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Review

Development of human visual function

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ABSTRACT

By 1985 newly devised behavioural and electrophysiological techniques had been used to track development of infants' acuity, contrast sensitivity and binocularity, and for clinical evaluation of developing visual function. This review focusses on advances in the development and assessment of infant vision in the following 25 years.

Infants' visual cortical function has been studied through selectivity for orientation, directional motion and binocular disparity, and the control of subcortical oculomotor mechanisms in fixation shifts and optokinetic nystagmus, leading to a model of increasing cortical dominance over subcortical pathways. Neonatal face processing remains a challenge for this model.

Recent research has focussed on development of integrative processing (hyperacuity, texture segmentation, and sensitivity to global form and motion coherence) in extra-striate visual areas, including signatures of dorsal and ventral stream processing. Asynchronies in development of these two streams may be related to their differential vulnerability in both acquired and genetic disorders.

New methods and approaches to clinical disorders are reviewed, in particular the increasing focus on paediatric neurology as well as ophthalmology. Visual measures in early infancy in high-risk children are allowing measures not only of existing deficits in infancy but prediction of later visual and cognitive outcome. Work with early cataract and later recovery from blinding disorders has thrown new light on the plasticity of the visual system and its limitations.

The review concludes with a forward look to future opportunities provided by studies of development post infancy, new imaging and eye tracking methods, and sampling infants' visual ecology.

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1. Introduction: scope of this review

Between 1975 and 1985, there was a rapid development of work on the development in human infants of acuity, contrast sensitivity, refraction and accommodation, and binocularity. Basic methods were established that could be applied in the clinic to assess visual function in infants and young children such as the Teller acuity cards, Cambridge Crowding cards, photo/videorefraction and the sweep VEP.

Work in the last 25 years has built on this foundation to explore how higher level aspects of visual processing develop. This period has seen increasing insights into the emergence of characteristic aspects of selective processing in V1, including orientation- and direction-selectivity, and into the developing interactions between cortical and subcortical systems, particularly in relation to oculomotor control. In the last decade, a major focus has been the development of integrative functions depending on extra-striate visual

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areas, for example texture segmentation and pop-out, hyperacuity, grouping, illusory contour formation, global form and global motion sensitivity. This work has highlighted questions of developmental relations between the dorsal and ventral cortical streams. This division between cortical streams has proved to be an increasingly important area for work on visual correlates of developmental disorders, which have shown wide-ranging 'dorsal stream vulnerability'. It has also contributed to an increasing trend to unify visual development with other aspects of developmental cognitive neuroscience (e.g. attention and the control of action). A summary neurobiological model is presented of visual development in the first year of life, which includes eye and brain networks integrating sensory visual processing with systems of visuo-motor control of action and selective attention.

The clinical application of the science of visual development has extended from the ophthalmology clinic (ocular disorders, strabismus and amblyopia) to an increasing engagement with paediatric neurology, where vision can provide a uniquely early functional window into the typically and atypically developing infant brain. Applications to perinatal brain injury, very premature infants, and genetic neurodevelopmental disorders are reviewed, as well as refractive screening for amblyogenic conditions. Work is also

reviewed on the effects of short- and long-term visual deprivation, which has increased our knowledge of the developmental plasticity of the visual system in and beyond V1.

The volume and range of work on human visual development is too great to be covered in the scope of this article: *Vision Research* alone has published over 270 papers on visual development in the period 1985–2010. Our coverage, therefore, will reflect the authors' particular interests and expertise in spatial pattern vision, cortical mechanisms, and their application to neurodevelopmental disorders. Major omissions include infant colour vision, scotopic vision and light/dark adaptation (these areas received a thorough review in this journal by Brown (1990)), visual fields and temporal/nasal differences, and pictorial depth cues; their absence does not reflect any judgment on either the scientific or the clinical importance of these topics. We have also concentrated on development in infancy. This has been the most intensively studied part of the life-span for visual development, but as we comment in the concluding section, there is increasing awareness of the ways in which visual capabilities, and their underlying brain bases, continue to develop through adolescence (see Skoczenski and Norcia (2002), and Knoblauch, Vital-Durand, and Barbur (2001) for two examples). However, a critical review that could do justice to work on development beyond infancy would stretch the bounds of this paper to breaking point. Some other areas – amblyopia, oculomotor development, vergence and accommodation, refractive development, temporal sensitivity, and face processing – will be touched on through connections with our major themes, but cannot be reviewed as fully as the amount of interesting work on these topics would deserve. We have reviewed many of these areas more extensively elsewhere (Atkinson, 2000; Atkinson & Braddick, in press, chap. 12; Braddick & Atkinson, 2009).

Prospects for future development of the field are discussed, including the continuity of visual development through childhood, the application of technical advances in neuroimaging and eye tracking, and sampling the visual ecology of the developing infant.

2. Infant vision: the early years

When *Vision Research* was born in 1960, human visual development barely existed as a scientific field. Paediatric ophthalmologists had to cope with the visual disorders of infants and children, and developmental psychologists tried to understand how they gained an understanding of the world which depended heavily on vision. But visual scientists generally did not see the early years of development as within their scope, and certainly did not see them as a subject for empirical investigation.

Vision Research published almost nothing recognisable as a developmental paper before 1969, and the first involving any investigation of human infant behaviour came with Tronick and Clanton's (1971) study of infant looking patterns. However, the field had been effectively seeded by Fantz's (1961) invention of preferential looking and habituation-recovery (Fantz, 1964) as means of revealing infants' visual discriminative abilities. In the mid 70s these were picked up first by Teller, Morse, Borton, and Regal (1974) who innovated the combination of preferential looking with forced choice by a 'blind' observer (forced-choice preferential looking = FPL), and then by others who saw the possibilities of combining them with the methods of visual psychophysics and new display technologies such as contrast sensitivity measurements (Atkinson, Braddick, & Braddick, 1974; Atkinson, Braddick, & Moar, 1977a, 1977b; Banks & Salapatek, 1978), and random-dot stereograms (Atkinson & Braddick, 1976; Fox, Aslin, Shea, & Dumais, 1980). The other methodological driver of progress was the realisation that visual evoked potentials could be recorded from infants and provided evidence on their development of

spectral sensitivity (Dobson, 1976), acuity (Sokol, 1978), contrast sensitivity (Atkinson, Braddick, & French, 1979; Harris, Atkinson, & Braddick, 1976; Pirchio, Spinelli, Fiorentini, & Maffei, 1978) and binocular interaction (Braddick et al., 1980; Petrig, Julesz, Kropfl, Baumgartner, & Anliker, 1981).

Visual development was the subject of a personal retrospective by Teller and Movshon (1986) in the issue marking the first 25 years of *Vision Research*, which gives a good view of the emphases and motivation of the early years of infant vision research. As well as the opportunity to exploit new techniques, it is clear that a major stimulus was the discovery in animals of plasticity of visual cortical organization during a critical period, pioneered by Wiesel and Hubel (1963), and accompanying studies on the normal development of this organization (e.g. Hubel & Wiesel, 1963; Wiesel & Hubel, 1974). The opening up of this field of developmental neuroscience brought to the forefront an inspiring goal: the development of infants' visual capabilities might be understood in terms of the structural and functional development of the visual system. Work on early plasticity also highlighted the relevance of physiological studies to the common problems of paediatric ophthalmology such as strabismus and amblyopia – a link which, if it was to be realised in practice, needed solid scientific knowledge of human visual development.

The links to the physiological studies and to amblyopia/strabismus meant that infant vision research up to the early 1980s focussed particularly on two areas: the development of visual acuity (since this was the commonest functional measure in clinical practice) and binocular interaction (the main area of plasticity that had been studied, and the key to studying strabismus). By 1980 there was a clear picture of how acuity develops rapidly in the first months of life, from neonatal values typically found to be around 1 c/deg, although some debate continued about discrepancies between behavioural and VEP measures (see reviews by Atkinson and Braddick (1981), Boothe, Dobson, and Teller (1985), Dobson and Teller (1978), Norcia and Tyler (1985)). Later, these different acuity and contrast sensitivity values, estimated from VEP and behavioural measures were not evident if similar stimuli and measures were compared across techniques on the same child (Atkinson, 2000). These measures of acuity in early life raised the question: what developing properties of the visual system determine the limits on acuity and contrast sensitivity in infancy? Visual optics and accommodation provide one potential limit which was investigated in this period, both by dynamic- and near-retinoscopy (Banks, 1980; Mohindra, Held, Gwiazda, & Brill, 1978) and by new methods of photorefractometry (Howland, Atkinson, Braddick, & French, 1978; Braddick, Atkinson, French, & Howland, 1979; Hainline, Riddell, Grose-Fifer, & Abramov, 1992). This work introduced the potential of large-scale refractive screening of infants (Atkinson, 1993; Atkinson, Braddick, Nardini, & Anker, 2007); it also showed that, in early infancy, while the accuracy of accommodative responses increased, even the youngest infants focussed sufficiently well at the normal distance for acuity testing that optical factors were not generally a significant limit.

A more interesting potential limit is imposed by the immature outer segment morphology and packing density of the foveal cones, and small eye diameter, in newborn infants (Youdelis & Hendrickson, 1986). Banks and Bennett (1988) calculated what would be the effect of these immaturities if the infant visual system then uses the information supplied by the cones as efficiently as the adult's. The calculation suggests that if the improvement of acuity from 1-month to adult is taken as 12-fold, only about 25% of this change can be attributed to the photoreceptors and to increasing eye size. However, anatomical information on cone structure in infants is inevitably very limited, and provides almost no data to track the correspondence between functional and anatomical development over the marked changes of the first 6 months. Thus,

while the role of receptor development is certainly significant, major changes must occur higher up, in the organization of the neural pathways that transmit visual spatial information.

Binocular interaction is unambiguously 'higher up', and so the insight into development of a central visual process, as well as the clinical significance and the link to animal studies of cortical organization, provided a strong motivation for investigating binocularity in infants. Work around 1980 from different laboratories using diverse behavioural and VEP approaches (Birch, Gwiazda, & Held, 1982; Braddick, Wattam-Bell, Day, & Atkinson, 1983; Braddick et al., 1980; Fox et al., 1980; Held, Birch, & Gwiazda, 1980; Petrig et al., 1981) showed a remarkable concordance that binocular interaction and the detection of stereo disparities typically emerge between about 11 and 18 weeks of age, but with a substantial degree of individual variation. The work from Held and Birch's group showed a remarkably rapid improvement of stereoacuity following its initial emergence. Our knowledge of binocular development has continued to be refined, including its relationship to vergence control (Birch, Gwiazda, & Held, 1983; Birch & Stager, 1985; Hainline & Riddell, 1995). However, there remain some major areas of controversy and ignorance. One concerns the way in which inputs from the two eyes are organized before the onset of disparity sensitivity. Work by Shimojo, Bauer, O'Connell, and Held (1986; see also Held, 1993) suggested that in the first months, the two eyes made undifferentiated connection to the same cells in layer IV of primary visual cortex, leading effectively to binocular superposition without disparity detection or rivalry. It is hard to see how such a system would not yield differential signals for correlated and anti-correlated dot patterns in the two eyes – the diagnostic for infant binocularity used by Braddick et al. (1980) and Braddick et al. (1983) – and Shimojo's original observations on infants' preferences between compatible and rivalrous binocular stimuli have more recently failed to be replicated (Brown & Miracle, 2003). An alternative, but unproven possibility is the inputs from the two eyes are segregated and do not combine until binocular, disparity sensitive neurons emerge in the upper cortical layers around age 3–4 months.

Another persisting puzzle is the association between strabismus and refraction. Hyperopia has long been known to be associated with early esotropic strabismus, and screening studies have shown that hyperopic refraction can be a precursor of strabismus (Atkinson et al., 1996, 2007). However, the conventional wisdom, that over-accommodation required by hyperopic eyes leads to a breakdown of the coupling between convergence and accommodation, has never been convincingly demonstrated and is perhaps not very plausible as a sole explanation. The relation between blur and convergence is an example of a sensory-motor mapping. Most such mappings have to be highly plastic during development. For example, the relation between distance perception and limb movement for grasping has to be modified as the biomechanics of the arm changes with growth; as has the relation between disparity and vergence as interocular distance changes. It is not clear why the linkage of accommodation and vergence should be an exception.

In the remainder of this article we move on, to review in more detail the progress of work on human visual development since the early 1980s, and some of the prospects for future research.

