Visual Neuroscience (2013), **30**, 185–195.
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doi:10.1017/S0952523813000497

SPECIAL ISSUE

Linking Hypotheses in Visual Neuroscience: A Tribute to Davida Teller

PERSPECTIVE

Inferences about infants' visual brain mechanisms

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(Received March 10, 2013; Accepted October 24, 2013; First Published Online November 13, 2013)

Abstract

We discuss hypotheses that link the measurements we can make with infants to inferences about their developing neural mechanisms. First, we examine evidence from the sensitivity to visual stimulus properties seen in infants' responses, using both electrophysiological measures (transient and steady-state recordings of visual evoked potentials/visual event-related potentials) and behavioral measures and compare this with the sensitivity of brain processes, known from data on mammalian neurophysiology and human neuroimaging. The evidence for multiple behavioral systems with different patterns of visual sensitivity is discussed. Second, we consider the analogies which can be made between infants' behavior and that of adults with identified brain damage, and extend these links to hypothesize about the brain basis of visual deficits in infants and children with developmental disorders. Last, we consider how these lines of data might allow us to form "inverse linking hypotheses" about infants' visual experience.

Keywords: Infant, Visual development, VEP, Visual behavior

Introduction: Linking hypotheses in infant vision

The classical instance of a "linking hypothesis" is the proposal of Brindley (1970) examining relationships between the observer's experience and questions about the neural mechanisms underlying that experience. Davida Teller wrote thoughtfully about the problems in defining and testing such psychophysical linking hypotheses (Teller, 1984). Although these discussions focused on inferences from experiments with adult observers, most of Teller's own scientific contributions were in her quest to understand the development of vision in human infants (Teller, 1997). For infants, we do not have the knowledge of their experience provided in adults by verbal reports or verbally instructed responses. The underpinnings of work on infant vision must then be hypotheses that link the measurements we can make with infants, to inferences about their developing neural mechanisms. If we want to say anything about infants' visual experiences, it must be derived from these measurements combined with neural inferences—an inverse linking hypothesis. We return to this question at the end of this overview.

The first approach we take in thinking about linking hypotheses in infancy is to examine evidence from the sensitivity to visual stimulus properties seen in infants' responses and compare this with the sensitivity and specificity of brain processes, identified from sources such as mammalian neurophysiology and human neuroimaging data. In the first part of this article, we consider some examples, in particular in relation to visual evoked potential/visual event-related potential (VEP/VERP) measures of infants' sensitivity. Both VEP and behavioral methodologies for studying infant vision, and the advantages and disadvantages of particular techniques, are discussed in detail by Atkinson and Braddick (1998).

A second approach is to seek analogies between infants' visual capabilities and those of adults with identified brain damage. This approach can be extended to hypotheses on the brain basis of visual deficits in infants and children with developmental disorders. In taking this approach, we must maintain awareness that disabling a structure within an adult's already developed neural system is not the same as an anomaly of that system occurring in a dynamic process of development of the whole brain (see Karmiloff-Smith, 1998). Nonetheless, such analogies can provide highly suggestive pointers to the neural underpinnings of developmental disorders, and we discuss some examples below. Advances in neuroimaging measures of the structure and function of the typically and atypically developing brain may provide more direct test of such analogies.

In summary, we will examine below what we can infer about developing visual brain mechanisms from (a) comparison of infants' visual responses to the known properties of specific neural systems in adulthood and (b) comparison of both typical and atypical development with the performance of adults having known damage to specific systems. We will present some specific findings by way of illustration, but we do not attempt a review of the current state of knowledge about infants' visual development, which we have recently undertaken elsewhere (Braddick & Atkinson, 2011).

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https://doi.org/10.1017/S0952523813000497 Published online by Cambridge University Press

The VEP (VERP) as a route to understanding infant vision

One of the methods that brings us closest to direct knowledge of the infant's visual nervous system is through recording VEPs (or VERPs—the terms are synonymous). These scalp recordings of mass neuronal activity in the EEG are sometimes, particularly in a clinical context (e.g., Strasburger et al., 1996) described as "objective" in contrast to behavioral measures of vision. This description is questionable—first, because observations or measurements of an infant's behavior are (or should be) as objective, as the trace of a voltage recorded from the scalp; second, because successful recording of a meaningful VEP, like meaningful behavioral measures, depends on the infant's overall behavioral state and specifically on extended periods of visual attention to the stimulus. In addition, although the VEP may be a direct product of neural activity, to infer from it the development of significant neural function is not straightforward. We will argue that the most secure knowledge of infant vision comes from attempts to provide converging evidence from VEPs and behavior. VEP measurements have the advantage that parallel measurements can be made with the same basic technique, throughout the age range from newborns to adults. It is not safe, however, to assume that the same neural generators produce the recorded signal throughout the age range.

VEP methodologies—transient *versus* steady-state recording

VEP recording depends on identifying neural responses which are time-locked to a stimulus event (e.g., the reversal of contrast in a grating or checkerboard pattern). Within this general constraint, there have been two contrasting approaches to VEP measurement. The more traditional is "transient" recording, in which the scalp voltage following a stimulus is recorded (averaged over multiple stimulus presentations), with a sufficiently long interval between stimulus events that the response to one stimulus is believed to be complete before the next is delivered. The goal is to identify a characteristic waveform, typically containing a series of components which provide peaks and troughs at characteristic latencies after the stimulus event. It should be noted, however, that components arising from different neural mechanisms cannot be safely identified from peaks and troughs alone because the recorded waveform is a superposition of overlapping signals from these mechanisms, in which a peak from one source may be distorted, shifted, or abolished by the contributions from other sources (Otten & Rugg, 2004). An alternative approach is from "steady-state" recording, in which the visual stimulus events are repeated at a sufficiently rapid rate that discrete waveforms from each repetition cannot be separated, but instead there is a periodic signal at the stimulus frequency (and/or its harmonics). Analysis of such signals is therefore performed in the frequency rather than the time domain. A variant of the steady-state method is the "sweep VEP" (Norcia & Tyler, 1985) in which stimulus events are presented at a high rate and a stimulus parameter such as contrast is varied continuously over time, yielding a function relating signal amplitude at the stimulus frequency to contrast, which is extrapolated to estimate a threshold.

