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Abstract-

Little is known about the neural development underlying high order visual perception. For example, in detection of structures by coherently moving dots, motion information must interact with shape-based information to enable the recognition objects. Tasks involving these different motion-based discriminations are known to activate distinct specialized brain areas in adults. Here, we investigate neural development of normal developing children using functional magnetic resonance imaging (fMRI) during perception of randomly moving point-light dots (RM), coherently moving dots that formed a 3D rotating object (SFM), and static dots. Perception of RM enhanced neural activity as compared with static dots in motion processing related visual areas, including visual area 3a (V3a), and middle temporal area (hMT+) in ten adults (age 20-30 years). Children (age 5-6 years) showed less pronounced activity in area V3a than in adults. Perception of SFM induced enhanced neural activity as compared to RM in adults in the left parietal shape area (PSA), whereas children increased neural activity within dorsal (V3a) and ventral brain areas (lingual gyrus) of the occipital cortex. These findings provide evidence of neural development within the dorsal pathway. First, maturation was associated with enhanced activity in specialized areas within the dorsal pathway during RM perception (V3a) and SFM perception (PSA). Secondly, high order visual perception related neural development was associated with a shift in neural activity from low level shape and motion specialized areas in children, including partially immature area V3a, to high order areas in the parietal lobule (PSA) in adults.

Introduction

Research on visual perception and cognition has led to the understanding that vision is not merely a matter of passive perception; but rather an intelligent process of construction ((Zeki, 2001) and references therein). These constructive processes are age-dependent and reflect the integration of colour, shape and motion information into the representation of the child's environment. A neurobiological theory of visual development postulates at least three visual systems: one early, rudimentary subcortical and two cortical systems (Atkinson, 1984; Atkinson, 2000). One cortical system comprises areas located in the ventral occipital and temporal lobes. It is commonly referred to as the "what" pathway because damage to these regions leads to deficits in the ability to discriminate between visual objects. The other cortical system includes areas located in the dorsal occipital and parietal lobes. It is commonly referred to as the "where" pathway because damage to these regions leads to deficits in the ability to identify the locations of visual objects in space (Haxby et al., 1991; Milner and Goodale, 1995; Ungerleider and Mishkin, 1982). Whereas the ventral pathway is prone to process, among others, visual identity and feature information (e.g. colour, luminance, faces and object identities), the dorsal pathway is inclined to process spatial relations and motion direction information.

There is strong evidence that the dorsal stream is more vulnerable to neurodevelopmental disorders than the ventral stream, which has been described in children aged 4 years and older (Braddick et al., 2003). In normally developing children the parsing of the visual array into globally organized forms appears to develop more securely than the equivalent parsing by relative motion. The integration of local motion into the perception of coherent translational global motion is a basic integrative process of the motion pathway, for which norms of behavioural performance in the 4-10 year age range are already established (Gunn et al., 2002; Parrish et al., 2005). Recent findings, however, animated the unresolved debate on the neural mechanisms underlying the development of motion processing, particularly after four years of age. For example, a recent functional brain imaging study showed that full development of coherent motion in hMT+ is not reached until adolescence (Bucher et al., 2006). Tasks inducing dynamic visual adaptation (Schrauf et al., 1999), configural object recognition (Rentschler et al., 2004) and haptic priming upon configural visual stimuli (Jüttner et al., 2006) require even stronger visual processing demands and possibly the

involvement of dorsal stream processing in object recognition. It has been shown that these functions do not mature until adolescence.

The detection of structures-from-motion (SFM) at least partly depends on the detection of coherent motion. At some stage, however, shape processing needs to be activated by coherent motion. Braddick and colleagues (2003) suggested that the development of integrative processing in structure from motion is constrained by the development of global coherent motion processing. This idea was based on findings that perception of biological motion or structure from motion develops at about the same age as the detection of coherent motion. For example, 3-6-month-old infants can already detect SFM (Arterberry and Yonas, 1988; Arterberry and Yonas, 2000; Kaufmann-Hayoz et al., 1986; Yonas et al., 1987). Others, however, suggested that a third area, probably in the posterior, superior parietal cortex, needs to be activated that binds both motion and shape processing areas (Zeki, 2001). This (temporary) binding between shape and motion may be related to attention or spatial processing, and which may have a different developmental time course (Oakes et al., 2006; Rentschler et al., 2004; Ross-Sheehy et al., 2003). Thus, it remains unknown to what extend neural development of SFM processing depends on both the development of motion processing related areas and areas that are not directly related to shape or motion processing.

