VISUOSPATIAL AND VISUOMOTOR DEVELOPMENT

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Introduction

'Visual spatial development' has many different definitions and levels of analysis with different perspectives from neuropsychology, developmental cognitive neuroscience, paediatric neurology and ophthalmology, education and rehabilitation. It covers many areas including brain processing related to spatial representations, an understanding of relative motion, of objects in space, the processes underpinning acts of mental rotation and location memory, reaching, grasping and spatial attention. The neurobiological approach taken in this chapter will attempt to link findings from normal adults and patients with neurological damage, animal neurophysiology and psychological studies on spatial development in infants and children, so as to identify relationships between changing behaviour and brain function and to devise models of these processes.

In some areas attempts have been made to separate 'perception' from 'cognition' in spatial development. For example some developmental psychologists have defined cognitive acts as those in which infants demonstrate 'intentionality', while 'perception' is more automatic and less goal oriented. Some argue for limiting 'visual perception' to lower centres in the eye and occipital lobes, while 'cognition' is mediated by 'higher centres' – parietal, temporal and frontal cortices. Such divisions are somewhat artificial in that many visual spatial actions involve complex circuitry running from subcortical centres such as the superior colliculus and basal ganglia to occipito-parietal areas for spatial representations, including cortical and subcortical motor areas, specialist temporal lobe areas for object recognition, top- down attentional control from frontal areas, and feedback loops between all of these networks. In fact it has been estimated that over half of the brain is involved in even simple spatial tasks such as pouring water from a jug into a glass. However, in many developmental studies there is an attempt to delineate and separate processes within a network by designing stimulus conditions with dimensions known to elicit responses in specific populations of tuned neurons within particular brain areas- these we might call 'designer stimuli'. Other studies have adapted tests for children and infants from adult visual spatial tasks, where failures have been related to specific locations of brain damage in the patient.

Of course in human development immaturity of processing in any one or more of these networks may limit behavioural performance on any specific visuospatial task. If analogies are found between infant and adult patient behaviour this does not necessarily mean that the cascading

processes of human development follow the same course as the adult with specific brain damage. It can only be used as a first approximate step.

The chapter is divided into eight sections. These are:

1. Current neurobiological models of normal infant development of spatial vision

2. Development of spatial attention for action in infancy

3. Development of dorsal and ventral streams

4. Development of action modules for reaching, grasping, and motor planning

5. Development for action modules for locomotion and navigation

6. Development of spatial localization in location memory tasks

7. Summary of abnormal spatial development

8. Summary of the developmental model of visual spatial development

Examples of abnormality of development and their neurobiological underpinnings are briefly reviewed in each section, and are summarized in Section 7.

1. Current neurobiological models of normal infant development of spatial vision

1.1. Two visual systems – subcortical and cortical

Early models of visual spatial development started from the idea of two visual systems, a phylogenetically older retinotectal system and a newer geniculostriate system. The tectal system defines 'where' an object is located to trigger orienting, while cortical mechanisms define 'what' is actually in the selected location (Sprague & Meikle 1965; Schneider 1969). Bronson's (1974) model for human visual development was based on this dual system. Since newborns orient by head and eye movements to conspicuous stimuli, but show little evidence of pattern discrimination, he proposed that vision is subcortically controlled for deciding 'where' a stimulus was located, with the cortex maturing postnatally for deciding 'what' was in the fixated location.

Extensive studies with typically developing infants have allowed more detailed models to be devised for these two systems. These studies have included behavioural measures (for example, preferential looking) and electrophysiological measures of brain waves (EEGs, visual evoked potentials or event related potentials- VEP/ERP). In Atkinson and Braddick's initial model (Atkinson 1984; Braddick et al. 1989) distinct functional modules or channels for the different visual attributes for colour, pattern and motion were proposed, which had their underpinnings in populations of cortical neurons with distinct profiles of response to different visual stimuli.

The visual cortex undergoes very rapid development in neuronal selectivity in the first 6 months after birth, the beginning of a period during which the number of synapses in visual cortex increases dramatically (Huttenlocher et al. 1982), providing the rich connectivity on which the selective cortical processing proposed in the model depends. Atkinson and Braddick's VEP and behavioural studies with normal infants suggested that the various attributes of selectivity do not emerge together in this wiring-up of the cortex; rather, there is a clear developmental ordering. Mechanisms or channels for orientation for shape discrimination become functional closely after birth, followed by direction selectivity for visual motion, and then selectivity to binocular disparities for stereoscopic vision.

1.2. Magnocellular and parvocellular systems

Sensitivity to motion direction (directionality) and stereo depth information (binocularity) is associated with input to the cortex from the magnocellular pathway, and processing within the cortex by the dorsal stream (Livingstone & Hubel 1988). The initial development of this pathway may be slower than that of the parvocellular-ventral pathway which specialises in processing form (orientation or slant) and colour (Atkinson, 1992). Motion and disparity processing both require the comparison of information between separated locations in the visual field and hence the establishment of relatively long, orderly, horizontal connections in cortex. The fact that, after the initial onset, there is a development of infants' directional sensitivity to progressively greater displacements (Wattam-Bell 1992, 1996), and of binocular sensitivity to progressively greater disparities (Wattam-Bell, 1995) suggests that the range of these connections, increasing with age, may be a limiting factor in the development of these aspects of cortical selectivity.

1.3. Dorsal and ventral streams

Pioneering electrophysiology starting in the 1970s and 1980s mapped distinct brain areas beyond primary visual cortex containing neurons responding to particular visual attributes, including an area selective for motion information (V5/MT) and a colour specific area (V4) (reviews - Zeki 1993; Felleman & Van Essen 1991). Ungerleider and Mishkin (1982) proposed two broad, functionally distinct processing streams, the 'dorsal' and 'ventral' streams. The dorsal stream, including area MT/V5, transmits information to parietal lobe networks for localising objects within a spatial array ('where') and is intimately linked to eye movement mechanisms of selective attention. The ventral stream processes information for the temporal lobe (including V4), concerned with the 'what' aspects of objects, such as form, colour and face recognition.

Supporting evidence came from other studies on primates (e.g. Van Essen and Maunsell, 1983; Boussaoud et al 1990; Merigan and Maunsell 1993) and from clinical observations of patients with specific deficits of spatial processing (e.g. Damasio and Benton 1979), movement perception (Zihl et al. 1983) or object recognition (Milner & Goodale 1995).

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Figure 1 here

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Figure 1 shows a schematic of the current model of Atkinson and Braddick, based on both developmental studies and the neurophysiology from other species. In this figure there are some additional divisions between onset of functioning in 'local' and 'global' processing (discussed below).

Milner and Goodale (1995; Goodale and Milner, 2003) suggested that the ventral and dorsal cortical streams have different functions in the visual control of behaviour; the ventral stream is concerned with perceptual processing (including, for example, object recognition) and the dorsal with visual control of action. This is a functional description of the two streams rather than one based on the types of selectivity of cells.

1.4. Action modules in the dorsal stream

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INSERT FIGURE 2 ABOUT HERE (dorsal stream modules)

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There now exists substantial information about many distinct action modules in primates. Figure 2 shows a schematic model of some of these dorsal circuits, drawing on the extensive reviews of Milner and Goodale (1995) and Jeannerod (1997). For example, Jeannerod has argued that the dorsal stream, transmitting visual information to primary motor cortex (M1), has separate divisions for reaching and grasping.

Both dorsal and ventral streams project to prefrontal cortex and in the mature brain the two systems are heavily interconnected. Visual spatial development can be divided into processes

more dependent on dorsal stream functions, such as visual control of action, and those dependent on ventral, such as recognition. However, for many visuospatial tasks processing across two or more modules must be combined. For example in reaching for an object the object must be identified as the correct object for the goal of the action using ventral stream networks before the appropriate action is planned using dorsal stream processing. In looking at development of the first stages of dorsal and ventral stream processing, stimuli have been designed to artificially separate one stream from the other, but even here there can be some debate about their separation.

The eye movement control systems are the first to develop in young infants. These action systems control saccadic tracking and smooth pursuit of objects of interest and switches of attention involving head and eye movements to scrutinize different objects of interest sequentially. These two systems are schematized in Figure 2. However, before discussing development in each of these early action streams, mechanisms for controlling attention must be considered, as the action and attention processing systems are heavily interlinked in development.

1.5. Links between attention and spatial action

Mechanisms of attention play an essential role in perceptually "filtering out" irrelevant stimuli and enhancing those of interest. Traditionally, visual attention has been viewed as a unitary, supramodal mechanism subserved by anatomical systems separate from those involved in sensory and perceptual processing (e.g. Posner 1980; LaBerge & Brown 1989; Posner & Petersen 1990). More recently two attentional brain systems have been postulated, a posterior system which subserves spatial attention and an anterior system involved in various complex cognitive tasks related to executive function (Posner and Dehaene 1994).

Effects of "covert attention" are seen in subjects' advantages in responding to a stimulus when they know where it will appear, even when they do not move their eyes to fixate the relevant place (Posner & Cohen 1980). Attention has also been described as a mechanism which enables 'selection for action' (e.g. Allport 1989), the action being either an eye movement (a saccade to fixate the object), or a bodily movement such as a reach towards the object. Such motor acts have been taken as indicators *overt* attention shifts. Rizzolatti and others (e.g. Rizzolatti 1983; Rizzolatti & Camarda 1987; Berthoz 1996) have proposed a 'premotor' theory of attention, according to which *covert* attention (without fixating the object of interest) exploits the same selection-for action mechanism. On this theory, selective attention to a spatial location would involve a number of action modules. In Figure 2 areas related to selective attention overlapping

with areas in the dorsal stream are highlighted in square boxes. This suggests considerable overlap between the attention and action systems. Whether or not the premotor theory can provide a complete account of adult attention, it is valuable in a developmental context where evidence for attention control comes from overt orienting acts. In the next section development of these linked attention and action systems in early infancy is discussed.

2. Development of selective attention for action in infancy

The most basic visual spatial action system to develop in young infants involves control of eye movements to track moving objects and people and to stabilize objects on the retina.

2.1. Newborn eye movements

Optokinetic nystagmus (OKN): With a large visual field of conspicuous vertical stripes, moving horizontally at a constant speed of around 10 deg/sec, optokinetic nystagmus (cycling eye movements – each cycle showing a brief period of smooth following in the direction of the motion followed by a rapid saccadic return in the opposite direction) can be observed in newborns. These stabilizing eye movements act to keep the head and eyes fixating on objects of interest in the real world. OKN is the first directional action system to operate in newborns, but does not seem to be one of which there is conscious awareness.

