Accommodative and vergence responses to conflicting blur and disparity stimuli during development

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Accommodative and vergence responses of the typically developing visual system are generated using a combination of cues, including retinal blur and disparity. The developmental importance of blur and disparity cues in generating these motor responses was assessed by placing the two cues in conflict with each other. Cue-conflicts were induced by placing either -2 D lenses or 2 MA base-out prisms before both eyes of 140 subjects (2.0 months to 40.8 years) while they watched a cartoon movie binocularly at 80 cm. The frequency and amplitude of accommodation to lenses and vergence to prisms increased with age (both $p < 0.001$), with the vergence response (mean ± 1 *SEM* = 1.38 ± 0.05 MA) being slightly larger than the accommodative response (1.18 ± 0.04 D) at all ages ($p = 0.007$). The amplitude of these responses decreased with an increase in conflict stimuli (1 to 3 D or MA) (both $p < 0.01$). The coupled vergence response to -2 D lenses (0.31 ± 0.06 MA) and coupled accommodative response to 2 MA base-out prisms (0.21 ± 0.02 D) were significantly smaller than (both $p < 0.001$) and poorly correlated with the open-loop vergence ($r = 0.12$; $p = 0.44$) and open-loop accommodation ($r = -0.08$; $p = 0.69$), respectively. The typically developing visual system compensates for transiently induced conflicts between blur and disparity stimuli, without exhibiting a strong preference for either cue. The accuracy of this compensation decreases with an increase in amplitude of cue-conflict.

Introduction

Focused and corresponding retinal images are a prerequisite for normal postnatal visual development (Banks, Aslin, & Letson, 1975; Kiorpes, Kiper, O'Keefe, Cavanaugh, & Movshon, 1998; Mitchell & Timney, 1984). In adults, they are achieved and maintained through neurally cross-coupled accommodative and vergence responses that are driven using a combination of cues including retinal blur (primary cue for accommodation) and disparity (primary cue for vergence) (Fry, 1983; Judge & Cumming, 1986; Mays & Gamlin, 1995; Morgan, 1968; Schor & Ciuffreda, 1983). By approximately 3 months of age, infants demonstrate the ability to dynamically change their accommodation and vergence, with gains that are typically well matched to the stimulus demands under naturalistic binocular viewing conditions (Banks, 1980; Bharadwaj & Candy, 2008; Haynes, White, & Held, 1965; Tondel & Candy, 2007; Turner, Horwood, Houston, & Riddell, 2002). The accommodative and vergence systems are also cross-coupled by this age, indicating that, like adults, the developing visual system could also use combinations of retinal blur and disparity cues to drive

these near-motor responses (Aslin & Jackson, 1979; Bharadwaj & Candy, 2008; Bobier, Guinta, Kurtz, & Howland, 2000; Currie & Manny, 1997; Turner et al., 2002). The relative importance of these two cues in driving accommodation and vergence during development is however not fully understood.

Recent studies have observed that the gain of accommodation and vergence and the maximum amplitude of accommodation of typically developing infants and children are smaller under monocular conditions (i.e., when retinal disparity feedback is made open-loop) than under full-cue binocular conditions (Bharadwaj & Candy, 2008; Currie & Manny, 1997; Sterner, Gellerstedt, & Sjostrom, 2004, 2006; Turner et al., 2002; for similar results in naïve uninstructed adults, see Horwood & Riddell, 2008). Adult-like monocular accommodative gains are achieved only by 7 to 10 years of age (Bharadwaj & Candy, 2008)—after the time by which the optics of the eye and spatial visual processing are expected to support this performance (Bradley & Freeman, 1982; Green, Powers, & Banks, 1980; Teller & Movshon, 1986). While the reduction in monocular vergence gain is expected given the absence of retinal disparity under monocular conditions, the reduction in monocular gain

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of accommodation is somewhat unexpected, indirectly suggesting that the retinal disparity cue might play an important role in generating appropriate near-motor responses during normal visual development. These responses measured under disparity open-loop conditions do not necessarily reveal how blur and disparity cues are combined under fully closed-loop naturalistic conditions. However, the closed-loop interaction is likely to be complex as the final responses could consist of combinations of responses driven by the primary cues, plus the coupling, and negative feedback used to correct any remaining errors (Schor & Narayan, 1982; Semmlow & Hung, 1979; Semmlow & Venkiteswaran, 1976; Semmlow & Wetzel, 1979).

The goal of this study was therefore to determine the relative importance of blur and disparity when all cues are available to the typically developing visual system. Relative importance of the two cues was assessed by placing them in conflict with each other. A blur cue was provided with minimal change in retinal disparity using negative lenses (lens conflict condition; LC) while a disparity cue was provided with no change in blur cue by placing base-out prisms in front of the eyes (prism conflict condition; PC).

The responses of infants and children to apparently conflicting blur and disparity stimuli are also important from the clinical perspective. Infants are typically born hyperopic (Mayer, Hansen, Moore, Kim, & Fulton, 2001) and with a narrow inter-pupillary distance (IPD) (MacLachlan & Howland, 2002). The accommodative stimulus of infants is therefore typically larger than that of adults while their vergence stimulus (expressed in angular units of eye rotation) is smaller than that of adults (Aslin & Jackson, 1979). The typically developing visual system therefore experiences sustained levels of apparent conflict between blur and disparity cues even under naturalistic viewing conditions. Some children are able to maintain normal binocular vision in the presence of such apparent cue-conflict, while others, with matched levels of refractive error, develop binocular abnormalities such as refractive esotropia (Anker et al., 2003; Chin & Breinin, 1967; Ingram, Gill, & Goldacre, 1994; Parks, 1958; von Noorden & Avilla, 1990). The accommodative and vergence performance of the developing visual system should therefore also be considered in relation to the underlying hyperopic refractive error and vergence demand to define the total amount of apparent conflict between blur and disparity. The current study addressed this question in two ways: by comparing the accommodative and vergence responses in the LC and PC conditions to mismatches implied by the subject's cycloplegic refractive error and by measuring accommodative and vergence performance to three different amplitudes of experimentally-induced conflict between blur and disparity.

The ability of the adult visual system to compensate for conflicting blur and disparity stimuli is well established. In the clinic, this is routinely assessed by stimulating either blur-driven accommodation ("relative accommodation") or disparity-driven vergence ("relative vergence"), while the other cue is held constant and the subject is instructed to maintain a clear and single percept of a visual target (Fry, 1983; Morgan, 1944a, 1944b, 1968). Using subjective estimates of when the visual target first appears blurred or diplopic (at a typical viewing distance of 40 cm), the typical adult ranges of relative accommodation and vergence have been estimated to extend from -3.00 D to $+2.25$ D and from 24 PD base-out to 23 PD base-in, respectively (Goss, 1986; Morgan, 1944a). Objective measurements of accommodative and vergence responses to such "conflicting" stimuli confirm that the motor responses are indeed dissociated, with accommodation responding more to the lens stimulation and vergence responding more to the prism stimulation (Fincham & Walton, 1957; Jaschinski, 1997; Ogle, Mussey, & Prangen, 1949; Ramsdale & Charman, 1988). However, the responses of the stimulated system (accommodation in LC and vergence in PC) under cue-conflict conditions are less accurate (i.e., larger accommodative "lag" and exo-fixation disparity for stimuli requiring an increased response) than under cue-consistent binocular viewing conditions (Fincham & Walton, 1957; Hung & Ciuffreda, 1994; Jaschinski, 1997; Ogle et al., 1949; Ramsdale & Charman, 1988). The coupled system (vergence in LC and accommodation in PC) also responds in the direction predicted by the coupling (i.e., accommodative "lead" and eso-fixation disparity), even though there is no change in stimulus demand (Fincham & Walton, 1957; Hung & Ciuffreda, 1994; Jaschinski, 1997; Ogle et al., 1949; Ramsdale & Charman, 1988). The size of this coupled response is much smaller than that predicted by the open-loop coupling gain (Fincham & Walton, 1957; Ramsdale & Charman, 1988), indicating dissociation, albeit an incomplete one, between the two motor responses. Overall, these observations indicate that the adult visual system is capable of compensating for a range of conflicting stimulus demands, without exhibiting a strong bias towards either the blur or disparity cue.