Brain imaging studies in adults showed that random motion (RM) activates areas at different levels of the cortical motion pathways, including dorsal visual area 3a (V3a), area V5 (middle temporal area hMT+), the inferior/superior parietal lobule and ventral areas in the lingual and fusiform gyrus (Cornette et al., 1998; Sunaert et al., 1999). In contrast to RM, coherent motion activates areas in the parietooccipital junction, but also enhances activity in extrastriate areas responding to RM (Braddick et al., 2001; Braddick et al., 2000). As compared to RM, 3D SFM also activates areas within the parietooccipital cortex and parietal cortex, but some studies also reported enhanced activity in extrastriate areas related to RM perception (Murray et al., 2003; Orban et al., 1999; Paradis et al., 2000). The question is whether young children up to the school age show differences in brain activity during RM perception, and whether these differences are limited to the certain parts of the dorsal stream. A further question is whether the limitations observed in high order visual capacities of 5-6 year old children are associated with high order visual areas and functions. In this case one may hypothesize that age related differences only occur in stimuli that require high order visual processing. Alternatively, age related differences may be due to maturation in low

order visual processing areas, in which case stimuli requiring both low and high order visual processing would induce age related differences in neural activity. Here, we measured neural activity in adults and 5-6 year old children in an fMRI experiment while they perceived RM stimuli and SFM stimuli. Because of limitations in scanning time in young children we did not include an intermediate coherent motion condition. We found that adults activated dorsal and ventral occipital areas during RM perception in contrast to perception of static dots and that children showed less pronounced activity in dorsal area V3a. High order perception of SFM stimuli enhanced neural activity in adult parietal cortex as compared with RM. Children showed less pronounced activity in this area, but more in lower visual areas related to shape and motion processing.

Methods

Subjects

Ten normal achieving pre-school children (mean age 6 years, range 5 y 6 m – 6 y 9 m, 4 male) and ten right handed adults (mean age 26 years, range 20-29, 4 male) were scanned. All subjects and parents of the children gave written informed consent prior to participation. All subjects had no history of neurological or psychiatric disorder. The children were slowly introduced to the scanner and its equipment. For all children, a teddy bear was positioned on the scanner table in order to explain the scanning procedure to the child in an attempt to ease reservations about the procedure an alleviate anxiety. Children were able to watch a cartoon video during anatomical acquisitions. In order to improve compliance and reduce head motion, children listened to a story presented on the headphone. Because of a limitation in head space within the MR head coils we chose to not use a headphone in adults. Parents stayed outside the scanner room but were able to talk to the children between the scans. The study was approved by a local ethics committee. The families were given a child's story-CD as a token of our appreciation. Adult volunteers were given financial compensation for their participation.

Stimuli

Subjects viewed randomly moving dots (RM), moving dots that formed a 3-D rotating structure by coherent movement (SFM) and static dots (STAT) as control stimuli. The stimuli were downloaded from the reference provided by Murray and colleagues (http://redwood.uncdavis.edu/scott/research/sfm/; see Figure 1a for a schematic illustration, adapted from Murray et al. 2003). All stimuli consisted of an array of 450 dots subtending 10° of visual angle. For RM stimuli each dot moved in a random direction with constant speed

(4°/s). The dots in the SFM condition were projections of rigid, transparent, geometric shapes including a cube, cylinder and 'house shaped' figures. Dots were randomly selected from a uniform distribution on the object surface and kept fixed relative to the rotating object surface and orthographically projected onto the image plane. Dots were rotated on a randomly chosen 3-D axis for 40° in 1.5° increments. Both motion stimuli had the same direction and speed, but direction and speed were randomly reassigned to different dots to create random motion. The motion stimuli were generated by creating moving sequences at a rate of 20 Hz with 28 frames stored as a bitmap. A sequence of 80 frames was played forward and backward so that motion was continually observed. The first frame was the same for every SFM and RM. The baseline (STAT) presented the 25th frame from the RM stimuli. The total presentation time of each stimulus was 4000 ms. Stimuli were presented through optical goggles during a 12 minute scanning session. The three conditions were presented in a balanced order of 18 blocks of trials that were separated by a 2 second interval (54 trials per condition, 4 seconds per trial). All subjects were instructed to passively view the stimulation.