2.2. Smooth pursuit eye movements: Differences have also been found developmentally

between newborns and three month- olds in the extent and gain of smooth pursuit, which implies that at least in human development, there are different stabilizing mechanisms for smooth pursuit, enabling targets to be tracked, and saccadic movements, enabling orienting. Detailed studies of the development of these stabilizing mechanisms in infants have been made by Claes von Hofsten and his colleagues (see for example von Hofsten & Rosander 1996, 1997). They recorded smooth pursuit eye movements even in newborns, if targets of sufficient size and contrast were used and their velocity was kept relatively low. However, saccadic tracking is much more commonly observed than pursuit in the newborn. They also looked at the development of the initial coupling of eye and head movements, as the infant develops these stabilizing mechanisms. Fairly accurate coupling and a mature vestibular ocular response is achieved in the first few months of life, although many of the tracking eye movements observed in everyday situations in this period are saccadic, rather than continuous smooth pursuit. This changeover from passive saccadic tracking to smooth pursuit eye movements has been taken to imply anticipation of the end point of the object in space and a planning mechanism used to control eye movements.

Further evidence for this comes from the infant's ability to anticipate where an object will be in space when moving behind an occluder. There are extensive studies in this area concerning the factors, such as path trajectory, velocity and target appearance, which will change this anticipatory behaviour (for a review see von Hofsten 2005).

2.3. Eye/head eye movement systems for switching attention

For switching attention there is general agreement that the newborn has a 'where?' system, which is largely under subcortical control, and is used for orienting the head and eyes to abrupt and significant changes in the world. In the visual domain these are usually changes in luminance or movement. This system has been studied using the fixation shift paradigm (e.g. Atkinson & Braddick, 1985; Atkinson et al, 1992). Newborn infants make a shift of the head and eyes from a central target to a target in the peripheral fields appearing at the moment when the central target disappears. The orienting system used when only one target is visible at one time (non-competition) is likely to operate supramodally, across domains and sensory modalities, as a non-specific alerting system. The superior colliculus is strongly implicated within this system, although there may be a number of subcortical circuits involved in different components of the responses (see Figure 2 for likely areas involved).

2.4. Disengagement and switching attention when targets compete

The crude subcortical system, described above, will orient to a single salient target. However, it works much less effectively in the fixation shift paradigm when a peripheral stimulus appears but the central target remains visible. Responses to a peripheral stimulus when the central target continues to engage fixation require modulation and disengagement of this orienting system by cortical processes. Both right and left parietofrontal areas, linked to subcortical eye movement systems have been implicated as necessary for development of these attention switching systems in infancy (Atkinson & Braddick 1985; Atkinson et al, 1992; Atkinson & Hood, 1994). The cortical system appears to become functional around 3-4 months of age in normally developing infants. This modulation by the cortex can be mapped out by varying the interval between offset of one target and onset of another (Hood & Atkinson, 1993). In some infants who have suffered perinatal brain damage involving both cortical and subcortical areas (and in particular the basal ganglia) even the primitive orienting system may not be functional (Atkinson & Hood 1994; Mercuri et al. 1996, 1997a, b).

2.5. Abnormalities of switching attention

The cortical contribution is vulnerable to brain damage, particularly in the parietal lobes. Two infants who underwent hemispherectomy (removal of one complete hemisphere), one at 4 months of age and the other at 8 months, to relieve intractable epilepsy, postoperatively failed to show disengagement and shifts of eyes and head from a centrally viewed target to one appearing in the periphery when the central target remained visible while the peripheral target appeared (i.e fixation shift under competition). Failure to shift under competition was on the side of space opposite the removed hemisphere, but good shifts of gaze were made on the side controlled by the remaining functional hemisphere, and to either side when only one target was visible –i.e. fixation shifts without competing targets (Braddick et al. 1992). In other studies, infants with either focal lesions or diffuse hypoxic-ischaemic damage showed this 'sticky fixation' – an inability to easily switch visual attention from one target to another when two targets are present at once (Atkinson & Hood 1994; Hood & Atkinson 1990; Mercuri et al. 1996). This behaviour resembles the problems often seen in adult stroke patients as part of a 'visual neglect' syndrome.

In this section the first spatial selective attention systems have been discussed. However, attention is not a unitary function. Besides neural systems controlling selective attention and switches of attention there are those for sustaining attention and those for inhibiting actions and learning new ones (the later sometimes being called 'attentional control'). Many of these attentional systems mature in later childhood. Development of attention in spatial tasks in childhood will be considered later in the chapter, together with abnormalities in these component systems.

3. Development of dorsal and ventral streams

3.1. Development of cortical motion systems: local and global processing

The first stage of development of the dorsal stream underpinning spatial development is the development of sensitivity to motion. Behavioural and VEP/ERP studies for infants and young children have been designed to distinguish 'local' from 'global' processing in the dorsal and ventral streams. Local motion processing can be defined as the sensitivity to direction in a small region of the image, such as a short segment of contour, while global motion processing allows the representation of motion over extended regions that may correspond to surfaces and objects. In adults and other species, global processing has been identified with the integrative properties of neurons in visual area V5, while local processing is identified with neurons in V1 (Braddick and Qian, 2000). Several aspects of infant performance indicate that global processes operate at an early stage of development. In a dot pattern containing a proportion of randomly moving dots,

processing the motion of individual dots cannot yield the overall direction of motion; this requires integration of motion signals over many dots, a process which can be assessed in terms of the motion coherence threshold, the proportion of coherently moving dots required for detecting the global direction. Such thresholds can be measured using preferential looking where it can be shown that by about 3-4 months of age, a strip of coherently moving dots is preferred over an area of random motion; this closely follows the emergence of local direction discrimination at around 2 months (Wattam-Bell 1994). These results suggest that very soon after local motion signals are first available in the developing brain, the processes which integrate them into global representations are operating quite efficiently. It may be that connectivity between V1 and extrastriate areas including V5, on which this integration is based, exists early at least in a crude form, awaiting the organization of local directional selectivity in V1 - perhaps because the latter requires some minimum level of temporal precision before it can function. Deficits in global motion processing, which have been called 'dorsal stream vulnerability' may originate in problems processing temporal information at these very early stages of motion processing.

3.2. Comparison of global form and global motion processing

The development of global motion processing - a function of extrastriate dorsal stream processing - can be compared with global processing of form in the ventral stream, where analogous thresholds can be measured. Here subjects must detect the organization of short line segments into concentric circles, with 'noise' introduced by randomizing the orientation of a proportion of the line segments. Neurons responding to concentric organization of this kind have been reported in area V4 in macaques (Gallant, Braun & Van Essen 1993), an extrastriate area at a similar level in the ventral stream to V5 in the dorsal stream. In infants form coherence discrimination is apparent from 4-5 months of age from preferential looking and VEP /ERP studies (Braddick et al, 2002a), with children's coherence thresholds reaching adult levels at around 7-8 years (Gunn at al, 2002). When dynamic rotating and static versions of the same, circularly organized stimulus are compared, later maturity for motion coherence than for form is found – a reversal of the early development where form detection appears to be before motion (Atkinson & Braddick 2005).

Specific areas associated with form and motion coherence tasks have been identified for comparable stimuli in fMRI studies of normal adults (Braddick et al. 2000, 2001). This work has shown that anatomically distinct circuits are activated in global processing of form and motion, although each circuit involves parts of both the parietal and temporal lobes, and cannot therefore

be said to be strictly 'dorsal' and 'ventral' in the human brain. However, the activated areas do include dorsal stream areas V5 and V3A for motion, and anatomically ventral areas for form. It has also been found that the BOLD response in fMRI studies increases linearly with degree of coherence in an area analogous to V5 (Rees, Friston & Koch, 2000) and that areas in the lingual/fusiform gyrus, which may include V4, similarly show a linear response for form coherence (Braddick et al., 2002b).

In summary, although local orientation sensitivity emerges earlier in development than directional selectivity, global organization based on form, pattern or orientation is found to be less effective in determining infant behaviour than global organization based on motion. This may reflect the importance of global motion for segmentation and depth organization of the visual world for early spatial tasks. Such segmentation arises both from the independent movement of objects, and from parallax due to self-motion; the latter is effective for infants (e.g. Kellman and Spelke, 1983) even though their self-motion is largely passive rather than actively controlled in the first six months. Later in childhood, sensitivity to form coherence attains adult levels rather earlier for than motion coherence, and is less sensitive to developmental impairments; this 'dorsal stream vulnerability' is discussed in the following section.

3.3. Abnormalities of dorsal and ventral stream development

The broad division between the functions of dorsal and ventral cortical streams is reflected in abnormal development. We have studied development of these functions in a number of groups of young children with atypical developmental profiles (children with Williams syndrome, autism, Fragile X, perinatal brain damage resulting in focal lesions and hemiplegia). Across all these groups, a general finding has been that tasks designed to compare the two streams, the development of the dorsal action stream is more likely to be affected than the ventral. This has led us to a general hypothesis of 'dorsal stream vulnerability' (Atkinson et al. 1999; Spencer et al. 2000; Atkinson et al, 2001). Children with Williams Syndrome (WS or infantile hypercalcaemia) typically show a very uneven profile of neuropsychological development, with relatively strong expressive language abilities combined with unusual semantics, good face recognition, but spatial cognition severely impaired (see for example Bellugi et al. 1988, 1990, 1994, 1999; Bertrand et al, 1996; Karmiloff-Smith, 1998; Klein & Mervis 1999; Pezzini et al, 1999). They reach motor milestones later than typically developing children, are often delayed in learning to walk and in the development of fine motor skills, and on a standardised test of motor function (Motor ABC: Henderson & Sugden 1992) they show an average delay of at least 2 years (Atkinson *et al.*

1996a). Problems that persist into later life include uncertainty when negotiating stairs or uneven surfaces (Atkinson *et al.* 1996), awkward gait and joint contractures in some children (Kaplan *et al.* 1989), and difficulty with the use of everyday tools.

This neuropsychological profile is consistent with the possibility that ventral stream processes (e.g. face recognition), are relatively unimpaired but dorsal stream function for visual control of action is developmentally abnormal. We have explored this possibility in several ways. First, we have compared tests of motion and form coherence which require global integration by extra-striate visual areas. Many children with Williams syndrome (WS) have considerable difficulty with the motion task relative to the form task (Atkinson et al. 1997, 2003). These WS children are found across the age range from 3 years to adulthood (Atkinson et al, 2006a) . The same pattern is found in some younger, typically developing children (4-5 years) and so, although the results are in line with the 'dorsal vulnerability' hypothesis, they suggest a more general delay with ability never approaching adult levels, but asymptoting at the 4-5 year level.

3.4. Use of motion information for more complex discriminations in infancy

In the previous section psychophysical sensitivity of infants to simple stimuli varying in form, pattern and motion has been measured. These abilities are useful to young infants for understanding the spatial world around them. For example recognising the pattern of motion of a human being rather than a rocking chair is fundamental to separating objects in space, and for separating one's own motion from intrinsic motion of objects and people. Detecting 3D information from the distribution of optic flow information is also a necessary starting point for segmenting objects from their background.