Methods

Subjects

One hundred forty subjects (2.0 months to 40.8 years) with no significant ocular or medical conditions (by report) took part in the data collection, after informed consent had been provided by a parent or the subject

themselves. The research adhered to the tenets of the declaration of Helsinki and had been approved by the local Indiana University institutional review board. Infants and children were recruited from local birth records and were born within 3 weeks of their due date. Adults who were pre-presbyopic and near-emmetropic were recruited from the local academic department. They were naïve to the goals of the experiment. They reported no accommodative abnormalities or ocular symptoms and had low amounts of hyperopia or up to 1 D of myopia. The myopia was corrected during the experiment using soft contact lenses. The infants and children were expected to have typical amounts of developmental hyperopia (Mayer et al., 2001) and did not wear any refractive correction during the experiment to mimic their daily natural viewing conditions. Cycloplegic refractions were collected from a subset of the subjects.

Procedure

Accommodative and vergence responses were measured simultaneously using a video-based eccentric photorefractor recording at 25 Hz (PowerRefractor (PR), Multi Channel Systems) (Choi et al., 2000; Schaeffel, Wilhelm, & Zrenner, 1993). Detailed descriptions of the technique can be found elsewhere (Roorda, Campbell, & Bobier, 1997; Schaeffel et al., 1993) and only a brief description will be provided here. The subject was aligned at 1.0 m from a set of LED light sources immediately beneath the PR camera aperture. Light from the LED's passed into the eye and was reflected back from the retina through the pupil. The dioptric focus of the eye in the vertical meridian is derived from the slope of a linear regression fit to the distribution of reflected light across the pupil. Vergence responses (in degrees) were measured using the relative displacement of the first Purkinje image with respect to the image of the pupil center in each eye. These estimates were converted and scaled into meter angles (MA, m^{-1}), to compensate for changes in IPD with age, using each subject's IPD measured using the PR.

The PR uses a population-average defocus calibration based on data collected from adults (Choi et al., 2000; Schaeffel et al., 1993). Similarly, a population-average Hirschberg ratio is used to calculate gaze position and vergence (Riddell, Hainline, & Abramov, 1994; Schaeffel et al., 1993). While individual defocus and eye position calibrations could not be performed on all subjects due to lack of cooperation, they were performed on 68 out of 100 subjects who gave usable data in all conditions (age range = 2.2 months to 40.2 years), in order to confirm the absolute gains of accommodation and vergence. The calibration slope, obtained using the procedure described in detail by Bharadwaj and Candy (2008) and Choi et al.

(2000), was used to scale the individuals' raw data. If a calibration function was unavailable, then the default PR calibration was used.

Subjects watched a high contrast cartoon movie with naturalistic spatial frequency amplitude spectra [the average slope of the spatial amplitude spectra in log–log coordinates was -1.47 ± 0.03 (Bharadwaj & Candy, 2008)] displayed on an LCD screen at a constant viewing distance of 80 cm (1.25 D or MA). Perceived distance and size cues therefore remained approximately constant during the entire experiment. The target subtended $5.4° \times 5.4°$ at the 80-cm viewing distance. The image from the LCD screen was reflected from a beamsplitter to reach the subject (Figure 1, panel a). The subject was carefully aligned so that the visual target and the PR camera were centered on the midline between their eyes (Figure 1, panels b and c—confirmed during data collection using a gridline that is not visible in these images). An experimenter gently supported each infant or young child's chin during the entire experiment to keep them aligned and to minimize head movements. Older children and adults were instructed to hold their heads as stable as possible. No specific instructions were given to the subjects regarding the task; they were
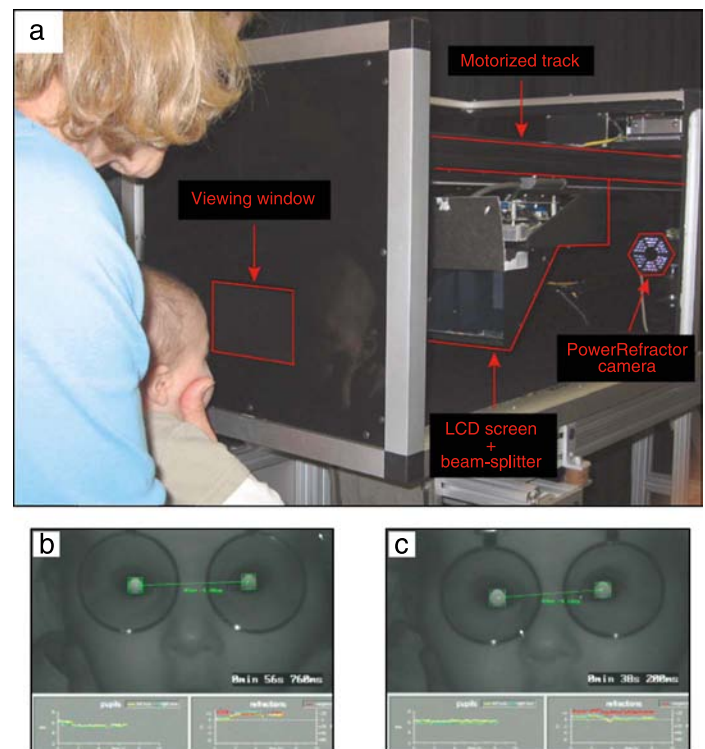

Figure 1. Panel a: The experimental equipment. The core components are labeled. Panels b and c: A sample PowerRefractor (PR) image of a 4-month-old infant looking through a pair of -2 D lenses (panel b) and 2 MA base-out prisms (panel c).

Analysis	Purpose
a. Experiment 1. LC accommodation vs. PC vergence	Comparison of the stimulated systems' responses to conflict between blur and disparity
b. Experiment 1. LC vergence vs. PC accommodation	Comparison of the coupled systems' responses to conflict between blur and disparity
c. Experiment 2. LC accommodation vs. DOL accommodation	Comparison of accommodative performance under conflict with absence of conflict
d. Experiment 2. PC vergence vs. BOL vergence	Comparison of vergence performance under conflict with absence of conflict
e. Experiment 2. LC vergence vs. DOL vergence	Comparison of coupled vergence responses in the conflict condition and in the open-loop condition
f. Experiment 2. PC accommodation vs. BOL accommodation	Comparison of coupled accommodative responses in the conflict condition and in the open-loop condition

Table 1. The purpose of the analyses performed in Experiments 1 and 2.

merely asked to watch the movie (Horwood, Turner, Houston, & Riddell, 2001; Stark & Atchison, 1994).