fRMI data acquisition and analysis

Brain images were acquired on a 3.0 T Scanner (General Electric, Milwaukee USA) using a standard 8-channel head coil. To estimate blood oxygenation level dependent (BOLD) contrast 343 echo planar imaging (EPI) scans were acquired including 2 dummy scans. The scans were aligned perpendicular to the V1 coronal axis thus covering the occipital and parietal lobe (see Figure 1b for an example). Scan parameters were: number of slices (NS): 26; slice thickness (ST): 2.7 mm; matrix size (MS): 96×96 zero-filled to 128×128; field of view (FOV): 230 mm; flip angle (FA): 50°; echo time (TE): 32 ms; repetition time (TR): 2 s. The task was presented via video goggles (MRI Audio/Video System, Resonance Technology, Inc., USA) using Presentation software (www.neurobs.com). Additionally, a high-resolution anatomical reference T2-weighted scan was acquired (NS: 52; ST: 2.7 mm; MS: 256×256; FOV: 230 mm; FA: 90°; TE: 12.3 ms; TR: 10.6 s). Functional MRI data analysis was done using Statistical Parametric Mapping 2 (SPM2, www.fil.ion.ucl.ac.uk/spm/). Pre-processing included realignment with unwarping. No subject was excluded from the analysis because of excessive movement, since only one child had maximum movement of 3.5 mm in z-direction. All other subjects did not exceed 2.5 mm movement in z-direction and 1.5 mm in all other directions, which was less than 1 voxel size. We transferred functional and anatomical data from adults and children into a common stereotactic space. For this purpose, T2 images of all subjects were segmented, and

normalization parameters were estimated for grey matter images on a standard grey matter template in Montreal Normalization Institute space. The EPI images data were coregistered upon the T2 image and normalization parameters were applied to both the T2 images (1 mm^3) and EPI images (3 mm^3). EPI data were then smoothed with a 6 mm full width at half maximum Gaussian kernel. The hemodynamic response was modelled by a stick function to each stimulus presentation in each category convolved with a canonical hemodynamic response function and its temporal derivative. Parameter images were generated for each adult and child for the contrasts STAT, RM and SFM. We applied two-sample t-tests in a second level random-effect analysis for the contrasts RM-STAT and SFM-RM. Significant voxels are reported ($p<0.001$, uncorrected) within clusters of 20 voxels, which was the threshold of a significant cluster after correction for multiple comparisons ($p<0.05$). We further performed a region of interest (ROI) analysis on signal changes from voxels within 10 mm spheres around mean local maxima in the left and right hemisphere reported by Murray and colleagues (2003). These ROIs were related to motion processing (LOS left x = -27/y= -91/z = 8, right 34/-88/4; V3a left -19/-91/24, right 21/-90/22; hMT+ left -45/-73/5, right 48/-66/2), shape (LO left -39/-82/-2, right 41/-81/2, SLO left -33/-82/15, right 37/-78/12, PF left -43/-70/-7, right 45/-65/-8) and structure-from-motion processing (parietal shape area, PSA left -34/-49/58, right 35/-47/59). For contrasts RM-STAT and SFM-RM ANOVAs were performed on the within-subject factors stimulus, ROI (7), hemisphere (left, right) and between-subject factor group (adult, child).

It is not trivial to generalize ROIs from adult subjects to children, because the location of specialized brain areas may be shifted within the developing brain. Previous studies have tested the possibility to generalize across age within a common space for 7 year old children (Burgund et al., 2002; Kang et al., 2002). The children were one (maximally 2) years younger than in the study by Kang and colleagues, which was considered to be a similar age group. In order to verify the normalization procedure and the choice of ROIs the contrast between RM and STAT was calculated in two exemplary subjects at two significance levels ($p<0.05$ corrected for the whole brain and $p<0.001$ uncorrected). Percent signal changes were also calculated from two ROIs (areas V3a and hMT+). It could be shown (Figure 2C) that similar clusters were activated by RM in adults and children, but that the level of activity was different, particularly in area V3a. This result justifies the choice of ROIs and do not suggests that brain areas are shifted with age in this sample.