A diverse range of studies have tested infants for complex discriminations for motion information in spatial tasks. Discrimination has been demonstrated between rigid and non-rigid transformations of a 3-D object (Walker et al. 1980). Others have shown quite subtle discrimination of 3-D structure from motion (Arterberry & Yonas 1988, 2000) (e.g. the presence of an interior corner on a cube, represented by random dot kinematograms), and kinetic depth information leading to recognition of a 3-D shape subsequently provided through disparity cues. Infants' sensitivity can be demonstrated to the temporal direction of apparently causal event sequences (e.g. Leslie 1984), and a preference has been reported for dynamic event sequences with simple shapes that adults categorise as social interactions (Rochat, Morgan & Carpenter

1997). Infants have also shown sensitivity to the patterns of point-light motion that characterise biological motion (e.g. Bertenthal et al. 1985; Booth, Pinto & Bertenthal 2002). Most of these discriminations have been in tests of 3-6 month old infants, and none have been shown so early that they require us to revise the view that the general ability for directional discrimination emerges after 7 weeks of age. On the other hand, they demonstrate that, only a few weeks after infants acquire any ability to discriminate motion directions, they can exploit this ability in a wide variety of complex perceptual functions. Together with the findings on global motion, these results support the idea that the emergence of motion processing in development is constrained by the development of relatively low-level directional mechanisms, rather than by immaturity of processes that elaborate and integrate motion information.

3.5. Dorsal and ventral pathways beyond extrastriate areas

The possibility of different courses of development for dorsal and ventral streams has already been mentioned, but there are also important developmental differences between different modules within a stream.   The major milestones of exploratory head and eye movements, directed reaching and grasping, and locomotion each involves integrated function of a different spatial action module processing dorsal stream information. All these action programs must involve some spatial analysis of the visual layout, but the different systems need representations at different scales and with different frames of reference. For reaching and grasping the infant only needs representation of space near to the body and an egocentric frame of reference to match object locations to hand actions. For locomotion, the child needs to represent the environment on a scale beyond arm's length, and with a reference frame that remains stable in space as the body moves. Next in this chapter we will briefly describe studies on development of reaching, grasping and locomotion which are all underpinned by dorsal stream circuitry.

4. Development of action modules for reaching, grasping, and motor planning
4.1. Reaching and grasping in infancy

Typically developing infants usually start to reach and grasp successfully for objects in near distance at around 4-6 months of age. Two kinds of visual information must be processed within the visual action system controlling reaching and grasping. First, the location of the object, laterally and in distance, must be identified. Second, visual analysis is required to determine whether the object is a suitable target for reaching and grasping.

For the first, the coincidence in timing between the development of binocularity around 4 months (Braddick 1996) and the emergence of visually guided reaching suggests that binocular disparity information, associated with convergence, is a key input to the visuomotor module for reaching. This is confirmed by the finding that binocular information is critical in determining the kinematics of infants' reaches (Braddick, Atkinson & Hood 1996).

From 6-9 months, reaching appears as a quite compulsive behaviour for small objects presented within range. This behaviour raises the question of the visual information by which an infant determines that an object is graspable and hence a suitable target for reaching.

4.2. Preferential looking and preferential reaching

The development of distinct visuo-motor modules, and their ultimate integration, is illustrated by experiments which combine preferential looking with preferential reaching (Newman et al,. 2001). In preferential looking infants make an orienting response of head and eyes towards the most salient object or region in the visual field. Presentation of paired stimuli allows the relative salience of these stimuli to be assessed. Depending on the development of various cortical modules, salience is a function of luminance, colour, motion or depth contrast, and of spatial structure defined by such contrast. It is also modulated by novelty (as in habituation tests) and by the special significance of certain stimuli such as faces. Salience, so defined, is the visual computation characteristic of the set of cortical modules which contribute to the orienting system (providing output through the superior colliculus). In the case where an infant is presented with two 3-D objects, similar in shape and surface but different in size, the infant tends to orient to the larger object (King et al. 1996; Newman et al. 2001).

However, reaching is only an appropriate response for objects which are small enough to be grasped. Thus the visual modules which provide information controlling this response need to compute, as well as the spatial direction for the reach, the size of the potential target. This computation is not necessarily possible for the infant at the age when the motor schema of reaching becomes available, but when it is possible, it will cause reaching to be preferentially directed to the smaller object of a pair, when the larger is beyond the span on the infant's hand.

Thus the two visuo-motor dorsal stream systems, for orienting and reaching, may be driven by different visual information from the same pair of objects. The studies of King and Newman showed that these systems interact differently at different ages; possible organization of the two

systems at each stage is schematized in Figure 3. When infants first start to reach (up to 8 months), they do not show a significant reaching preference between large and small objects. However, their reaching is predominantly directed to the object they initially fixate. We infer that processing of the specific visual attributes signifying graspability is not yet linked into a visuomotor module for reaching, and that at this stage there is a substantial coupling between the system controlling reaching and that determining orienting.

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FIGURE 3 INSERT ABOUT HERE

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Between 8 and 12 months a strong preference emerges for reaching for the smaller object, which is within the span of the infant's hand. Thus an effective visual analysis of graspability has developed and serves as an input to the reaching control system. Infants at this age show a noticeable decoupling of reaching and initial orienting – they are more likely than younger or older infants to first fixate one object and then reach for another. This decoupling can be emphasised by manipulating visual salience: marking a schematic face on one object increases preference for looking at that object, without altering its graspability and hence without a corresponding increase in the tendency for it to elicit reaching in competition (Newman et al, 2001).

After 12 months, reaching becomes less selective towards the smaller object, perhaps because it has become a less compulsive behaviour, and also because the infant's grasp can encompass larger objects. At the same time, reaching and initial looking become more congruent again. It appears that the orienting and reaching systems can be integrated into a single piece of goal-directed behaviour.

There is an extensive literature on factors affecting reaching in infants (for reviews see von Hofsten 1991; Berthier & Keen 2006). A number of studies have found changes in development during the first 2 years of life in the kinematics, dependent on the size of the target (e.g. Fagard & Jacquet, 1996; Fagard, 2000). For example in a recent study cubed objects were varied across a wide range of sizes (Braddick and Atkinson, 2003). For infants between 4 and 6 months smaller objects elicited more grasping actions than non grasp contacts. Between 6 and 10 months the proportion of bimanual reaches for the larger objects increased, with different kinematics of the

speed profiles in grasp compared to non-grasp reaches. Some of these differences in kinematics may reflect an understanding of the 'graspability' of the object. This suggests that areas such as AIP may be to be operating to identify salient object properties for guiding actions in the first year of life.

4.3. Bimanual Coordination

Alongside reaching and grasping with one hand comes bimanual coordination for the many tasks requiring two hands to reach a goal. Early bimanual coordination patterns are typically similar for the two hands in that both hands reach or grasp synchronously and involve proximal control. With improvements in posture and visuomotor skill at around 6 months of age the infant starts to explore objects placed in their hand and transfers the object from one hand to the other. These actions form the basis of later developing complementary bimanual patterns of coordination. In these early object explorations only one hand is active at a time, but towards the end of the first year the two hands are capable of carrying out two different actions simultaneously, e.g. lifting and holding open the lid of a box in order to retrieve a toy. The first bimanual attempts are often poorly timed and clumsy but by 18 months of age the infants perform these tasks smoothly and efficiently with good spatial and temporal organization (e.g. Bruner, 1970; Diamond, 1991; Fagard 1994). Bojczyk and Corbetta (2004) demonstrated that with repeated exposure (training) infants were able to develop well coordinated bimanual actions by 8-9 months and thus outperform age-matched infants with no previous experience of the task.

4.4. Visual information in motor planning : abnormalities in Williams syndrome

For everyday motor planning many visual factors need to be taken into account. For example, for an object to be grasped, its distance, size and orientation must be judged accurately. One experimental paradigm that gives insight into more complex visual control of action is the "postbox task" used by Goodale et al (1991) to study a ventral-stream impaired patient. Goodale and colleagues found a striking dissociation. This patient could accurately post a card through an oriented slot (dependent on dorsal-stream control of action) but failed on perceptual matching of the slot orientation (dependent on ventral-stream processing for perceptual judgments). On a task of this kind, children with Williams Syndrome showed much greater inaccuracy in posting the card than in matching the card's orientation to that of the slot, compared with normally developing children (Atkinson et al 1997). This results supports the account of a dorsal stream deficit, although again the degree of deficit was quite varied between individuals.

When picking up square shapes, children with WS were also impaired on adjusting grip aperture to target size, and made slower reaches, with more movement segments, suggesting that they were less able to program accurately the reach as a whole (Newman 2001). There thus appears to be a continuing immaturity in WS in the dorsal stream units controlling reaching and grasping. However, they also show poor performance on a matching test (judgment for the squares' size without picking them up), indicating that problems in WS appear in both 'ventral' and 'dorsal' aspects of the task (Newman 2001).

In the post-box task discussed above (Atkinson *et al.* 1997), children with WS often found their hands in awkward postures as they rotated the card, suggesting inefficiency in end-state planning, the ability to take into account the intended use or end-state of the object. End-state planning is likely to involve the integration of dorsal stream information with pre-frontal areas involved in inhibiting inappropriate actions and co-ordinating the elements of action sequences. An end-state planning deficit in WS was explicitly tested by Newman (2001) using a handle rotation task adapted from adult studies by Rosenbaum *et al.* (1992). Results from this study indicate that children with WS either do not attempt end-state planning or are unable to make the spatial transformations required to predict the end-state correctly.

Overall, these studies found subtle and variable deficits in the use of dorsal stream information to control manual action, although these were not always dissociated from ventral stream performance. The deficits were most striking beyond the early stages of visual processing for actions, in the use of visuospatial information for end-state planning. There may well be a 'cascade' effect, with early abnormalities in more basic parts of the dorsal pathway affecting later development of complex feedback loops involved in visuomotor planning, which show deficits even if the lower level effects are overcome. The individual variability highlights the degree to which adaptive strategies may lead to differently configured systems even if there is a common initial developmental deficit.

5. Development of action modules for locomotion and navigation

The integration of different dorsal stream modules is required when locomotion becomes part of the infant's behavioural repertoire. For instance a desired object is processed in far space as a target for locomotion, and brought into near space as a target for reaching. The child must

become able to switch attention from near to far, and to engage the visual processes required at these two scales. Other aspects of visual behaviour also require such shifts – e.g. joint attention invoked by an adult's pointing gesture, which is also achieved around the beginning of the second year (Butterworth & Grover 1990). It remains a challenge for further research to characterize and understand these processes of integration and switching.

A key component of successful locomotion is balance. The use of visual information to maintain balance starts as young as 15 months (Lee & Aronson, 1974) and develops throughout childhood (Shumway-Cook & Woollacott, 1985). Real-world locomotion also depends on avoiding obstacles or accommodating movement to them (Patla, 1991). The visual decisions involved are: can I step over this or should I walk round it? And: if I step over this, what height should I raise my feet to? These considerations are important when planning both single steps and longer routes.

