Human infants can generate vergence responses to retinal disparity by 5 to 10 weeks of age

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Vergence is defined as a binocular eye movement during which the two eyes move in opposite directions to align to a target in depth. In adults, fine vergence control is driven primarily by interocular retinal image disparity. Although infants have not typically been shown to respond to disparity until 3 to 5 months postpartum, they have been shown to align their eyes from hours after birth. It remains unclear what drives these responses in young infants. In this experiment, 5- to 10-week-old human infants were presented with a dynamic random noise stimulus oscillating in disparity at 0.1 Hz over an amplitude of 2° for 30 s. Fourier transforms of the horizontal eye movements revealed significant disparity-driven responses at the frequency of the stimulus in over half of the tested infants. Because the stimulus updated dynamically, this experiment precluded the possibility of independent monocular fixations to a sustained target. These data demonstrate cortical binocular function in humans by five weeks, the youngest age tested here, which is as much as two months younger than previously believed.

Introduction

The two eyes of a primate must be actively aligned in a dynamic three-dimensional environment to take advantage of a typical binocular view of the world. This binocular function facilitates perception of space and behaviors such as reaching, grasping and locomotion (Hibbard & Bradshaw, 2003; Melmoth, Storoni, Todd, Finlay, & Grant, 2007; Theys, Pani, van Loon, Goffin, & Janssen, 2013). Failure to achieve sustained binocular eye alignment during early development results in disrupted synaptic refinement in the cortex of monkeys with strabismus (e.g., Bi et al., 2011; Boothe & Brown, 1996; Crawford & Harwerth, 2004; Fenstemaker, Kiorpes, & Movshon, 2001; Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998; Shooner et al., 2015), and amblyopia and loss of perceptual binocular function in humans (e.g., Atkinson & Braddick, 1983; Ingram, Lambert, & Gill, 2009). Fine adjustment of alignment in adult humans is achieved using retinal disparity cues (Erkelens & Collewijn, 1985; Westheimer & Mitchell, 1969), and the use of disparity to control vergence eye movements is a prerequisite for normal binocular vision in human adults.

Although there is evidence that infants as young as 8 weeks show some binocular summation at the level of visual cortex (Braddick, Wattam-Bell, Day, & Atkinson, 1983), along with somatic physiological responses to disparity, such as increased heart rate (Appel & Campos, 1977), classical studies of sensitivity to disparity (assessed with VEP or preferential looking) have typically suggested that human infants fail to demonstrate responses to binocular disparity until 3 to 5 months of age (Atkinson & Braddick, 1976; Birch, Gwiazda, & Held, 1983; Fox, Aslin, Shea, & Dumais, 1980; Held, Birch, & Gwiazda, 1980; Petrig, Julesz, Kropfl, Baumgartner, & Anliker, 1981) with only one study demonstrating as many as 65% of 2-month-olds responding to a large-amplitude clinical stereo-test (Birch & Salomao, 1998). These studies have been used to propose a lack of reliable binocular function until that age (e.g., Braddick, 1996; Held, 1993; Riddell, Horwood, Houston, & Turner, 1999; Teller, 1997).

Nonetheless, infants have been shown to realign their eyes in depth from hours after birth (Riddell et al., 1999; Seemiller, Wang, & Candy, 2016; Slater & Findlay, 1975). One possibility is that these oculomotor

responses are capable of being driven by interocular disparity signals. Another possibility is that these vergence eye movements were responses to monocular cues to depth (Enright, 1987; Maddox, 1893; Mitchell, 1970; Schor, 1992; Semmlow & Hung, 1981). A third possibility suggests that infants may be utilizing independent monocular eye movements to refixate a target; each eye arrives on a target without input from the other eye. These "monocular foveations" would give the outward appearance of vergence without being a truly binocular response (Riddell et al., 1999). Currently, therefore, it is not clear which cues or processes are contributing to vergence in infants younger than three months and whether retinal disparity can be a useful cue.