Evidence for detection from transient VEPs

VEP studies may address various different questions. In infant research, the question asked often is: is there evidence that the brain responds to a particular type or level of stimulus event? For such questions, the steady-state approach has some distinct advantages. It does not require specific components to be identified or quantified, which is a hazardous business with infants, since both the shape and latencies of specific VEP waveforms show radical changes in early development (Spekreijse, 1978; Brecelj, 2003). An example from higher-level visual processing is in response to human faces. In adults, a component N170 (i.e., contributing a negative voltage peak at 170 ms latency) is believed to be face-specific. Researchers have found a response-dubbed "N290" in 3-month infants, which shows some, but not all, aspects of this stimulus specificity for faces, and is more spatially and temporally diffuse (Halit et al., 2003; de Haan, 2008). However, the continuity of developmental progression really needs to be demonstrated, if it is to be argued that N290 represents an immature form of the mechanism generating the adult N170.

Evidence for detection from steady-state VEPs

The steady-state, compared to the transient, approach can provide more straightforward evidence for detection, since relatively simple procedures allow the statistical significance of a periodic component in a steady-state waveform to be assessed (Moore, 1980; Wattam-Bell, 1985; Dobie & Wilson, 1993), whereas determining the statistical evidence for the presence of a specific transient VEP component is more complex and rarely attempted.

If we have statistical evidence that a VEP response occurs at the stimulus frequency, what can we infer about neural mechanisms? When the stimulus is contrast reversal, the response indicates that information about the presence of spatial contrast is reaching the cortex. This has been interpreted as a measure of acuity or contrast sensitivity (e.g., Harris et al., 1976; Sokol, 1978; Norcia & Tyler, 1985). However, the VEP signal arises from the summated synchronized activity of many thousands of neurons. This activity may not be summated within the nervous system, to provide an input to the control of behavior, across the same neural population whose combined activity is detected at the scalp. (Who knows how subjective awareness of contrast may relate to neural population activity, either in adults or in infants?)

Furthermore, the VEP signal we measure is typically the average over many repeated epochs, since the EEG is typically too noisy to reveal the response to single visual presentations. Although many of the noise sources will not impact on information transmission within the nervous system, some will, and the neural systems which control decisions or behavior cannot reduce noise by averaging over minutes of recording. The meaning of VEPs for absolute sensitivity, in a functionally meaningful sense, is therefore doubtful. However, in infant studies, we can typically be content with comparisons, rather than absolutes. For example, the response to reversal of high contrast gratings at increasingly high spatial frequencies between 1 and 3 months of age can be taken as evidence of developmental increase of acuity. As another example, the linear function relating VEP amplitude to the logarithm of contrast has been shown to relate to psychophysical thresholds in adults (Campbell & Kulikowski, 1972), providing a basis for using this approach to infer contrast and acuity threshold in infants (Harris et al., 1976; Atkinson et al., 1979); it is the basis of the sweep VEP approach cited earlier.

In common with behavioral measures of infant vision, positive evidence for a VEP response can provide evidence that stimulus-related information is present in the visual system, but the failure to detect a response does not necessarily mean this information is absent or functionally insignificant. Responses might be undetectable for various reasons, for example:

- neurons carrying the information may be too few in number, buried too deep within the cranium, or nonoptimally configured to generate a detectable VEP (the scalp voltages depend

https://doi.org/10.1017/S0952523813000497 Published online by Cambridge University Press

on intracranial current flows being at right angles to the surface of the scalp, as occurs when they arise from pyramidal neurons in a cortical gyrus that is parallel to the scalp). We have to consider the possibility that functionally significant information could be transmitted by very small populations of neurons.

- The magnitude of the VEP will depend on the synchrony of neural responses among the thousands or millions of neurons which contribute to the scalp potential. It is plausible that, as myelination of the visual pathway develops, this synchrony will become tighter, enhancing the measured VEP signal. However, it may well be that for some purposes, neurons whose responses are poorly synchronized in early development may nonetheless contribute effectively to functional vision.
- Contrast-reversal VEPs, and those for other stimulus events discussed below, depend on nonlinearities in the system. When a dark/light edge in the visual pattern reverses contrast, on-center cells with receptive field centers on the side that becomes bright will give a positive signal, but a presumably equal number of cells on the other side of the edge will give a negative signal. (Responses of off-center cells would match in the opposite way.) If the system was truly linear, these signals would be equal and opposite, and cancel out. The response we observe at the reversal frequency therefore must reflect a nonlinearity that generates an asymmetry between positive and negative effects. This requirement might conceal the presence of functionally meaningful responses which include primarily linear components.

All these possibilities indicate potentially important developmental changes, but we must be alert to the possibilities of changes in the number or topography of neurons with a given sensitivity, the synchronization of their signals, or the emergence of significant nonlinearities, as well as the changing functional sensitivity of the overall system.

In summary, steady-state VEPs have some advantages over transient measures for infant testing and yield a latency measure with different properties to that of the latency of a transient peak. Steady-state signals can yield statistical evidence for the occurrence of a response to specific stimulus events, such as contrast threshold. However, the absence of a significant VEP signal might reflect various forms of immaturity (in timing, number, topography, or linearity) of the neurons concerned.