Four experiments were conducted.

Experiment 1—Effect of induced conflict between blur and disparity cues on accommodative and vergence performance. The aim was to assess the effect of transiently induced conflict between blur and disparity on binocular accommodative and vergence responses (Table 1, analyses a and b). In the lens conflict (LC) condition (*n* = 140; 2.0 months to 40.8 years), a step change in retinal blur was induced, without a change in retinal disparity, by introducing −2 D lenses in front of each eye of the subject (Figure 1, panel b). Thus, the absolute stimulus to blur-driven accommodation changed from 1.25 to 3.25 D in this condition. Simultaneous clear and single vision would be maintained in this condition by eliciting an accommodative response with no change in vergence. In the prism conflict (PC) condition (*n* = 136; 2.0 months to 40.8 years), a step change in retinal disparity was induced, without a change in retinal blur, by introducing 2 MA of base-out prism divided equally between the eyes (Figure 1, panel c). The amount of prism (in prism diopters) was scaled to the subject's IPD to achieve a constant vergence demand of 2 MA. Thus, the absolute stimulus to disparity-driven vergence changed from 1.25 to 3.25 MA in this condition. Simultaneous clear and single vision would be achieved in this condition by eliciting a vergence response with no change in accommodation. Accommodative response in the LC condition and vergence response in the PC condition will be referred to as the "stimulated response" and vergence response in the LC condition and accommodative response in the PC condition will be referred to as the "coupled response." Both lenses and prisms were held approximately 14 to 16 mm in front of the subject's eyes on custom built mounts that were separated by the individual's IPD, so that the optical center of each lens (or prism) was aligned with the subject's pupillary axis. Any small decentration of the lenses (or prisms) from the eyes' pupillary axes, due to head movement for example,

would therefore introduce only yoked changes in visual direction, with no change in retinal disparity, as it would affect both eyes equally. The lenses and prisms were introduced at least three or four times for approximately 10 s each time. For most subjects both types of stimulation were attempted during the same experimental session, with the order pseudo-randomized across subjects. As the viewing distance remained at 80 cm during the entire experiment, perceived distance and size cues were consistent with the disparity cue but in conflict with the blur cue in the LC condition and they were consistent with the blur cue but in conflict with the disparity cue in the PC condition.

In a separate pilot experiment, the LC and PC conditions of Experiment 1 were repeated at three different viewing distances (80, 50, and 30 cm) for 11 subjects (1.4–11.9 years) and 13 subjects (2.4–11.8 years) to assess the impact of target viewing distance on accommodative and vergence performance, respectively, under cue-conflict conditions (Ramsdale & Charman, 1988). The group average accommodative response for the 2-D lens stimulation and vergence response for the 2-MA prism stimulation across all three viewing distances fell within a range of 0.2 D or 0.2 MA. Therefore, the remaining experiments were conducted at a viewing distance of 80 cm.

Experiment 2—Comparison of accommodative and vergence performance under conflicting conditions with performance under open-loop conditions. This experiment compared accommodative and vergence performance in the LC and PC conditions with that under disparity open-loop (DOL) and blur open-loop (BOL) conditions. Blur and disparity cues are rendered unreliable when their negative feedback loop is opened and therefore they are incapable of guiding accommodative and vergence motor responses (Schor, 2003). Measurements of accommodation and vergence made under open-loop conditions therefore reflect performance in the absence of conflict between blur and disparity cues. A comparison of performance under conflicting and open-loop conditions

quantifies the effect of cue-conflict on accommodation and vergence performance in the LC and PC conditions. With regard to the stimulated response, accommodation in the LC condition (with cue-conflict) can be compared to accommodation in the DOL condition (without cue-conflict) to assess the influence of the disparity conflict on blur-driven accommodation (Table 1, analysis c). A similar comparison between the PC and BOL conditions can be made to assess the influence of blur conflict on disparity-driven vergence (Table 1, analysis d). With regard to the coupled response, vergence in the LC condition and accommodation in the PC condition can be compared to open-loop vergence in the DOL condition and open-loop accommodation in the BOL condition, respectively, to determine whether the coupled responses in the cue-conflict conditions are completely defined by the strength of the accommodative-vergence and vergence-accommodation cross-coupling (Table 1, analyses e and f) (Hung & Ciuffreda, 1994) or whether there is evidence of apparent dissociation.

DOL and BOL measurements were collected from 44 (3.2–37.8 years) and 28 (3 months–37.8 years) subjects who took part in Experiment 1, respectively. The subjects were positioned in front of a large box containing a 58-cm diameter beamsplitter at an orientation of 45° about the vertical axis. The subject viewed through an aperture in one side of the box, the PR was aligned with the subject's eyes through an aperture on the opposite side, and the visual target, reflected in the beamsplitter, was presented in an aperture in a third side (see Figure 1, panel b in Tondel & Candy, 2008). This arrangement allowed the visual target and the PR to be on the same optical axis. Disparity-driven vergence was made open-loop in the DOL condition by having the subjects watch the cartoon movie monocularly at 80 cm. The left eye was occluded using a Kodak Wratten #87 IR transmitting filter that enabled photorefractor images to be collected from both eyes. A step stimulus to accommodation was introduced by placing a −2 D lens in front of the unoccluded eye while accommodative and vergence responses were measured using the PR. Blur-driven accommodation was made open-loop in the BOL condition by having the subjects watch a spatially filtered version of the same movie in binocular viewing conditions. The cartoon movie was projected with approximately 5 D of optical defocus onto a form of diffuser paper (manufactured by The Crafty PC®), using a DLP projector. The diffuser paper acted as a rear projection screen. In addition, a difference-of-Gaussian mask was also printed on the diffuser paper to low-pass filter the edges of the stimulus to a cut-off spatial frequency of 0.2 cpd. Low-pass filtering of the spatial content of the target has been shown to be effective at opening the feedback loop for blur-driven accommodation (Kotulak & Schor, 1987; Suryakumar & Bobier, 2004; Tsuetaki & Schor, 1987). A step stimulus to vergence was provided by placing a 2-MA base-out prism

in front of one eye, while the accommodative and vergence responses were measured using the PR.

Three hypothetical patterns of results were predicted from Experiments 1 and 2, each providing insights into the weighting of blur and disparity cues. First, the results could indicate a complete weighting of accommodative and vergence motor responses to one cue. For instance, if retinal blur was the critical cue, accommodation would always respond in the LC condition and the amplitude of the coupled vergence response in the LC condition would equal the open-loop vergence response in the DOL condition. In addition, vergence would not respond in the PC condition (Table 1, analyses a and e). Second, there may be a more equal weighting of the two cues, with no dissociation of the accommodative and vergence motor responses. A stimulated response (accommodation to lenses and vergence to prisms) would therefore indicate that the cue that is dynamically stimulated assumes the dominant role during cue-conflict. The stimulated accommodative and vergence responses might have similar amplitudes in the LC and PC conditions, respectively, while the coupled responses are entirely predicted by the open-loop coupling gains (Table 1, analyses a, e, and f). Third, the cues may be relatively equally weighted again, but the coupled responses might be smaller than predicted by the open-loop coupling gains, indicating an active compensation for the mismatch in stimuli in the conflicting conditions (Table 1, analyses a, e, and f). In this case, both cues stimulate the near-response at the same time and compensate for the cross-coupling interaction.