Several studies of adult macaques have suggested that absolute retinal disparity cues may be available to drive vergence responses and eye alignment at earlier stages of processing in visual cortex (V1) than relative disparity for depth perception (V2, MT, MST; Cumming & Parker, 1997; Cumming & Parker, 1999; Thomas, Cumming, & Parker, 2002). Neurophysiological evidence from neonatal monkeys has also suggested that disparity sensitive neurons are present in V1 and V2 at 6 to 10 days after birth and are largely limited by the spatial resolution of monocular inputs (Chino, Smith, Hatta, & Cheng, 1997; Maruko et al., 2008). Thus, it may be possible that young infants are able to access coarse absolute disparity information for vergence at a younger age than they can respond to finer relative disparities.

Given the physiological evidence for disparity selectivity early in life, the current study asked whether retinal disparity alone could drive a vergence eye alignment response in 5- to 10-week-old human infants. Large field dynamic random noise stimuli were modulated sinusoidally in disparity while eye position was recorded. This stimulus differs from those used previously, in that disparity was the only information available to drive vergence. For example, physical objects presented at near distances (e.g., Slater & Findlay, 1975) present multiple consistent cues, such as blur and pictorial information. Realignment responses elicited by prism deviation could in theory be two separate monocular eye movements independently fixating a sustained moving target (Hainline, Riddell, Grose-Fifer, & Abramov, 1992; Held, 1993; Riddell et al., 1999). We presented a dynamic transient target that only changed in binocular disparity—there was no monocular motion cue. Vergence responses at the temporal frequency of the stimulus modulation would suggest that infants are using binocular cues to drive vergence sooner after birth and would require a revision of models of the development of human binocular function.

Methods

Subjects

Twenty-two full-term, typically developing human infants were recruited between the ages of 35 and 65 days postpartum. The median age at the first visit was 55 days. Eleven prepresbyopic adults with no known binocular abnormalities, wearing any habitual optical correction, were also recruited. Informed consent was obtained from all adult subjects and the infants' guardians. The study was approved by the Indiana University Institutional Review Board and adhered to the Tenets of the Declaration of Helsinki.

Stimulus and data collection

Subjects viewed stimuli presented on a rear projection screen (S-60-3-D; Screen-Tech, Hamburg, Germany). Left and right eye images were presented dichoptically using circular polarizing filters over two vertically stacked projectors (Casio XJS 52; Casio, Shibuya, Tokyo, Japan). The rear-projection screen preserved the polarization of the light forming the images, which were then viewed through corresponding filters worn in glasses for adults or goggles for the infants.

The stimulus was drawn using functions based in MATLAB (MathWorks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The stimulus consisted of binary random noise patterns subtending 86° horizontally by 60° vertically at the viewing distance of 45 cm, with a pixel size of 6 minutes of arc. Individual green noise elements subtending 5.75° horizontally by 8.65° vertically, were placed at uniformly random horizontal and vertical coordinates on a black background and could overlap other nearby noise elements. In any single frame, between 45% and 50% of the screen was black (luminance $= 11$ cd/m^2) with the remaining area being green (luminance $= 204$ cd/m^2). The noise field updated at 3 Hz so that a new field of static spatially random elements was presented every 333 ms. Individual trials lasted for 30 s, during which a trained lab member held the infant gently in place or the adult maintained their head in a stable position. If an infant became restless and more than two seconds of continuous data collection were missed the trial was discarded.