2.1. The emergence of cortical function

Based on reviewing the limited discriminative abilities that had been demonstrated in newborns, Bronson (1974) had proposed that these abilities were mediated by subcortical systems – a suggestion which in fact goes back to Koffka (1924). This idea was developed by Atkinson (1984), using the much wider range of evidence on infant vision that emerged in the 1970s and early 80s to highlight the changes in performance that occur in the first few

months of life. She proposed that these reflected not just the emergence of specifically cortical processes, but also the function of descending pathways through which these processes modulate and control subcortical visual pathways.

It is well established that pattern-reversal VEPs can be recorded from birth and even some weeks preterm in prematurely born infants (e.g. Atkinson et al., 1979; Harding, Grose, Wilton, & Bissenden, 1989; McCulloch, Orbach, & Skarf, 1999). This might be taken as evidence of visual cortical function. However, the consensus is that VEPs arise not from spiking activity of neurons but from longer lasting potentials, e.g. postsynaptic potentials (Wood & Allison, 1981). Thus, the presence of a pattern-reversal VEP demonstrates that contrast-related signals are reaching the cortical neurons, but not necessarily that these neurons are responding to contrast.

Two kinds of evidence have been used to identify infants' cortical processing. First, mammalian neuroscience has found that the neurons of striate cortex (V1) show selective responses to stimulus properties – particularly orientation, spatial frequency, direction of motion, and binocular relationships – that are not found in the earlier stages of the visual pathway. The emergence of such selective responses in infant vision therefore provides an indicator that cortical function is emerging. Second, the direct pathways from the retina to midbrain centres (in particular the superior colliculus) serve oculomotor functions which undergo striking changes when subject to descending control from the cortex.

As outlined above, VEP and behavioural evidence concurred that binocular interaction in human visual cortex appeared around the 3rd–4th month of life. VEPs were measured time-locked to transitions in binocular relationships (e.g. correlated to anti-correlated) (Braddick et al., 1980; Julesz, Kropfl, & Petrig, 1980; Petrig et al., 1981). It was fundamental to this approach that the binocular transitions were embedded in a series of random dot replacements, so that the binocular component of the response to the transitions could be distinguished from that to local changes in each eye's sequence of random patterns. This approach – extracting a VEP to a high-order transition from events which shared low-level changes – could be applied to other forms of cortical specificity.

In interpreting developmental VEP results, it is important to bear in mind the origin of the VEP as the summated activity in large numbers of neurons. Thus increases in the VEP signal with age may reflect overall changes in neuronal sensitivity, an increased number of neurons showing a particular response, or increasing synchrony in responses across a pool of neurons – an issue discussed below in connection with myelination and temporal precision.

2.1.1. Orientation selectivity

To reveal orientation-selective responses, Braddick, Wattam-Bell, and Atkinson (1986a) isolated infants' VEPs to reversals of grating orientation between opposite obliques by embedding them in a series of random shifts in the gratings' spatial phase. The initial experiments showed that orientation-selective responses first appeared around 6 weeks of age, although later exploration found that at lower reversal frequencies, the response could be recorded at 3 weeks (Braddick, 1993). This aspect of cortical processing, therefore, could not be found at birth but was seen to emerge in a few post-natal weeks.

Orientation-specific masking has been an alternative approach to testing infants for selective cortical channels. Morrone and Burr (1986) found that parallel and orthogonal masks showed no difference in their effect on a grating VEP at 3.5 months, showed differential masking at 4 months, but only showed an adult-like effect of these masks on contrast gain after 6 months. This was interpreted as an initial emergence of orientation-selective channels, followed later by the maturation of inhibitory interactions between these

channels. An analysis of intermodulation responses between test and mask gratings led Candy, Skoczenski, and Norcia (2001) to similar conclusions, albeit expressed in terms of contrast normalization. Overall then, orientation-selective neurons emerges early in human postnatal life, but the dynamics of their responses, and the intracortical interactions on which these may depend, continue to develop at least over the first 6 months: this timetable is consistent with anatomical evidence on the postnatal development of inter-columnar connections in infant visual cortex (Burkhalter, Bernardo, & Charles, 1993).

Behavioural orientation discrimination provided a third line of evidence, which needs to be reconciled with VEP results. Both Atkinson, Hood, Wattam-Bell, Anker, and Tricklebank (1988a) and Slater, Morrison, and Rose (1988) showed using habituation methods that even newborns could discriminate gratings of opposite oblique orientations. However, these stimuli were static, while the VEP of Braddick et al. (1986a) requires dynamically alternating gratings. When the same dynamic frequencies (3 and 8 reversals/s) were used for behavioural testing, discrimination performance appeared at similar ages as the VEP responses (Braddick, 1993; Hood, Atkinson, Braddick, & Wattam-Bell, 1992). This does not simply reflect overall improvement of temporal response to rapidly changing stimuli; the simpler pattern-reversal VEP can be seen for either frequency at birth. There are two alternative interpretations: either orientation selective cortical neurons are present at birth, but have extremely sluggish dynamics; or newborns base their discrimination on some other process, perhaps subcortically based (e.g. if infants' patterns of eye movements are anisotropic, then different contour directions would generate different spatio-temporal contrast as the eyes sweep over them).

2.2. Spatial frequency tuning

Another aspect of cortical selectivity is the tuning of neurons to relatively narrow bands of spatial frequency, compared to earlier levels of the visual pathway (Blakemore & Campbell, 1969; de Valois & de Valois, 1990). This has been less explored in infancy. Banks, Stephen, and Hartmann (1985) used a preferential looking method to test infants' detection of gratings in narrowband masking noise, and found spatial-frequency specific masking in 12-week old but not 6-week-old infants. However, Fiorentini, Pirchio, and Spinelli (1983) report frequency specific masking effects on the VEP for 6-week olds and Suter et al. (1994), using a sweep VEP measure, report evidence for frequency-specific adaptation as young as 3 weeks, although the selectivity is less evident in their data plots for the younger groups. The Banks et al. results suggest a comparable developmental course to the orientation selectivity reviewed above, and Fiorentini's results are compatible with this, while Suter et al. suggest that spatial frequency selectivity is present earlier. Orientation and spatial frequency need to be tested using the same methods and the same age groups, for a more conclusive comparison of the development of these two dimensions of cortical selectivity.

2.2.1. Directional selectivity

Directional responses to motion are another form of selectivity which is seen in primary visual cortex but not in its input. In particular, the evidence is that direction selective responses in the cortex emerge postnatally. By analogy with the methods described for orientation and binocularity, VEPs can be isolated for reversals of motion direction which are embedded in a series of non-directional transitions (Wattam-Bell, 1991). This response was not seen in infants under 10–12 weeks of age. Detailed comparison of orientation selective and direction-selective VEP responses in the same infants shows that these two aspects of cortical processing do not emerge together, but that direction consistently lags orientation in development (Braddick, 1993; Braddick, Birtles,

Wattam-Bell, & Atkinson, 2005). Preferential looking towards a random-dot field that is segmented by opposite directions of motion demonstrated a somewhat earlier onset of directional sensitivity (Wattam-Bell, 1992, 1996a) but still at 7 weeks postnatal or later. It might be expected that motion-based segmentation develops later than overall directional selectivity; however, tests of the ability to distinguish different directions of uniform motion do not demonstrate any earlier onset (Wattam-Bell, 1996b, 1996c, 1996d). Younger infants show a preference for moving over static stimuli (Volkman & Dobson, 1976) but such a preference could be based solely on the salience of temporal transients, without any registration of direction which is the intrinsic spatio-temporal characteristic of motion. Thus despite the importance of motion for diverse perceptual purposes (Nakayama, 1985) it is not the first aspect of cortical processing to develop.

The infant's initial directional sensitivity is limited to quite a narrow range of velocities around 5–10 deg/s. This range extends to higher speeds with development (Wattam-Bell, 1992, 1996b), possibly reflecting (along with a similar extension in the range of disparity handled by the developing stereo system (Wattam-Bell, 2009)) an extension in the range of the intracortical connections that are needed to recognise large displacements. In parallel, the range of velocities and displacements which infants respond to is also extended at the low speed/small displacement end (Aslin & Shea, 1990; Banton & Bertenthal, 1997; Wattam-Bell, 1996b). Since, for a given temporal interval, low-speed discrimination requires the differentiation of small spatial separations, this latter development is in keeping with the coarse-to-fine development seen in resolution acuity and other visual functions.

Responses to motion require the transmission and analysis of rapidly varying visual signals. Infants, at both the photoreceptor (Horsten & Winkelman, 1962) and behavioural levels (Regal, 1981) show responses to remarkably high flicker rates at 1 month and younger. However, as we have argued in a review elsewhere (Braddick & Atkinson, 2009), while individual optic nerve fibres may convey high temporal frequencies to the infant brain, the effective integration of this information, for motion detection and other purposes, is delayed in development – perhaps because signals in incompletely myelinated fibres of the optic nerve are not yet well synchronised.

The full account of how motion processing develops has to take into account optokinetic nystagmus (OKN) – the pattern of following slow eye movements interspersed with rapid 'flicking back' saccades; that is elicited by large field movements. Brisk OKN responses can be elicited even in newborn infants (Dayton et al., 1964; Kremenitzer, Vaughan, Kurtzberg, & Dowling, 1979). While OKN must depend on a directional neural mechanism, evidence reviewed below strongly supports the view that this mechanism is subcortical in the newborn. Mason, Braddick, and Wattam-Bell (2003) showed that the OKN and preferential looking responses depended on two distinct mechanisms, which could be distinguished by the different developmental course of their sensitivity to random-dot motion coherence. Infants under 6 weeks show some other motor responses to motion patterns, such as head withdrawal to an expanding flow field (Jouen, Lepecq, Gapenne, & Bertenthal, 2000; Nanez & Yonas, 1994 – see reviews by Braddick, Atkinson, and Wattam-Bell (2003) and Banton and Bertenthal (1997)); these sensory-motor links are less well investigated than OKN, but may also represent initially subcortical mechanisms to maintain visual stability through motor adjustments.

In summary, the characteristic selectivities of cortical neurons emerge postnatally in human infants. However, this is not a unitary 'switching on' of the cortex, but a staged emergence, with orientation selectivity and perhaps spatial frequency tuning first, followed by directional selectivity and later, specificity for binocular correlation and disparity.

2.3. Cortical modulation of subcortical oculomotor systems

As noted above, newborn infants give directional OKN responses. However, these responses turn out to be asymmetrical; in common with newborn kittens (Van Hof-Van Duin, 1978) and infant monkeys (Atkinson, 1979; Distler, Vital-Durand, Korte, Korbmayer, & Hoffmann, 1999) non-binocular species such as rabbits, when the infant under 2–3 months views monocularly, OKN can only be driven by motion in the temporal-to-nasal direction (Atkinson, 1979; Atkinson & Braddick, 1981) and the nasal-to-temporal response emerges progressively thereafter (Lewis, Maurer, Chung, Holmes-Shannon, & Van Schaik, 2000; Naegel & Held, 1982). If both directions are present, as in a stationary counterphase reversing grating, monocular stimulation elicits only temporal to nasal OKN responses in 2-month infants (Teller, Succop, & Mar, 1993).

This asymmetry is consistent with the directional bias of neurons in the nucleus of the optic tract (NOT), with these neurons having an 'ipsiversive' preferred direction (i.e. the right NOT responds to rightward motion, and the left NOT to leftward motion (Hoffman, 1986)). There is a direct pathway from each retina to the contralateral NOT, so this direct subcortical pathway could mediate a response to temporal-to-nasal motion only. In the mature system, a descending pathway from cortical binocular neurons to the ipsilateral NOT provides a route for information from the each eye to the contralateral NOT, and hence for driving a response to nasal-to-temporal motion (Hoffman, 1986, 1989; Ilg & Hoffmann, 1993). The neonatal OKN asymmetry has therefore been interpreted as a signature of this subcortical pathway, and the emergence of nasal-to-temporal OKN in infancy as the development of a cortical input to this subcortical sensory-motor loop.

This hypothesis has been supported by findings with infants who have undergone surgical hemispherectomy to relieve intractable epilepsy caused by unilateral cerebral malformations. If the operation is early, such infants initially show the neonatal pattern of OKN asymmetry with either eye (Morrone, Atkinson, Cioni, Braddick, & Fiorentini, 1999), consistent with an intact subcortical loop on both sides. However, the nasal-temporal sensitivity that would, on the hypothesis described above, be served by the missing hemisphere, does not emerge (Braddick et al., 1992; Morrone et al., 1999).