Imaging results

Motion

Figures 2A and 2B show fMRI results from adults and children. As compared with static stimuli RM yielded enhanced neural activity in adults in the lateral and dorsal part of the occipital cortex, as well as in the ventral occipital cortex and posterior middle temporal gyrus (Figure 2A). These areas correspond to previously described bilateral lateral occipital sulcus (LOS), visual area 3a (V3a) and middle temporal area (hMT+) (Murray et al., 2003; Orban et al., 1999; Sunaert et al., 1999; Tootell et al., 1997). A similar pattern of brain activity was found in children (Figure 2B), with few apparent differences in the distribution. Children showed enhanced activity in bilateral LOS, but less in medial occipital areas that extend into dorsal and ventral parts of the occipital cortex (see Table 1 for detailed results) and in hMT+. Whole head analysis showed no significant differences between groups except for a larger effect for RM in children than adults in the left precentral gyrus (Talairach coordinates x = -36, y = -15, z = 45, Z = 4.2, $p<0.001$).

The ROI analysis (collapsed over left and right hemisphere, Figure 3A, top part) showed differences in the neural response to RM in different regions (ROI: $F_{6,108}= 11.0$, $p<0.001$). Significantly enhanced activity was found in adults and children in motion processing related areas (LOS, V3a, hMT+, all $p<0.001$) as well as in shape related areas lateral occipital (LO), superior lateral occipital (SLO) and posterior fusiform (PF) (all $p<0.001$), but not in SFM related area parietal shape area (PSA). A significant interaction between group and ROI ($F_{6,108}= 4.5$, $p=0.004$) indicated that RM induced larger neural activity in adults than in children in motion sensitive area V3a (adult > child $t_{18} = 2.9$, $p < 0.01$). A trend to significance was found in hMT+ ($t_{18} = 1.8$, $p < 0.09$). Further, there was a significant hemispheric lateralization effect in LO that did not depend on maturation (right > left LO, $p < 0.01$).

In a more general analysis, we separated the ROIs into larger functional areas to investigate whether RM affected shape or motion areas differently in children than in adults. Figure 3B shows neural responses to RM (dark grey) in motion (orange), shape (blue) and shape/motion related areas (orange/blue). The data suggests a larger difference between motion and shape related areas in adults than in children during RM perception (dark gray). This observation was confirmed in a significant interaction between age and visual feature specialized area ($F_{1,18} = 21.4$, $p < 0.001$). This result indicated that RM enhanced activity specifically in motion areas of adults, whereas children showed less neural specialization.

To further investigate whether RM related activity depended on age, we calculated regression coefficients on age within ROIs (Figure 3C). We found significant age-dependent increases in V3a activity (regression coefficient R^2 = 0.3, p=0.01). A slightly better fit was found for a logarithmic increase in activity within V3a than for a linear increase (R^2=0.27, p=0.02). No other area showed correlations between age and brain activity (hMT+ R^2=0.13, p=0.11; all other R^2<0.05, p>0.5). Thus, neural specialization could be shown by larger differences in response to RM between motion and shape areas in adults than in children, but particularly in dorsal area V3a.

Structure-from-motion

Functional brain imaging data in adults replicated findings that SFM enhanced neural activity as compared with RM in several areas related to shape processing, and also in areas not involved in elementary shape or motion perception, particularly on the occipitotemporal and occipitoparietal junction and further upward into the dorsal stream of the parietal cortex (Figure 2A). The former areas probably correspond with VIPS/POIPS (Orban et al., 1999) or POJ (Paradis et al., 2000). The latter area corresponds with PSA (Murray et al., 2003), cIPS (James et al., 2002), or DIPSL/DIPSA (Orban et al., 1999). In children, however, SFM yielded enhanced activity in dorsal and ventral parts of the occipital cortex, but not in the parietal lobule (Figure 2B).

Whole head analysis yield group differences for SFM. Adults showed enhanced neural activity as compared to RM in the inferior and superior parietal lobule (detailed results are listed in Table 1). The superior parietal activity was located medial and superior to area PSA in Brodmann area 7, whereas the left lateral area was located in the inferior parietal lobule on the border of the precentral gyrus in Brodmann area 40. In contrast, SFM yielded enhanced neural activity in children in the lingual gyrus on the border of the parahippocampal gyrus and fusiform gyrus. This area partially overlaps with area PF. Activity was primarily found in the right hemisphere, but at a lower statistical threshold (p<0.005) also left fusiform activity was found. The areas may be identical or adjacent to area posterior part of LO as reported earlier (x = -36, y = -71, z = -13) (Grill-Spector et al., 1999) or with ventral surface areas involved in motion and shape processing (Braddick et al., 2000).