VEP signatures of processing beyond contrast detection

The capability to respond to contrast and high spatial frequencies (acuity) tells us only about the most basic stages of visual processing. We would like to know about the developing capability of the infant's brain to encode higher-level visual attributes such as orientation, motion direction, binocular relationships, vernier alignment, pattern features, and global structure. The problem is that a change in any of these attributes cannot be achieved without changes in local contrast in the image. When a VEP is elicited by such a change, how can we distinguish whether it is a response to local contrast changes or to the higher-level attribute that we are manipulating?

An early attack on this problem was made by Julesz et al. (1980) who tested VEP responses in adults to random-dot correlograms and stereograms. A change in binocular correlation or disparity in a random dot pattern would change some or all of the dots in one eye's view, potentially generating a contrast-based VEP. However, if the patterns are replaced with fresh random dots at the display frame rate, then the local changes accompanying the disparity change are in no way distinctive, and a signal specifically associated with this change must reflect a response to the binocular relationship. This method was used with infants by Braddick et al. (1980, 1983), and Petrig et al. (1981) to make the first attempts to chart the development of neural systems that combine binocular input, in the first few months of life. This work showed that the newborn brain was not sensitive to binocular correlation and disparity and that such sensitivity emerged around 3–5 months of age, with substantial and reliable variability between individual infants (Braddick et al., 1983; Braddick, 1996); more recently, the method has been used to examine the sensitivity of binocularity development to visual experience in preterm infants (Jandó et al., 2012).

It is intrinsic to this approach that it uses steady-state recording, since it depends on the separation of two VEP signals in the frequency domain (a high-frequency response to the changing dots and a low-frequency response to the binocular configuration). The binocular correlogram method is an example of embedding the event of interest in a sequence of events which control lower level transitions. It has served as a model for a range of similar techniques. The development of orientation-specific responses has been demonstrated, using an "orientation-reversal" sequence in which changes of a grating's orientation are embedded in a sequence of random shifts in the spatial phase of the grating, without orientation change (Braddick et al., 1986; Braddick, 1993). Similarly, responses specific to the direction of motion of a random-dot pattern can be revealed, when reversals of direction are interspersed with events where the random dots are replaced without a change in direction (Wattam-Bell, 1991; Braddick et al., 2005). These methods have provided a principal line of evidence for the postnatal emergence of the characteristic selectivities (orientation, direction, and binocular) of cortical neurons, leading to models of the development of cortical function (Atkinson, 1984; Atkinson & Braddick, 1990; Atkinson, 2000; Braddick & Atkinson, 2011). This approach has also proved fruitful in identifying delays and deficits in cortical development in infants with perinatal brain damage and those born very preterm, where delayed development or absence of the orientation-reversal response has proved to be a useful early marker for abnormal brain development in infants and predictor of later cognitive and neurological status (Mercuri et al., 1998, 1999; Atkinson et al., 2008).

However, care is needed in specifying just what neural properties can be isolated by this approach. For example, consider the expected response of cortical simple cells (Hubel & Wiesel, 1962) to the orientation-reversal sequence outlined above. A simple cell shows linear summation of stimulus effects in the excitatory and inhibitory regions of its receptive field (Movshon et al., 1978*b*). In different phase positions, the balance of excitation and inhibition will change, and so each random phase shift will change the cell's response (somewhere between a maximum when a bright bar activates the excitatory region and a minimum when a bright bar lies in the inhibitory region). The response to an orientation change will be somewhere within this range of responses to the phase shifts and so will not lead to a distinctive component in the VEP signal. In contrast, it is characteristic of cortical complex cells that their response to an optimally oriented grating is insensitive to the spatial phase (Hubel & Wiesel, 1962; Movshon et al., 1978*a*), so their response will be little affected by the phase shifts, and the VEP contribution from such cells will therefore arise primarily from responses to the orientation reversals (Braddick, 1993). The onset of orientation reversal responses in infancy, then, may reflect the functional emergence of orientation-selective complex cells, and it

https://doi.org/10.1017/S0952523813000497 Published online by Cambridge University Press

remains possible that orientation-selective simple cells have a different developmental course.

A related method is to devise a stimulus sequence where some high level ("global") organization, such as the arrangement of elements into concentric patterns (e.g., Pei et al., 2005; Wattam-Bell et al., 2010), vernier alignment (Skoczenski & Norcia, 1999), or the layout of pixels to form a face or object image (e.g., Farzin et al., 2012) periodically appears and disappears. Local changes necessarily occur at each transition, but these are, at least statistically, symmetrical between the onset and offset of the global organization. Only a mechanism which is sensitive to the global structure will respond differentially. Thus, if the fundamental frequency of the stimulus corresponds to the complete cycle of two transitions (global-onset and global-offset), a response at the first harmonic (F1) must represent the activity of mechanisms responding to the global structure, whereas the second harmonic (F2, reflecting symmetrical responses to each transition) will reflect in whole or in part the local changes. Again, this method is naturally cast in the frequency domain using steady state recording, although a similar logic can be applied to examining a difference signal between measured transient responses at global onset and offset. The presence of an F1 signal confirms the presence of a mechanism sensitive to global structure, but it should be noted that such a mechanism might not be revealed if it gave an equal response (across the neural population yielding the scalp potential) to the onset and offset of structure, since such a response would appear in the signal at F2.

In summary, steady-state VEPs have indicated the successive emergence in the first 6 months of life of cortical responses to changes in orientation, directional motion, and disparity. This approach depends on designing stimulus sequences which control for accompanying low-level contrast changes. A second approach, demonstrating infants' responses to global structure (e.g., concentric form or motion, vernier alignment), depends on the difference between neural responses to the onset and offset of coherent structure. Such global sensitivity develops very rapidly after sensitivity develops to the local properties.