Experiment 3—Effect of increasing conflict amplitude on accommodative and vergence performance. The steady-state errors in adult accommodation and vergence responses increase with the amplitude of conflict between blur and disparity stimuli (Fincham & Walton, 1957; Ramsdale & Charman, 1988). To determine whether the developing visual system also exhibited this behavior, the LC and PC conditions of Experiment 1 were repeated in 14 (3.4 months to 12.4 years) and 12 subjects (4.3 months to 11.2 years) with 1 D (or MA), 2 D (or MA), and 3 D (or MA) lenses or prisms, respectively. The order and type of stimulation was pseudo-randomized across subjects. In all other respects, the protocol remained the same as for Experiment 1.

Experiment 4—Cycloplegic spherical equivalent refractive error (SER). Infants are typically born hyperopic, with an average SER of approximately 2.0 D and a standard deviation of approximately ±2.0 D (Mayer et al., 2001). The blur and disparity demands of infants and children are therefore in potential conflict with each other relative to a typical emmetropic adult, even before additional lenses or prisms are added in the LC and PC conditions. The accommodative and vergence responses of infants and children in the LC and PC conditions were therefore compared with SER in a subset of children. Cycloplegic retinoscopy was performed on 85 infants and

children (2.7 months to 11.7 years) who took part in Experiment 1 to determine whether the amplitude of the stimulated accommodative and vergence responses were related to their refractive error. Cycloplegia was achieved 20–30 min after instilling one drop of 1% cyclopentolate.

Data analysis

Data analyses were performed using MacSHAPA[®], Matlab[®], Microsoft Excel[®], and SPSS[®]. Video of each experimental session was recorded and analyzed offline using MacSHAPA[®] to determine the frame during which introduction or removal of the lenses or prisms occurred. These times were used to create the stimulus profile which was compared with the raw data obtained from the PR. The raw stimulus and accommodation and vergence data were all smoothed using a 200-ms averaging window, thereby maintaining the temporal relationship between them. The accommodative and vergence responses to each step stimulus were then included in the analyses if they met the following criteria:

a. The accommodation data were within the linear operating range of the instrument (+4.0 to −6.0 D) and the pupil diameters were between 3 and 8 mm (required for the instrument to collect data) (Choi et al., 2000; Schaeffel et al., 1993).

b. The data were collected from a gaze eccentricity of less than 15° from the pupillary axis. The optical quality of the adult eye changes with gaze eccentricity (Jennings & Charman, 1981; Navarro, Artal, & Williams, 1993) and therefore the effects of peripheral refraction during intermittent peripheral fixations could not be distinguished from changes in accommodation. This threshold criterion was based on adult data as there are currently no comparable data from infants. The infants and adults typically maintained stable gaze on the target, and so very little data were excluded as a result of this criterion.

c. The immediate offset in the focus or eye position data caused by introduction of the lenses or prisms was reliable and within 25% of the expected value (e.g., between 1.50 and 2.50 D for a −2 D lens). The lens and prism-induced offsets were subtracted from the refraction and eye position traces, respectively, to compute the accommodative and vergence responses. Any significant error in measuring this offset would otherwise translate into an error in the estimated response amplitude. Data from a total of 11 subjects in the LC and PC conditions were rejected as a result of this criterion.

d. In the LC condition, the difference in refraction between the two eyes (anisometropia) observed before and after lens stimulation was within 0.5 D of each other. Since the left and right eyes' accommodative responses are well correlated with each other (Bharadwaj & Candy, 2008; Campbell & Westheimer, 1959), the anisometropia is expected to remain equal before and after lens stimulation. Any significant change in anisometropia after lens stimulation reflects an error in determining the shift in refraction induced by the lens. Data from nine subjects were rejected as a result of this criterion.

After applying the inclusion criteria, the final accommodative and vergence responses were obtained by averaging 2 s of steady-state data (50 data points) collected before and after stimulation (Figure 3). The amplitudes of the stimulated and coupled responses were calculated as the difference in response before and after stimulation. In any given trial, the stimulated response was only considered valid when its response to lenses or prisms was greater than 25% of the stimulus amplitude. It is feasible that the measured accommodative responses could be over-estimated and the measured vergence responses could be under-estimated as a result of the negative lens induced minification of the PR image. However, the minification induced by −2 D lenses is small (0.5% to 1.4% for thin lenses with vertex distances ranging from 10 to 20 mm; Brooks & Borish, 2007) and therefore its influence on the accommodative and vergence response estimates is likely to be negligible.

If a subject provided multiple responses in each condition, the response amplitudes were averaged to obtain the overall mean accommodative and vergence response amplitude. For each subject, the accommodative responses obtained from the left and right eye were averaged to obtain a mean accommodative response. The intra-examiner repeatability for calculation of the accommodative and vergence response amplitude for a sample of 160 responses distributed across age showed no bias or relationship between the difference in response estimates and their mean (data not shown) (Bland & Altman, 1986). The mean difference between the two accommodation estimates was −0.06 D (SD = 0.18 D) and between the two vergence estimates was −0.01 MA (SD = 0.22 MA).

The data obtained from Experiment 1 were divided into the following five age groups: ≤1 year, >1 to ≤4 years, >4 to ≤8 years, >8 to ≤12 years and adults (≥20 years) in order to keep the number of subjects approximately constant in each group. The effects of age, stimulation type, and responding system on the frequency and amplitudes of responses were examined using ANOVA.

Results

Experiment 1—Effect of induced conflict between blur and disparity cues on accommodative and vergence performance. In the LC and PC conditions, the difference in mean accommodative and vergence response amplitudes

Age (years)	LC condition						PC condition					
	<1	1.1–4	4.1–8	8.1–12	Adults	Total	<1	1.1–4	4.1–8	8.1–12	Adults	Total
Number of subjects recruited	27	36	29	26	22	140	24	36	28	26	22	136
Number of subjects who met inclusion criteria	21	28	25	21	20	115	18	27	24	21	20	110
Number of subjects with usable data in both conditions	17	26	21	17	19	100	17	26	21	17	19	100
Number of subjects who responded at least once to lens or prism stimulation	12	24	19	17	18	90	15	23	17	15	19	89

Table 2. Details of subject inclusion in analyses based on Experiment 1. For all subjects who met the inclusion criteria, a stimulated response (accommodation in LC and vergence in PC) was considered valid only if the amplitude of the response was greater than 25% of the stimulus amplitude.

obtained by averaging the data of subjects with individual calibrations (68 out of 100 subjects who gave usable data) and by averaging the data from all subjects (i.e., those with and without individual calibrations) was only 0.05 D and 0.04 MA, respectively. The rest of the analyses of the means were therefore completed on the entire group of subjects.

