items that were specifically designed to capture developmental changes in childhood. Therefore, these results do not exclude the possibility that the ability to recognize objects from unusual perspectives can still improve with increasing object experience in adulthood.

We did not identify any age-related changes in tool-selective tissue in any of (1) a whole brain analysis, (2) a structurally defined ROI analysis, or (3) a functionally defined ROI analysis. We clearly show that at an age as young as six, mere passive tool viewing preferentially activates parietal regions of the cortex, including AIP, without any explicit requirements to grasp. We did not find any evidence for protracted tuning of any regions with a tool preference (Hypothesis 1). We therefore conclude that the dorsal and ventral stream tool network shows an adult-like spatial distribution and tool preference relatively early (Hypothesis 2). This is in line with previous reports that a preference for other non-social objects in the ventral stream is adult-like by 5 years of age (Golarai et al., 2007; Scherf et al., 2007). Because a tool preference during passive object viewing was already present and organized in an adult-like way in our youngest age group, we could not explore the developmental relationship between the dorsal and ventral visual stream. Future studies will need to track the development of the tool preference in the cortex at younger ages to establish whether category specialization in the two streams develops (1) in tandem or (2) whether development of organization-by-category in the dorsal stream precedes and perhaps drives the development of the ventral stream (Mahon et al, 2007; Mounoud et al., 2007) or (3) whether the development of organization-by-category in the ventral stream precedes and perhaps drives the development of the dorsal stream (Braddick et al, 2003; Klaver et al., 2008).

The consistent organization of a tool preference from 6 years onwards contrasts with previous reports on the developing cortical preference for faces (Cohen-Kadosh and Johnson, 2007). The two regions with an animal preference that we detected in the right FFG (in an omnibus analysis of all 44 subjects) and the LOC in adults are in fact often reported as regions with a face preference and have been shown to keep tuning to faces until the teenage years (Golarai et al., 2009). Compared to the developmental continuity that we found in regions with a preference for tools, there was a distinctly less consistent preference for animals across age in these two animal-preferring regions. In adults, but not in children the FFG and LOC showed a significant animal preference in the BOLD response. However, direct comparison of age group differences did not reach statistical significance. This pattern indicates that a preference for animals in these cortical regions only gradually emerges. Further exploration of the possible protracted development of cortical animal processing and animal face processing in LOC and FFG may have important implications for theories on the development of cortical

face processing. Such research may, for example, provide insight into whether the protracted development of a face preference in these regions is restricted to human adult faces, or extends to the processing of animal faces as well.

In the bilateral intraparietal cortex and the FFG, we found regions where the sensitivity to objects (irrespective of category) was correlated with performance on the unusual perspective task that improves between age 6 and 10. Specifically, the response to objects in the left and right intraparietal sulcus and regions in the left and right inferotemporal cortex decreased when children got better at recognizing graspable objects from unusual viewpoints outside the scanner. The story becomes more complicated when comparing object processing in children and adults. In adults, the response in the above-mentioned regions was not related to performance on the unusual perspective task. In addition, the response to objects in the intraparietal cortex and fusiform regions increased after 10, resulting in a U-shaped pattern of BOLD response across age. We suggest that this complex developmental pattern may be the result of different cognitive strategies employed by adults and children. Indeed, U-shaped patterns of behavior are typically associated with changes in cognitive strategy (Karmiloff-Smith, 1992; Karmiloff-Smith and Inhelder, 1978; Seigler, 2004). Here, for example, adults may be more proficient at the passive viewing task and allocate fewer resources to passively viewed scrambled stimuli vs objects. Developmental patterns in regions that are typically associated with regulation of attention such as the posterior cingulate lend some support to this idea.

Possibly, the decreasing response to objects with improving performance in childhood reflects that children who are better at recognizing objects process the stimuli in the scanner more efficiently, leading to a decrease in the inferotemporal and intraparietal BOLD response to objects in general. A developmental decrease in activation with age and improving performance is frequently reported in the developmental literature and is generally attributed to more efficient or sparse processing (Casey et al., 2005; Durston et al., 2006; Poldrack, 2010). Although the neural mechanisms that result in decreasing activation with development remain to be elucidated, Peelen et al. (2009) used an adaptation paradigm to show that developmental changes in the FFA were linked to increasingly selective internal representations, and thus provide some evidence that this is a plausible explanation. The volume of the brain does not change much after age 6, but dynamic changes in long and short range connectivity and the ratio of gray to white matter density continue until late in adolescence and are most pronounced in the prefrontal cortex, the inferotemporal cortex and the intraparietal cortex (Casey et al., 2005; Fair et al., 2007; Giedd et al., 1999; Gogtay et al., 2004). In line with the protracted development of parietal and inferotemporal regions during childhood our findings suggest that the intra- and inter-regional networks that support object representations in dorsal and ventral high-level visual regions continue to fine-tune during childhood (Johnson, 2001, 2010). A challenge for future research will be to disentangle the role that experience and brain maturation play in tuning these networks for object processing.