The neural origin of VEP responses

To link VEP measures to details of neural processing, we need to know from what neural processes the VEP arises. This has two aspects: microscopic and macroscopic. At the microscopic level, it is generally believed that evoked potentials represent the summation of slow potentials, such as postsynaptic potentials, rather than spiking activity (Wood & Allison, 1981). In the specific case of the functional development of area V1, this means that the presence of a VEP, for example to contrast onset or reversal, may reflect the postsynaptic effects in cortical cells of a barrage of input arising from the optic radiation due to contrast changes in the stimulus, but does not necessarily indicate that action potentials are being generated in those cells. For instance, it is well established that evoked potentials to contrast reversal can be measured in newborn or even preterm-born infants (Atkinson et al., 1979; Harding et al., 1989; McCulloch et al., 1999). This might be taken to indicate that visual cortical neurons are functioning at birth, despite the evidence discussed above that the characteristic selective responses of cortical neurons only emerge in the postterm months in human infants. However, it would be consistent with synaptic input to these cortical cells that was not yet able to evoke spiking activity. (Alternatively, it is also quite possible that cortical neurons are generating action potentials in response to visual stimulation at birth, but that these responses are not yet selectively tuned in terms of orientation, motion direction, etc.)

On a more macroscopic scale, there is much interest in assigning the origin of VEP components to particular brain structures. High-density sensor arrays can give quite a fine-grained picture of the distribution of VEP signals over the scalp. However, locating the distribution of electrical dipoles within the brain that give rise to a particular scalp distribution is a complex "inverse problem" which is only solvable with some assumptions and with detailed anatomical information about the topography and electrical properties of cranial tissues. This is particularly problematic for analyzing brain activation in infants. First, adult source localization is usually based on geometry derived from MRI scanning of the individual participant's head. This is rarely available for nonclinical infants, although some work using MRI with individual infants has recently been reported (Reynolds & Richards, 2009; Richards et al., 2010). Second, the electrical properties of different tissues in the head are not necessarily the same in infants and adults, and data on the infant tissues are sparse (Gibson et al., 2000). The effects of the fontanelles in the infant skull (gaps where the cranial bones have not yet fused in development) have not generally been modeled. The source of particular VEP components has been argued to be in area V1 by reason of polarity reversals that are taken to reflect the retinotopic layout of V1. However, it has been argued that this does not reliably distinguish signal arising in V1 from other early visual cortical areas such as V2 and V3 (Ales et al., 2013).

Consequently, we are at present more secure in assigning infant VEP signals to particular brain systems by identifying their functional properties with those of known cortical areas, than through topographical approaches, although this may change as source localization methods for infants become more refined. However, this does not mean that the scalp topography of infant VEPs has no value. First, differences in scalp topography of responses to different stimulus events can be taken to indicate that anatomically distinct systems respond to these events [e.g., the distinct responses to global form and global motion structure found by Wattam-Bell et al. (2010)], and so contribute to understanding the development of differential processing systems. Second, changes in the distribution of scalp potentials during development can reveal significant reorganization of the brain systems which underlie specific forms of processing, as in the case of global form and motion processing (Wattam-Bell et al., 2010).

In summary, at the cellular level, VEP responses are probably dominated by slow potentials rather than spiking activity, and the developmental course of these is not necessarily the same. Localizing the source structures from the scalp topography of VEP signals requires information about tissue properties and individual anatomy, which is currently very limited when we test individual infants. However, differences in scalp topography have yielded important information about the separate sources of responses to different stimuli and the reorganization of underlying systems with age.

Timing of neural events in the developing visual system

VEPs, unlike most other methods of investigating neural activity noninvasively, have a fine temporal resolution. This means that the timing of VEP signals can provide an index of the maturation of function in the visual pathway of the developing infant. The latency of the first major component of the VEP to contrast reversal ("P1," with a latency of about 100 ms in adults) becomes markedly shorter in the first 6 postterm months (McCulloch et al., 1999; Lee et al., 2012*a*), a development which is commonly taken to reflect the myelination of the visual pathway to the cortex. However, as

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discussed in the preceding section, this early response, reflecting the effects of an initial barrage, is not necessarily informative about the time course of processing within the cortex. An alternative measure, based on the phase of the steady-state response at different frequencies, provides an indicator of the time course of the entire neural response contributing to the VEP and therefore presumably includes contributions from intracortical processing as well as the arrival of visual information at the first cortical synapses. This measure, calculated from the slope of the plot of phase *versus* temporal frequency (Lee et al., 2012*a*,*b*), shows a much more prolonged developmental course than the transient latency of P1. This development must be associated with response components later than P1, which may reflect a combination of afferent activity in cortical neurons, the effect of intracortical connections within V1 (and possibly other early visual areas), and transmission, including feedback, between cortical areas. The phase-based measure also shows differential patterns of development between the responses to pattern reversal (Lee et al., 2012*a*), orientation reversal (Lee et al., 2012*b*), and direction reversal (Lee et al., 2013). This developmental dissociation supports the idea that discrimination of these different visual parameters of the stimulus depends on populations of neurons that have different properties.

It is likely that during early development, response times of neural elements involved in visual processing not only become faster but also that the variance of response times decreases, as discussed earlier. As well as affecting the measured magnitude of VEP responses, this could also change the waveform shape and (depending on the skewness of the distribution of response times) the timing of an identified peak.

In summary, reducing VEP latencies with age reflect the maturation of the infant's visual pathway, in both faster and less variable transmission. A measure calculated from the phase of steady-state VEPs shows a longer developmental course than standard measures of latency from transient VEPs, presumably because it reflects later development in the timing of cortical processes beyond the early transient peak.