During test condition trials, the entire stimulus field oscillated sinusoidally in disparity at 0.1 Hz, with an amplitude of 2° (4° peak-to-trough). The entire images were shifted in opposite directions on the projection screen, generating a consistent binocular disparity across the full screen. There were three cycles of
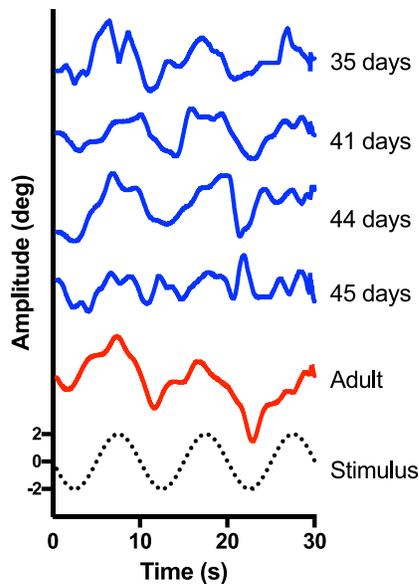
Figure 1. The vergence responses of the four youngest infants tested and one adult. The dotted sinusoid represents the stimulus profile. The data were smoothed over a 1 s window for presentation in this figure, to emphasize the low frequency content in the response. Individual trials are shifted vertically for clarity.

disparity modulation during each thirty-second trial. A video-based Purkinje image eye tracker (PowerRef 3; Plusoptix, Nuremberg, Germany) was aligned above the rear-projected image at a distance of 1 m from the subject's eyes. It captured images of the participants' eyes using beamsplitters that reflected infrared light while transmitting visible light to prevent occlusion of the stimulus on the screen. An experimenter started the eye movement recording and stimulus presentation manually using simultaneous key-presses. The beamsplitters were held in place using transparent plastic strips that also did not interfere with the projected images. The eye tracker recorded horizontal gaze binocularly at 50 Hz and vergence position was calculated by subtracting the right from the left horizontal eye position. A single Hirschberg ratio (the ratio of ocular rotation to Purkinje image displacement in the pupil image) of 20.89 pd/mm was used to calibrate the data for both infants and adults (Riddell, Hainline, & Abramov, 1994; Schaeffel, 2002).

Data analysis

A fast Fourier transform (MATLAB) was used to derive the amplitude spectrum of each stimulus and response vector. Missing data (either due to blinks, small pupils, or the subject looking away from the screen) for epochs of less than two seconds were interpolated using simple linear interpolation. The

amplitude of the response at 0.1 Hz, the modulation frequency of the stimulus, was compared with the response averaged across the two adjacent frequencies (0.0667 and 0.133 Hz) as an estimate of ocular motor noise (Norcia & Tyler, 1985).

If the subject remained cooperative after five test trials, a control condition was also performed. The interocular disparity was held constant for 30 s while the noise patterns updated at 3 Hz, thus providing no disparity cue to modulate vergence. These data were analyzed using the same approach as the test condition, so that the response at 0.1 Hz could provide an additional estimate of unrelated vergence activity at the stimulus frequency of the test condition.

A paired t test was performed for each age group, to test the significance of the responses at 0.1 Hz relative to the intratrial noise estimates (each noise estimate being the mean of the adjacent frequencies for the relevant trial). When more than one trial was collected within a session, the trial with the median amplitude was used for analysis (if an even number of trials were collected, the median two were averaged). We also computed Hotelling's T^2 to assess the statistical significance of the temporal relationship between the stimulus and vergence responses. The statistical significance level was set at 0.05. When possible, data from the first two trials were used to assess repeatability. In addition, longitudinal data were then collected from five infants on subsequent visits, until 67 days postpartum.

Results

Usable data were collected from 16 of 22 infants and 10 of 11 adults. Six infants were excluded as a result of restlessness and one adult was excluded as a result of her pupil size being below the minimum required for the instrument to collect data. Examples of raw data from the four youngest infants and one adult are shown in Figure 1. Response amplitudes for all trials from all of the included infants are shown in Figure 2. For the group analysis, we used the median trial amplitude from each subject's first visit, and compared this with responses at the adjacent frequencies on the same trials. Responses at the stimulus frequency were significantly larger than the noise estimation (paired t test, $t = 4.926$, $p = 0.0002$).