The descending pathway consists of binocular neurons, and the development of the symmetrical response requires normal development of binocularity (Atkinson & Braddick, 1981; Birch, Fawcett, & Stager, 2000a; Crone, 1977). Also linked to disorders of binocularity, and presumably somehow associated with the OKN asymmetry, is an asymmetry in the VEP elicited by alternating displacements of a grating (Norcia et al., 1991). However, consistent with the findings that directional cortical responses emerge postnatally, Birch et al. (2000a) found that the VEP asymmetry is absent in 6-week and younger infants. Since the OKN asymmetry is conspicuous at this age, it cannot be an asymmetry in the cortical signals that drives the OKN asymmetry. We discuss this rather puzzling relationship in more detail in reviews by Braddick et al. (2003) and Braddick (1996).

A second apparently subcortical oculomotor loop is that controlling the fixation response to a suddenly appearing target. This is present in the first 3 months, provided that there is not a target already engaging the infant's fixation (Aslin & Salapatek, 1975; Tronick, 1972). However, in the 'competition' situation, where the infant must disengage from an initially fixated target, shifts to the newly appearing target are extremely sluggish or absent; prompt fixation shifts under competition start to appear around 3 months of age (Atkinson & Hood, 1997; Atkinson, Hood, Braddick, & Wattam-Bell, 1988b; Atkinson, Hood, Wattam-Bell, & Braddick, 1992). The superior colliculus contains superimposed

visual and oculomotor maps, which provide a subcortical loop to generate fixation saccades; however in the mature system there is also a inhibitory drive from frontal eye fields which has a controlling effect on the fixation loop (Hikosata & Wurtz, 1983). It is proposed, therefore, that the improvement in competition performance reflects development of the cortical system and/or its connection to the colliculus. This development can be mapped out by varying the interval between offset of one target and onset of another (Hood & Atkinson, 1993). Again, tests with the hemispherectomised infants support this account of emerging cortical function; these infants tested postoperatively at 8 months of age and later show shifts under competition to targets in the half-field served by their intact hemisphere, but will only fixate in the other half field, where there is no cortical control, if there is no central competing stimulus (Braddick et al., 1992).

2.4. Encoding spatial relationships

Elementary cortical detectors may signal the presence of visual pattern elements, but pattern vision requires the spatial relationships between these elements to be encoded. One approach to the development of this encoding has been to test infants' sensitivity to the phase relationship between spatial frequency components; another has been to examine the development of vernier acuity and other spatial 'hyperacuities'.

Braddick, Atkinson, and Wattam-Bell (1986b) used a habituation method to test whether infants discriminated a square-wave grating from the same frequency components with scrambled phase. They found that while 1-month and 2–3-month-old infants both showed this discrimination, it was abolished in the younger group when peak-trough contrast was eliminated as a cue, while the older group showed a genuine discrimination of the phase pattern, which also dominates the appearance of the stimulus for adult observers. A similar transition was in tests of preferences for schematic face images against images in which either the phase or the amplitude spectrum was interchanged with that of a non-face pattern. For newborns, the preference for face-like images was dominated by the amplitude spectrum (Kleiner, 1987), while 2-month-olds' preferences followed the phase spectrum (as do adults' judgments) (Kleiner & Banks, 1987). The conclusion is that the configurational properties carried in the phase relations have relatively little impact on the perception of the youngest infants, although Kleiner showed that phase effects could be demonstrated when the amplitude spectrum was constant. The amplitude spectrum (the 'linear systems account') was also been found to predict 8- and 13-week infants' preferences for geometrically simpler stimuli (Banks & Stephens, 1982; Gayl, Roberts, & Werner, 1983).

Infants' rapidly improving sensitivity to vernier breaks has been tested both behaviourally (Shimojo, Birch, Gwiazda, & Held, 1984; Skoczenski & Aslin, 1992, 1995; Zanker, Mohn, Weber, Zeitler-Driess, & Fahle, 1992) and using VEP measures (Manny, 1988; Skoczenski & Norcia, 1999, 2002). Although it is questionable to compare quantitatively the threshold gap for vernier acuity with that for grating resolution (Shimojo & Held, 1987; Shimojo et al., 1984), the age trends can be meaningfully compared, and have shown that vernier performance increases much more rapidly than grating acuity between 2 and 6 months, and continues to mature for longer, asymptoting in adolescence (Skoczenski & Norcia, 1999, 2002). Brown, Adusumilli, and Lindsey (2005) present evidence that the difference between 12-week-old infants' and adults' vernier performance can be accounted for by the difference in contrast discrimination thresholds for the two groups, which would argue against the idea that a specific sensitivity to spatial relationships underlies the developmental trend. However, Skoczenski and Aslin (1995) examine a rather similar argument, on how far the developmental change in vernier acuity reflects 'intrinsic blur'

within the visual system. They conclude that the development from 3 to 5 months can be accounted for in this way, but that the further large improvement from 5 months to adulthood required also improved spatial processing.

The precise neural basis is not well established for either phase discrimination or for vernier acuity, although there is evidence that vernier acuity depends on cortical integrity (e.g. Skoczenski & Good, 2004) and that cortical neurons are sensitive to vernier breaks (Swindale & Cynader, 1986). It is likely, then, that the development of these functions reflects the increasing spatial organization and precision of cortical visual mechanisms, although the changing basic limitations on contrast processing must also be taken into account.

Vernier acuity is often taken as an example of 'hyperacuity', requiring spatial information to be integrated to define locations with higher precision than the separation of the photoreceptor mosaic. However different hyperacuity tasks do not necessarily involve the same integrative processes, and so may not show the same developmental course. For instance, the early development of stereo- and vernier acuity is not parallel (Brown, 1997). Sensitivity to radial deformation (Birch, Swanson, & Wang, 2000b) is another hyperacuity which develops through infancy, but may involve global pattern processes of the kind described in the next section as well as sensitivity to local offsets.

A range of evidence, then, has suggested that visual cortical function is at best very rudimentary at birth, but develops rapidly from about 1 month onwards. This evidence from visual function is consistent with the neuroanatomical finding that the number of synapses in human striate cortex increases only at a shallow rate for the first 1–2 months, but then accelerates rapidly, with a peak around 6–9 months (Huttenlocher, 1990; Huttenlocher, de Courten, Garey, & van der Loos, 1982) about tenfold higher than at birth. However, these studies show a subsequent decrease in synapse number, with only about half of the maximum remaining at 10 years. The initial exuberance presumably establishes the receptive field organization underpinning the abilities we have discussed. The later decrease is believed to be selective pruning that refines this organization, but we do not yet know what particular improvements in visual performance during early childhood can be ascribed to it. In any case, the development of function is not driven simply by a generic process of synaptogenesis: the differential time courses for orientation, directional, and binocular development indicates that distinct developmental processes must establish the neuronal connectivity that underlies each of these types of receptive field organization.

2.5. Integrative, extra-striate processing

The years since 1980 have seen an explosion of our knowledge of the multiple, specialised extra-striate cortical visual areas, both from neuroanatomy and physiology in non-human primates, and from fMRI investigations in humans. Successive tiers of these extra-striate areas typically show a progressive increase in receptive field size and in the complexity of stimulus properties to which they respond (see Maunsell and Newsome (1987) for an early review, and Orban (2008) for a recent one), both trends reflecting integration of the signals received from V1 which encode only local properties of visual stimuli. Developmental researchers in visual development have therefore turned to these integrative processes to examine how vision develops beyond the basic receptive field properties of V1.

2.5.1. Segmentation

One relatively simple function which requires spatial integration is the segmentation of the visual field to define distinct objects and surfaces for perceptual analysis. Such segmentation can be

based on a number of different dimensions – e.g. colour, motion, texture orientation – and is closely related to the phenomenon of pop-out where an element in a visual array is salient because of its difference from neighbouring elements. Given its importance for organizing the visual world, it is not surprising that segmentation emerges early in infancy. In adult perception, colour differences play a key role in visual segmentation of different surfaces, and is a particularly powerful cue for 'pop-out' (Nothdurft, 1993). Colour segmentation in infants has not been explored as thoroughly as it deserves, but there is evidence that 3- to 4-month-old infants can detect a pop-out target on the basis of colour alone (Franklin, Pilling, & Davies, 2005; Gerhardstein, Renner, & Rovee-Collier, 1999).

Salapatek (1975) pioneered studies on whether a discrepant element or region within a patterned texture, including orientation differences, attracted preferential looking in 8–11 week-old infants. His early results demonstrated preferences for particular element types (e.g. vertical over horizontal line segments), but no evidence for detection of texture segmentation at this age. Atkinson and Braddick (1992) demonstrated infants' preference for targets segmented by texture orientation by 4 months. Sireteanu and Rieth's (1992) initial results with a similar paradigm but smaller stimulus patches did not show segmentation before 9 months but a later habituation experiment by the same group (Rieth & Sireteanu, 1994) confirmed orientation-based segmentation by 5 months.

While some theorists have ascribed texture segmentation to horizontal interactions within V1 (e.g. Li, 2003) there is evidence that it depends on extra-striate areas, perhaps via feedback connections to V1 (e.g. Allen, Humphreys, Colin, & Neumann, 2009). The postnatal development of such connections from V2 to V1 has been demonstrated anatomically (Burkhalter, 1993).

The inverse of segmentation is grouping. There are studies which are interpreted as showing the presence of Gestalt grouping of local elements in newborns (Cassia, Simion, Milani, & Umiltà, 2002; Farroni, Valenza, Simion, & Umiltà, 2000). However, as Cassia et al. point out, the infants' performance in these studies can be explained on the basis of a dominance of the low-spatial-frequency band in their pattern processing. While this may be an important aspect of 'global' processing in both infants and adults, unlike the texture experiments cited above it does not require a process of explicit 'second-order' linkage of pattern elements, and so does not bear on the suggested mechanism based on long-range horizontal cortical connections or feedback connections.

Segmentation based on orientation appears to develop with some delay from the initial cortical sensitivity to orientation. In contrast, motion-based segmentation appears to develop at the same time as cortical directional selectivity. Wattam-Bell (1992, 1994, 1996a) demonstrated the onset of directionality using directionally-based segmentation to produce preferential looking. Kaufmann-Hayoz, Kaufmann, and Stucki (1986) and Johnson and Mason (2002) demonstrated recognition of motion-segmented shapes in 2- to 3-month-olds. It might seem that segmentation of different directions requires a prior developing ability to identify a single direction, but Wattam-Bell (1996b, 1996c, 1996d) found that directional discrimination for a uniform field developed *later* than the ability to discriminate direction within a segmented array.

In fact, the success of Wattam-Bell's (1992) preferential looking procedure suggests that motion-based segmentation is rather salient in driving infants' visual attention, compared with the relatively weak preferences found by Atkinson and Braddick (1992) and Sireteanu and Rieth (1992) for targets segmented by oriented texture. We have speculated that motion-based segmentation is of particular importance in learning to organize the visual world, since it occurs whenever parallax is generated either by the independent movement of objects, or by self-motion. This

motion-based organization may serve as a scaffolding for the infant to learn that discontinuities in properties such as surface texture can also be diagnostic of the boundaries between objects and surfaces.

Visually significant boundaries are signalled not only by luminance contrast and by discontinuities in motion, texture and colour, but also by the presence of aligned contour terminators and collinear contour segments, generated by occluding surfaces – the so-called ‘subjective contours’ exemplified by the Kanisza triangle figure (Peterhans & von der Heydt, 1991). Curran, Braddick, Atkinson, Wattam-Bell, and Andrew (1999) found that infants as young as 2 months could detect such boundaries. However, this required aligned terminators to be associated with common motion. A number of studies have shown that, by 3–4 months, infants are also sensitive to the figural organization created by aligned elements in Kanisza figures (Ghim, 1990; Kavsek, 2002; Kavsek & Yonas, 2006; Otsuka & Yamaguchi, 2003; Yonas, Gentile, & Condry, 1991); again, this sensitivity is demonstrated earliest when the alignment is coupled to common motion in a dynamic display, consistent with the idea that motion supports the development of other cues for segmentation.

2.5.2. Integrative motion processing

Segmentation is just one of a range of perceptual functions which require the integration of local motion information, and which have been demonstrated in infants. Arterberry and Yonas (1988, 2000) showed quite subtle discriminations of three-dimensional structure defined by dot motions corresponding to surfaces of a rotating solid. Kellman and Spelke (1983) and Jusczyk, Johnson, Spelke, and Kennedy (1999) have shown that infants link the parts of a partially occluded object by their common motion, and Johnson et al. (see review in Johnson, 2004) has explored in detail the conditions for this to occur. Leslie (1984) and Wickelgren and Bingham (2001) demonstrated sensitivity to the dynamics of causal event sequences, and Rochat, Morgan, and Carpenter (1997) report a preference for dynamic event sequences with simple shapes that adults categorise as social interactions. Infants are also sensitive to the patterns of point-light motion that characterise biological motions (Bertenthal, Proffitt, & Cutting, 1984; Bertenthal, Proffitt, Spetner, & Thomas, 1985; Booth, Pinto, & Bertenthal, 2002; Fox & McDaniel, 1982). Most of these tests have been with 3–6 month-old infants, and so do not require any revision of the view that directional motion information is available only after 7 weeks of age. However, they demonstrate that, only a few weeks later, infants can exploit this directional information in complex perceptual functions.