VEPs require dynamic stimuli

A VEP signal is defined by its temporal relation to a discrete stimulus event. It follows that VEPs can only be used to analyze stimuli which undergo change, and in the case of steady-state VEPs, stimuli which change several times per second. This may limit the scope of VEPs for revealing responses with very slow dynamics, which may be characteristic of the youngest infants, as revealed by the measurements of response timing discussed in the preceding section. The restriction on the temporal properties of stimuli used in VEP tests provides one of the reasons why VEP and behavioral methods provide essential complements in measuring infants' visual abilities. For example, there appeared to be a discrepancy between VEP measures of the emergence of cortical orientation selectivity in the first 2 months (Braddick et al., 1986; Braddick, 1993) and behavioral evidence for orientation discrimination in newborns (Atkinson et al., 1988; Slater et al., 1988). However, the behavioral (habituation) tests used static oriented gratings, while the orientation-reversal VEP method depended on a steady-state signal to gratings whose orientation changed at up to 8 times per second. When the behavioral tests used the same temporal parameters as the VEP stimulus (orientation changes embedded in a sequence of phase shifts, discriminated from a grating with the same phase shifts but constant orientation), the developmental course of the two measures of orientation sensitivity fell into line (Hood et al., 1992).

In summary, some apparent discrepancies between VEP and behavioral measures of infants' capabilities are due to the need for rapid temporal changes to generate the VEP and are resolved when comparable temporal frequencies are used in behavioral tests. The comparison of VEP and behavioral measures is discussed further in a later section.

Interpreting behavioral responses

Much of the evidence on infants' visual development comes from eliciting differential behavior toward differential stimuli. The best known example is preferential looking (PL), either based on intrinsic preferences [e.g., the measurement of behavioral acuity, contrast, or chromatic sensitivity from fixation of a patterned *vs.* blank field (e.g., Atkinson et al., 1974; Teller et al., 1974; Atkinson et al., 1977; Dobkins et al., 1997)] or from preferences induced by habituation to one type of stimulus. However, inferences have also been drawn from diverse behavioral responses, including optokinetic nystagumus (Dayton et al., 1964), tracking eye movements (Fox et al., 1980), reaching responses (Atkinson & French, 1983; Yonas et al., 1985), and head withdrawal from looming displays (Yonas et al., 1979; Jouen et al., 2000).

The simple, and incontestable, inference from behavioral studies is that if two stimuli elicit different responses, then they must be differently represented somewhere in the infant's brain. If our question is "what information do the infant's eyes deliver to the brain?," then the finding of differential behavior may answer this question. This may be the goal, for example, of measurements of infants' acuity. However, the occurrence of different behavioral responses leaves open the question of where in the brain this differential representation occurs. Different forms of behavior engage distinct brain systems, and it has become increasingly apparent that these systems may use different properties of the visual input and perform their own characteristic computations on that input.

Multiple behavioral systems: Motion processing

An example comes from examining brain systems and behavior in directional motion processing. PL studies reveal that detection of motion segmentation, which must be based on direction selectivity, first emerges between about 6–8 weeks of age (Wattam-Bell, 1992, 1994, 1996*c*), and neither habituation (Wattam-Bell, 1996*b*) nor VEP (Wattam-Bell, 1991; Birch et al., 2000) measurements provide any evidence for earlier development of directional responses (see review by Braddick et al., 2003). However, optokinetic nystagmus (OKN), which requires a directional motion signal, is present from birth (e.g., Dayton et al., 1964; Kremenitzer et al., 1979) This apparent contradiction can be resolved if we take into account the evidence that the form of OKN seen in very young infants is controlled by a subcortical mechanism (Atkinson 1979; Atkinson & Braddick, 1981; Braddick et al., 1992; reviewed by Braddick et al., 2003). The idea that PL is supported by a different mechanism of motion processing is supported by the finding that coherence thresholds for the two behavioral indicators follow very different developmental courses (Mason et al., 2003). Given the knowledge that directional processing in the geniculostriate pathway emerges at the cortical level, and the finding that VEP signatures of directionality are not apparent before 6–10 weeks, it has been inferred that the PL response to segmented motion depends on cortical processing.

https://doi.org/10.1017/S0952523813000497 Published online by Cambridge University Press

In summary, different behavioral responses used as indicators of infants' capabilities may depend on distinct neural systems. These differences have helped to dissociate the development of, for example, the sensitivity of cortical *versus* subcortical systems.

PL, fixation shifts, and attention

However, it cannot be assumed that PL in general is a cortically mediated process. Infants from birth can orient toward a salient target, but data on infants' ability to shift fixation show that the youngest infants will only do this if there is no competition from a visible object which they are already fixating. The ability to disengage promptly (under 2 s) from one object to fixate another develops only after about 3 months of postterm age (Atkinson et al., 1992). Thus in the youngest infants, PL for a stimulus paired with a blank field (as in the measurement of acuity and contrast sensitivity) may be an efficient method for assessing visual sensitivity, since there is effectively no competition. However, when a PL test of discrimination pairs a stimulus with a "foil" which itself contains competing detail, the looking behavior of infants up to 3 months of age is likely to be at best sluggish in switching between the stimuli. The stimuli used in motion PL experiments provide a potential example. Here, the infant is presented with a stimulus which on one side of the center contains a region of moving dots, which is segmented from its surround by opposite directions of motion, with a second region on the opposite side in which all the dots move uniformly (Wattam-Bell, 1992), meaning that there is dynamic detail for both the test stimulus and the foil.