We know that children avoid objects based on the visual information they have about their size. For example the classic 'visual cliff' experiment showed that young infants avoided crawling on an area they perceived to be dangerously deep (Gibson & Walk, 1960). Some new work considers how visual information is used to accommodate movements appropriately. This work shows that step descent is divided into 'transport' and 'placement' phases. The transition between phases is marked by the lead leg swinging in to contact the step. The vertical distance traveled by the knee during the transport phase increases in proportion to the step's riser height. This pattern is lost when vision is removed. Strikingly, this ability to scale movement to riser height is present in children as young as 3 years old. However, these children depend more than adults on online visual control to accomplish this (Cowie et al., in preparation). These studies illustrate that children use vision to control accommodative processes as well as avoidance decisions.

Successful locomotion involves not only using visual information but combining it with information about one's own locomotor abilities and current body state. Toddlers take locomotor decisions based on their own walking skill and experience (Kingsnorth & Schmuckler, 2000) and body dimensions (Adolph & Avolio, 2000). In a new 'stepping stones' task children must choose to follow one of two paths of 'stepping stones' across a pretend 'river'. Children as young as 3 years are influenced in their planning by their own body states - in this case the need to make anticipatory changes in foot position before the start of the task (Cowie et al. 2006a; 2006b).

As with other visuomotor tasks, the visual control of locomotion is likely to be mediated by the dorsal stream. There is little work on this, but the patient DF, with damage to the ventral stream but a spared dorsal stream, can accurately scale her stepping-up movements (Patla & Goodale, 1996), though not her verbal estimates of step-height; while young children with Williams syndrome, who show other dorsal-stream impairments, cannot scale stepping-down movements in the task reported above (Cowie et al, 2006c; Atkinson et al, 2006b).

6. Development of spatial localization in location memory tasks

Further important aspects of spatial development depend on the systems underpinning accurate spatial localization in memory tasks. From studies of adults using psychophysics, brain imaging and TMS (transcranial magnetic stimulation), and from animal lesion studies, dorsal stream parietal networks are the primary processing areas for basic spatial localization, while the hippocampus, parahippocampal gyrus and entorhinal cortex are involved in more complex spatial memory tasks (see review by Stiles et al, in press).

6.1. Location memory in infants

In the classic Piagetian "A not B" task, an object is repeatedly hidden at location A, before a test trial on which it is hidden in novel location B. Infants aged around 9 months continue to search incorrectly in the "familiar location" (A); this is the "A not B" error. AB tasks have been used to test *object permanence*, that is, the infant's knowledge that objects exist independently over space and time. However, they also reveal the spatial framework that infants use to define the location of an object.

Children's ability to overcome the AB error depends on many factors. Self-locomotion reduces the likelihood of the error (Horobin and Acredolo 1986; Kermoian and Campos 1988; Bertenthal and Campos 1990), and looking-time measures indicate that children are aware of the difference between the A and B locations before they are able to avoid the AB error in their reaching responses (e.g. Baillargeon and DeVos 1991; Hofstadter & Reznick 1996).

In non-human primates bilateral lesions of dorsolateral prefrontal cortex disrupt AB performance, but bilateral lesions to parietal cortex (Diamond, 1991; Diamond, Werker & Lalonde 1994) or hippocampus (Diamond, Zola-Morgan & Squire, 1989) have little effect. These findings suggest that children's solution of the task depends on frontal maturation. Further evidence from changes

in frontal metabolic activity in the first year (Chugani, Phelps & Mazziotta, 1987; Jacobs et al. 1995) supports this view, as does data from EEG and near infrared spectroscopy measures (Fox & Bell 1990; Baird et al. 2002). Bell and Fox (1992) found increased anterior-posterior EEG coherence associated with improved performance on the AB task, suggesting that long range axonal connections may contribute to the change in performance. As discussed earlier, these pathways may be critical for control of reaching. Thus maturation of the anterior-posterior system may account for the differences in performance on reaching and looking tasks.

Infants make a related error when looking for an object after changing position. 6 – 12 month olds often search *egocentrically* after they have moved, i.e. they seem not to appreciate that a target that was previously on their left is now on their right (e.g. Acredolo, 1978). As with the AB error, infant egocentrism is moderated by many factors. It can be overcome, particularly when a visual cue that directly indicates the target is available (*e.g.* Rieser 1979). Crucial for mature navigation however is the later-developing ability to use indirect landmarks, which do not directly indicate a target.

6.2. Development of location memory in childhood

Improvements in location memory in mid- childhood follow prefrontal, posterior parietal, and hippocampal maturation. Children's use of different spatial frames of reference to remember a location develops gradually. Egocentric representations, using the body as a reference, provide a good basis for immediate action towards objects. More robust representations are provided by encoding where objects are relative to stable landmarks (using an allocentric reference frame). This would enable objects to be found even when the viewer changes position. Another way to deal with a change of position is to track where an object is while the observer is moving ('updating' the egocentric representation as the observer moves); adults use these different frames of reference and updating processes in complementary ways.

Representations using external landmarks are reliably used for action by the second year (Huttenlocher et al, 1994). At 16 – 36 months, children retrieve objects hidden in a sandbox after walking around to the other side (Newcombe et al 1998), showing coding relative to landmarks and/or spatial updating with self-motion. A more difficult problem is processing a change of viewpoint caused by the rotation of an object, rather than one's own displacement. In this case the self-motion information that could be used to maintain an accurate egocentric representation while walking is not available. Judging what would be where if the viewer's viewpoint changed

presents a "perspective problem" (Huttenlocher & Presson 1973), potentially a test of children's ability to use a purely viewpoint-independent, or allocentric frame of reference. Piaget and Huttenlocher's perspective-taking studies were not usually solved until around 10 years, although, similar tasks have been solved earlier with a modified procedure (Newcombe & Huttenlocher 1992).

Nardini et al (2006a) tracked both egocentric coding, suitable for simple spatial recall, and allocentric codings, capable of solving the "perspective problem", in 3 - 6 year olds within the same task. Children saw a toy hidden under one of 12 cups on a board with landmarks attached to two of its edges, and had to find it after a manipulation. The task systematically varied whether the same view of the board was seen at hiding and test – *i.e.*, whether the toy kept its place relative to the *body*, and whether the array was rotated, *i.e.* whether the toy kept its place relative to the *room*. In 3 – 6 year olds, as in adults (Wang & Simons 1999), there were parallel, additive effects of both *body* and *room* frames of reference. The performance improvement when a familiar view allowed egocentric coding was already seen at 3 years. From five years children showed successful recall after changes of viewpoint caused by rotation, which could only be solved by attending to the array and its local landmarks (a "perspective problem"). This ability may depend on codings relative to landmarks, supported by the hippocampus (O'Keefe & Burgess 1996), and may also include mental rotation, which has elsewhere been demonstrated from 5 years (Marmor 1975; Kosslyn et al. 1990), and shows activation including parietal areas (e.g. Booth et al., 2000) in children and adults.

A separate question concerns how children combine different kinds of visual information to maintain their sense of orientation. The human environment includes discrete landmarks such as trees or buildings, which could be individuated by colour or shape, as well as elements of layout, such as the shape of a room or a field, whose geometric aspects could be coded. Hermer & Spelke (1994; 1996) found that 18-24 month olds, disoriented in sparsely-featured enclosures, re-established their orientation using geometry (enclosure shape), but not the colours of the walls. They argued that early reorientation depends on a specialised geometric module "encapsulated" with respect to colour, and that the eventual solution of the task depends on language (Hermer-Vazquez, Spelke, & Katsnelson 1999).

Solution of the task by nonlinguistic animals (reviewed by Cheng & Newcombe 2005), and children in larger enclosures (Learmonth, Nadel, & Newcombe 2002), argues against this account;

the ability of 18-24 month olds to reorient using wall colours in small square enclosures (Nardini, Atkinson & Burgess 2007a) also demonstrates that reorientation is not encapsulated with respect to colour. Nevertheless, the early dominance of room geometry over colour for spatial orientation, when both are available, remains an interesting phenomenon that has not been fully explained. Geometric judgements might be favoured in small, but not large rooms, as relative wall lengths are easier to judge when standing at a corner (Sovrano & Vallortigara 2006). In addition, children's poor use of colour may not be specific to disorientation, but could represent a more general phenomenon. Oriented 18 - 24 month olds searching in boxes on a table top were poor at using box colour alone as a cue, and especially likely to disregard colours when they had to be combined in memory with actions (Nardini, Braddick & Atkinson, 2006; Nardini et al, submitted a). At 30-36 months children no longer showed this disregard for colour, but did show it for monochromatic textures. "Disregard of colour" may therefore be a part of more general developmental phenomenon linked to the uneven development of links between the dorsal and ventral visual streams and prefrontal mechanisms for working memory.

6.3. Impairments of spatial representation in memory in atypical development

Early focal cortical injury in the right hemisphere is associated with deficits in organising spatial elements coherently, while left hemisphere injury is associated with poor encoding of detail in complex forms (Stiles-Davis, et al 1985; Stiles, et al 1996). Although these patients often show remarkable recovery compared with those obtaining similar injuries in adulthood, fine grained analysis indicates persistent deficits (Stiles 2000).

Children born very premature, who show a range of cognitive deficits by school age (Bhutta et al, 2002; Marlow et al, 2005), have especially marked deficits in the visuospatial and visuomotor domains (Atkinson *et al.* 2006c). On a spatial memory task assessing recall using different frames of reference, 6-year olds born at 25 - 30 weeks gestation had an average delay of more than one year across conditions (Nardini et al, 2006b). On average this group's deficit was as large for external frames of reference (landmarks) as for egocentric recall. However correlations with other cognitive and motor tests indicate subgroups with differential patterns of impairment. Impairments to spatial updating for changes of viewpoint produced by walking may be predicted by poor detection of coherent motion (related to visual processing of optic flow), while performance on the "perspective problem" (changes of viewpoint produced by movement of the array) is predicted by 'frontal' tests of inhibition and response selection, suggesting that a 'frontal' inhibition or selection process is involved in this task.

In addition to their visuomotor problems (Atkinson *et al.* 1997), children and adults with Williams syndrome (WS) show deficits on the purely perceptual task of egocentric localisation for locations on a screen (Paul et al, 2002; Vicari, et al 2006). Impairments to representations of location may therefore underlie their visuomotor and constructional difficulties. To compare the development of egocentric and landmark-based recall in Williams syndrome, we tested children and adults with WS on the "frames of reference" task. Overall, individuals with WS showed parallel, additive, use of *body* and *room* based reference frames; however these were combined anomalously in development, and performance in adulthood was not better than at 4 years in typical development (Nardini et al, submitted b). Crucially, adults with WS showed only marginal ability to use local landmarks to solve the "perspective problem", solved by typical children at 5 years. Visuomotor and constructional deficits in WS may thus be caused in part by the unusual integration of different frames of reference in development, and the poor ability to select local frames of reference even in adulthood.

7. Summary of abnormal spatial development

Abnormalities of development have been seen in every aspect of spatial vision. Examples have already been given in each section of this chapter; these are summarised here together with a brief description of a number of relatively new tests for diagnosing spatial deficits in infants and very young children.