Table 2 shows the number of subjects in each age group on whom the LC and PC conditions were attempted and the number of subjects whose data met the inclusion criteria. To permit within-subject comparison of the LC and PC conditions, only data from subjects who gave usable responses in both conditions are reported in the rest of the table and analyses. Some infants and young children did not respond to either lens or prism stimulation—i.e., the stimulated response was less than 25% of the stimulus amplitude. Since this experiment did not employ an independent measure of subject cooperation, it remains uncertain whether the lack of a stimulated response indicated an inability to respond to the stimulus or poor subject cooperation.

The mean response frequency of the stimulated response (excluding those who did not respond even once to the stimulation) increased significantly with age ($F(4, 179) = 9.36$, $p < 0.001$) (Figure 2, panel a). A post hoc Games–Howell test (with no assumption about equal variance) showed that the response frequency in age groups 1 and 2 was statistically significantly different from those of age groups 3, 4, and 5. Post hoc tests comparing age groups 1 and 2 and comparing age groups 3 to 5 were not statistically significant. The main effect of stimulation type on response frequency ($F(1, 179) = 0.47$, $p = 0.50$) and the interaction between age and stimulation type were not statistically significant ($F(4, 179) = 1.58$, $p = 0.18$). This result indicates that the frequency of response to both lens and prism stimulation increased similarly up to 4 years of age, beyond which it appeared to saturate. To look at individual differences, a ratio of the number of valid stimulated vergence responses in the PC condition to the total number of valid stimulated responses

in the LC and PC conditions combined was calculated (response proportion) for each subject and plotted as a function of their age (Figure 2, panel b). In this figure, data along the bottom red line represent subjects with no valid vergence response in the PC condition (indicating absolute bias to responding to the blur stimulus), data along the top blue line represent subjects with no valid
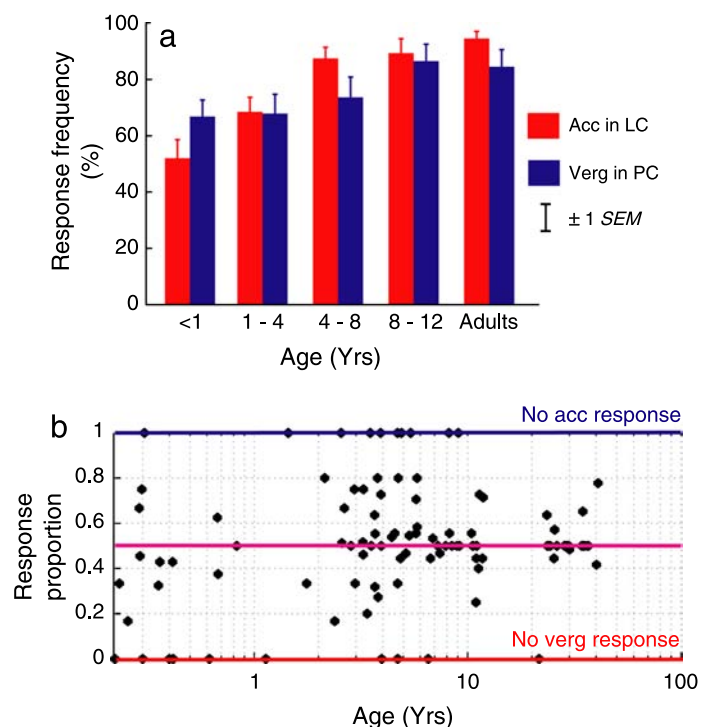

Figure 2. Panel a: Mean (±1 *SEM*) response frequency of accommodation in LC and vergence in PC for all subjects within an age group. Panel b: Response proportion (i.e., ratio of the number of valid vergence responses in the PC condition to the total number of valid responses in the LC and PC conditions combined) of individual subjects plotted as a function of their age. Subjects with no valid response in both LC and PC conditions were not included in these analyses.
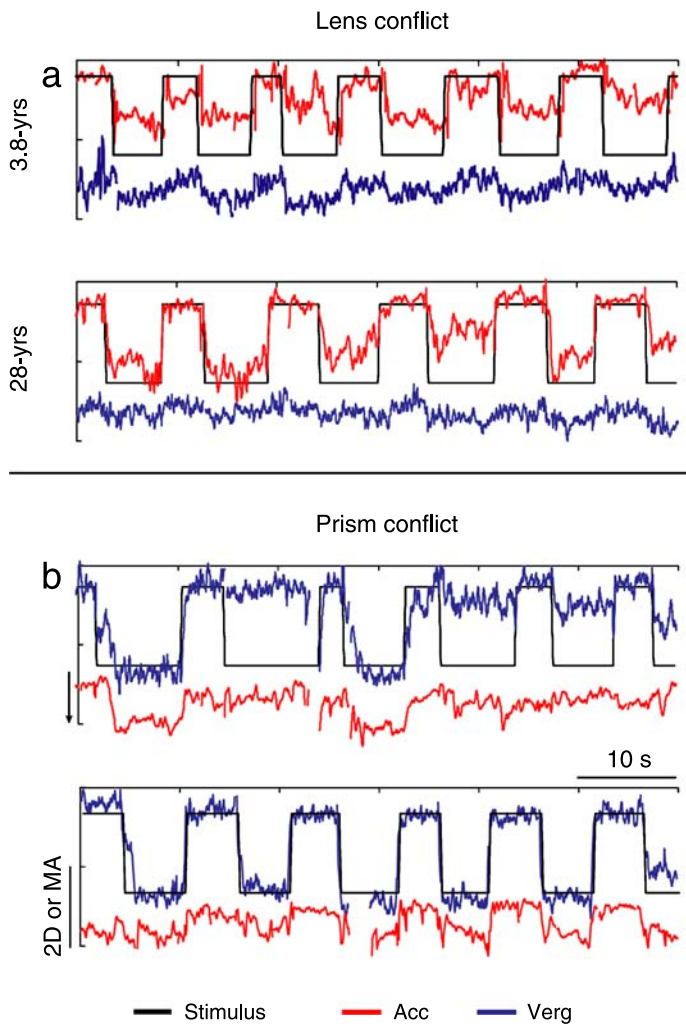
Figure 3. Representative raw traces of accommodation and vergence from a 3.8- and a 28-year-old in the LC condition (panel a) and PC condition (panel b). Raw traces from other age groups were similar to the traces shown here. The raw traces have been vertically shifted for clarity, with no shifting of the horizontal (time) axis. Downward on the ordinate indicates an increasing stimulus or response.

accommodative response in the LC condition (indicating absolute bias to responding to the disparity stimulus), and data along the middle purple line represent subjects with equal numbers of valid responses in the LC and PC conditions. The majority of the values are clustered around the middle line, with no apparent age-related trend, indicating that, at a population level, there was no strong preference for responding to either lenses or prisms (Figure 2, panel b). Nineteen subjects (distributed across age) fell along the red and blue lines, suggesting that they exhibited a bias.

Figure 3 shows raw accommodation and vergence responses to the lens (panel a) and prism (panel b) stimulation in a representative adult (28 years) and child (3.8 years). The raw data demonstrate that while a stimulated response was elicited to lens and prism

stimulation in both subjects, the size of the stimulated response was, on an average, larger in the adult than in the child. Second, every time a stimulated response occurred, a change in the coupled response was also elicited (vergence changed in the LC condition and accommodation changed in the PC condition). However, the size of the coupled response was small and it was similar for the adult and the child.