In general, the point is well known that negative results in PL, whether between a target stimulus and a blank field (as in acuity testing) or between target and foil that both contain visual detail (as in the segmented motion test) cannot yield any definitive conclusion, since the infant may discriminate the stimuli but not manifest any fixation preference. Thus, converging studies using VEP and habituation methods are important in inferring that the PL results on directionality are constrained by the neural processing of motion information and not just by the competitive demands of the two stimuli in the PL display.

Quite apart from its role in PL, the process of shifting fixation is important in its own right for inferring the development of infants' brain mechanisms underpinning orienting and localized attention. Work on nonhuman primates has shown that the superior colliculus in the midbrain contains superimposed visual and oculomotor maps and provides outputs to the oculomotor nuclei. This provides the basis for a robust but primitive "unconscious" automatic orienting system, which can direct fixation to significant events in different sensory modalities (see Calvert et al., 2001; Wallace & Stein, 2001). Newborns' responses to localized stimuli, both auditory and visual, show that this orienting system is functional from birth. Evidence from hemispherectomized infants indicates that lateralized shifts of fixation, when there is no competition between two visible targets, do not require an intact cortical representation of the target object, but that fixation shift under competition does (Braddick et al., 1992). Results from studies on nonhuman primates indicate a pathway from frontoparietal cortex, which can inhibit the collicular maintenance of fixation (Schiller & Tehovnik, 2005). This combination of evidence has been used to infer that the newborn's orienting can be mediated by a subcortical (collicular) system and that in development, this comes to be modulated by a cortical mechanism which can initiate disengagement from the current fixation object when a new target appears elsewhere in the field (Atkinson et al., 1992; Atkinson & Hood, 1997).

The fixation shift paradigm, comparing infants' ability to shift gaze with and without a competing target, has proved a valuable method for assessing cortical function and predicting outcome in infants with early brain damage, including focal lesions (Hood & Atkinson, 1990), neonatal hypoxic-ischemic encephalopathy (Mercuri et al., 1999), and very premature birth (Atkinson et al., 2008) (see review by Atkinson & Braddick, 2012). It has also indicated deficits in attention networks in Williams Syndrome (Atkinson et al., 2003). However, given the complexity of attention networks in the mature brain, discussed below, we should be cautious in interpreting all these deficits in terms of the same neural systems.

The system connecting frontoparietal cortex to colliculus is just one element in a more extensive network of brain areas involved in the attentional control of brain function. Imaging and neuropsychological evidence has been used to distinguish three distinct systems within this, concerned respectively with selective attention (including the orienting function), sustained attention, and executive control (Fan et al., 2005; Posner & Rothbart, 2007). Psychometric studies with a new battery of age-appropriate attention tests designed to tap these systems (the Early Childhood Attention Battery, ECAB: Atkinson & Braddick, 2012; Breckenridge et al., 2013) have found that these functions do not become differentiated before about 4 years of age; factor analysis across the whole battery (including tests designed for selective, sustained, and executive control of attention) indicates that performance before this age is best modeled by a single factor. One interpretation of this would be that with age, there is an increasing specialization of brain systems for different components of attention. However, another is that before 4 years of age, these systems might have a distinct neural basis, but that performance of all three systems is limited by some common general constraint. This area of the components of attention provides an example both of the light that adult neuropsychology can throw on development and the caution needed in making developmental inferences about brain systems in infants and young children. A different kind of example is provided by the finding that damage to the basal ganglia, which is not reported to have significant visual implications in adults, appears critical for early development of visual function in infancy (Mercuri et al., 1997*a*).

In summary, PL performance depends in part on the development of attention systems, in particular on the cortically mediated ability to disengage from one stimulus and switch fixation to another. Attentional systems are a key element in linking the processing of the visual input to behavior. Specific neural systems for sustained attention, selective attention, and executive control emerge in development and are particularly important for assessing functional vision in children with clinical problems. In children with severe cerebral visual impairment (CVI), there is often a statement made from behavioral testing that these children have a visual loss, although it would often be more reasonable to conclude that they have a deficit of visual attention (often a deficit in disengaging from one stimulus to another) rather than a sensory visual loss.

Control of visuomotor actions: Interactions between dorsal and ventral streams

We have discussed how the development of motion processing must be understood in terms of distinct brain systems underpinning different kinds of behavior. Other examples of multiple behavioral systems come from manual behavior. Between about 6 and 18 months of age, infants show an almost compulsive tendency to reach, grasp, and manipulate objects of an appropriate size relative to the hand, that are placed within arms' reach. This behavior can serve as the

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basis of a "manual psychophysics" of visual distance perception, demonstrating sensitivity to binocular information (Braddick et al., 1996; Braddick & Atkinson, 2013) and to a range of perspective and other depth cues (Yonas et al., 1985, 2002), and also sensitivity to the object size (Newman et al., 2001; Braddick & Atkinson, 2007). These relationships are specific to the system controlling reaching, so for instance, the size of the object which is preferred as the target for a reach is not necessarily the same as the preferred target for visual fixation (Newman et al., 2001; Braddick & Atkinson, 2013).

The translation of visual information into the control of action is proposed to be the major function of the cortical dorsal stream, connecting occipital visual processing to the parieto-frontal systems which program and control spatially directed actions (Milner & Goodale, 1995). Different kinds of visual information are important for different types of action, and there is evidence that visuomotor translation involves distinct modules involved in the control of different actions (saccades, smooth pursuit, reaching, grasping, locomotion, etc.) (Goodale, 1996; Jeannerod, 1997). The differences between visual stimuli engaging infants' fixation and those evoking reaches indicate the distinctive properties of different visuo-motor modules. In infants aged between 8 and 12 months, it can lead to a dissociation in which the larger (more visually salient) of two objects is treated as the initial target for looking, but a reach is directed toward the smaller (more readily graspable) object, on the same presentation (Newman et al., 2001; Braddick & Atkinson, 2013).