7.1. Deficits in the development of spatial attention linked to action

Earlier in the chapter results from studies of infants who underwent hemispherectomy showed abnormal attentional control of actions, such as foveating or reaching for a target in peripheral vision on the side of space opposite the hemisphere lacking a normal cortex. This was only seen in conditions where two targets were competing for attention (Braddick et al.,1992). This failure to disengage and to make eye and head movements to a salient peripheral target when a central target is still visible is a common finding in many children with perinatal brain damage involving parietal and frontal areas. When damage extends to subcortical networks, then even without competition shifts of gaze (and presumably attention) can be absent and/or slow.

7.2. Deficits in spatial attention in childhood

In school age children there are many studies of deficits related to attentional loss. In normally developing children there is considerable improvement in attentional capacities throughout

childhood and adolescence. Three different components of attention have been identified from adult studies and patient populations, each with rather different neural underpinnings. The first component is linked to selective visual attention in visual search tasks. The second component is "sustained attention", which can be measured in vigilance tasks, and the third component involves inhibition of a prepotent response to switch and make a new association. Studies indicate that developmental trajectories differ for different attention components. Earlier maturity in selective attention (before 6-7 years), for example, contrasts with the continued development of sustained attention into adolescence, and rapid development of executive function between 7 and 11 years (McKay et al. 1994; Rueda et al. 2004; Kelly 2000). One test battery used to study attentional development is the Test of Everyday Attention for Children (TEA-Ch; Manly et al. 2001), which examines components of attention between ages 6 and 16 years. Data from this battery support the notion that distinct components of this function exist in childhood, and suggest differential impairment of these components in clinical samples including ADHD (Manly et al. 2001; Heaton et al. 2001) and traumatic brain injury (Anderson, Fenwick, Manly & Robertson 1998).

A number tasks have been developed to examine executive function in preschool children (e.g. Hughes & Russell 1993; Gerstadt, Hong & Diamond, 1994; Hood 1995; Backen-Jones, Rothbart & Posner 2003; Zelazo, Frye & Rapus 1996; Kirkham, Cruess & Diamond 2003); these show significant changes in the ability to inhibit prepotent responses and shift attention flexibly between the ages of 3 and 4 years. Many of these inhibitory tasks involving inhibition of a prepotent response are thought to have their underpinnings in frontal lobe circuitry. In one such test, "counterpointing", the child first points as rapidly as possible to a target which appears to either the left or right of a fixation spot. The rule is then changed and the child is asked to point as rapidly as possible to the opposite side to where the target appears. On this test inhibitory control is achieved on average by 4 years of age in typically developing children, but can be considerably delayed in clinical populations (Atkinson et al, 2003). Measures have also emerged in recent years that allow for more formal assessment of selective and sustained attention in preschoolers, demonstrating improvement in these abilities between the age of 3 and 6 years (Prather, Sarmento & Alexander 1995; Mahone et al ,. 2005; Corkum, Byrne & Ellsworth 1995).

Despite the clear changes in attention through the preschool age range, however, comprehensive batteries of attention measures are not generally available for children between 2 and 6 years. A new battery of attention measures is being developed for typically developing 3-6 year olds and

children in this mental age range, such as chronologically older children with Down syndrome or Williams syndrome (Breckenridge et al. in preparation).

7.3. Deficits in development of the dorsal stream relative to ventral stream

In section 3.3 the general hypothesis of 'dorsal stream vulnerability' (Atkinson et al., 1999; Spencer et al. 2000; Braddick et al, 2003) has been discussed. This refers to the general finding that across a number of clinical populations with very diverse aetiologies (e.g. Williams syndrome, Fragile X, congenital cataract patients, Autism, children with hemiplegia), when tasks are carefully designed to compare and isolate responses related to the dorsal and ventral streams, the development of the dorsal stream is more likely to be affected than the ventral (review, Braddick et al. 2003).

7.4. Planning and execution of actions in spatial tasks

Taken together with a comparison of dorsal and ventral stream function in the post-box task (see section 4.4) and in other motor planning tasks, Atkinson and Braddick have proposed that Williams syndrome is as an example of broader dorsal stream vulnerability. Support for this relative deficit in dorsal stream networks in WS comes from a structural MRI study with 2 year olds (Mercuri et al, 1997c) and from structural and functional MRI studies with WS adults (Reiss et al, 2004, Meyer-Lindenberg et al, 2004). Frontal executive functions have been found to be an additional area of deficit for WS, even relative to verbal IQ. The extent of this deficit depends on the nature of the task and is much greater when it requires inhibition of a prepotent spatially directed response, notably in counterpointing (see above) and also in a spatial detour task (Biro and Russell, 2001). Inhibition of a verbal response is considerably less affected. Thus the transmission of spatial information to frontal systems within the dorsal stream seems to be specifically disrupted in WS.

7.5. New tests of spatial development

Shape matching and block construction copying tasks have been normalized and standardized as part of a battery (ABCDEFV- Atkinson Battery of Child Development for Examining Functional Vision) to measure functional vision in children of mental ages between birth and five years (Atkinson et al, 2002a). All tests have been standardized with typically developing children, failure on a particular subtest usually corresponding to a score below the 15th percentile for the appropriate age. The battery is divided into tests of 'core vision', requiring minimal saccadic tracking eye movement, including measures of acuity, refraction and field perimetry, and

additional visuomotor, visuocognitive and spatial tests (requiring minimum motoric skills of reaching and pointing or grasping with one hand). Some sub- tests measure spatial vision related to more ventral or more dorsal stream processing, whereas some involve integration across both processing streams.

The ABCDEFV has been used to test spatial development in a number of clinical populations. In a large scale population infant vision screening programme (N=5000) for detection of strabismus and refractive errors in 9 month- old infants and prevention of later onset strabismus and amblyopia through spectacle correction in infancy (Atkinson et al, 1996b), children who had significant hyperopia in the first year of life were significantly worse on many of the visuospatial ABCDEFV tests throughout the preschool years. However, none of the items on the Griffiths scales of paediatric development showed a difference, arguing against a general developmental delay in this clinical group. Overall, these results indicate mild deficits in the hyperopic group, concentrated in areas of visual perception and visuo-motor control related to both dorsal and ventral stream development (Atkinson et al 2002b).

A second battery which has been developed is the Movement ABC (Henderson and Sugden, 1992), a standardised assessment of everyday visuo-motor and spatial competence for 4-16 year olds. The Movement ABC includes tasks to assess visuo-motor development within three categories: manual dexterity, balance, and ball skills. At 3 and 5 years, children who had been significantly hyperopic as infants scored lower on these tests (Atkinson et al, 2005). The pattern did not show a subgroup of poorly performing children, but suggested a mild but widespread deifict in the formerly hyperopic group. There was no significant difference between children who had worn spectacles to correct refractive errors in infancy and those who had not, which suggests that there may not be a direct causal connection between poorer sensory vision in infancy and poorer preschool visuomotor and visuocognitive abilities, but rather that abnormal refraction and strabismus in infancy is a soft sign of poorer brain development, affecting not only specific eye-brain networks for sensory vision, but those of selective attention and spatial cognition involving temporal, parietal and frontal lobe areas with links to subcortical networks.

In longitudinal studies of very premature infants (under 32 weeks gestation) a comparison has been made between their visual spatial development, brain imaging at birth and term, and their general neurological and cognitive development over a period from birth to 5 years of age. Diffuse excessive high signal intensity (DEHSI) is a common feature of white matter

abnormality in very premature infants when scanned around term. The presence and degree of white matter damage (DEHSI or PVL) correlated with the measures of early attention on the fixation shift test, deficits in onset of cortical functioning measured with orientation- reversal VEPs, and deficits on spatial tasks in the ABCDEFV and preschool attentional tests of frontal lobe function (Atkinson et al., in prep. a).

In a second cohort children who were born very prematurely were intensively studied between 6 and 7 years of age. Across the group deficits in visuomotor, visuospatial and attention tasks are found, with relative sparing of verbal performance and language. From this analysis, an overall model of brain development for premature infants is that as in other developmental disorders, there is vulnerability in the more dorsally controlled areas with attentional deficits arising from poor frontal lobe connections, whereas development of language and communication and ventral stream function is relatively good (Atkinson et al., in prep. b). For some children in the premature group these deficits are relatively mild, but many are likely to have subtle learning difficulties (e.g. mild ADHD) which persist and have cascading effects on later academic abilities.

8. Summary of the developmental model of visual spatial development

Figure 1 illustrates Atkinson and Braddick's (2003) account of the developmental sequence and the broad neural processes corresponding to it. From an initial subcortical stage, there is development of functioning in specific cortical channels, followed by development of integrative processes across channels within a single stream so that the infant can build up internal representations of objects and individuals. This aspect of the developing processes takes place largely in the ventral stream, with dynamic on-line information contributed from the dorsal stream to control orienting by eye and head movements. Of course, for objects to be represented, information about colour, shape and texture must be integrated with motion information at a relatively early stage so that objects can be segregated from each other and from their background. These processes provide object representations which must be integrated with dorsal-stream spatial information to allow, later, emergence of the visual action systems associated with reaching/grasping and with locomotion. These action systems are a combination of visual attentional and motor systems. It is over-simple, however, to show this as a linear sequence; there are likely to be important feedback loops, by which the consequences of a new development can affect the way that earlier established processes work. Furthermore, a description of the sequence is only the start. We still cannot explain timing differences in functional onset and

plasticity in one system as opposed to another – why do some processes in certain networks start to function earlier than others? How far are we seeing the unfolding of a maturational sequence, and how far does the developmental trajectory depend on exposure to the environment, including the kinds of exposure made possible by earlier networks becoming functional? There are still many unanswered questions.

A model of deficits in spatial development has been suggested - 'dorsal stream vulnerability'. This is based on the general finding that tasks related to more dorsal stream areas show higher levels of deficit that those related to ventral across many different clinical conditions including children with developmental disorders related to genetic abnormalities such as Williams syndrome and Fragile X. We still need to find the basic cause of this difference in plasticity between dorsal stream and ventral stream modules. It may have its origin in very low level timing mechanisms in subcortical or early cortical areas, it may depend on a misbalance between the number of functional magnocellular and parvocellular cells and their integration, or it may depend on integration of information from processing in many different occipital, parietal and frontal areas before the planning and decision for action is taken. Of course we do not know whether a deficit which seems similar behaviourally arises because of identical faults in its neural processing. Hopefully with improved imaging methods and specific behavioural measures we may be able to answer these questions in the future and provide appropriate interventions, tuned to the individual, to alleviate spatial difficulties in children.

Acknowledgments

Figure Legends

Figure 1. Atkinson and Braddick model of visual spatial development of dorsal and ventral streams in infancy

Figure 2.   Schematic model of different action modules within the dorsal stream

Figure 3. Schematic model of development of preferential looking and preferential reaching for objects in infancy

References

Acredolo, L. P. (1978). Development of Spatial Orientation in Infancy. Developmental Psychology, 14, 224-234

Adolph, K. E. & Avolio, A. M. (2000). Walking infants adapt locomotion to changing body dimensions. *Journal of Experimental Psychology: Human Perception and Performance, 26*: 1148-1166.