A dynamic interaction between accommodation and vergence was evident in the raw data of 12 subjects (4.3 months to 11.8 years) in the PC condition (Figure 4). In these subjects, the prism stimulation elicited a convergence response that was accompanied by an accommodative response. Unlike convergence, the accommodative responses of these subjects were transient and returned to a steady state in between the peak of the transient response and the position before prism stimulation. Interestingly, it was not possible to detect a similar transient change in the disaccommodative response when the prisms were removed. It was also not possible to detect a similar transient change in the vergence response after lens stimulation in the LC condition, potentially due to technical limitations.

The mean amplitude of the stimulated response increased significantly with age ($F(4, 179) = 6.27$, $p < 0.001$) (Figure 5, panel a). A post hoc Games–Howell test showed that the
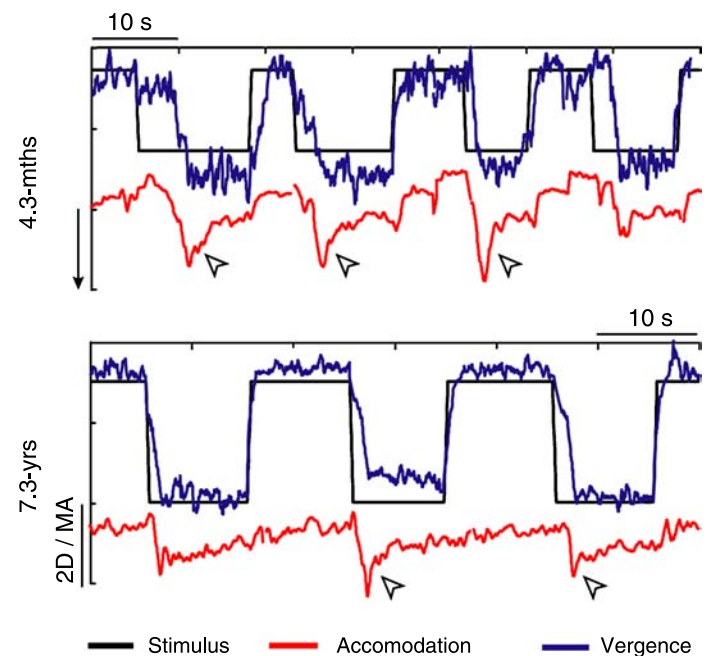

Figure 4. Raw traces from a 4.3-month-old and a 7.3-year-old illustrating dynamic interaction between accommodation and vergence in the PC condition of Experiment 1. The arrowheads illustrate apparent dynamic compensation for the convergence driven accommodation. The raw traces have been vertically shifted for clarity. The horizontal (time) relationship between the stimulus and response is maintained. Downward on the ordinate indicates an increasing stimulus or response.
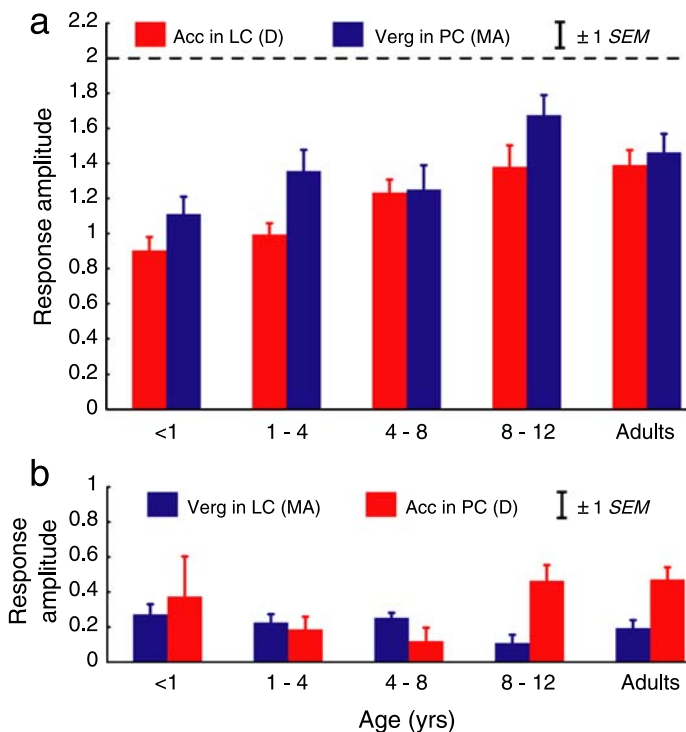
Figure 5. Mean (±1 *SEM*) amplitude of the stimulated response (panel a) and the coupled response (panel b) in the LC and PC conditions of Experiment 1. Only subjects with at least one stimulated response (i.e., response frequency >0%) were included and the mean for each subject only includes their responses that met the inclusion criteria.

mean response amplitudes of age groups 1, 2, and 3 were not statistically significantly different from each other ($p > 0.1$) but the mean response amplitude of age group 1 was statistically significantly different from that of age groups 4 and 5 ($p = 0.01$). The mean response amplitude of age groups 4 and 5 was not statistically significantly different from each other ($p = 0.95$). The grand mean vergence response to prism stimulation (mean ± *SEM* across all ages = 1.38 ± 0.05 MA) was statistically significantly larger than the grand mean accommodative response to lens stimulation (1.18 ± 0.04 D) ($F_{(1, 179)} = 7.41$, $p = 0.007$) (Figure 5, panel a; analysis a in Table 1). Both responses were however smaller than the stimulus, indicating that the stimulated response to lenses and prisms was inaccurate (Figure 5, panel a). The interaction between age and stimulation type was not statistically significant ($F_{(4, 179)} = 0.97$, $p = 0.43$). Overall, these results indicate that the amplitude of the stimulated response increased gradually with age for both lenses and prisms and that the stimulated response to prisms was slightly larger than to lenses.

The corresponding coupled responses were small but above zero for both lens (mean ± *SEM*: 0.21 ± 0.02 D) and prism (0.31 ± 0.06 MA) stimulation (Figure 5, panel b). There was no main effect of age ($F_{(4, 179)} = 0.51$, $p = 0.73$) or stimulation type ($F_{(4, 179)} = 0.11$, $p = 0.74$)

(analysis b in Table 1), and the interaction between age and stimulation type was also not significant ($F_{(4, 179)} = 1.62$, $p = 0.17$) in the coupled response. These results indicate that a coupled response was elicited along with the stimulated response for both lens and prism stimulation and that the size of the coupled responses was similar for both forms of stimulation.