The raw traces, including those for adult observers, show large deviations from binocular alignment to the stimulus. This reflects two important limitations of working with infant subjects. First, the head (and body) is free to move. Second, no independent calibration of the eye position measures was possible. These deviations are therefore also likely to reflect calibration offsets (i.e., true Hirschberg ratios that are not equal to
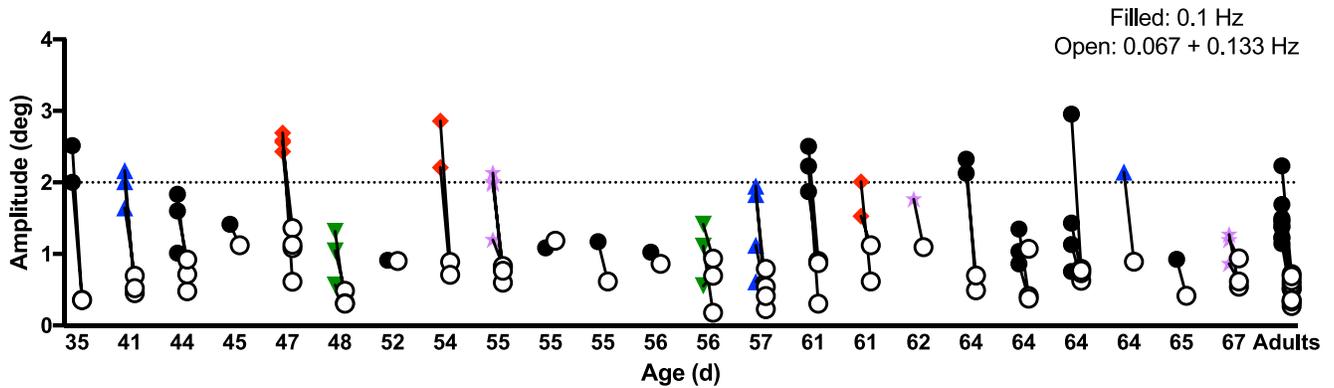
Figure 2. Summary of all the usable trials collected from each infant and the first trial from each adult. Filled circles are the response amplitudes at 0.1 Hz (the frequency of the stimulus). Open circles are an average of the amplitudes at the adjacent frequencies (0.0667 and 0.133 Hz). Data from individual trials are connected with a line. For infants, multiple trials are plotted separately in the same column. Longitudinal data collected from four infants are distinguished by unique colors and symbols. The amplitude of the stimulus is represented for comparison by the dotted horizontal line at 2°. Although all trials are shown here, only the trial with the median amplitude from the first visit was used for statistical analyses.

the one estimated here). It is for this reason that responses to a periodic stimulus were recorded—a systematic modulation in the response at the stimulus frequency provides clear evidence of disparity driven vergence that does not depend on instrument calibration.

Static control data were collected from nine infants and 10 adults. During those trials, the stimulus was matched in all characteristics to the disparity modulation condition, but the disparity was held at a constant value of zero (relative to the screen) for the full 30-s trial. The response at 0.1 Hz from 16 of these trials from infants (four trials from one infant, two trials each from four infants, and one trial from four infants) was used as an additional estimate of vergence noise. The mean response amplitude at 0.1 Hz from these trials was 0.48° ($SD \pm 0.36$), as compared with a mean estimate averaging adjacent frequencies during the test condition of 0.68° ($SD \pm 0.42$).

Four infants were tested longitudinally over two or three visits, between 41 and 67 days. These data are plotted as individual colors and symbols in Figure 2. No statistical analyses were performed on these data because of the small sample size, but there is no obvious developmental trajectory.