For many of these functions, there is little specific knowledge of how motion information is integrated in extra-striate cortex. However, some integrative functions have been studied at the single-cell level, in particular in area V5 (MT). For example, the combination of motion signals from contours in different orientations to solve the ‘aperture problem’ is known to occur in the ‘pattern motion cells’ of V5 (Movshon, Adelson, Gizzi, & Newsome, 1986). The perceived direction of plaids, made by superimposing two moving gratings, is the classic test of this integration (Adelson & Movshon, 1982) and has provided a paradigm for testing functional development of this area. Manny and Fern (1990) found that, even at 1 month, OKN eye movements were driven in the direction of ‘pattern motion’ perceived by adults, suggesting that such integration was occurring. However, Manny and Fern suggested that a subcortical mechanism, depending on a different process than combination of motion signals in V5, might drive neonatal OKN in this way. This seemed to be supported by Smith and Harris’s (1991) observations of OKN in cats which showed that subcortical processes contributed a pattern motion signal. However, Harris, Lewis, and Maurer (1993) later found evidence that, in human

adults, directional integration in OKN had a cortical origin, so the case for young infants is unresolved. Dobkins, Fine, Hsueh, and Vitten (2004) used a stimulus with spatially separated grating components (which would not generate pattern motion by the subcortical summation suggested for superimposed plaids) and found directional integration in the youngest group they tested (2 month infants).

In ‘type 2’ plaids (Adelson & Movshon, 1982) two gratings are superimposed with very asymmetrical motion vectors and the resulting pattern motion is very different from the mean direction of the two components. Such plaids distinguish the integration process seen in adult perception (and pattern-motion V5 neurons) from a simpler combination process that averages the motion vectors of each component grating. Harris et al. (1993) found that adult OKN showed the more complex integration process with type 2 plaids. However, no infant studies appeared to have yet used such patterns. Nor has there yet been a human infant study using a behavioural discrimination technique; this is urgently needed since infant macaques have been shown to develop the ability to discriminate plaid direction (Hall-Haro & Kiorpes, 2008) much later than direction discrimination for dot patterns (Kiorpes & Movshon, 2004). The 10–18 weeks at which macaques show this discrimination is argued to be equivalent to 30 weeks + in human development, although it is not clear how far any consistent developmental scaling can be applied between the two species (Hall-Haro, Johnson, Price, Vance, & Kiorpes, 2008).

A second form of motion integration with a known extrastriate mechanism is the detection of globally coherent motion in a dot pattern containing a proportion of randomly moving dots. The coherence threshold – the minimum percentage of dots sharing a common direction of motion that is required for detection of that motion – provides a measure of this integration. This threshold has been shown to depend on area V5 in macaques (Newsome & Pare, 1988) and humans (Baker, Hess, & Zihl, 1991) and individual V5 neurons in macaque show coherence thresholds which are comparable to the overall behavioural threshold (Britten, Shadlen, Newsome, & Movshon, 1992). Neuroimaging results show that human V5 is sensitive to the level of motion coherence (Rees, Friston, & Koch, 2000). Other extra-striate cortical areas, such as V3a, share this strongly coherence-dependent responses (Braddick, O’Brien, Wattam-Bell, Atkinson, & Turner, 2000), but it seems clear that the detection of global coherent motion is an extra-striate function.

Infants’ coherence thresholds, assessed by preferential looking, develop rapidly from the initial onset of directional discrimination, falling to about 30% by 24 weeks (Mason et al., 2003; Wattam-Bell, 1994) compared to adult values around 20% with the same display. A related test, in which coherence is varied by changing the spread of motion directions about the mean value, shows that infants of 12 weeks and over can make direction discriminations that require integration of directional distributions with standard deviations of 68° (Banton, Bertenthal, & Seaks, 1999). (The wider range of distributions which adults can integrate (Williams & Sekuler, 1984) was not tested in infants). These findings are supported by VEP/VERP experiments, discussed further below, in which 5-month infants gave responses to a stimulus sequence that isolates global motion integration from local directional responses (Wattam-Bell et al., 2010) and other VEP recordings of responses to global flow patterns at this age (Gilmore, Hou, Pettet, & Norcia, 2007; Hou, Gilmore, Pettet, & Norcia, 2009).

These results, along with the diverse complex motion-based discriminations discussed above, 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. We have speculated (Braddick et al., 2003) that the connectivity between V1 and extra-striate areas including V5, on which this integration is based, may exist early in some

crude form, awaiting the organization of local directional selectivity in V1 – perhaps because the latter requires some minimum level of temporal performance in the developing visual pathway before it can function (Braddick & Atkinson, 2009).

Single unit studies of infant monkeys indicate that V5 neurons show directional responses, albeit sluggish, at 1 month of age, but are considerably slower to develop pattern-motion responses and sensitivity to global coherence (Movshon, Rust, Kohn, Kiorpes, & Hawken, 2004; Kiorpes, Hawken, Movshon, Kohn, & Rust, 2007). This is consistent with the behavioural results in this species (Hall-Haro & Kiorpes, 2008). Distler, Bachevalier, Kennedy, Mishkin, and Ungerleider (1996) found that metabolic activity in macaque V5 was immature in newborns but rose rapidly to near adult-levels around 3 months of age. In humans, Rosander, Nystrom, Gredeback, and von Hofsten (2007) measured VEP responses to motion in 2–3 month-olds that they argued arose from V5, but the stimuli did not require the specific integrative functions of V5. It will be important to determine how far high-level motion-based perception depends on the refinement of V5 properties, and whether other extra-striate pathways are involved.

Long-range integration of motion between parts of an occluded object may have a slower developmental course: Kochukhova and Rosander (2008) found that pursuit eye movements for a diamond figure, whose edges were visible through four separated apertures, reflected adult-like integration in 9-month-old but not 5-month-old infants. It is not known whether motion integration in displays of this kind depends on later-developing processes in V5, or on other motion processing areas with large receptive fields.

2.5.3. Integrative pattern processing

Analogous to the integration of local motion signals, a number of processes integrate the orientations of local contour segments to define contours, textures, regions and shapes. For example, area V4, at a similar level in the extra-striate hierarchy to V5 contains receptive fields that are sensitive to large scale concentric or radial organization (Gallant, Braun, & Van Essen, 1993).

Above we discussed the segmentation of oriented textures seen around 4 months. The related ability to discriminate coherent parallel texture from the same elements randomly oriented has been demonstrated using a VEP technique by Norcia, Pei, Bonneh, Hou, Sampath, and Pettet (2005), in a group of infants aged 2–5 months (albeit with higher coherence thresholds than adults (Pei, Pettet, & Norcia, 2007)). A variety of studies (Palomares, Pettet, Vildavski, Hou, & Norcia, 2010; Braddick & Atkinson, 2007; Wattam-Bell et al., 2010) have shown infants' VEP responses specific to the kind of concentric or radial organization seen in V4 receptive fields. However, direct comparison of sensitivity to global pattern structure and global motion, both behavioural (Braddick & Atkinson, 2007; Braddick, Curran, Atkinson, Wattam-Bell, & Gunn, 2002) and VEP-based (Braddick & Atkinson, 2007; Wattam-Bell et al., 2010) indicate that the former matures more slowly during infancy. We return to this comparison in the next section.

Grouping of elements into a texture is a 'region-based' integrative process, and can be contrasted with the 'contour-based' grouping of near-collinear line segments (Hess & Field, 1999). This latter process also develops during the postnatal months. Gerhardstein, Kovacs, Ditre, and Feher (2004) and Baker, Tse, Gerhardstein, and Adler (2008) showed detection of grouped contour segments in a noise background, in 3-month and 6-month-old infants respectively, although the level of noise tolerated is much lower than for adults, and indeed remains so at 5–6 years (Kovács, Kozma, Fehér, & Benedek, 1999). A satisfactory VEP demonstration of this effect does not yet seem to have been achieved in infants (Pei et al., 2007), although the alignment of segments may contribute to the results found for global concentric and radial organizations which include some degree of alignment.

One specialisation of extra-striate cortex for high-level pattern properties is the detection and recognition of human faces, particularly in the 'fusiform face area' (FFA) (Kanwisher, 2000). Tests of infants' preferences for faces date back to Fantz's (1961) first preferential looking experiments. The large body of work on what drives this preference is beyond the scope of this article; Pascalis and Slater (2003), Simion, Leo, Turati, Valenza, and Dalla Barba (2007) and Simion, Di Giorgio, Irene Leo, and Bardi (2011) give recent overviews. However, we need to consider the challenge it offers to the idea that visual cortical function develops postnatally. Much evidence exists that, at an age before the onset of visual cortical functions more generally, newborn infants are specifically sensitive to some aspect of facial configurations (Dziurawiec and Ellis, 1986; Goren, Sarty, & Wu, 1975; Johnson & Morton, 1991; Simion, Valenza, & Umiltà, 1998) or at least have visual preferences which bias them to acquire face-related information (Turati, 2004). Johnson and Morton (1991) proposed that a 'CONSPEC' mechanism, possibly subcortical, determined initial newborn fixation biases towards face-like stimuli. However, there is not yet any direct evidence for any subcortical face-specific responses.

Simion and her group (see review by Simion, Di Giorgio, Irene Leo, and Bardi (2011)) suggest that face preferences at birth are the result of combining a set of non-specific constraints stemming from general characteristics of the immature visual system and some general structural properties that attract newborns' attention. For example, newborns may attend preferentially to patterns that are top-heavy with contrast, because of a possible upper-visual-field advantage in visual sensitivity.

In adults, face-related information has been found to bypass V1 in a pathway that drives emotional responses in the amygdala (Morris, Degelder, Weiskrantz, & Dolan, 2001; see also review by Johnson (2005)), but the role of this pathway in development, what subcortical and cortical structures it involves, and its relation to the FFA, are matters for speculation. There are other face-responsive areas in the adult cortex, notably the occipital face area (OFA) (Gauthier et al., 2000) which may represent an earlier level in the face-processing network than the FFA (Liu, Harris, & Kanwisher, 2010; Pitcher, Walsh, & Duchaine, 2011) but their role does not alter the underlying issue of whether there is any cortical contribution to newborns' face preferences. Thus in relation to the model of emerging cortical function, there remain two alternatives: either crude face-specificity, or a pattern of preferences which favours faces, is a precocious property of the newborn cortex, or it is embodied in subcortical structures such as the superior colliculus, guiding fixation biases to favour visual stimulation which then promotes the development of face-specific systems in the cortex.

It has recently been suggested that neonates display a preference for biological motion patterns (Simion, Regolin, & Bulf, 2008; Simion et al., 2011) – an analogy to the face question, since such performance would reflect sensitivity to a biologically significant visual configuration in advance of the cortical development which might be expected to underpin it. Again the question remains whether such performance depends on a specialised early-developing cortical module, or on previously unknown subcortical capabilities.

2.6. Dorsal and ventral stream development

The extra-striate areas whose functions are discussed above are components of two major processing streams: the 'ventral stream' which includes V4 and other areas (including the FFA) projecting to the temporal lobe, which is believed to be responsible for object, face, and scene recognition, and the 'dorsal stream' including motion-sensitive areas V5 and V3A, which connects to a network of parietal areas and is believed to underlie perception of spatial

relationships and the visual control of actions (Felleman & van Essen, 1991; Milner & Goodale, 1995; Mishkin, Ungerleider, & Macko, 1983; Zeki, 1993). This division has highlighted questions of the developmental relations between the two streams and the parvo and magno-pathways which respectively feed them. As will emerge in discussion, there is no simple answer that one stream develops ahead of the other; the answer depends on the stage of development considered and on whether functional onset, rate of development, or vulnerability is taken as an indicator.