Such findings mean that it may be misleading to think of the infant's various behavioral responses as routes for revealing the information present within a unitary visual representation in the infant's brain. In the development of reaching, following the age at which there may be differently specified target objects for reaching and looking, these two behaviors become more closely coupled, with the fixation system acquiring the target to which a reach is intended (Newman et al., 2001; Braddick & Atkinson, 2013). However, even in normal adults, the information used in the dorsal stream to control reaches is not necessarily available for conscious report (Castiello et al., 1991; Binsted et al., 2007), and in a patient with ventral stream damage, such a dissociation can be very striking (Milner & Goodale, 1995).

Locomotor responses to optic flow (Barbu-Roth et al., 2009) provide another example which may show a developmental trajectory for specific processing of visual stimuli associated with a particular visuomotor translation system.

In summary, we must expect that when we tap infants' visual processing through different action systems, we will find different patterns of sensitivity. On the one hand, this complicates attempts to define the visual information available to the infant and "experienced" by the infant. On the other hand, it potentially allows us to dissect the development of the different brain systems, subcortical, ventral-stream, and dorsal-stream, which process visual information.

Comparison of behavioral and VEP measures

From the discussion above, it will be clear that behavioral and VEP measures of infant vision involve different assumptions and constraints and do not necessarily tap the same neural mechanisms. For a secure and comprehensive understanding of what visual discriminations the infant can make, we therefore need to combine information from both approaches.

In the past, there has been considerable discussion of whether VEP measurement, compared to PL, provides a more sensitive measure of the development of infants' acuity (e.g., Sokol et al., 1983). More generally, however, the relation between the measures can be quite different in different cases. In the case of directional selectivity discussed above, the average age of onset measured from PL is several weeks earlier than the age at which a VEP can be elicited by direction reversal (Wattam-Bell, 1996*a*; Braddick et al., 2003). In contrast, the onset of cortical binocularity, as indicated by a VEP elicited by binocular correlation, occurs on average 2 weeks earlier than PL measures using closely similar stimuli (Smith et al., 1988; Braddick, 1996). This latter study is one of the few where the two methods were used with the same individual infants. The high correlation between the developmental onset measured by VEP and PL increases confidence that in this case at least, both methods reflect a common underlying process of neural development.

In another case, longitudinal acuity and contrast sensitivity measurements were made with the same individual infant over the first 3 months of life and results compared using PL, OKN, and VEP as parallel measures of grating detection (Atkinson, 2000, ch. 4). The stimulus parameters, the size of the field, and statistical analyses were matched as closely as possible across these different methods. A good agreement of acuity and contrast sensitivity estimates and trajectories was shown across these different methodologies, supporting the idea that, over the age range covered (up to 3 months), these measures reflect a common limiting factor, presumably early in the visual pathway. However, optical, retinal, and cortical limitations on acuity have different developmental courses, and these factors may have a different balance in their effects on the three types of measure at later ages (see review by Braddick & Atkinson, 2011).

In principle, in cases where different VEP and behavioral methodologies yield systematically different results, it might be possible to understand these differences in terms of different neural systems determining the performance seen with each measure. Such arguments will be most compelling where there is a good basis, from neuropsychology, nonhuman neuroscience, and other sources for inferring which brain systems underlie a particular type of behavioral or electrophysiological response.

These issues become particularly relevant in clinical applications where the normal developmental relations between different visual mechanisms may not hold (e.g., Hood & Atkinson, 1990; Mercuri et al., 1999). Discrepancies between measures that are normally correlated in development, such as PL acuity and orientation reversal VEP, are potentially revealing about which neural systems have been affected by pathology.

Levels of processing: The example of dorsal stream vulnerability

The study of infants' visual development has become progressively concerned with the information transmitted beyond the early stages of the visual pathway. For some aspects of processing in extrastriate visual areas, we have sufficiently good evidence of the areas' function that the logic discussed above can be applied. For instance, first, the relatively larger receptive field size of neurons in area V5 (MT) compared to those in V1 (Mikami et al., 1986), second, their sensitivity to global motion coherence (Britten et al., 1993), and third, the fMRI activation of areas V5 and V3a by the contrast between dot patterns in coherent and incoherent motion (Braddick et al., 2000), all provide converging support for the idea that infants' sensitivity to motion coherence is mediated by this level of the hierarchy of extrastriate processing. Such sensitivity, in

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infants aged 3–5 months, has been demonstrated both behaviorally (Braddick & Atkinson, 2007) and through VERP activation measures (Wattam-Bell et al., 2010).

However, the fact that this level of processing is functional in the infant does not mean that it operates in the same neural network as in the adults. Wattam-Bell et al. (2010) showed that, although both infants and adults gave reliable VERP responses to the onset of motion coherence, the topography of the scalp distribution of these responses was quite different in infants to that of adults. This result implies that, between infancy and adulthood, there is significant reorganization of the network involved. For example, one interpretation consistent with the data is that the VERP response in adults is dominated by a feedback loop from extrastriate areas to area V1, which is not yet operating in infants (Wattam-Bell et al., 2011). However, there are other possible models of reorganization which will need to be distinguished in future research. There are also changes between infancy and adulthood in the spatiotemporal properties (Hou et al., 2009) of the system which responds to radial optic flow, and in the relative responsiveness to expanding and contracting flow (Brosseau-Lachaine et al., 2008; Shirai et al., 2009); exploration of these changes may help us to understand the developmental reorganization of global motion systems.