The ROI analysis (Figure 3A) showed that adults and children exhibited different responses to SFM in some but not all areas (Interaction ROI × GROUP: $F_{6,108}$= 4.2, p=0.004). SFM induced enhanced activity in adult PSA (p<0.003), but not in children (n.s., adults > children p=0.057). In contrast, SFM enhanced neural activity in children more than adults in

areas hMT+ (children p=0.051; adults n.s.; children > adults p=0.042) and PF (children p=0.001; adults n.s.; children > adults p=0.035).

In a more general analysis, we separated the ROIs into larger functional areas to investigate whether SFM affected shape or motion areas differently in children than in adults. Figure 3B suggests that SFM enhances neural activity in shape related areas more strongly than in motion related areas. This observation is supported by a significant interaction between shape vs. motion related ROIs (excluding PSA) and SFM-RM ($F_{1,18}$ = 5.2, p=0.034). We found no significant group effect or interaction between shape vs. motion related ROIs and group. This result indicates that both adults and children recruit neural activity in shape related areas during SFM perception.

To further investigate whether SFM related neural activity dependent on age, we calculated regression coefficients on age within ROIs after averaging the percent signal change over the left and right hemisphere ROIs (Figure 3C). We found significant results and trends to significance for an age dependent logarithmic decrease in neural activity in motion processing related areas hMT+ (p=0.04) and V3a (p=0.07) and shape related area PF (p=0.03). This decrease indicated that these areas exhibited enhanced activity for SFM as compared with RM in children, but that this activity attenuated in the maturing brain. On the other hand PSA showed a trend to a logarithmic increase in activity (p=0.06), which indicated that SFM enhanced neural activity in PSA in more mature subjects. Except for area PF (R^2=0.23) all areas (R^2: hMT+ = 0.21, V3a= 0.17, PSA= 0.18) showed a better fit for a logarithmic age dependent change in activity than for a linear change. Together, the results indicate that SFM enhanced neural activity as compared with RM in dorsal areas within the parietal lobule in adults. Children on the other hand showed enhanced activity under same conditions within dorsal and ventral areas of the occipital lobe that are related to motion and shape processing, including areas that may not be fully mature such as areas hMT+ and V3a. Parietal areas showed no significant neural activity during perception of SFM in children.

Discussion

The aim of the current study was to investigate the neural basis of development in visual perception. As far as we know, this is the first study to show direct evidence that neural activity in the dorsal stream of the occipital cortex and parietal lobule was not mature by the age of 6 years. We also suggest that age dependent neural activity depends on the complexity of the motion stimulus and that high order processes are substituted by low order processes in the immature brain. These claims are discussed in more detail.

In line with previous studies we found that RM activated areas in the ventral and dorsal part of the occipital lobe (Cornette et al., 1998; Sunaert et al., 1999). Ventral activity was found in the lingual gyrus (predominantly in the right hemisphere), whereas dorsal stream activity was found in areas V3a, LOS and hMT+. There was clear evidence that differences in neural development of visual perception can be linked to the dorsal stream. Adults showed neural specialization within dorsal brain areas, particularly area V3a, whereas children activated both dorsal and ventral areas, with less apparent neural specialization. For SFM a different pattern was found. SFM increased activity as compared with RM in both adults and children in the left lateral part of the middle occipital gyrus (SLO) and a dorsal area at the parietooccipital junction. Adults showed enhanced SFM related neural activity only in dorsal areas, including several areas within the parietal lobule, whereas children enhanced neural activity during SFM perception in dorsal and ventral stream areas of the occipital cortex. These data provide evidence for maturation in the parietal lobule and are in line with general anatomical delayed development of the M-pathway in the dorsal stream including the parietal lobule, which showed that grey matter does not reach maturity by the age of 6 years (Braddick et al., 2003; Gogtay et al., 2004; Sowell et al., 2004). For the frontal cortex it has been suggested that task unrelated activity decreases during maturation, whereas task related activity increases (Booth et al., 2003; Bunge et al., 2002; Casey et al., 2005; Schlaggar et al., 2002). As far as we know, this is the first study to show that a similar developmental mechanism occurs within the parietal lobule and in area V3a within the dorsal part of the occipital cortex.