Allport, A. (1989). Visual attention. In M. I. Posner (ed.), Foundations of cognitive science. Cambridge, MA: MIT Press.

Anderson, V., Fenwick, T., Manly, T., & Roberston, I. (1998). Attentional skills following traumatic brain injury in childhood: A componential analysis. *Brain Injury, 12,* 937-949.

Arterberry ME, Yonas A (1988). Infant's sensitivity to kinetic information for 3-dimensional object shape. Perception & Psychophysics, 44: 1-6.

Arterberry ME, Yonas A. (2000). Perception of three-dimensional shape specified by optic flow by 8-week-old infants. Perception and Psychophysics, 62, 550-556.

Atkinson J & Hood B (1994). Deficits of selective visual attention in children with focal lesions. Infant Behaviour and Development, 17: 423.

Atkinson J., King J, Braddick O.J, Nokes L, Anker S, and Braddick F. (1997) A specific deficit of dorsal stream function in Williams' syndrome. NeuroReport, 8, 1919-1922.

Atkinson, J. & Braddick, O. J. (1985). Early development of the control of visual attention, Perception, 14: A25.

Atkinson, J. (1984). Human visual development over the first six months of life. A review and a hypothesis. Human Neurobiology, 3: 61-74.

Atkinson, J. (1992). Early visual development: differential functioning of parvocellular and magnocellular pathways. Eye 6: 129-135

Atkinson, J. (2000). *The developing visual brain*. Oxford: OUP (Oxford Psychology Series 32).

Atkinson, J., & Braddick, O. (2005). Dorsal stream vulnerability and autistic disorders: The importance of comparative studies of form and motion coherence in typically developing children and children with developmental disorders. *Cahiers de psychologie cognitive (Current Psychology of Cognition) 23* (1-2): 49-58.

Atkinson, J., Anker, S., Braddick, O., Nokes, L., Mason, A., & Braddick, F. (2001). Visual and visuo-spatial development in young Williams Syndrome children. Developmental Medicine & Child Neurology 43: 330-337.

Atkinson, J., Anker, S., Rae, S., Hughes, C., & Braddick, O. (2002a). A test battery of child development for examining functional vision (ABCDEFV). *Strabismus 10*(4): 245-269.

Atkinson, J., Anker, S., Nardini, M., Braddick, O., Hughes, C., Rae, S., & Atkinson, S. (2002b). "Infant vision screening predicts failures on motor and cognitive tests up to school age". *Strabismus*, 10, 187-198.

Atkinson, J., Braddick, O. J., Lin, M.-H., Curran, W., Guzzetta, A., & Cioni, G. (1999). Form and motion coherence: is there dorsal stream vulnerability in development? Investigative Ophthalmology & Visual Science 40/4: S395.

Atkinson, J., Braddick, O., Rose, F. E., Searcy, Y. M., Wattam-Bell, J., & Bellugi, U. (2006a. Dorsal-stream motion processing deficits persist into adulthood in Williams Syndrome. *Neuropsychologia* [Short Communication] *44*(5): 828-833.

Atkinson J, Braddick O, Nardini M, Cowie D, Breckenridge K, Anker S, Birtles D (2006b) Spatial cognition, locomotion planning and problems of attention in Williams syndrome (WS) : new tests developing the model of 'dorsal stream vulnerability' in WS. *Presentation at Williams Syndrome Foundation Professional Meeting, Richmond VA, August 2006.*

Atkinson, J., Braddick, O. J., Nardini, M., Anker, S. E., Cowan, F. M., & Edwards, A. D. (2006c). 'Dorsal Vulnerability' and Patterns of Visuo-Cognitive Deficit Following Very Premature Birth. *Perception (Suppl.)*, 35S, 3-4

Atkinson, J., Braddick, O., Anker, S., Curran, W., & Andrew, R. (2003). Neurobiological models of visuospatial cognition in children with Williams Syndrome: Measures of dorsal-stream and frontal function. *Developmental Neuropsychology 23*(1/2): 141-174.

Atkinson, J., Braddick, O., Anker, S., Ehrlich, D., Macpherson, F., Rae, S., King, J., Mercuri, E., Nokes, L., & Braddick, F. (1996a) Development of sensory, perceptual, and cognitive vision and visual attention in young Williams Syndrome children. Presentation and poster at the Seventh International Professional Conference on Williams Syndrome, King of Prussia, PA.

Atkinson, J., Braddick, O., Bobier, B., Anker, S., Ehrlich, D., King, J., Watson. P., & Moore, A. (1996b). Two infant vision screening programmes: prediction and prevention of strabismus and amblyopia from photo- and videorefractive screening. *Eye 10*(2): 189-198.

Atkinson, J., Hood, B., Wattam-Bell J., & Braddick, O.J. (1992). Changes in infants' ability to switch visual attention in the first three months of life. Perception, 21: 643-653.

Atkinson, J., Nardini, M., Anker, S., Braddick, O., Hughes, C., & Rae, S. (2005). Refractive errors in infancy predict reduced performance on the Henderson Movement Assessment Battery for Children at 3.5 and 5.5 years. *Developmental Medicine and Child Neurology* 47, 243-251.

Atkinson et al (in preparation a). Cortical visual function, neonatal MRI, and developmental outcome in preterm infants.

Atkinson et al (in preparation b).

Backen Jones, L., Rothbart, M. K., & Posner, M. I. (2003). Development of executive attention in preschool children. *Developmental Science, 6,* 498-504.

Baillargeon, R., and J. DeVos. 1991. Object permanence in young infants: further evidence. *Child Development* 62:1227-1246

Baird, A. A., J. Kagan, T. Gaudette, K. A. Walz, N. Hershlag, and D. A. Boas. (2002). Frontal lobe activation during object permanence: data from near-infrared spectroscopy. Neuroimage 16:1120-1125.

Bell, M. A., and N. A. Fox. (1992). The relations between frontal brain electrical activity and cognitive development during infancy. Child Development 63:1142-1163.

Bellugi, U., Bihrle A, Trauner, D, Jernigan, T & Doherty, S (1990) Neuropsychological, neurological, and neuroanatomical profile of Williams syndrome children. American Journal of Medical Genetics (Supplement), 6, 115-125

Bellugi, U., Lichtenberger, L., Mills, D., Galaburda, A. & Korenberg, J. R. (1999) Bridging cognition, the brain, and molecular genetics: evidence from Williams syndrome. Trends in Neurosciences, 22, 197-207.

Bellugi, U., Sabo, H. & Vaid, J. (1988). Spatial deficits in children with Williams syndrome. In J. Stiles-Davis, M. Kritchevsky & U. Bellugi (eds) Spatial Cognition: Brain Bases and Development. Hillsdale NJ: Lawrence Erlbaum.

Bellugi, U., Wang, P.P. & Jernigan, T.L. (1994). Williams syndrome: An unusual neuropsychological profile. In S. H. Broman & J. Grafman (eds.) Atypical cognitive deficits in developmental disorders: Implications for Brain Function (pp.23-56). Lawrence Erlbaum, Hillsdale NJ.

Bertenthal BI, Proffitt DR, Spetner NB, Thomas MA (1985) The development of infant sensitivity to biomechanical motions. Child Development, 56: 531-543

Bertenthal, B. I., & J. J. Campos. (1990). A systems approach to the organizing effects of self-produced locomotion during infancy. *Advances in Infancy Research* 6:1-60.

Berthier, N., & Keen, R. (2006). Development of reaching in infancy. Experimental Brain Research 169: 507-518.

Berthoz, A. (1996). Neural basis of decision in perception and the control of movement. In Damasio, A. R., Damasio, H., & Christen, Y. (Eds.) Neurobiology of decsion making. Berlin: Springer.

Bertrand J., Mervis C. B., & Eisenberg J. D. (1997) Drawing by children with Williams syndrome: A developmental perspective. Developmental Neuropsychology, 13, 41-67.

Bhutta, A. T., Cleves, M. A., Casey, P. H., Craddock, M. M., & Anand, K. J. (2002). Cognitive and Behavioral Outcomes of School-Aged Children Who Were Born Preterm: a Meta-Analysis. *Journal of the American Medical Association*, 288, 728-737.

Biro, S. & Russell, J. (2001). The execution of arbitrary procedures by children with autism. *Development and Psychopathology,13,* 97-110.

Bojczyk, K.E. & Corbetta, D. (2004). Object retrieval in the 1st year of life:learning effects of task exposure and box transparency. *Developmental Psychology*, 40, 54-66.

Booth A E, Pinto J, Bertenthal B I (2002). Perception of the symmetrical patterning of human gait by infants. Developmental Psychology, 38: 554-563.

Booth, J. R., B. MacWhinney, K. R. Thulborn, K. Sacco, J. T. Voyvodic, and Feldman, H. M. (2000). Developmental and lesion effects in brain activation during sentence comprehension and mental rotation. Dev Neuropsychol 18:139-169.

Boussaoud, D., Ungerleider, L. G. & Desimone, R. (1990). Pathways for motion analysis: cortical connections of the medial superior temporal and fundus of the superior temporal visual areas in the macaque. J. comp. Neurol, 296: 462-495.

Braddick O J, O'Brien J M D, Wattam-Bell J, Atkinson J and Turner R (2000). Form and motion coherence activate independent, but not dorsal/ventral segregated, networks in the human brain. *Current Biology* 10: 731-734.

Braddick, O., Curran, W., Atkinson, J., Wattam-Bell, J., & Gunn, A. (2002a). Infants' sensitivity to global form coherence. *Investigative Ophthalmology & Visual Science 43*: E-Abstract 3995.

Braddick O J, O'Brien J, Rees G, Wattam-Bell J, Atkinson J, Turner R (2002b) Quantitative neural responses to form coherence in human extrastriate cortex. Presentation at Society for Neuroscience. Program no 721.9. Available online.

Braddick O, Atkinson J, & Hood B. (1996). Monocular vs binocular control of infants' reaching. Investigative Ophthalmology & Visual Science, 37, S290.

Braddick O., Atkinson J., Hood B., Harkness W., Jackson G., Vargha-Khadem F. (1992). Possible blindsight in infants lacking one cerebral hemisphere. Nature 360: 461-463.

Braddick, O J, O'Brien J M D, Wattam-Bell J, Atkinson J, Hartley T, Turner R (2001). Brain areas sensitive to coherent visual motion. Perception, 30: 61-72.

Braddick, O. (1996). Binocularity in infancy. Eye, 10: 182-188.

Braddick, O. J., & Atkinson, J. (2003). Top-down, bottom-up, and sideways in infants' development of visual object organisation. *Perception 32*(Suppl.): 49-50.

Braddick, O. J., Atkinson, J., & Wattam-Bell, J. (1989). Development of visual cortical selectivity: binocularity, orientation, and direction of motion. In von Euler (Ed,), *Neurobiology of early infant behaviour* (pp. 165-172). London: MacMillan.