In summary, we investigated three hypotheses with regard to the development of object processing during human development. We obtained some evidence for the protracted developmental tuning of certain animal selective regions (Hypothesis 1), but we did not observe any such developmental changes in those regions with a tool preference, which looked adult-like from at least 6 years (Hypothesis 2). The relative stability of neural representations of tools across ages is consistent with the critical role that objects and actions play in many theories of learning and education, namely bootstrapping the development of knowledge from early ages onwards (Bruner, 1966; Mounoud et al., 2007; Piaget, 1952, 1954; Vygotsky, 1934, 1978). In the light of these theories one might indeed expect that by age 6, children have the neural machinery in place to learn about the world

through their interactions. The early mature parietal specialization for tools that we report here is in line with this. To examine our third hypothesis we investigated whether the response to both tools and animals in object sensitive cortex showed a protracted development with age and increasing object-processing proficiency. The results for general object sensitive cortex were consistent with this hypothesis in that we observed a decreasing cortical response to both types of objects in the dorsal and ventral higher-level object sensitive visual cortex that correlated with developing object recognition ability between age 6 and 10.

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2010.11.005.

References

Arbib, M.A., 2005. From monkey-like action recognition to human language: an evolutionary framework for neurolinguistics. Behav. Brain Sci. 28, 105–124.

Augustine, J.R., 1996. Circuitry and functional aspects of the insular lobe in primates including humans. Brain Res. Rev. 229–244.

Aylward, E.H., Park, J.E., Field, K.M., Parsons, A.C., Richards, T.L., Cramer, S.C., Meltzoff, A.N., 2005. Brain activation during face perception: evidence of a developmental change. J. Cogn. Neurosci. 17 (2), 308–319.

Barsalou, L.W., 2008. Grounded cognition. Annu. Rev. Psychol. 59, 617–645.

Beauchamp, M.S., Lee, K.E., Haxby, J.V., Martin, A., 2003. fMRI responses to video and point-light display of moving humans and manipulable objects. J. Cogn. Neurosci. 15 (7), 991–1001.

Beckmann, C.F., Jenkinson, M., Smith, S.M., 2003. General multi-level linear modeling for group analysis in FMRI. Neuroimage 20, 1052–1063.

Bova, S.M., Fazzi, E., Giovenzana, A., Montomoli, C., Signorini, S.G., Zoppello, M., Lanzi, G., 2007. The development of visual object recognition in school-age children. Dev. Neuropsychol. 31, 79–102.

Braddick, O., Atkinson, J., Wattam-Bell, J., 2003. Normal and anomalous development of visual motion processing: motion coherence and 'dorsal-stream vulnerability'. Neuropsychologia 41, 1769–1784.

Bruner, J.S., 1966. On cognitive growth. In: Bruner, J.S., Olver, R.R., Greenfield, P.M. (Eds.), Studies in Cognitive Growth. Wiley.

Casey, B.J., Tottenham, N., Liston, C., Durston, S., 2005. Imaging the developing brain: what have we learned about cognitive development? Trends Cogn. Sci. 9, 104–110.

Chao, L.L., Martin, A., 2000. Representation of manipulable man-made objects in the dorsal stream. Neuroimage 12 487–484.

Cohen-Kadosh, K., Johnson, M.H., 2007. Developing a cortex specialized for face perception. Trends Cogn. Sci. 11, 367–369.

Crookes, K., McKone, E., 2009. Early maturity of face recognition: no childhood development of holistic processing, novel face encoding, or face space. Cognition 111 (2), 219–247.

Diedrichsen, J., Shadmehr, R., 2005. Detecting and adjusting for artifacts in fMRI time series data. Neuroimage 27 (3), 624–634.

Durston, S., Davidson, M.C., Tottenham, N.T., Galvan, A., Spicer, J., Fossella, J.A., Casey, B.J., 2006. A shift from diffuse to focal cortical activity with development. Dev. Sci. 9 (1), 1–8.

Fair, D.A., Cohen, A.L., Dosenbach, N.U.F., Church, J.A., Miezin, F.M., Barch, D.M., Raichle, M.E., Petersen, S.E., Schlaggar, B.L., 2007. The maturing architecture of the brain's default network. PNAS 105 (10), 4028–4032.

Fransson, P., Marrelec, G., 2008. The precuneus/posterior cingulate cortex plays a pivotal role in the default network: evidence from a partial correlation network analysis. Neuroimage 42, 1178–1184.

Gathers, A.D., Bhatt, R., Corbly, C.R., Farley, A.B., Joseph, J.E., 2004. Developmental shifts in cortical loci for face and object recognition. NeuroReport 15 (10), 1549–1553.