Beyond infancy, poor behavioral sensitivity to motion coherence, compared to an analogous task detecting coherence of static form, has been identified as a deficit in a wide range of neurodevelopmental disorders. The areas processing global motion form part of the dorsal stream of cortical processing (in contrast to global aspects of static pattern which are processed in ventral-stream areas such as V4), and so, this widespread pattern of deficit has been characterized as "dorsal stream vulnerability" (Atkinson et al., 1997; Gunn et al., 2002; Braddick et al., 2003; Atkinson & Braddick, 2007, 2011*a*). This concept has gained strength with findings that the disorders which show this pattern are characterized in middle childhood by deficits in spatial cognition, attention, and visuomotor performance, all functions with dorsal stream involvement. [It should be recognized, though, that these disorders may involve other brain structures also, for example the cerebellum in Williams syndrome (Mercuri et al., 1997*b*).]

The dorsal steam, considered in this broader sense, is a complex system which gains spatial visual input through the extrastriate areas we have already cited but distributes this information through multiple networks in parietal, frontal, and medial temporal cortex. Kravitz et al. (2011) have used adult fMRI imaging and nonhuman primate data to delineate anatomically and functionally these dorsal stream networks. We need to question then, at what level of this network do the dorsal stream deficits arise (Atkinson & Braddick, 2011*b*)? This question has two components: first, what brain system, or systems, are abnormal at the time the behavior is assessed? and, second, at what levels of the system did the abnormal development originate? Does the pattern of deficit derive from cascading effects of an early failure in extrastriate areas such as V5 to provide the visual information needed for higher level functions to develop properly? The answers to such questions await data on the correlation between different aspects of dorsal stream vulnerability (motion processing, visuomotor, spatial, and attentional abilities) both at a given stage of development and longitudinally in childhood, together with randomized control trials of intervention to discover whether training and improvement in one domain, for example, improvements in motion coherence sensitivity, has consequences for spatial and attentional abilities. However, the questions highlight that, in the context of infants', young children's, and adolescents' vision, linking hypotheses between brain and behavior are not only restricted to synchronous relationships but also have a cascading developmental dimension.

In children with developmental disorders, we need to consider how far deficits in performance reflect an overall neurocognitive delay—that is, brain development simply equivalent to typical children of a younger age—and how far they indicate anomalies of development in specific subsystems. The idea of dorsal stream vulnerability is that dorsal stream systems lag behind ventral in development, so that the relative sensitivity does not correspond simply to overall delay. In WS, this anomaly of relative sensitivity between the two streams persists into adulthood (Atkinson et al., 2006).

In summary, the finding of dorsal stream vulnerability in developmental disorders raises the question of how different levels of brain processing relate to each other in development. The initial evidence was based on relative sensitivity to global motion and forms coherence, but subsequent studies show selective deficits in higher-level functions of the dorsal stream (visuo-motor coordination, spatial cognition, and attention). It remains a key question for future research whether these deficits result from these higher-level processes receiving abnormal visual information.

Infants' visual experience

When we have both evidence on infants' behavioral capabilities and VEP responses, and inferences made from these about the underlying neural mechanisms, there remains the question of the "inverse linking hypothesis" mentioned in the introduction: what visual experience do these mechanisms provide to the infant? James (1891) famously asserted that the newborn's world was a "blooming buzzing confusion," but this is more poetic than informative. Attempts are sometimes made to illustrate the effects of infants' limited acuity and contrast sensitivity at different ages [see Fig. 22 of Teller (1997) for an example]; these may give an indication about what information is potentially available for visual processing but say little about what experience that processing delivers. Simulating a blurry and low contrast view does not help us imagine a world in which we cannot discern contour orientation and motion direction, which appears to be the case for the visual world of an infant in the first weeks of life. We have a similar problem in penetrating the visual experience of some neuropsychological patients, for example, a sufferer from agnosia who can describe an object's color and texture but be quite incapable of identifying it; who can draw a good apple from memory but is quite incapable of reproducing the shape of an apple in front of her (Milner & Goodale, 1995). We can appreciate some analogies from our own experience under extreme conditions; for example, with high-velocity motion of low spatial frequencies, we have a sense of rapid change but no appreciation of direction, and this seems to be the case for young infants presented with motion at all velocities (Wattam-Bell, 1996*c*; Braddick & Atkinson, 2009). It may also be possible to make connections with neuropsychology; for example, the "blindsight" shown in the visual responses of individuals who have V1 lesions (Weiskrantz, 1996) may have some analogy to the visual world of the infant in whom cortical responses have not yet emerged (Braddick et al., 1992). However, our ability to appreciate the visual experience of the infant, even though it is part of the individual experience of all of us, must remain indirect and tentative.

Conclusions and prospects

We now have considerable understanding of how developing neural mechanisms underlie the visual capabilities of infants, most

https://doi.org/10.1017/S0952523813000497 Published online by Cambridge University Press

securely when we have been able to apply converging methods from electrophysiology and multiple behavioral systems. To extend this understanding will require methodological innovation. We will need to improve the analysis of the sources of VEP signals and use fine-grained temporal analyses of these to build a fuller picture of how feedforward and feedback mechanisms develop in the human visual brain. Advances in functional MRI may make it possible to build on the limited studies that have managed to apply this method to infant vision (e.g., Born et al., 1998, 2000). We can also expect continuing insights from parallel studies of development of the visual brain in other species, as exemplified by Kiorpes et al. (2012). Insights may also come from studies that exploit individual differences in development, possibly linked to genetic differences, in longitudinal studies; for example, does the early ability to control fixation shifts predict the later development of attentional systems? Such approaches may lead us from a series of snapshots of visual brain function at different ages, to a more truly dynamic developmental perspective.

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