Braddick, O., & Qian, N. (2000). The organisation of global motion and transparency. In J. M. Zanker & J. Zeil (Eds.), *Motion vision* (pp. 86-112). Berlin: Springer Verlag.

Braddick, O., Atkinson, J., & Wattam-Bell, J. (2003). Normal and anomalous development of visual motion processing: Motion coherence and 'dorsal stream vulnerability'. Neuropsychologia 41(13): 1769-1784.

Breckenridge et al (in preparation). The structure of attention in preschool-age children.

Bruner, J.S. (1970). The growth and structure of skill. In K Connolly (Ed.), *Mechanisms of motor skill development* (pp. 62-94). New York: Academic Press.

Butterworth G, & Grover L. (1990) Joint visual-attention, manual pointing, and preverbal communication in human infancy. Pp. 605-624 in Attention and Performance XIII Cambridge MA: MIT Press.

Cheng, K. & Newcombe, N. S. (2005). Is There a Geometric Module for Spatial Orientation? Squaring Theory and Evidence. Psychonomic Bulletin and Review, 12, 1-23.

Chugani, H. T., M. E. Phelps, and J. C. Mazziotta. 1987. Positron emission tomography study of human brain functional development. Annals of Neurology 22:487-497.

Corkum, P.V., Byrne, J.M., & Ellsworth, C. (1995). Clinical assessment of sustained attention in preschoolers. Child Neuropsychology, 1, 3-18.

Cowie, D., Smith, L., Braddick, O., & Atkinson, J. (2006a Stepping stones across the river: Visually guided planning of locomotion in children and adults. Perception, S35: 95

Cowie, D., Smith, L., Braddick, O., Atkinson, J., & Nardini, M. (2006b The development of visually guided locomotor planning. Cognitive Processing, 7 (S5), 123.

Cowie, D., Smith, L., Braddick, O., & Atkinson, J. (2006c Locomotor planning in Williams syndrome. Presentation at the 3rd Williams Syndrome Workshop, Reading.

Cowie et al., in preparation

Damasio, A. R. & Benton, A. L. (1979). Impairment of hand movements under visual guidance. Neurology, 29: 170-178.

Diamond, A. (1991). Neuropsychological insights into the meaning of object concept development. In S. Carey & R. Gelman (Eds), Biology and knowledge: Structural constraints on development (pp. 37-80). Hillsdale, NJ: Erlbaum.

Diamond, A., J. F. Werker, and C. Lalonde. 1994. Toward understanding commonalities in the development of object search, detour navigation, categorization, and speech perception. In

Human behavior and the developing brain., G. Dawson, K. W. Fischer and et al., eds. New York, NY: The Guilford Press, pp. 380-426.

Diamond, A., S. Zola-Morgan, and L. R. Squire. 1989. Successful performance by monkeys with lesions of the hippocampal formation on AB and object retrieval, two tasks that mark developmental changes in human infants. Behavioral Neuroscience 103:526-537.

Fagard, J. (1994). Manual strategies and interlimb coordination during reaching, grasping, and manipulating throughout the first year of life. In S. Swinnen, H. Heuer, J. Massion, & P. Casaer (Eds.) Interlimb coordination: Neural, dynamical and cognitive constraints (pp. 439-460). San Diego, C.A: Academic Press.

Fagard, J. (2000). Linked proximal and distal changes in the reaching behaviour of 5- to 12-month-old human infants grasping objects of different sizes. Infant Behaviour and Development, 23, 317-329.

Fagard, J., & Jacquet, A.Y. (1996). Changes in reaching and grasping objects of different sizes between 7 and 13 months of age. British Journal of Developmental Psychology, 14, 65–78.

Felleman, D.J. and Van Essen D.C. (1991) Distributed hierarchical processing in primate cerebral cortex. Cerebral Cortex 1:1-47.

Fox, N. A., and M. A. Bell. (1990). Electrophysiological indices of frontal lobe development: Relations to cognitive and affective behavior in human infants over the first year of life. Annals of the New York Academy of Sciences 608:677-704.

Gallant, J. L., Braun, J. & Van Essen, D.C. (1993). Selectivity for polar, hyperbolic, and Cartesian gratings in macaque visual cortex. Science, 259, 100-103.

Gerstadt, C.L., Hong, Y.J. and Diamond, A. (1994). The relationship between cognition and action: performance of children 3 1/2 - 7 years old on a Stroop-like day-night test. Cognition, 53, 129-153.

Gibson, E.J. & Walk, R.D. (1960). The "visual cliff". *Scientific American*, 202, April, 64-71.

Goodale MA & Milner AD. (2003) Sight Unseen: An Exploration of Conscious and Unconscious Vision. Oxford: Oxford University Press

Goodale, M.A, Milner, A.D., Jakobsen LS. and Carey, D.P.(1991) A neurological dissociation between perceiving objects and grasping them. Nature, 349, 154-156.

Gunn, A., Cory, E., Atkinson, J., Braddick, O., Wattam-Bell, J., Guzzetta, A., & Cioni, G. (2002). Dorsal and ventral stream sensitivity in normal development and hemiplegia Neuroreport 13(6): 843-847.

Heaton, S. C., Reader, S. K., Preston, A. S., Fennell, E. B., Puyana, O. E., Gill, N. et al. (2001). The Test of Everyday Attention for Children (TEA-Ch): Patterns of performance in children with ADHD and clinical controls. Child Neuropsychology, 7, 251-264.

Henderson, S. E. & Sugden, D.A. (1992). The Movement ABC manual. The Psychological Corporation, London.

Hermer, L. & Spelke, E. (1994). A Geometric Process for Spatial Reorientation in Young Children. Nature, 370, 57-59.

Hermer, L. & Spelke, E. (1996). Modularity and Development: the Case of Spatial Reorientation. Cognition, 61, 195-232.

Hermer-Vazquez, L., Spelke, E. S., & Katsnelson, A. S. (1999). Sources of Flexibility in Human Cognition: Dual Task Studies of Space and Language. Cognitive Psychology, 39, 3-36.

Hofstadter, M., and J. S. Reznick. 1996. Response modality affects human infant delayed-response performance. Child Development 67:646-658.

Hood, B. & Atkinson, J. (1990). Sensory visual loss and cognitive deficits in the selective attentional system of normal infants and neurologically impaired children. Developmental Medicine and Child Neurology, 32: 1067-1077.

Hood, B. & Atkinson J. (1993) Disengaging visual attention in the infant and adult. Infant Behaviour and Development, 16: 405-422.

Hood, B. (1995). Gravity rules for 2-4 year olds. Cognitive Development, 10, 577-598.

Horobin, K., and L. Acredolo. 1986. The role of attentiveness, mobility history, and separation of hiding sites on Stage IV search behavior. Journal of Experimental Child Psychology 41:114-127.

Hughes, C. & Russell, J. (1993) Autistic children's difficulty with mental disengagement from an object: its implications for theories of autism. Developmental Psychology 29, 498-510.

Huttenlocher, J. & Presson, C. C. (1973). Mental rotation and the perspective problem. Cognitive Psychology, 4, 277-299.

Huttenlocher, J., Newcombe, N., & Sandberg, E. (1994). The coding of spatial location in young children. Cognitive Psychology, 27, 115-147.

Huttenlocher, P.R., de Courten, C., Garey, L.G. & van der Loos, H. (1982). Synaptogenesis in human visual cortex - evidence for synapse elimination during normal development. Neuroscience Letters 33: 247-252.

Jacobs, B., H. T. Chugani, V. Allada, S. Chen, M. E. Phelps, D. B. Pollack, and M. J. Raleigh. (1995). Developmental changes in brain metabolism in sedated rhesus macaques and vervet monkeys revealed by positron emission tomography. Cerebral Cortex 5:222-233.

Jeannerod, M. (1997). The Cognitive Neuroscience of Action. Oxford: Blackwell.

Karmiloff-Smith, A. (1998). Development itself is the key to understanding developmental disorders. Trends in Cognitive Sciences 2, 389-398

Kaplan, P., Kirsschner, M., Watters, G. and Costa, M.T. (1989) Contractures in children with Williams syndrome. Pediatrics, 84(5), 895-899.

Kellman PJ, Spelke ES (1983). Perception of partly occluded objects in infancy. Cognitive Psychology, 15: 483-524.

Kelly, T. P. (2000). The clinical neuropsychology of attention in school-aged children. Child Neuropsychology, 6, 24-36.

Kermoian, R., and J. J. Campos. 1988. Locomotor experience: A facilitator of spatial cognitive development. Child Development 59:908-917.

King, J.A., Atkinson, J., Braddick, O.J., Nokes, L. and Braddick, F. (1996). Target preference and movement kinematics reflect development of visuomotor modules in the reaching of human infants. Investigative Ophthalmology and Visual Science, 37, S526.

Kingsnorth, S. & Schmuckler, M.A. (2000) Walking skill versus walking experience as a predictor of barrier crossing in toddlers. *Infant Behaviour and Development*, 23, 331-350.

Kirkham, N. Z., Cruess, L., & Diamond, A. (2003). Helping children apply their knowledge to their behavior on a dimension-switching task. Developmental Science, 6, 449-476.

Klein B.P. & Mervis C.B. (1999). Contrasting patterns of cognitive abilities of 9 and 10-year-olds with Williams syndrome or Down syndrome. Developmental Neuropsychology, 16, 177-196.

Kosslyn, S. M., J. A. Margolis, A. M. Barrett, E. J. Goldknopf, et al. (1990). Age differences in imagery abilities. Child Development 61:995-1010.

LaBerge, D. & Brown, V. (1989). Theory of attentional operations in shape identification. Psychological Review, 96: 101-124.

Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Childrens' Use of Landmarks: Implications for Modularity Theory. Psychological Science, 13, 337-341.

Lee, D.N., & Aronson, E. (1974). Visual proprioceptive control of standing in human infants. Perception and Psychophysics, 15, 529 – 532.

Leslie AM, (1984). Spatiotemporal continuity and the perception of causality in   infants. Perception, 13:287-305

Livingstone, M. & Hubel, D. H. (1988). Segregation of form, color, movement and depth: anatomy, physiology and perception. Science, 240: 740-749.

Mahone, E. M., Pillion, J. P., Hoffman, J., Hiemenz, J. R., & Denckla, M. B. (2005). Construct validity of the auditory continuous performance test for preschoolers. Developmental Neuropsychology, 27, 11-33.

Manly, T., Nimmo-Smith, I., Watson, P., Anderson, V., Turner, A., & Roberston, I. H. (2001). The Differential Assessment of Children's Attention: The Test of Everyday Attention for

Children (TEA-Ch), Normative Sample and ADHD Performance. Journal of Child Psychology and Psychiatry, 42, 1065-1081.

Marlow, N., Wolke, D., Bracewell, M. A., Samara, M., & EpiCure Study Group (2005). Neurologic and Developmental Disability at Six Years of Age After Extremely Preterm Birth. New England Journal of Medicine, 352, 71-72.

Marmor, G. S. 1975. Development of kinetic images: When does the child first represent movement in mental images? Cognitive Psychology 7:548-559.