Giedd, J.N., et al., 1999. Brain development during childhood and adolescence: a longitudinal MRI study. Nat. Neurosci. 10, 861–863.

Gogtay, N., Giedd, J.N., Lusk, L., Hayashi, K.M., Greenstein, D., Vaituzis, A.C., et al., 2004. Dynamic mapping of human cortical development during childhood through early adulthood. Proc. Natl Acad. Sci. USA 101, 8174–8179.

Golarai, G., Ghahremani, D.G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J.L., Gabrieli, J.D., Grill-Spector, K., 2007. Differential development of high-level visual cortex correlates with category-specific recognition memory. Nat. Neurosci. 10 (4), 512–522.

Golarai, G., Liberman, A., Yoon, J.M.D., Grill-Spector, K., 2009. Differential development of the ventral visual cortex extends through adolescence. Front. Hum. Neurosci. 3 (80). doi:10.3389/neuro.09.080.2009.

Grill-Spector, K., 2003. The neural basis of object perception. Curr. Opin. Neurobiol. 13, 159–166.

Grill-Spector, K., Knouf, N., Kanwisher, N., 2004. The fusiform face area subserves face perception, not generic within category identification. Nat. Neurosci. 7 (5), 555–562.

Grill-Spector, K., 2009. Object perception: physiology. In: Goldstein, B. (Ed.), Encyclopedia of Perception. Sage Publications.

Hayden, B.Y., Nair, A.C., McCoy, A.N., Platt, M.L., 2008. Posterior cingulate cortex mediates outcome-contingent allocation of behavior. Neuron 60, 19–25.

Hasson, U., Harel, M., Levy, I., Malach, R., 2003. Large-scale mirror-symmetry organization of human occipito-temporal object areas. Neuron 37, 1027–1041.

Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and overlapping representation of faces and objects in ventral temporal cortex. Science 293, 2425–2429.

Jenkinson, M., Bannister, P.R., Brady, J.M., Smith, S.M., 2002. Improved optimisation for the robust and accurate linear registration and motion correction of brain images. Neuroimage 17 (2), 825–841.

Johnson, M.H., 2001. Functional brain development in humans. Nat. Rev. Neurosci. 2, 475–483.

Johnson, M.H., 2010. Developmental Cognitive Neuroscience, 3rd Ed. Wiley-Blackwell Publishing, Oxford.

Johnson, M.H., Grossmann, T., Cohen-Kadosh, K., 2009. Mapping functional brain development: building a social brain through Interactive Specialization. Dev. Psychol. 45, 151–159.

Johnson-Frey, S.H., 2004. The neural basis of complex tool use in humans. Trends Cogn. Sci. 8 (2), 71–78.

Joseph, J.E., Gathers, A.D., Bhatt, R.S., 2010. Progressive and regressive developmental changes in neural substrates for face processing: testing specific predictions of the Interactive Specialization account. Dev. Sci, 1–15. doi:10.1111/j.1467-7687.2010.00963.x.

Juttner, M., Muller, A., Rentschler, I., 2006. A developmental dissociation of view-dependent and view-invariant object recognition in adolescence. Behav. Brain Res. 175, 420–424.

Kang, H.C., Burgund, E.D., Lugar, H.M., Petersen, S.E., Schlagger, B.L., 2003. Comparison of functional activation foci in children and adults using a common sterotactic space. Neuroimage 19, 16–18.

Karmiloff-Smith, A., 1992. Beyond Modularity: A Developmental Perspective on Cognitive Science. Mass.MIT Press/Bradford Books, Cambridge (Reprinted 1995).

Karmiloff-Smith, A., Inhelder, B., 1978. If you want to get ahead, get a theory. In: Johnson-Laid, Ph., Wason, P. (Eds.), Thinking: Readings in Cognitive Science. Cambridge University Press, Cambridge, pp. 293–306.

Klaver, P., Lichtensteiger, J., Burcher, K., Dietrich, T., Loenneker, T., Martin, E., 2008. Dorsal stream development in motion and structure-from-motion perception. Neuroimage 39, 1815–1823.

Klingberg, T., Forssberg, H., Westerberg, H., 2002. Increased brain activity in frontal and parietal cortex underlies the development of visuo-spatial working memory capacity during childhood. J. Cogn. Neurosci. 14 (1), 1–10.

Konen, C.S., Kastner, S., 2008. Two hierarchically organized neural systems for object information in human visual cortex. Nat. Neurosci. 11 (2), 224–231.

Mahon, B.Z., Milleville, S., Negri, G.A.L., Rumiati, R.I., Martin, A., Caramazza, A., 2007. Action-related properties of objects shape object representations in the ventral stream. Neuron 55 (3), 507–520.