The phase lag of the response at 0.1 Hz was also calculated relative to the stimulus (while noting that the stimulus and data recording were started with simultaneous physical key presses, potentially introducing small offsets). These results are shown in polar form in Figure 3. The lag of the mean vector for adults was equivalent to 0.305 s (amplitude = 1.54°). The phase lag of the mean infant vector was equivalent to 0.200 s (amplitude = 1.49°). Though the infants appear to have a shorter lag than adults, there is likely influence from four low amplitude responses with apparently leading

phases in the infant cohort. Hotelling's T^2 revealed statistically significant differences between test and static control results for both adults ($T^2 = 40.1$; $p = 0.00010$) and infants ($T^2 = 50.3$; $p = 0.000015$).

To assess the repeatability of the data, multiple test trials were run during each visit for both infants and adults. The full variation within sessions can be seen graphically in Figure 2. The 95% limits of agreement (LOA) were calculated as a summary of the variation. This metric describes the 95% confidence interval for the difference between pairs of trials. For infants who provided more than two usable trials in their first visit (8 out of 16), the first two recorded trials were used. The 95% LOA for the response at 0.1 Hz was ±1.01° for infants. The mean difference between Trial 1 and Trial 2 for infants was −0.081° (mean unsigned difference of 0.38°). For adults, the 95% LOA was
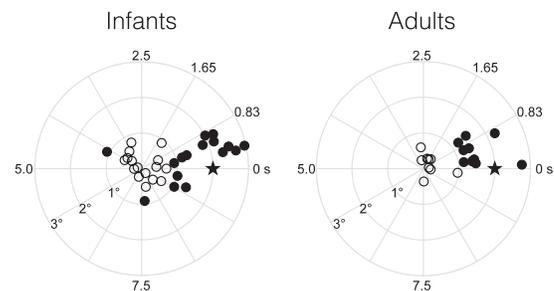

Figure 3. Polar plots showing lag in seconds (theta) relative to the stimulus and amplitude in degrees (rho) for infant (left) and adult (right) responses at 0.1 Hz. The median amplitude trials from the first visit for the test condition for infants are included while all control trials are included. For adults, only the first trial is included. Filled circles represent the disparity test condition while open circles represent the static zero disparity modulation control condition. The stimulus is shown as a pentagram.
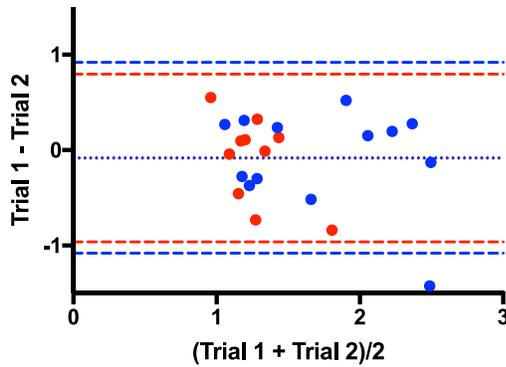
Figure 4. Tukey mean-difference plot to assess repeatability for infants (blue) and adults (red). The dotted lines are the mean differences (superimposed at this scale) and the dashed lines are the bounds of the 95% limits of agreement. Units are degrees. The first two usable trials recorded in the same session are used for each individual plotted.

$\pm 0.882°$. The mean difference between trials was -0.087 (mean unsigned difference of $0.32°$). These results are plotted in Figure 4.

Discussion

These data demonstrate that some infants at 35 to 65 days can make tracking vergence responses to a 0.1 Hz oscillating disparity of 2° amplitude, in the absence of any other cues that could drive vergence. Twelve of 16 infants showed evidence of a signal-to-noise ratio (the response at 0.1 Hz over the mean response at the adjacent frequencies) greater than 1.96 by 65 days postpartum along with all adults who gave usable data (Figure 2). Although other studies have demonstrated alignment responses to a prism-induced disparity by two months (Aslin, 1977; Riddell et al., 1999), they were unable to rule out the possibility that the two eyes were arriving independently at a sustained target feature. Horwood and Riddell (2013) also showed vergence responses in 8 of 30 6- to 9-week-olds viewing a low spatial frequency cartoon image scaled to remove proximal cues. Again, however, the image features were maintained and, therefore, did not preclude the possibility of independent monocular eye movements. The current study is the first to demonstrate tracking responses to interocular retinal disparity alone, in the absence of a persistent feature for monocular fixation. Additionally, because the stimulus frames were temporally uncorrelated, there was no systematic interocular velocity signal, which can drive vergence in adults (Sheliga, Quaia, FitzGibbon, & Cumming, 2016).