The second question was whether developmental differences were stimulus dependent and limited to high order visual processing. The present results support this hypothesis. First, RM and SFM showed developmental effects in different areas. Area V3a showed age dependent differences in response to RM, whereas areas in the parietal lobule showed age related differences in response to SFM. There was no area that showed common age dependent difference related to RM and SFM. Second, the same area V3a that was not specifically activated in children during RM perception showed enhanced activity during SFM perception, which strongly suggests that neural activity in area V3a depends on both maturation and stimulus complexity. Third, age dependent effects related to SFM perception were different in high order processing areas than in areas related to motion and shape processing. Areas in the parietal lobule were only activated by adults, whereas common neural activity was found in both age groups on the occipital parietal junction, suggesting that both groups similarly processed coherent motion (Paradis et al. 2003). Children, however,

showed increased neural activity during SFM perception in shape and motion related areas. Thus, we assert that children and adults use different neural mechanisms in the perception of high order visual stimuli and that age related differences in neural activity arise from the high order visual features of the SFM stimulus.

It remains an open question as to whether increased activity in children in the occipital lobe during SFM has a functional role in perception. Behavioural developmental studies show that SFM can be detected by infants (Arterberry and Yonas, 2000) and reach a mature level at the age of 7 (Parrish et al., 2005). Dependent on the perceptual features and the attentional demands during the task, however, developmental differences occur even until adolescence (Schrauf et al., 1999). In our task we used passive viewing instructions, so that the perceptual demands are low, but the relation to perceptual performance and attentional demands are unclear. Thus, given that perceptive capabilities are different between adults and children, and that children can principally perceive SFM stimuli, we tend to suggest that reduced maturation is substituted by increased neural activity in areas involved in feature specific analyses, whereas the engagement of adult dorsal areas in the parietal lobule during SFM perception relates to maturation. The relation between neural activity in these areas and perceptual capability remains to be answered in future studies.

The present results partially differed from previous studies. For example, in contrast to Murray and colleagues (2003) we found no reduced activity in V1 by SFM as compared with RM. They argued that SFM induced a top-down suppression of V1 activity. In contrast to that study we did not use an attention demanding perceptive task. Studies that used a passive viewing task, reported no stimulus dependent V1 difference in activity (Paradis et al., 2000). Our results are in line with the latter findings. Further, we found no direct evidence that SFM activated motion processing related areas. SFM did not significantly enhance areas related to RM in adults, though it enhanced shape processing related areas. This result contrasts with Murray and colleagues (2003) who showed increased activity in area hMT+ by SFM in adults. Again, these results may be related to the use of a passive viewing task, since they are in line with findings that SFM does not enhance neural activity in hMT+ when a passive viewing task is used (Paradis et al., 2000).

Another difference between the current and several other studies with adults on high order perception is that we used no coherent motion condition. We know from previous reports that such stimuli activate intermediate areas within the dorsal stream on the border of the occipital and parietal cortex (Braddick et al., 2001; Braddick et al., 2000; Orban et al., 1999; Paradis et al., 2000). Since we scanned young children we were limited in scanning

time (approximately 12 minutes). We thus chose to use a more complex condition of 3D SFM instead of a coherent motion condition to contrast with RM. Future studies are needed to provide a more fine-grained analysis of neural development.

Other aspects might cast doubt on our conclusions. First, it is not trivial to spatially normalize young children with an adult anatomical template. Yet, the present results seem to be anatomically valid. Structural imaging studies reported that particularly the parietal and frontal cortex differ in both grey and white matter (Sowell et al., 2002). The present results support a functional-anatomical development particularly in the parietal lobule, which cannot be entirely attributed to general differences in brain activity, since children show some activity in these areas in the contrast between RM and static control stimuli. Rather, these age-related differences are stimulus specific. Further, the normalisation procedures as applied here are in line with normalisation comparison studies. Two studies reported that both timing and peak activations were comparable between 7 to 8 year old children and adults after normalization into a common stereotactic space (Burgund et al., 2002; Kang et al., 2002). The children tested here were one to two years younger than in those studies. We further showed in an individual subject analysis that activity within ROIs was present in both adults and children, but that the level of neural activity differed. This suggests that functional brain areas in children were not spatially shifted as compared with adults. Nevertheless, the way in which maturation is expressed in neural activity in younger children is still under debate, and cannot be entirely solved here.