Experiment 2—Comparison of accommodative and vergence performance under conflicting conditions with performance under open-loop conditions. Figure 6, panel a compares the mean accommodative and vergence response amplitudes obtained in the DOL and LC conditions. The stimulated accommodative response in the DOL condition (mean ± *SEM* = 1.36 ± 0.21 D) was moderately correlated with ($r = 0.53$; $p = 0.006$) and statistically insignificantly different ($p = 0.23$) from that obtained in the LC condition (1.29 ± 0.19 D) (analysis c in Table 1). The coupled open-loop vergence response in the DOL condition (0.65 ± 0.10 MA) was poorly correlated with ($r = 0.12$; $p = 0.44$) and statistically significantly larger ($p < 0.001$) than the mean vergence response in the LC condition (0.20 ± 0.03 MA) (analysis e in Table 1). The ratio of vergence to accommodation in the DOL condition (i.e., the gain of accommodative-vergence coupling; 0.48 ± 0.04 MA/D) was statistically significantly larger than that in the LC condition (0.18 ± 0.03 MA/D) ($p < 0.001$). Figure 6, panel b compares the mean accommodative and vergence responses for the BOL and PC conditions. The mean stimulated vergence response in the BOL condition (1.80 ± 0.34 MA) was poorly correlated with ($r = 0.15$; $p = 0.45$) and statistically significantly larger ($p = 0.006$) than the mean vergence response obtained in the PC condition (1.38 ± 0.26 MA) (analysis d in Table 1). Similarly, the mean coupled open-loop accommodative response in the BOL condition (0.92 ± 0.17 D) was poorly correlated with ($r = -0.08$; $p = 0.69$) and statistically significantly larger than that obtained in the PC condition (0.28 ± 0.05 D) (analysis f in Table 1). The ratio of accommodation to vergence in the BOL condition (i.e., the gain of vergence-accommodation coupling; 0.52 ± 0.03 D/MA) was statistically significantly larger than that in the PC condition (0.17 ± 0.04 D/MA) ($p < 0.001$). The age of the subject was poorly correlated with the difference in coupled vergence responses obtained in the DOL and LC condition ($r = -0.24$; $p = 0.12$) and with the difference in coupled accommodative responses obtained in the BOL and PC condition ($r = 0.28$; $p = 0.15$).

Taken together, the results show that the coupled response obtained in the presence of cue-conflict is not determined by the strength of the cross-coupling between accommodation and vergence (as defined by the coupling gain in the open-loop condition) and that the subject's age has minimal influence on the coupled responses under cue-conflict conditions. With regard to the stimulated responses, the presence of the conflicting disparity cue does not appear to influence the stimulated accommodative
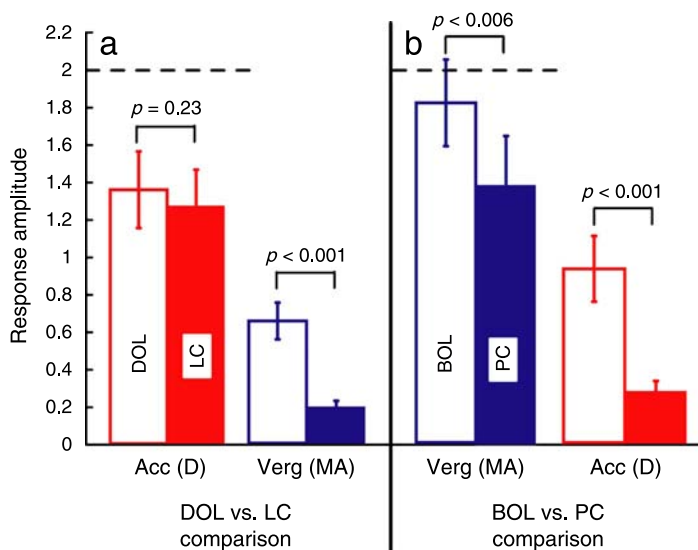
Figure 6. Panel a: Mean (±1 *SEM*) amplitudes of the stimulated accommodative response and coupled vergence response in the LC condition of Experiment 1 and in DOL condition of Experiment 2. Panel b: Mean (±1 *SEM*) amplitudes of stimulated vergence response and coupled accommodative response in the PC condition of Experiment 1 and in BOL condition of Experiment 2.

increase in conflict amplitude ($F(2, 34) = 6.10$, $p = 0.006$). A post hoc Games–Howell test showed that the vergence responses for the 1- and 3-MA stimuli were statistically significantly different from each other ($p < 0.001$). The amplitude of the coupled accommodative response did not show any statistically significant changes with increasing conflict amplitudes ($F(2, 34) = 0.07$, $p = 0.93$). Overall, these results show that an increase in the size of the conflict between blur and disparity stimuli—induced by higher powered lenses or prisms—reduces the amplitude of the stimulated response. The amplitude of the coupled response however remains the same for the range of conflict amplitudes tested.

Experiment 4—Cycloplegic spherical equivalent of refraction (SER). Cycloplegic refractive errors were available from 69 subjects (2.7 months to 11.7 years) who gave usable data in the LC condition in Experiment 1 and from 63 subjects (2.7 months to 11.7 years) who gave usable data in the PC condition in Experiment 1. As expected (Mayer et al., 2001), the cycloplegic spherical equivalent refraction (SER) was hyperopic in infants and then gradually reduced until near-emmetropia in the pre-school years (Figure 8, panel a). The response proportion (ratio of the number of valid vergence responses in the PC condition to the total number of valid responses in LC and
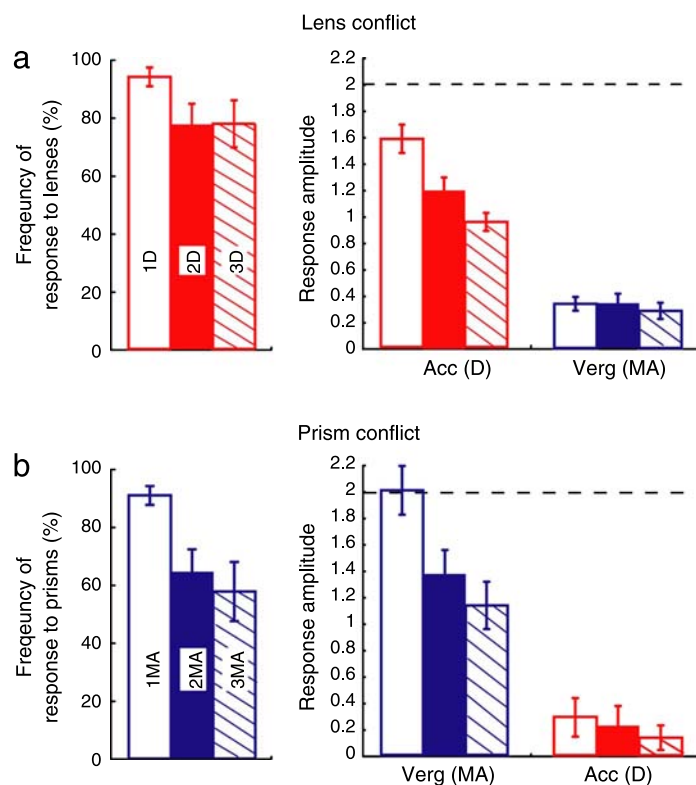
response in the LC condition, while the presence of blur cues does seem to influence the stimulated vergence response in the PC condition.