Mahon, B.Z., Anzellotti, S., Schwarzbach, J., Zampini, M., Caramazza, A., 2009. Category-specific organization in the human brain does not require visual experience. Neuron 63 (3), 397–405.

Mondloch, C.J., Le Grand, R., Maurer, D., 2002. Configural face processing develops more slowly than featural face processing. Perception 31, 553–566.

Mondloch, C.J., Geldart, S., Maurer, D., Le Grand, R., 2003. Developmental changes in face processing skills. J. Exp. Child Psychol. 86, 67–84.

Mondloch, C.J., Ahola, S., Maurer, D., 2006. Becoming a face expert. Psychol. Sci. 17, 930–934.

Mounoud, P., Duscherer, K., Moy, G., Perraudin, S., 2007. The influence of action perception on object recognition: a developmental study. Dev. Sci. 10, 836–852.

Muzik, O., Chugani, D.C., Juhasz, C., Shen, C., Chugani, H.T., 2000. Statistical parametric mapping: assessment of application in children. Neuroimage 12 (5), 538–549.

Nelson, E.E., McClure, E.B., Monk, C.S., Zarahn, E., Leibenluft, E., Pine, D.S., Ernst, M., 2003. Developmental differences in neuronal engagement during implicit encoding of emotional faces: an event-related fMRI study. J. Child Psychol. Psychiatry 44 (7), 1015–1024.

Nishimura, M., Scherf, S., Behrman, M., 2009. Development of object recognition in humans. F1000 Biol. Rep. 1, 56. doi:10.3410/B1-56.

Passarotti, A.M., Paul, B.M., Bussiere, J., Buxton, R., Wong, E., Stiles, J., 2003. Development of face and location processing: a fMRI study. Dev. Sci. 6 (1), 100–117.

Passarotti, A.M., Smith, J., DeLano, M., Huang, J., 2007. Developmental differences in the neural bases of the face inversion effect show progressive tuning of face-selective regions to the upright orientation. Neuroimage 34 (4), 1708–1722.

Peelen, M.V., Glaser, B., Vuilleumier, P., Eliez, S., 2009. Differential development of selectivity for faces and bodies in the fusiform gyrus. Developmental Science 12 (6), F16–F25. doi:10.1111/j.1467-7687.2009.00916.x.

Pelphrey, K.A., Lopez, J., Morris, J.P., 2009. Developmental continuity and change in responses to social and nonsocial categories in human extrastriate visual cortex. Front. Hum. Neurosci. 3 (25). doi:10.3389/neuro.09.025.2009.

Piaget, J., 1952. The Origins of Intelligence in the Child. InternationalUniversities Press, New York.

Piaget, J., 1954. The Construction of Reality in the Child. Basic Books, New York.

Poldrack, R.A., 2010. Interpreting developmental changes in neuroimaging signals. Hum. Brain Mapp. 31, 872–878.

Reiss, A.L., Abrams, M.T., Singer, H.S., Ross, J.L., Denckla, M.B., 1996. Brain development, gender and IQ in children — a volumetric imaging study. Brain 119, 1763–1774.

Rizzolatti, G., Matelli, M., 2003. Two different streams form the dorsal visual system: anatomy and function. Exp. Brain Res. 153, 146–157.

Saygin, A.P., Sereno, M.I., 2008. Retinotopy and attention in human occipital, temporal, parietal, and frontal cortex. Cereb. Cortex 18, 2158–2168.

Scherf, K.S., Behrmann, M., Humphreys, K., Luna, B., 2007. Visual category-selectivity for faces, places and objects emerges along different developmental trajectories. Dev. Sci. 10 (4), F15–F30.

Siegler, R.S., 2004. U-shaped interest in U-shaped development–and what it means. J. Cogn. Dev. 5, 1–10.

Sereno, A.B., Maunsell, J.H., 1998. Shape selectivity in primate lateral intraparietal cortex. Nature 395, 500–503.

Smith, S.M., 2002. Fast robust automated brain extraction. Hum. Brain Mapp. 17 (3), 143–155.

Thesen, S., Heid, O., Mueller, E., Schad, L.R., 2000. Prospective acquisition correction for head motion with image-based tracking for real-time fMRI. Magn. Reson. Med. 44, 457–465.

Valyear, K.F., Cavina-Pratesi, C.S., Stiglick, A.J., Culham, J.C., 2007. Does tool-related fMRI activity within the intraparietal sulcus reflect the plan to grasp? Neuroimage 36, T94–T108.

Vygotsky Tool and symbol in child development, 1934.

Vygotsky mind in society: the development of higher psychological processes, 1978.

Woolrich, M.W., Ripley, B.D., Brady, J.M., Smith, S.M., 2001. Temporal autocorrelation in univariate linear modelling of FMRI data. Neuroimage 14 (6), 1370–1386.