Directionality and binocularity, the later-developing aspects of primary cortical function, are associated with magnocellular input to the cortex and dorsal-stream areas (Livingstone & Hubel, 1988), suggesting that the initial development of this pathway may be slower than that of the parvocellular-ventral pathway which specialises in the processing of form (orientation or slant) and colour discrimination (Atkinson & Braddick, 1992). We have suggested (Braddick & Atkinson, 2009; Braddick et al., 2003) that the magnocellular/dorsal stream lag may reflect the demands for temporal precision in a motion-processing network, and/or the need for horizontal transmission of information by intracortical connections. It should be noted, however, that it has been argued from VEP temporal-frequency responses that the precortical stages of the magno pathway may mature earlier than parvo (Dobkins, Anderson, & Lia, 1999). It should also be noted that the division of processing between the two streams may be subject to developmental change: for example Dobkins (2009) discussed evidence that chromatic information, which is absent from the magno pathway in the adult, provides input to motion mechanisms in infants in the early months of life.

The tests of global processing discussed in the last section allow the direct comparison of comparable functions of extra-striate areas in the two streams. Specifically, the detection of motion coherence and form coherence have analogous requirements of information integration for the dorsal and ventral streams respectively, and behaviourally make similar demands on attention. A neuroimaging study by Braddick, O'Brien, Wattam-Bell, Atkinson, and Turner (2000) has shown that the two forms of coherence activate independent networks of extra-striate cortex (and do not activate V1 differentially compared to incoherent arrays of the same elements). We have cited above that young infants appear to segment visual arrays much more readily by motion than by static texture orientation, and this also seems to be the case for coherent motion patterns than for the corresponding form coherence test. In particular Braddick and Atkinson (2007) have used matching concentric organization for coherent form (short static arc segments) and motion (short trajectories rotating about a common centre). In preferential looking the response to motion coherence was already statistically significant at age 8 weeks and changed little over the following 10 weeks. In contrast the response to global form was initially at chance and showed an increasing preference over the same period. This developmental course is consistent with VEP responses to incoherent-coherent transitions, which at 4–5 months are robustly present for motion coherence in the majority of infants, but are statistically reliable for form coherence in a minority (Atkinson, Birtles, Wattam-Bell, & Braddick, 2005; Braddick & Atkinson, 2007). This has recently been confirmed in high-density VEP/VERP recording, which allows the spatial distribution of the response to be mapped (Wattam-Bell et al., 2010). While the responses were of approximately equal amplitude in adults, in 5-month infants the form response was typically around half the amplitude of the motion, and reached statistical reliability in only 50% of infants.

The high density study also showed that, in infants who showed both responses, the form and motion patterns yielded spatially distinct voltage distributions over the scalp, indicating that they were activating anatomically distinct mechanisms, as they did in adults.

However these distributions were markedly different in infants from adults, with the motion signal focussed on the posterior midline in adults but predominantly lateral in infants, while the form signal showed the opposite relationship. Wattam-Bell et al. (2010) proposed that each of these signals arises from a network of extra-striate areas (including, e.g. V5, V3a, and probably V6 for motion in adults) but that the relative contribution of the areas within each network undergoes substantial re-organization between infancy and adulthood.

In summary, although the local directional analysis for motion develops later than that for orientation, motion signals are integrated to generate a global response (dorsal stream) earlier in development than oriented elements are integrated to yield global form (ventral stream). However, the neural basis of each stream is far from its mature anatomical organization in infancy.

2.6.1. Development in childhood and 'dorsal stream vulnerability'

Children aged 4 years and over are capable of identifying verbally or by pointing a region of coherence in a computer display – the 'ball in the grass' or the 'road in the snowstorm' (Atkinson, Braddick, Anker, Curran, & Andrew, 2003) – and so their global motion and form coherence thresholds can be tested psychophysically. Such tests show that at age 4–5, motion coherence thresholds are higher and more variable, relative to adult values, than for form coherence; both thresholds improve with age and converge at adult values around 10 years, with the form coherence thresholds reaching adult asymptote earlier (Armstrong, Maurer, & Lewis, 2009; Atkinson & Braddick, 2005; Gunn et al., 2002;).

Motion coherence thresholds are not just more variable and slower developing in childhood, they are also more susceptible to disruption. The greater impact of developmental disorders on global motion compared to global form was first identified in Williams Syndrome (Atkinson et al., 1997, 2006), a genetic disorder where other features suggest a dorsal stream deficit (Atkinson et al., 2003; Meyer-Lindenberg et al., 2004). However work from a number of groups showed that global motion was disproportionately impaired in a number of genetic and acquired developmental disorders, including hemiplegia (Gunn et al., 2002), autism (Koldewyn, Whitney, & Rivera, 2010; Spencer et al., 2000), fragile-X syndrome (Kogan et al., 2004); developmental dyslexia (Cornelissen, Richardson, Mason, Fowler, & Stein, 1995; Hansen, Stein, Orde, Winter, & Talcott, 2001; Ridder, Borsting, & Banton, 2001); premature birth (Atkinson & Braddick, 2007; Taylor, Jakobson, Maurer, & Lewis, 2009) and visual deprivation through early cataract (compare Elleberg, Lewis, Maurer, Brar, and Brent (2002) with Lewis et al. (2002)). This has led to the proposal of a general 'dorsal stream vulnerability' in development (Braddick et al., 2003).

The normal developmental relationship between dorsal and ventral streams, as assessed through form and motion coherence, is therefore a complex one. Sensitivity to pattern properties (e.g. orientation) is apparent earlier in cortical development than to directional motion, but global integration of these directional signals develops in infancy faster and more robustly than for static pattern elements. Through childhood, this relation reverses again and global motion development depends on a relatively delicate, vulnerable system whose disruption is apparent in a range of developmental disorders. How this changing relationship is linked to the re-organization of the two systems, apparent from high-density VEP, requires further exploration.

2.6.2. Dorsal stream function

Global motion sensitivity samples an early stage in the processing of information by the dorsal stream. Two higher level aspects of this stream are important for putting visual development in a wider context. First, it has the major role of providing the visual information needed for the control of action (Milner & Goodale,

1995), including oculomotor systems; second (and connected) it is intimately involved in the control of visual behaviour through spatially directed attention.

The visual control of action can be considered to involve a set of visuo-motor modules, each delivering the information required for a particular action system. Atkinson and Braddick (2000), using the extensive reviews of Jeannerod (1997), Milner and Goodale (1995) and Rizzolatti, Fogassi, and Gallese (1997) have schematized the connecting areas, primarily connecting through parietal to frontal lobe areas, which are likely to form the modules for the visually controlled actions which emerge in the first years of life, illustrated in Fig. 1.

The first developing visual action systems are for the control of gaze (saccades, head movements, and pursuit). Saccades and head orienting form the basis of the preferential looking methods which are usable from birth, and the dynamics of the saccadic system are mature at a surprisingly early age (Hainline, Turkel, Abramov, Lemerise, & Harris, 1984; Hainline, 1993). Smooth pursuit emerges more gradually (Aslin, 1981; Phillips, Finocchio, Ong, & Fuchs, 1997; von Hofsten & Rosander, 1996, 1997), reflecting at least in part the development of cortical directional motion systems. However, there is developmental continuity between slow phase of OKN (initially subcortically controlled) and (cortically controlled) smooth pursuit which both aim to match eye velocity to stimulus velocity to serve related goals of stabilizing the retinal image.

Visually controlled reaching and grasping develop from about 4 months, and are a prominent feature of infants' visuo-motor exploration during the rest of the first 2 years of life. There have a number of approaches to characterising the visual information which elicits this behaviour (von Hofsten & Spelke, 1985; Yonas, Arterberry, & Granrud, 1987; Newman, Atkinson, & Braddick, 2001; Braddick & Atkinson, 2007) and evidence that binocular depth information plays an important role in initiating and guiding the reach (Braddick, Atkinson, & Hood, 1996; Kavsek, Granrud, & Yonas, 2009).

A visuo-motor system which is not included in Fig. 1 is the control of locomotion, which begins towards the end of the first year. Developmental research on the stimulus information which elicits

and guides locomotion is starting to appear (Adolph, 2008; Cowie, Atkinson, & Braddick, 2010) and is likely to be an area of active research in the years ahead, hopefully alongside better understanding of the underlying neural systems (Drew, Andujar, Lajoie, & Yakovenko, 2008).

All these visuo-motor systems require a target object or location to be selected and maintained as a goal. Much if not all of the covert operation of selective attention can be regarded as 'selection-for-action' (Allport, 1989; Rizzolatti, Riggio, & Sheliga, 1994). It is therefore not surprising that many areas identified as belonging to attention networks in the brain (Kastner & Ungerleider, 2000; Posner & Dehaene, 1994) appear within the dorsal stream systems diagrammed in Fig. 1. A developmental account of visually controlled action must therefore be integrated into a developmental account of spatial attention (Hood, Atkinson, & Braddick, 1997), of which a few elements have been introduced above.

While spatially directed action and attention have been presented as dorsal stream functions, it is clear that for effective perception and action, dorsal and ventral systems must work in a closely integrated way – for example in reaching, an target must usually be selected using ventral-stream systems to recognise the appropriate object type before the appropriate action is planned and initiated using dorsal stream processing. Some aspects of the developmental course may reflect the need to develop this integration, as well as components of the separate streams.

The evidence outlined earlier for 'dorsal stream vulnerability' was derived from form and motion processing at the relatively early extra-striate levels of the two streams. However the higher level aspects of dorsal stream function, in visuo-motor control and attention, seem also to be particularly vulnerable in neurodevelopmental disorders. Some evidence on this point will be cited in the clinical section below.

2.7. Clinical applications

For many infant vision researchers, a primary or parallel goal has been to apply the new knowledge and new methods from the field to the detection, diagnosis, and management of children's

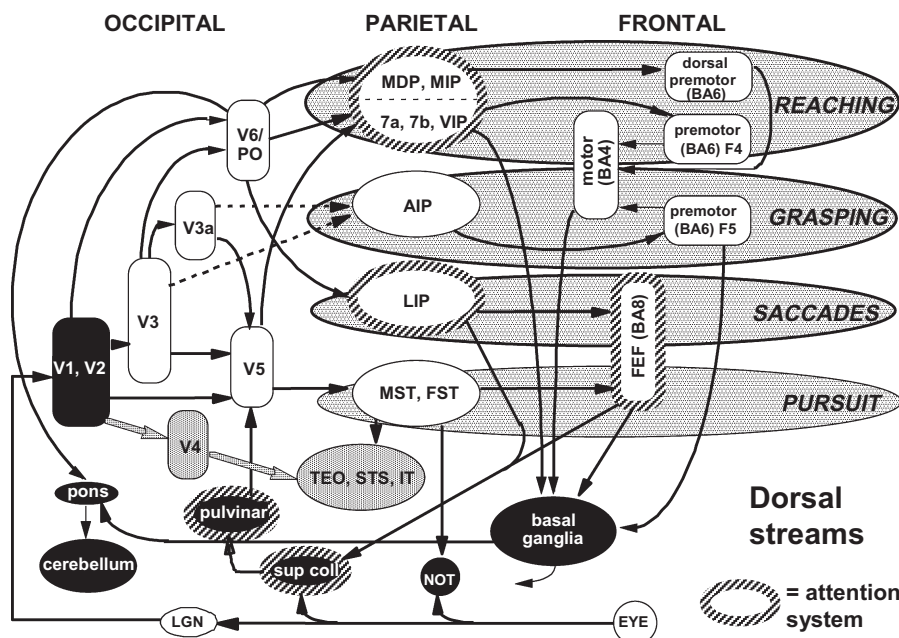


Fig. 1. Brain areas involved in visuo-motor modules and their connections, for four aspects of the development of visually controlled behaviour. Areas involved in spatial attention networks are highlighted by hatched borders. Based on data reviewed by Jeannerod (1997), Milner and Goodale (1995) and Rizzolatti et al. (1997). (Redrawn and updated from Atkinson and Braddick (2000)).

vision disorders. Atkinson and Braddick (1999a) provide an overview of many of these methods.

One of the first moves in this direction was to adapt the preferential looking procedure for measuring acuity from the specialised equipment used in the laboratory to the portable Teller Acuity Cards procedure (McDonald et al., 1985). This has been widely adopted in paediatric vision clinics, and used in a range of clinical research investigations, notably two major surveys and trials of treatment for the retinopathy of prematurity which is a problem associated with preterm birth (Dobson et al., 1990, 1995, 1999; Palmer, 1990). The approach using preferential looking cards has also been extended to stereopsis by Birch and Salomão (1998).