McKay, K. E., Halperin, J. M., Schwartz, S. T., & Sharma, V. (1994). Developmental analysis of three aspects of information processing: Sustained attention, selective attention, and response organization. Developmental Neuropsychology, 10, 121-132.

Mercuri, E., Atkinson, J., Braddick, O., Anker, S., Nokes, L. Cowan, F., Rutherford, M., Pennock, J. & Dubowitz, L. (1996). Visual function and perinatal focal cerebral infarction. Archives of Disease in Childhood, 75: F76-F81.

Mercuri, E., Atkinson, J., Braddick, O., Anker, S., Nokes, L. Cowan, F., Rutherford, M., Pennock, J. & Dubowitz, L. (1997a). Basal ganglia damage in the newborn infant as a predictor of impaired visual function. Archives of Disease in Childhood, 77: F111-F114.

Mercuri, E., Atkinson, J., Braddick, O., Anker, S., Cowan, F., Rutherford, M., Pennock, J. & Dubowitz, L. (1997b). Visual function in full term infants with hypoxic-ischaemic encephalopathy. Neuropediatrics 28: 155-161.

Mercuri, E., Atkinson, J., Braddick, O., Rutherford, M., Cowan, F., Counsell, S., Dubowitz, L., & Bydder, G. (1997c) Chiari I malformation and white matter changes in asymptomatic young children with Williams syndrome: clinical and MRI study. European Journal of Paediatric Neurology 5/6 177-181

Merigan, W. H. & Maunsell, J. H. R. (1993). How parallel are the primate visual pathways? Ann. Rev. Neuroscience, 16: 369-402.

Meyer-Lindenberg A, Kohn P, Mervis CB, Kippenhan JS, Olsen RK, Morris CA et al. (2004). Neural basis of genetically determined visuospatial construction deficit in Williams syndrome. Neuron, 43: 623-31.

Milner, A. D. and Goodale, M. A. (1995). The visual brain in action. Oxford: Oxford University Press.

Nardini, M. (2006). Components of Spatial Memory: a Developmental Analysis. PhD Thesis, University of London,

Nardini, M., Burgess, N., Breckenridge, K., & Atkinson, J. (2006a). Differential developmental trajectories for egocentric, environmental and intrinsic frames of reference in spatial memory. Cognition, 101, 153-172.

Nardini, M., Braddick, O., Atkinson, J., Cowie, D., Ahmed, T., & Reidy, H. (*submitted a*) Uneven integration for perception and action cues in children's working memory.

Nardini, M., Atkinson, J., Braddick, O., & Burgess, N. (2006b). The development of body, environment, and object-based frames of reference in spatial memory in normal and atypical populations. Cognitive Processing, 7, 68-69.

Nardini, M., Atkinson, J., & Burgess, N. (2007). Children reorient using the left / right sense of coloured landmarks at 18-24 months. *Cognition* doi:10.1016/j.cognition.2007.02.007

Nardini, M., Atkinson, J., & Burgess, N. & Braddick (*submitted b*). Developmental strajectories for spatial frames of reference in Williams Syndrome.

Nardini, M., Braddick, O., & Atkinson, J. (2006). Young children's errors combining visual information for recognition and action. Perception, 35S, 3-4.

Newcombe, N. & Huttenlocher, J. (1992). Children's early ability to solve perspective-taking problems. Developmental Psychology, 28, 635-643.

Newcombe, N., Huttenlocher, J., Bullock Drummey, A., & Wiley, J. G. (1998). The development of spatial location coding: Place learning and dead reckoning in the second and third years. Cognitive Development, 13, 185-200.

Newman, C. (2001). The Planning and control of action in normal Infants and children with Williams Syndrome. Ph D Thesis, University of London.

Newman, C., Atkinson, J., & Braddick, O. (2001). The development of reaching and looking preferences in infants to objects of different sizes. Developmental Psychology 37: 561-572.

O'Keefe J., Burgess N. (1996) Geometric determinants of the place fields of hippocampal neurones. Nature 381, 425-428.

Patla, A.E. (1991) Visual control of human locomotion. In *Adaptability of Human Gait*, Ed. Patla, Elsevier Science Publishers B.V. (North-Holland).

Patla, A.E., & Goodale, M.A. (1996) Obstacle avoidance during locomotion is unaffected in a patient with visual form agnosia. *NeuroReport* 8(1): 165-168.

Paul, B. M., Stiles, J., Passarotti, A. M., Bavar, N., & Bellugi, U. (2002). Face and Place Processing in Williams Syndrome: Evidence for a Dorsal-Ventral Dissociation. Neuroreport, 13, 1115-1119.

Pezzini, G., Vicari, S., Volterra, V. & Milani, L. & Ossella, M.T. (1999) Children with Williams syndrome: is there a single neuropsychological profile? Developmental Neuropsychology, 15, 141-155 (1999)

Posner, M. I. (1980). Orienting of attention. Quarterly Journal of Experimental Psychology, 32: 3-25.

Posner, M. I. & Petersen, S. E. (1990). The attention system of the human brain. Ann. Rev. Neurosci., 13: 25-42.

Posner, M. I. & Cohen, Y. (1980). Attention and the control of movements. In Tutorials in motor behavior (eds.), G. E. Stelmach & J. Requin (pp. 243-258). Amsterdam: North Holland Publishing.

Posner, M.I. & Dehaene, S. (1994). Attentional networks. Trends in Neurosciences, 17: 75-79.

Prather, P.A., Sarmento, N., & Alexander, A. (1995). Development of vigilance in preschoolers. Journal of the International Neuropsychological Society, 1, 153.

Rees, G., Friston, K., & Koch, C. (2000) A direct quantitative relationship between the functional properties of human and macaque V5. Nat Neurosci., 3, 716-23

Reiss AL, Eckert MA, Rose FE, Karchemskiy A, Kesler S, Chang M et al. (2004). An experiment of nature: brain anatomy parallels cognition and behavior in Williams syndrome. Journal of Neuroscience, 24: 5009-15.

Rieser, J. J. (1979). Spatial Orientation of Six-Month-Old Infants. Child Development, 50, 1078-1087.

Rizzolatti, G. (1983). Mechanisms of selective attention in mammals. In Ewwert, J.-P., Capranica, R. R. & Ingle, D. J. (eds.) Advances in vertebrate neuroethology, pp. 261-297. Amsterdam: Elsevier.

Rizzolatti, G. and Camarda, R. (1987). Neural circuits for spatial attention and unilateral neglect. In Jeannerod, M. (ed.) Neurophysiological and neuropsychological aspects of spatial neglect. pp. 289-213. Amsterdam: Elsevier.

Rochat P, Morgan R, Carpenter M (1997). Young infants' sensitivity to movement information specifying social causality. Cognitive Development, 12: 441-465.

Rosenbaum, D. A., Vaughan, J., Barnes, H. J., & Jorgensen, M. J. (1992). Time course of movement planning: selection of handgrips for object manipulation. Journal of Experimental Psychology: Learning, Memory & Cognition 18(5): 1058-1073.

Rueda, M. R., Fan, J., McCandliss, B. D., Halparin, J. D., Gruber, D. B., Lercari, L. P. et al. (2004). Development of attentional networks in childhood. Neuropsychologia, 42, 1029-1040.

Schneider, G. E. (1969). Two visual systems: brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions. Science, 163: 895-902.

Shumway-Cook, A. & Wollacott, M. (1985) The growth of stability: postural control from a developmental perspective. J Mot Behav, 17: 131-147.

Sovrano, V. A. & Vallortigara, G. (2006). Dissecting the Geometric Module. Psychological Science, 17, 616-621.

Spencer J., O'Brien J, Riggs K, Braddick O, Atkinson, J & Wattam-Bell J. (2000) Motion processing in autism: Evidence for a dorsal stream deficiency. NeuroReport 11: 2765-2767.

Sprague, J.M. & Meikle, T.H. (1965). The role of the superior colliculus in visually guided behavior. Experimental Neurology, 11: 115-146.

Stiles, J. (2000). Neural Plasticity and Cognitive Development. Developmental Neuropsychology, 18, 237-272.

Stiles, J., Stern, C., Trauner, D., & Nass, R. (1996). Developmental Change in Spatial Grouping Activity Among Children With Early Focal Brain Injury: Evidence From a Modeling Task. Brain and Cognition, 31, 46-62

Stiles-Davis, J., Sugarman, S., & Nass, R. (1985). The Development of Spatial and Class Relations in Four Young Children With Right Cerebral Hemisphere Damage: Evidence for Early Spatial-Constructive Deficit. Brain and Cognition, 4, 388-412.

Ungerleider, L. G. and Mishkin, M. (1982) Two cortical visual systems. In D. J. Ingle, M. A. Goodale & R. J. W. Mansfield (eds.) Analysis of Visual Behavior, pp.549-586. Cambridge, MA: MIT Press.

Van Essen, D.C. and Maunsell, J.H.R. (1983). Hierarchical organization and functional streams in visual cortex. Trends in Neurosciences, 6: 370-375.

Vicari, S., Bellucci, S., & Carlesimo, G. A. (2006). Evidence From Two Genetic Syndromes for the Independence of Spatial and Visual Working Memory. Developmental Medicine and Child Neurology, 48, 126-131.

Von Hofsten C & Rosander K (1996) The development of gaze control and predictive tracking in young infants. Vision Research 36: 81-96

Von Hofsten C & Rosander K (1997) Development of smooth pursuit tracking in young infants. Vision Research 37: 1799-1810.

von Hofsten, C. (2005). The development of prospective control in looking. In J. Lockman & J. Rieser (Eds.), Action as an organizer of perception and cognition during learning and development. Minnesota Symposium on Child Psychology. Vol 36. Mahwah, NJ: Lawrence Erlbaum.

Walker AS, Owsley CJ, Megaw-Nyce J, Gibson EJ, Bahrick LE (1980). Detection of elasticity as an invariant property of objects by young infants. Perception 9: 713-718.

Wang, R. F. & Simons, D. J. (1999). Active and Passive Scene Recognition. Cognition, 70, 191-210.

Wattam-Bell, J. (1992). The development of maximum displacement limits for discrimination of motion direction in infancy. Vision Research , 32: 621-630.

Wattam-Bell, J. (1994). Coherence thresholds for discrimination of motion direction in infants. Vision Research 34(7): 877-883.

Wattam-Bell, J. (1995). Stereoscopic and motion Dmax in adults and infants. Investigative Ophthalmology & Visual Science, 36: S910

Wattam-Bell, J. (1996). The development of visual motion processing. In F Vital-Durand, O Braddick, & J Atkinson (Eds). Infant Vision, Oxford University Press.

Zeki, S. (1993). A Vision of the Brain. Blackwell Scientific Publications, Oxford.

Zelazo, P.D., Frye, D., & Rapus, T. (1996). An age-related dissociation between knowing rules and using them. Cognitive Development, 11, 37-63.

Zihl, J., von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. Brain. 1983 106:313-40.