It is important to note that although 75% (12 of 16) of the infants shown in Figure 2 were capable of at least one trial with a strong response (SNR > 1.96), others did not appear to respond to the disparity. This variability could be the result of individual variation in the onset of disparity sensitivity (Birch & Petrig, 1996). However, this may also be the result of responses to monocular cues. Precisely because this stimulus isolates the disparity cue, it also places disparity in conflict with monocular cues (e.g., Backus, Banks, van Ee, & Crowell, 1999; Hillis, Watt, Landy, & Banks, 2004). That is, blur and proximal cues indicate that depth is not changing in the stimulus, and vergence responses of some infants could be tempered by this conflict.

These findings demonstrate that human infants as young as 35 days can be capable of responding to binocular disparity. This is weeks earlier than the youngest binocular responses previously recorded (Braddick et al., 1983) and the earliest laboratory estimates of disparity sensitivity (Birch & Petrig, 1996). It is important to note that these previous studies of disparity detection during infancy dealt primarily with stereopsis and relative disparity. The current experiment studied vergence, which in adults is primarily driven by absolute disparity (Erkelens & Collewijn, 1985; Mitchell, 1970; Rashbass & Westheimer, 1961). It has been demonstrated that the two types of disparity information may be first available in different areas of visual cortex: relative disparity in V2 (Clery, Cumming, & Nienborg, 2015; Thomas et al., 2002) and absolute disparity in V1 (Cumming & Parker, 1997; Cumming & Parker, 1999), and therefore development of these neural responses may follow different time-courses. Furthermore, sensitivity to absolute disparity is coarser than to relative disparity in adults. In adults, fine stereopsis has an upper limit (d_{max}), equivalent to approximately 100 minutes of arc depending on the parameters of the stimulus (Wilcox & Hess, 1995). However, the linear operating range of open-loop disparity-driven vergence extends out to at least 2° (Busettini, Fitzgibbon, & Miles, 2001), making larger disparities useful for vergence. It has been suggested that the development of disparity sensitivity may be critically limited by poor spatial vision and contrast sensitivity (Brown, Lindsey, Satgunam, & Miracle, 2007; Schor, 1985). It may simply be that larger disparities (such as those used in this study) can drive robust motor responses after being transmitted through immaturities in the anterior visual system that ultimately limit the relative disparity information reaching visual cortex (although the tracking behavior in Figure 1 suggests that some infants are sensitive to disparity amplitudes of less than 2°).

The results of this study are in agreement with studies of infant macaque (Chino et al., 1997; Maruko et al., 2008; Zheng et al., 2007) suggesting primate

visual cortex can routinely support disparity processing from soon after birth. In light of these findings establishing binocular function prior to the classically described sudden onset between approximately three and five months of age (reviews by Norcia & Gerhard, 2015 and Braddick, 1996), current models of the development of binocularity should be reformulated to include the early use of disparity cues for eye alignment. For example, Held and colleagues (Hainline & Riddell, 1995; Held, 1985; Held, 1993) have proposed that monocular neurons in young infants simply sum responses at the level of cortex. The results of this study necessitate a more sophisticated binocular interaction by the first month after birth and appear to confirm the presence of active disparity detecting neurons. Further research will elucidate the early role of binocular image alignment in cortical development and in space and scene interpretation as young humans begin to interact with the three-dimensional world.

Keywords: visual development, vergence, disparity

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