VEPs have also been used as a tool for measuring acuity and contrast sensitivity, including the development and application of the 'sweep VEP' method in which a steady-state VEP is measured as the spatial frequency or contrast of the grating stimulus is continuously varied (Norcia & Tyler, 1985; reviewed recently by Almqvist, Leat, and Irving (2008)). However measures of acuity from gratings, whether by FPL or VEP, do not capture the extent of visual deficits, particularly in amblyopia where 'crowding' effects (reduced acuity for a target that is surrounded by nearby detail) play a major role (Levi, 2008). Several groups have developed tests to measure crowded acuity in children too young to use a standard linear acuity chart. For example the Cambridge Crowding Cards (Atkinson, Anker, Evans, Hall, & Pimm-Smith, 1988c) in which children from 3 years upwards can match the central letter of an array without needing to name it, has been shown to yield values corresponding to a linear Bailey-Lovie chart in adults. Other recently developed acuity tests for young children include the HOTV and Lea symbols tests (Dobson, Maguire, Orel-Bixler, Quinn, & Ying, 2003; Hyvärinen, Näsänen, & Laurinen, 1980; VIP Study Group, 2010) and the Cardiff acuity cards (Adoh, Woodhouse, & Oduwaiye, 1992).

Another area of technical development has been photo- and videorefractometry, methods for assessing the refractive state of the eyes from the distribution of light, in the lens plane of a camera, returned from a flash source close to the camera lens. Howland (2009) has recently summarised the history and development of the various optical configurations and instruments ('orthogonal', 'isotropic' and 'eccentric' photorefractometry). These methods have the advantages over conventional retinoscopy, for work with infants and children with communicative disorders, that they operate at a distance around 1 m and so are not intrusive for the child; they measure both eyes and all axes simultaneously, and they make an instantaneous measure of a freely accommodating child, thus requiring a few seconds of cooperation for each picture and a few minutes for the entire test procedure including breaks. Photorefractometry has been used in a range of research studies of refractive and accommodative development (e.g. Braddick et al., 1979; Hainline et al., 1992; Howland et al., 1978; Suryakumar, Meyers, Irving, & Bobier, 2007) and its evident suitability for vision screening has been exploited in large-scale trials discussed below (Atkinson, Braddick, Durden, Watson, & Atkinson, 1984; Atkinson et al., 2007).

These are examples of exploiting new methods to improve the measurements usually made in the ophthalmology clinic – acuity, stereopsis, refraction – for young children and preverbal infants. However, another important development has been the recognition that visual function does not stop at the level of these measurements, and even for clearly ocular pathologies it is important to know the impact on higher level visual functions. Furthermore, an increasing proportion of visual impairment in children is cerebral visual impairment (CVI) due to early brain damage (e.g. Good, Jan, Burden, Skoczinski, & Candy, 2001), generally associated with wider neurological and cognitive problems, where the impairments can involve any of the levels of developing visual brain function reviewed in this article.

We have described above (and in Braddick, Atkinson, & Watam-Bell, 2011) a range of VEP methodologies that analyse cortical functions beyond simple contrast detection, and will cite below some applications of these to clinical groups (e.g. Mercuri et al., 1998). The use of VEP tests of extrastriate global function with clinical groups is promising, but still at an early stage (Atkinson et al., 2008). The fixation shift test under competition (discussed above under 'cortical modulation of subcortical oculomotor systems') has also given a method for probing, in children with neurological problems, function both of subcortical orienting networks and parietal and frontal cortical systems controlling disengagement processes and switches of attention.

A different approach is to assess behaviour and abilities that reflect the everyday requirements of visual function. This is the rationale of the ABCDEFV battery (Atkinson, Anker, Rae, Hughes, & Braddick, 2002a) which has been standardised for children from birth to 5 years of mental age. The battery is divided into 'core vision' tests requiring no motor abilities beyond minimal saccadic tracking eye movements, and a further set of age-specific tests which assess visuo-motor, cognitive and spatial functional visual behaviour which should be typically achieved at particular ages in the areas of vision. The core tests include measures of strabismus, tracking eye movements, visual fields, visual attention at distance, acuity (with optional use of a Rapid Acuity Screening Procedure (RASP), a shortened version of the TAC (Anker, Atkinson, Braddick, & Birtles, 2009)). The additional age-appropriate tests require the minimum motor skills of reaching, pointing and grasping; they test functions associated with dorsal stream, ventral stream function or their interaction e.g. picking up fine cotton thread, copying block constructions, detecting embedded figures. Some work using these tests with clinical populations is cited below. The Children's Visual Function Questionnaire (Birch, Cheng, & Felius, 2007) takes a questionnaire-based approach to similar questions of the effect of visual disability on everyday tasks.

As discussed above, attentional systems are intimately related to dorsal stream visual processing, and disorders of attention are one of the major consequences of extreme prematurity and other sources of perinatal brain injury (van de Weijer-Bergsma, Wijnroks, & Jongmans, 2008; Mulder, Pitchford, Hagger, & Marlow, 2009). Effective visual behaviour depends on cognitive control processes, in particular the control of attention. The abilities of selective, sustained, and controlled attention are believed to depend on distinct brain systems (Posner & Petersen, 1990) and subtests for each of these components have been incorporated into a battery – the Test of Everyday Attention for Children (TEA-Ch) (Manly et al., 2001). However, this test is designed for mental ages 6–12 years, and so it is too demanding either for younger children or for many of the children with potential cortical impairment, where assessment of attention is a major requirement. To overcome this, the Early Childhood Attention Battery (ECAB), a test on similar principles but adapted for the capabilities of mental age 3–6 has been devised (Breckenridge, 2007a, 2007b; Breckenridge, Braddick, & Atkinson, submitted for publication) and used to characterise groups with developmental disorders (Breckenridge & Atkinson, 2008). Both the TEA-Ch and ECAB have the advantage over many tests of attention of giving an individual profile of attentional abilities across the different attention components, which may be used to guide personalized specific intervention programmes, focussing on specific component deficits.

A wide range of clinical conditions can impact visual development in children and can be evaluated through the methods discussed. The use of many of these tests and methods has been reviewed previously by Atkinson (1989, 2000), Atkinson and Van Hof-van Duin (1993) and an overview of methods is provided by Atkinson and Braddick (1999b). Many of the techniques have been

used to investigate cerebral visual impairment – CVI, assessing children at risk of perinatal or early brain abnormality. For example these methods have been applied to infants who have undergone hemispherectomy to relieve intractable epilepsy (Braddick et al., 1992; Morrone et al., 1999), infants born prematurely (e.g. Atkinson et al., 2002b; Atkinson & Braddick, 2007), infants with perinatal infarcts (e.g. Hood and Atkinson, 1990; Mercuri et al., 1996, 1997, 1998, 2003), and hypoxic-ischemic encephalopathy (HIE) (Mercuri et al., 1997, 2004) with their prognostic value examined (e.g. Atkinson & Braddick, 2007; Mercuri et al., 1998, 1999).

Below we describe some examples of the areas where these new techniques and tests have been used. These are:

1. Refractive screening using photo and videorefraction in trials to prevent strabismus and amblyopia.
2. Visual development related to perinatal brain damage in term and preterm infants and children.
3. Visual development in Williams syndrome and other genetic developmental disorders.

2.7.1. Refractive screening and visual development

The development of photo- and videorefractive methods, outlined above, made non-invasive screening a practical possibility. These technologies were used in two population screening programs in Cambridge (UK), to detect significant refractive errors in a geographically based population of infants at 8–9 months of age (Atkinson et al., 1983, 2007). Over 8000 infants were screened in the two programs in the Cambridge Health District with a high attendance rate of around 80% of children born in the geographical area. Hyperopic infants ($\geq +4D$) were followed up alongside an emmetropic control group, with visual and developmental measures up to age 4–7 years, and entered a controlled trial of partial spectacle correction. These programs showed that hyperopic infants could be detected by either cycloplegic or non-cycloplegic photo or videorefraction, and were at increased risk of developing strabismus and poor acuity. The incidence of these conditions could be reduced by preventive refractive correction which did not prevent the normal refractive development of the eyes towards emmetropia.

The follow-up of these children indicated that, as well as purely visual effects, children who had significant hyperopia in the first year of life were significantly worse on many of the visuospatial ABCDEFV tests and visuomotor and attentional measures in the preschool years (Atkinson et al., 2002c, 2007). This raises the possibility of using infant refractive screening as a predictor of children at risk of preschool developmental delays of development and deficits and of intervention programmes at an early age to prevent later educational difficulties at school.

The conventional theory of accommodative strabismus would suggest that the group at greatest risk of strabismus would be those showing habitual accommodation in the face of their hyperopia. However, data from these screening programmes indicate that accommodative lag in infancy is an indicator of poor visual outcome. Given that detected hyperopia in freely accommodating infants was associated with modest delays in visuospatial and attentional development, it is possible that poor accommodative responses in infancy reflect a poor ability to attend to targets at different distances, and share a common link with later deficits in spatial attentional networks.

There have been several other studies to evaluate photorefractive screening (e.g. Schaeffel, Mathis, & Bruggemann, 2007; Williams, Harrad, Harvey, Sparrow, & ALSPAC Study Team. Avon Longitudinal Study of Pregnancy & Childhood, 2001) but apparently no attempt has been made to replicate or extend the Cambridge programmes in their scale, validation by cycloplegic refraction, or inclusion of a trial of prevention. As Howland

(2009) has commented “Whether [photorefraction] will play an important role in improving the ocular health and welfare of infants and children probably depends more on future developments in the healthcare system and the financial practicality of vision screening than on technological progress.”

2.7.2. Vision and perinatal brain insults

Vision is itself a key function for cognitive, behavioural and social development, but also, because it shows rapid early development in infancy, it provides an early measure of the wider integrity of brain function. As such, infant visual measures have been used to gauge the plasticity of both peripheral and central neural development in recovery from perinatal injury and to predict more complex later-developing abilities. Visual measures also have the potential to gauge the effectiveness of early treatment and intervention in neurologically at-risk infants.

For example, a series of longitudinal studies on infants born at term with focal cerebral lesions or hypoxic-ischemic encephalopathy (HIE), found that the generalised lesions in HIE were more frequently associated with abnormalities in fixation shift (FS) and orientation-reversal VEP (OR-VEP) measures of cortical visual function in the first 5 months (Mercuri et al., 1995, 1996). However, poor visual outcome was not necessarily most strongly associated with specific damage to classically ‘visual’ areas of the brain; for instance neonatal lesions in the basal ganglia were generally associated with a more severe visual outcome than visual cortical lesions, supporting the idea that certain circuits between subcortical areas and cortical areas are essential for normal visual development. Delayed or absent FS and OR-VEP responses were predictive of developmental testing and neurological outcome at 3 years (Mercuri et al., 1998, 1999), and showed a much higher sensitivity for this prediction than deficits in lower level visual function such as low acuity or a failure to show a binocular OKN response in both directions.

2.7.3. Sequelae of very preterm birth

Changes in obstetric practice and perinatal care have led to increased numbers and improved survival of infants born prematurely, as young as 24 weeks gestation. However, very preterm birth remains a major risk factor for childhood sensory, neurological and psychiatric impairment, (e.g. Marlow, 2006; Rennie, 2002; Robertson, Watt, & Dinu, 2009). Premature infants commonly suffer a different pattern of brain damage from that seen at term, with damage predominantly to the white matter (du Plessis & Volpe, 2002; Dyet et al., 2006). Nonetheless, the tests of cortical function which were predictive of outcome in term infants – OR-VEP and fixation shifts – again provide a general indicator of cerebral development; as for term-born infants these tests in children born before 33 weeks gestation also correlate with the level of brain damage seen on MRI, and show a similar specificity and sensitivity in predicting 2-year neurological outcome (Atkinson et al., 2008).

Premature infants without overt brain damage have a potential advantage compared to term infants at matched post-conceptual age (PCA); they have spent more time in a visually stimulating environment. There is little evidence for any developmental acceleration as a result: most studies have concluded that acuity matures in line with PCA with no evidence of preterm acceleration (e.g. van Hof-van Duin & Mohn, 1986; see review by Birch and O’Connor (2001)), although there is a contrary finding from VEP measurements of acuity (Norcia, Tyler, Piecuch, Clyman, & Grobstein, 1987). The maturation of orientation-specific cortical responses in healthy preterms appears to be in step with term-born infants of the same PCA (Atkinson et al. (2002b)). However; the picture is different for direction-specific responses, which are delayed by several weeks in healthy preterms (Birtles, Braddick, Wattam-Bell, Wilkinson, & Atkinson, 2007); this may perhaps be

taken as an early example of dorsal stream vulnerability, and the timing requirements of motion processing may be particularly vulnerable to subclinical white matter damage.