Secondly, children may have used different eye movement strategies during perception than adults, which might have biased imaging results based on the lack of eye tracking control and long stimulus presentation. The relation between eye movement and perception is an issue on its own. In the current study we preferred to minimize control over eye movement in order to not bias potential perceptual control mechanisms, which may differ between adults and children. Thirdly, stronger head movement during the task in children may bias fMRI results. Clearly, children moved generally more than adults, but no child moved beyond acceptable ranges and we found stimulus dependent neural activity that cannot be explained by movement alone. Fourth, children listened to a story while viewing whereas adults did not. This might be a potential confound inducing cross modal interference. However, the story barely exceeded scanner noise and could hardly be heard so that it is unlikely to interfere with neural activity during visual processing. Another reason is that the effect on visual processing is small. An interaction between highly demanding processing condition (mental imagery) and rest could only be verified in visual cortex in a PET study when scanner noise was

compared with a no noise condition. Only after ROI analysis in the cuneus a task by condition effect could be shown (Mazard et al., 2002). Thus, there is little reason to believe that these factors biased the main results. Taken together, the current study provides evidence that dorsal brain areas are not fully developed in six year old children, even during simple motion perception. Perception of SFM stimuli engages high order brain areas that show structural changes in neural development, whereas low order feature specific brain areas are used less with increasing maturation.

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Figure 1

(A) Three types of stimuli were presented, static dots, randomly moving dots and moving dots that formed a 3D-structure (cylinder, box or 'house shaped' figures). These stimuli were adapted from Murray et al. (2003). (B) An example of partial functional brain imaging perpendicular to the V1 coronal axis, thus covering the occipital cortex and parietal lobule.

Figure 2

(A) Statistical maps overlaid on coronal slices of a canonical structural MR image. Displayed are the within-subject contrasts for adults (red, $p<0.001$) and between-subject contrasts (yellow, adults > children, $p<0.05$) for random motion > static (top), structure-from-motion > static (centre), and structure-from-motion > random motion (bottom). (B) Same as 2a, but for within-subject contrasts in children and between-subject contrasts (children>adults). (C) Two exemplar adults (ad1/ad2) and children (ch1/ch2) are displayed at two statistical threshold (yellow $p<0.001$ uncorrected, orange $p<0.05$ corrected the whole brain). The left side shows left (dark blue) and right (dark red) area V3a (y = -90) and percent signal change within these ROIs. The right side shows the same for the left and right area hMT+ (y = -70). It shows that adults and children both show significant neural activity in areas V3a and hMT+, but with different levels of neural response.

Figure 3

(A) The top part shows percent signal changes for adults and children for random moving (contrasted against static dots) in regions of interest related to motion processing (blue: LOS= lateral occipital sulcus, V3a= visual area 3a, hMT+ = middle temporal area) or shape processing (orange: LO= lateral occipital, SLO=superior lateral occipital, PF= posterior fusiform) or shape and motion processing (blue/orange: PSA= parietal shape area). The bottom part shows the same for the contrast structure-from-motion against random motion. Significant and trends to significance for age related group differences are marker by asterisk and asterisks in brackets. (B) The ROI locations are illustrated on coronal slices of a canonical brain. The bar plot indicates percent signal change in motion (blue), shape (orange) and shape/motion (blue/orange) related areas for random motion (RM) against static dots and the additional neural activity that is induced during structure-from-motion (SFM) perception. (C) Percent signal changes for the contrast random>static and structure-from-motion> random-motion plotted against age (in months). The best fit (logarithmic) regression on age is plotted for each ROI.