Generally, very preterm infants taken as a group show long-term deficits in a range of visual and visuo-cognitive functions. Ophthalmological studies have normally concentrated on physical examination of the eyes, refraction, acuity, and binocularity. In all these areas, prematurely born children have a higher rate of defects than their term-born peers (e.g. Birch & O'Connor, 2001; Hellgren et al., 2007; Larsson, Rydberg, & Holmström, 2005). Some of these are associated with the occurrence of retinopathy of prematurity (abnormal retinal vascularisation, due to excessive oxygen delivered in intensive care to premature neonates) (Sylvester, 2008), others with general developmental delay ascribed to identifiable cerebral damage, but as a group, prematurely born children show worse vision even when these specific conditions have not been identified. It should be realised that strabismus, refractive error and acuity are not independent problems but in this group of children, as in others, are intimately interrelated.

The cerebral damage associated with prematurity has a continuing impact on high-level as well as low-level visual abilities. The infants studied with OR-VEP in the first year showed levels of failure on ABCDEFV component tests over years 1–5 that were also correlated to the severity of damage seen on neonatal MRI (Atkinson & Braddick, 2007). The functional impact of this damage depended on the complexity of the function concerned. For core visual functions, in particular binocularity and visual fields, deficits were associated with the most severe MRI group. Performance on the visuo-cognitive tests was impaired in the 'severe' and 'moderate' groups; for block construction and frontal executive function tests, especially the latter, even the 'normal/mild' group showed deficits compared to age norms. This conclusion is reinforced by the follow-up of such children at later ages.

In a preterm cohort born before 33 weeks gestation and tested between 6–7 years, overall performance of the group show a range of deficits (Atkinson & Braddick, 2007) including global motion coherence test, fine and gross visuomotor tests (Henderson & Sugden, 1992), subtests of TEA-Ch, and spatial memory (Nardini, Burgess, Breckenridge, & Atkinson, 2006). In contrast, IQ scores and language (vocabulary) tests of the group were normal. As discussed above, deficits of spatial processing, attention, and visual control of actions are those primarily associated with the dorsal stream. Factor analysis has shown that the different test results also show differential patterns of association with MRI findings of perinatal brain damage, gestational age at birth, as well as impairment in the group as a whole (see Atkinson & Braddick, 2007).

A variety of other studies have shown deficits of motion processing and dorsal stream functions in preterm born children at age 8–18 years: local and global motion thresholds (MacKay et al., 2005; Taylor et al., 2009); biological motion detection (Pavlova, Sokolov, Birbaumer, & Krageloh-Mann, 2006); motion-based form segmentation (Jakobson, Frisk, & Downie, 2006); execution of directed pointing movements (van Braeckel et al., 2008); drawing and three-dimensional constructional tasks (Luoma, Herrgård, & Martikainen, 1998) and other motor tasks (Marlow, Hennessey, Bracewell, Wolke, & EPICure Study Group, 2007). Attention deficits are another common finding among ex-premature children (Botting, Powlis, Cooke, & Marlow, 1997; van de Weijer-Bergsma et al., 2008; see also the meta-analysis by Bhutta, Cleves, Casey, Craddock, & Anand, 2002), in line with the broader concept of dorsal stream vulnerability.

2.7.4. Williams Syndrome and other genetic developmental disorders

As well as developmental disorders acquired through brain injury, there has been extensive research interest in visual problems associated genetically based neurodevelopmental disorders, both

because of the clinical and educational issues these children face, and because of the insights they might yield on the genetic basis of visual brain development. A particular focus has been on Williams Syndrome (WS), a rare disorder arising from a deletion of around 30 genes on one arm of chromosome 7 (reviewed by Atkinson and Braddick (2011)). WS is characterised by a very uneven cognitive profile, with relatively good language abilities, good face recognition, and object recognition in line with their mental age (Landau, Hoffman, & Kurz, 2006) but very poor performance on visuospatial and visuomotor skills such as drawing and block construction (e.g. Bellugi, Lichtenberger, Mills, Galaburda, & Korenberg, 1999). In a large scale study of 73 young children with WS (Atkinson et al., 2001), a high incidence of binocular disorders, reduced acuity and refractive errors (usually hyperopia rather than myopia) was found in around 50% of the group. Marked deficits were also found on many subtests of the ABCDEFV, with particularly poor performance on the block construction copying task. However, the severity of spatial deficits was not well correlated with sensory visual deficits such as strabismus, suggesting no direct causal link between sensory visual loss and problems of spatial cognition.

The discrepancy between face and object recognition abilities and spatial cognition, supported by findings on global motion vs. global static form perception and on the contrast between good orientation matching vs. poor visuomotor alignment to the orientation of a postbox slot, led to the hypothesis of 'dorsal stream vulnerability', that the dorsal stream was a focus of this disorder (Atkinson et al., 1997). Many later findings are consistent with this idea of a dorsal stream loss, examples are a massive delay on all visuo-motor planning tasks (e.g. Atkinson et al., 2001, 2003), problems of using visual judgments of step height in stair descent to scale leg and foot movements (Cowie, Braddick, & Atkinson, 2010), poor spatial location memory for hidden objects when allocentric frames of reference (relative to the external environment) need to be used (Nardini, Atkinson, Braddick, & Burgess, 2008), better face processing than processing the location of faces (Paul, Stiles, Passarotti, Bavar, & Bellugi, 2002) and neuroimaging evidence (Eckert et al., 2005; Meyer-Lindenberg et al., 2004). However, although some of these tests have isolated dorsal from ventral processing, many of the spatial deficits in WS may depend heavily not on dorsal stream functioning alone but on integration of ventral stream information with dorsal and it may well be this integration which is the main block for these children learning to overcome their difficulties.

Other genetic developmental disorders which have attracted studies of visual performance, with particular attention to disorders of motion processing, are Fragile-X syndrome (Farzin, Whitney, Hagerman, & Rivera, 2008; Kéri & Benedek, 2009; Kogan et al., 2004) and Prader-Willi syndrome (Woodcock, Humphreys, & Oliver, 2009). Autism has also attracted much attention, with visual findings recently reviewed by Simmons et al. (2009) and Kaiser and Shiffrar (2009). As well as motion processing problems, a striking finding in autism is the focus on local detail rather than global object or pattern organization, a focus which can actually enhance autistic individuals' performance on embedded figures tasks (Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005; Shah & Frith, 1983, 1993).

In many developmental disorders, including WS, marked deficits have been found on a range of tasks involving control of spatial attention. For example, many infants and very young children with WS could not disengage attention and shift their gaze to a newly appearing peripheral target, when two targets are visible simultaneously ('competition' condition in the fixation shift paradigm) and older children with WS cannot inhibit a familiar motor movement ('prepotent response') and point to the opposite side to the target, rather than point to the target when it appears in the

periphery ('counterpointing task') (Atkinson et al., 2003). Deficits in selective attention, sustained and executive control have been found in children with WS on the TEA-Ch battery and those with a mental age between 3 and 6 years on the ECAB described above (Breckenridge, Anker, Braddick, & Atkinson, submitted for publication; Breckenridge & Atkinson, 2008; Breckenridge, Braddick, Anker, Woodhouse, & Atkinson, submitted for publication).

Ultimately, findings in all these disorders will illuminate the connection between visual development and the broader genetic programs that determine the development of the brain. However, clear insights of this kind remain a hope for the future.

3. Plasticity and deprivation

The focus on visual development in the 1970s and 1980s was driven significantly by discoveries by Wiesel and Hubel (1963), Blakemore (1978) and others about the plasticity of the developing visual system, through which cortical binocularity, orientation, and directionality could be strikingly modified by early selective deprivation in a critical period. Recent neuroscience has concentrated on the cellular and molecular processes that underlie this plasticity (see Daw (2006) and Hensch (2005) for recent reviews).

These studies of animal models showed that early strabismus is associated with a loss of binocular input to cortical neurons, and led to a classic study by Banks, Aslin, and Letson (1975). They tested the interocular transfer of a visual after-effect in individuals whose strabismus had onset and surgical correction at different ages, leading to an estimate of the critical period for binocularity which tails off between 1 and 3 years. Animal models have also provided an analogy to clinical amblyopia – a functional loss of vision, usually in one eye – associated with visual deprivation, anisometropia (difference in refraction between the eyes), or strabismus, which has driven much of the interest in visual cortical plasticity. A proper review of the large, continuing volume of work on amblyopia is beyond the scope of this article; two short reviews on human research (Levi, 2006) and animal findings (Kiorpes, 2006) summarise many recent findings, and Barrett, Bradley, and McGraw (2004) highlight continuing topics of uncertainty. Work on animal models, exemplified by Boothe, Loudon, and Lambert (1996) and Mitchell and Sengpiel (2009), has provided valuable evidence, which should be applicable to clinical patching regimes, on the effects of schedules of monocular occlusion on V1 input and acuity for the two eyes. However, among the issues emphasised in the reviews cited above are (a) that effects on grating acuity are only a part of the visual deficit in amblyopia, for which spatial 'scrambling' effects among others are very important; (b) that although the emphasis has been on plasticity of the input to V1, there is also important plasticity at higher levels of visual processing. Furthermore, the patterns of visual function between strabismic, anisometropia and deprivation amblyopia are different, and complicated by associations between these conditions (McKee, Levi, & Movshon, 2003). Finally, the possibility of effective therapy for amblyopia beyond the classical 'critical period' raises the question of how early plasticity is related to the lifelong capacity for perceptual learning (Levi & Li, 2009). Given these open questions, the wider interest in the modifiability of brain mechanisms, and the progress on the cellular and molecular mechanisms of plasticity, amblyopia-related research is likely to continue as an area of intense and multidisciplinary activity.

The visual development of children with early, and early removed, cataracts has been a prime area of evidence on the plasticity underlying deprivation amblyopia (Birch, Stager, Leffler, & Weakley, 1998; Maurer & Lewis, 1993). However, recent work from the Ontario group has explored the long-term effects of such deprivation on higher level visual function, with striking results.

Functions including motion coherence sensitivity (Elleberg et al., 2002), form coherence sensitivity (Lewis et al., 2002), holistic face recognition (Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002; Le Grand, Mondloch, Maurer, & Brent, 2004) and integration of contour segments in a Kanisza figure (Putzar, Hötting, Rösler, & Röder, 2007) show impairment in children who had visual deprivation from cataracts for a period as short as 4 months after birth. Since these abilities are very immature in the first 4–6 months of life, Maurer, Mondloch, and Lewis (2007) characterise these as 'sleeper' effects, whereby deprivation interferes with the establishment of foundations that are necessary for development that normally takes place after the period of deprivation. Evidence for a critical period for these effects comes from the finding that cataracts with an onset after 4–6 months do not produce the impairment of motion coherence thresholds (Elleberg et al., 2002) (this 'late onset' group do not yet appear to have been tested on the other tasks discussed).

Deprivation amblyopia – the loss of acuity and contrast sensitivity resulting from early cataract – is a strongly competitive effect: the loss is greater in the affected eye with unilateral cataract than it is the two eyes of bilateral cataract cases. In contrast, the effects on global form and motion were much greater in bilateral cases than in the affected eyes following unilateral cataract, suggesting that rather than interocular competition, these effects are mediated by co-operative interactions between the eyes, through which the stimulated eye can provide 'scaffolding' which can be exploited by the input from the deprived eye, once the cataract is removed (Elleberg et al., 2002; Lewis et al., 2002). The relatively smaller effect of monocular deprivation also argues against the idea that the deficits in high-level function are simply secondary to the amblyopic loss of acuity and contrast sensitivity.

New data relevant to the plasticity of visual brain systems have also come from cases which suffered long-term visual deprivation. Fine et al. (2003) report an individual who was blind from corneal scarring at age 3 until a successful graft in his 40s. The patient MM has continuing poor acuity and contrast sensitivity, difficulty with face recognition, parsing overlapping figures, and interpretation of depth cues. On fMRI testing, he showed greatly reduced BOLD responses in V1 even within his spatial frequency range. Thus it was clear that prolonged deprivation later than infancy leads to a profound degeneration of both low and high levels of cortical visual processing. However, the most intact functions appeared to be associated with motion processing (segmentation, 3-d structure from motion) (although formal coherence thresholds, for instance, have not yet been reported), and his BOLD responses from MT+ are closer to normal than those from V1. Thus despite its vulnerability in childhood disorders, including deprivation by cataract in the first 6 months, motion processing in the dorsal stream seems better able to resist degradation from later, long-term deprivation, as shown both for MM and for the late-onset cataract group. Configural face processing, on the other hand, appears vulnerable both to early and to late visual deprivation.

Treatable but uncorrected visual deprivation is very rare in Western nations, but sadly common in the developing world. Project Prakash (<http://web.mit.edu/bcs/sinha/prakash.html>) has the goal of treating long-term cataracts and other blinding conditions in rural India, and at the same time investigating the visual capabilities of the treated individuals. Results with early subjects (Ostrovsky, Meyers, Ganesh, Mathur, & Sinha, 2009; Sinha, Ostrovsky, & Meyers, 2006) had much in common with those from Fine et al.'s patient MM, in finding a difficulty in parsing static images that was resolved by introducing structure from motion. However, study of an individual, who was reported to have 20 years of visual experience following 12 years of congenital visual deprivation, found recovery of many functions including face recognition, image segmentation, and pictorial depth cues (Ostrovsky, Andalman,

& Sinha, 2006). Cross-modal transfer between vision and touch is another intriguing area for these studies; early reports (Held, 2009) suggest that it is initially absent but very rapidly acquired with visual experience. More extensive series, of patients with different histories of deprivation and restored vision, will be required to understand whether a coherent account of these effects can be achieved, including dependence on residual plasticity in adolescence and/or recovery during very long periods of visual learning. It is to be hoped that Project Prakash may provide unique material for such an account. In the meantime, combining data from these subjects, the Ontario cataract studies, and MM, we can at least say that visual functions, both low- and high-level, require initial visual experience to establish the foundation for functional mechanisms, and continuing visual experience to sustain them.

3.1. Prospects

Can we foresee what advances in our knowledge of human visual development will appear in *Vision Research*, and its competitor and complementary journals, in the next quarter century? Almost certainly not, but some potential lines of progress can be suggested.

The early years were marked by applications of methodological innovation. Since then the ease with which we can generate rich, complex, dynamic stimuli has been transformed, but these more elaborate stimuli have largely been used to investigate new aspects of infant vision using the same basic armoury of methods – preferential looking, habituation, and evoked potentials. However, some new approaches, and new developments of old approaches, are in prospect.

3.1.1. The continuity of visual development

Infants aged under about 6–9 months are relatively tractable participants in visual research – they are highly visually engaged and generally look at what is put in front of them. As they become more capable of manipulation and locomotion they are less inclined to co-operate in obtaining psychophysical and electrophysiological data. As a consequence, most of the research reviewed above has studied infants in the first 6 months of life. Infant researchers never believed that development stopped after that point, but there has been a tendency to emphasise the rapid development of basic mechanisms during that early period.

Researchers in both development and adult vision have given increasing attention to higher levels of visual processing, including those processes in which vision interacts with motor control, object knowledge, and executive systems. These areas will demand understanding of stages of development beyond early infancy. Furthermore, modern anatomical neuroimaging has emphasised how far structural development of all parts of the brain, including visual areas, continues throughout childhood and into adult life (Toga, Thompson, & Sowell, 2006). Some of the studies discussed above (e.g. Gunn et al. (2002) on 'dorsal vulnerability') illustrate the insights to be gained from the differential development of visual capabilities during childhood. We anticipate that a future overview of human visual development would contain a much fuller picture of how development during childhood builds on the foundation based in early infant development. The work on visual deprivation described in the preceding section will also continue to inform our ideas on the contributions of visual experience over the lifespan.

We can also expect more attention to the other end of continuity in development – from fetus to infant. There is considerable work, some discussed above, on the visual consequences of pre-term birth. An increasing number of children now survive healthily from birth at ages as early as 24 weeks gestation, but knowledge of the state of their visual systems before term is very limited. It will be difficult to obtain such knowledge, but if it can be obtained it

would greatly improve the links that can be made between human development and our broader knowledge of visual developmental neurobiology (e.g. the role of spontaneous neural activity in forming the organization of the visual system, illustrated in the work of Shatz (1996) and others). The exposure of preterm infants to visual stimulation also offers one of the few 'natural experiments' on the role of environmental manipulations in human visual development (see Van Hof-van Duin and Mohn (1986) and Dobkins, Bosworth, and McCleery (2009) for examples of this approach).

3.1.2. Neuroimaging and high-density recording

Our understanding of the brain mechanisms of human vision has been transformed over the last 15 years by the progress of functional neuroimaging methods, in particular fMRI. We can confidently expect that the same methods will lead to progress in understanding the development of these brain mechanisms in infancy and childhood. Mapping infants' brain activity will be important not only for understanding how the organization of the visual brain emerges, but also for investigating its plasticity in the face of abnormal development, whether from genetic or traumatic causes.

As commented above, structural neuroimaging has increased awareness of the continuing changes in the brain through middle childhood and adolescence. Functional studies of development in this period are underway, confirming that the basic retinotopic organization of cortical areas is in place by 7–12 years (Conner, Sharma, Lemieux, & Mendola, 2004) although the metabolic demands are greater in children, perhaps due to less selective responses (Marcar, Strässle, Loenneker, Schwarz, & Martin, 2004). At the beginning of this period, extrastriate functional specificity is still markedly less focussed than the adult, both for motion processing in the dorsal stream (Klaver et al., 2008) and face- and place-selective areas in the ventral stream (Grill-Spector, Golarai, & Gabrieli, 2008).

However, to provide direct evidence on the brain development that underlies the striking functional changes of visual capacities in infancy, we will need results from fMRI and analogous methods in this early period. This presents great experimental challenges. Pioneering studies of cortical activity in the newborn have used flicker stimulation through the closed eyelids of sedated or sleeping infants (Born et al., 1998, 2000) but further progress will require fMRI scanning of infants who are awake with eyes open. The vulnerability of the method to movement artefacts requires minimal head movement during a scan period of many minutes – a serious obstacle to testing conscious young children. Algorithms which allow some correction of images for head movements are in use in research and clinical contexts, and we can hope that these will be developed to the level where they can provide reliable data from babies in a natural, alert, and happy state. Advances in scanner design may also improve the degree of physical contact which a sympathetic and experimentally sophisticated adult can maintain with the infant during scanning. If and when these technical advances materialize, we may expect a wealth of information which can clarify the developmental stability and change of the brain systems mediating many aspects of visual perception.

fMRI uses the Blood Oxygen Level-dependent (BOLD) signal as a proxy for neural activity, and records from developing children depend on the maturation of the metabolic and hemodynamic processes by which neuronal activity elicits changes in blood oxygen. In adults, the major effect is to increase oxygen in the cerebral vasculature, presumably because local increases in blood flow outweigh the depletion of oxygen due to metabolic demands. In contrast, the local changes around the calcarine fissure elicited by visual stimulation found by Born et al. (1998, 2000) were reductions in blood oxygen. This is consistent with the changes found by in our laboratory by Meek et al. (1998) during visual stimulation of awake infants, using near infra-red spectroscopy (NIRS), and this

result suggests that Born's 'negative' signals were not an result of sleep state or sedation. We do not yet know the age function for the transition between negative and positive BOLD signals. However, the fact of this reversal between infancy and adulthood means that studies of visual development using the BOLD signal will have to take into account the development of hemodynamic control as well as the development of neural processing.

While we wait for infant fMRI to deliver on its promise, other technical approaches can provide some information about infants' brain activity. NIRS measures infra-red absorption by oxy- and deoxyhemoglobin between an optical source and receiver ('optodes') placed on the infant's scalp and so provides measures analogous to BOLD. It gives good signals in infants due to the relative transparency of the infant tissues to infra-red, and since the optodes are head mounted, small head movements do not move the sensors relative to the source. Its spatial resolution has been very much poorer than MRI but is improving through technical advances in multi-optode arrays (Lloyd-Fox, Blasi, & Elwell, 2010) and in measures using photons' time of flight rather than simply optical density (Heiskala, Hiltunen, & Nissila, 2009). A number of studies have shown that NIRS recordings from infants are practical and can yield useful information about the activity of striate and extra-striate visual areas (Meek et al., 1998; Minagawa-Kawai, Mori, Hebden, & Dupoux, 2008; Otsuka et al., 2007; Lloyd-Fox et al., 2010), but the full potential of the method for visual developmental neuroscience has yet to be realised.

The best established approach for localising brain activity in infants is high-density EEG, and arrangements for attaching large arrays of sensors on the heads of infants and children are widely available. Mapping the distribution of voltage in evoked (or 'event-related') potentials over the surface of the scalp allows distinct visual mechanisms to be spatially distinguished and developmental changes to be tracked, yielding important insights on visual development (e.g. Arcand et al., 2007; de Haan, Humphreys, & Johnson, 2002; Izard, Dehaene-Lambertz, & Deharme, 2008; Rosander et al., 2007; Wattam-Bell et al., 2010). However, going beyond inferences from changes in scalp distributions, to identifying the location of sources in the 3-D volume of the head, is not straightforward. Solving this 'inverse problem' requires a model of the geometry and electrical properties of the various tissues and fluids of the head and brain; even for adults there is much scope for controversy about the assumptions of such modelling, and the modelling of the infant head has so far been very little explored. Furthermore, even a source that has been accurately localised in geometrical terms can only be located with respect to brain features if a structural brain image of the individual subject referenced to head landmarks is available. So far this has been rarely true for (non-clinical) infant subjects, but work with this approach is under way (Richards, Reynolds, & Courage, 2010). We anticipate that secure discoveries from this approach will emerge in step with the development of infant MRI methods.

EEG (recording the voltages arising at the scalp from evoked currents in brain tissue) has recently been complemented by magnetoencephalography (MEG) which records the magnetic fields arising at the scalp from the same currents. MEG has advantages over EEG – it is much less affected by the tissues between the source and the sensor array, leading to higher spatial resolution and a simpler inverse problem. However the sensors form a bulky, fixed (and very expensive) array which does not have the flexibility in use of an EEG array which forms a cap worn on an infant's head. Consequently, although the feasibility of MEG recording of auditory responses in sleeping infants has been demonstrated (Cheour et al., 2004), its use in developmental vision research faces similar obstacles to fMRI. As for EEG, accurate source localisation requires structural MRI information from the individual.

3.1.3. Infant eye tracking

Instrumental measures of infant eye movements have been important since the early days (e.g. Aslin & Salapatek, 1975; Hainline, Turkel, Abramov, Lemerise, & Harris 1984), but in the early years the technical difficulty of using systems that required accurate alignment with infants involved heroic efforts and large amounts of lost data. Modern digital systems using the corneal-reflection method allow rapid calibration and relatively good tolerance of head movements (Gredeback, Johnson, & von Hofsten, 2010), and have made measurements of infants' gaze much more accessible. They have been most prominently exploited for studying issues such as infant's ability to anticipate the path of moving objects behind occluder (e.g. Johnson, Amso, & Slemmer, 2003), or the intentional actions of a human agent (e.g. Falck-Ytter, Gredeback, & von Hofsten, 2006). There is also scope, however for using eye-tracking to refine the use of gaze data in preferential looking methods. For example the statistical efficiency of FPL would be greatly improved by using four or more target positions rather than just two; this is generally beyond the ability of human observers to discriminate gaze reliably, but should be readily achieved with an automated eye-tracking system. Currently such an automated system is being developed using the Tobii eye-tracking system; initial results suggest that this may be useful for clinical assessment before and after treatment such as gene therapy in infants and young children (Burton, Nardini, & Wattam-Bell, 2011).

It should be noted however, that the temporal and spatial precision required to analyse the dynamics of oculomotor mechanisms themselves are considerably more demanding (Schupert & Fuchs, 1988) and may require more sophisticated and less infant-friendly instrumentation.

3.1.4. Sampling the visual ecology of the infant

A well-founded account of visual development needs to describe how a programme of maturation interacts with the input that the developing child's visual system receives from the environment. In recent years there have been quite extensive studies of the statistics of visual images in natural scenes, with proposals about how visual mechanisms embody adaptation to these statistics (see reviews by Simoncelli (2003) and Geisler (2008)). The presumption is that an important part of this adaptation takes place during sensitive periods in infancy and early childhood. However, our knowledge of the visual input that infants actually receive has been based on intuitions. Attempts have now started, using lightweight head-mounted cameras, and records of infants' fixations (Aslin, 2009; Franchak, Kretch, Soska, Babcock, & Adolph, 2010; Sinha, Balas, & Ostrovsky, 2007; Yoshida & Smith, 2008) to determine what infants actually look at in natural situations. Given the challenges, it is not surprising that there are methodological limitations in all the cited studies. However they give a first look, notably at the high preponderance of face information in young infants' visual ecology, and of monitoring hand workspace in older, manipulating toddlers, and promise that this approach before too long will give the kind of quantitative data for input to visual learning systems that child language researchers have had for some time.

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