4. Table

Table 1

Effect	Area	BA	Coordinates LH			Z	P-value	Coordinates RH			Z	P-value
			x	y	z			x	y	z		
Adults												
Random > Static	Middle occipital g.	18/19	-18	-92	16	5.1	0.003	21	-93	13	4.3	0.006
	Middle temporal g.	19/39	-42	-70	-2	4.0	0.01	45	-70	6	5.0	0.003
	Middle occipital g.	19	-24	-87	10	3.9	0.02	33	-81	4	3.9	0.02
	Lingual g.	18/17	-27	-79	-9	4.1	0.009	18	-82	-1	4.4	0.006
SfM > Random	Superior parietal l.	7	-24	-58	61	5.0	0.007	27	-47	60	4.3	0.013
	Postcentral g.	5	-30	-43	66	3.9	0.014	30	-43	68	4.3	0.014
	Precuneus	7/19	-24	-71	39	4.5	0.01	18	-82	43	3.9	0.014
	Middle frontal g.	6	-18	3	55	4.6	0.01	27	-3	55	4.7	0.01
	Cingulate g.	31	-12	-18	40	4.3	0.013	15	-33	40	4.6	0.01
	Middle temporal g.	37	-48	-55	3	4.1	0.014					
	Middle occipital g.	39/19	-45	-80	26	4.1	0.014					
	Inferior parietal g.	40	-65	-30	37	3.7	0.014	50	-36	43	3.9	0.014
Children												
Random > Static	Middle occipital g.	18	-36	-84	10	4.1	0.056*	33	-81	4	3.9	0.056*
	Middle temporal g.	39	-45	-75	15	3.5	0.057*	45	-73	1	3.6	0.056*
	Lingual g.	17						9	-87	-1	4.1	0.056*
SfM > Random	Lingual g.	18/19	-30	-64	1	5.5	<0.001	30	-76	-4	5.1	0.001
	Middle occipital g.	18/19	-27	-81	15	4.5	0.003	36	-75	15	4.8	0.002
	Cuneus	18/19	-21	-89	29	4.8	0.002	21	-90	24	4.3	0.004
	Precuneus	7	-24	-74	37	4.0	0.006	24	-75	45	4.0	0.006
Adults > Children												
SfM > Random	Inferior parietal l.	40	-57	-45	39	3.9	0.001					
	Precuneus	7	-15	-47	52	3.9	0.057*					
Children > Adults												
Random > SFM	Precentral g.	4	-36	-15	45	4.2	0.046					
SfM > Random	Lingual g.	18				4.3	0.006	30	-76	-4	4.3	

Significant statistical comparisons are shown for random motion and structure from motion in children and adults. Talairach-coordinates (x/y/z) are listed from left (LH) and right hemisphere (RH) local maxima of significant clusters (FDR corrected $p<0.05$, * represent trends to significance). Z-values are listed for voxels at the local maxima. BA is the Brodmann area nearest to the coordinate and should be considered approximate (g. is gyrus, l. is lobule).

5. Figure

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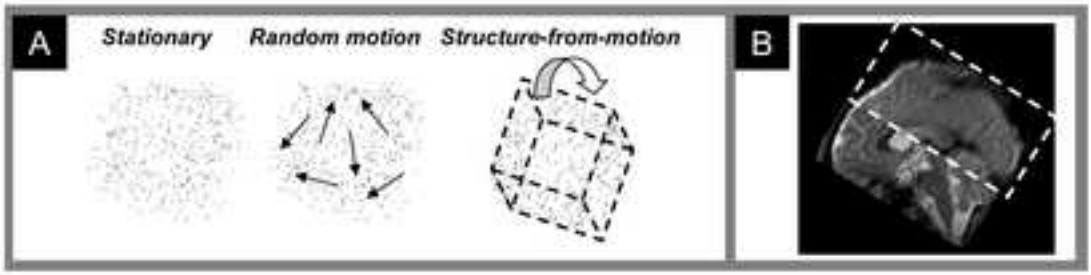

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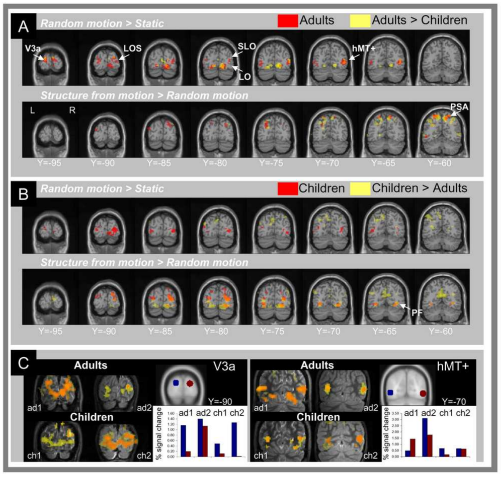

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