Experiment 3—Effect of increasing conflict amplitude on accommodative and vergence performance. Figure 7 shows the mean response frequencies and amplitudes of accommodation and vergence for the three conflict amplitudes in the LC (panel a) and PC (panel b) conditions. As the data from the LC and PC conditions were collected from different individuals in this experiment, the two sets of data are not directly compared with each other. In the LC condition, the frequency of accommodative response to lenses reduced with an increase in conflict amplitude (Figure 7, panel a), but this reduction was not statistically significant ($F(2, 41) = 2.05$, $p = 0.14$). The amplitude of the stimulated accommodative response reduced significantly with an increase in conflict amplitude ($F(2, 39) = 11.61$, $p < 0.001$). A post hoc Games–Howell test showed that the accommodative responses at the three conflict amplitudes were statistically significantly different from each other (for all combinations, $p < 0.001$). The coupled vergence response amplitude was greater than zero and it did not show any statistically significant change with the amplitude of the conflict ($F(2, 39) = 0.73$, $p = 0.49$). The results for the PC condition were qualitatively similar to those of LC condition (Figure 7, panel b). The frequency of vergence response to prisms reduced with an increase in conflict amplitude ($F(2, 35) = 4.06$, $p = 0.03$). The stimulated vergence response amplitude reduced significantly with an

Figure 7. Mean (±1 *SEM*) response frequency of stimulated responses and amplitudes of the stimulated and coupled responses in the LC (panel a) and PC (panel b) conditions for three different conflict amplitudes.
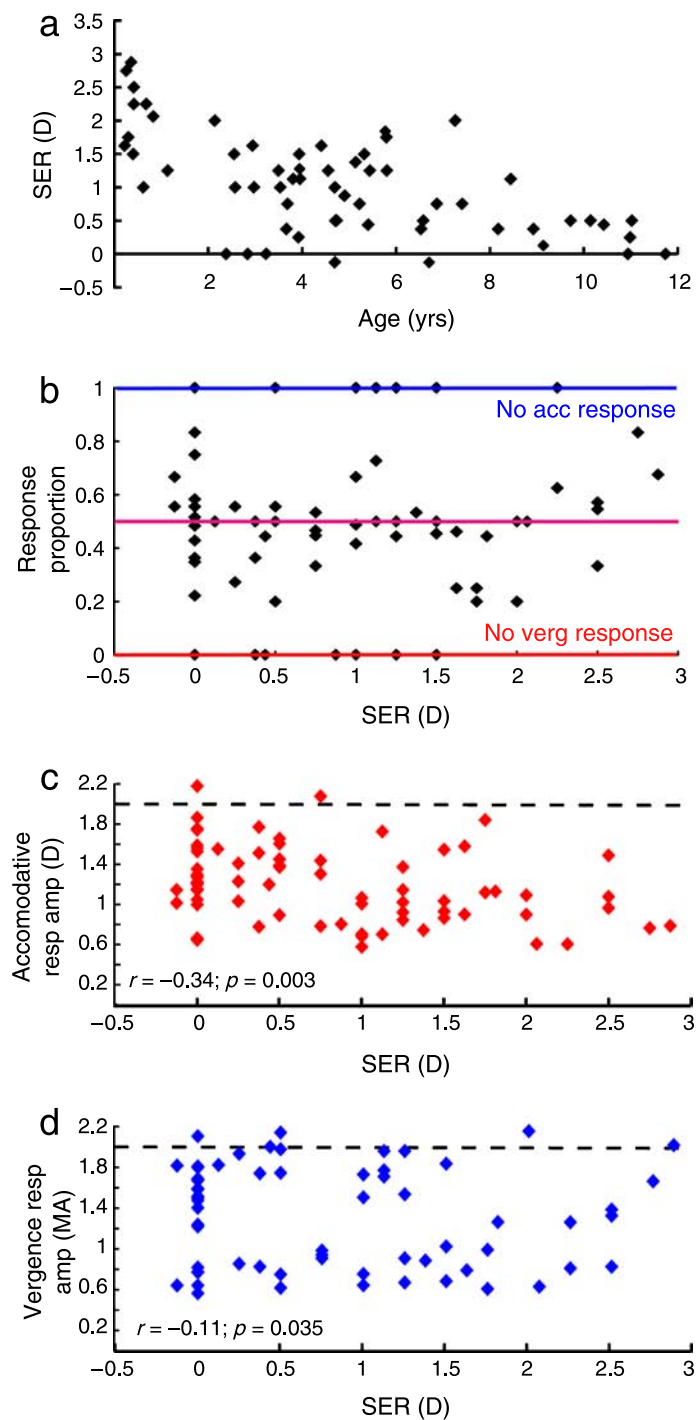
Figure 8. Panel a: Cycloplegic spherical equivalent refraction (SER) plotted as a function of subject's age. SER from right and left eyes were averaged. Panel b: Response proportion of individual subjects plotted as a function of their cycloplegic SER. Panel c: The response amplitude of accommodation plotted as a function of the cycloplegic SER in the LC condition. Panel d: The response amplitude of vergence plotted as a function of the cycloplegic SER in the PC condition.

PC conditions combined) of individual subjects is plotted as a function of their cycloplegic SER in Figure 8, panel b. The data were typically clustered around the middle purple line (response proportion of 0.5) with no apparent refractive error related trend, indicating that the subject's SER, over this range, did not strongly bias them in responding to either lens or prism stimulation. The frequency of accommodative responses to the LC condition was however modestly correlated with the SER ($r = -0.34$; $p = 0.001$), indicating that the response frequency did somewhat reduce with an increase in the subject's SER. The frequency of vergence response in the PC condition was poorly correlated with the SER ($r = -0.11$; $p = 0.21$). The amplitude of accommodative response in the LC condition was also modestly negatively correlated with the SER ($r = -0.33$; $p = 0.001$; Figure 8, panel c) while the amplitude of vergence response in the PC condition was poorly correlated with the SER ($r = -0.11$; $p = 0.35$; Figure 8, panel d). These results indicate that, for the range of refractive errors tested here, the frequency and amplitude of accommodation to lens stimulation decreased somewhat with an increase in the subject's hyperopic refractive error. The frequency and gain of vergence to prism stimulation, on the other hand, was not significantly influenced by the subject's hyperopic refractive error.

Discussion

This study was designed to determine how the developing visual system weights retinal blur and disparity in generating accommodative and vergence responses when both cues are present, as is the case under naturalistic binocular viewing conditions. Blur and disparity cues were placed in conflict with each other and the impact of this cue-conflict on accommodative and vergence performance was assessed across a wide range of ages (2.0 months to 40.8 years). Three hypothetical patterns of results were derived for Experiments 1 and 2 to provide insights into the relative use of the two cues. The data indicated that, when directly stimulated with lenses or prisms, both accommodation and vergence responded, although inaccurately, with the frequencies and amplitudes of vergence responses being slightly larger than those of the accommodative responses across all ages tested (Table 2, Figure 5, panel a). The mean accommodative response for the −2 D lens stimulus was 1.18 D (*SEM* = 0.42 D) (a mean accommodative error of 0.82 D) and the mean vergence response for the 2-MA base-out prism stimulus was 1.37 MA (*SEM* = 0.58 MA) (mean vergence error of 0.63 MA) across all ages tested (Figure 5, panel a). The vergence response to prism stimulation is expected to be somewhat larger than the accommodative response to lens stimulation given the smaller size of Panum's fusional area in adults (0.08 MA; Schor, Wood, & Ogawa, 1984)

than their depth of focus (0.18–0.25 D; Charman & Whitefoot, 1977). The size of Panum's area and the depth-of-focus however need to be determined in infants and children to expand these predictions. The mean stimulated accommodative responses in the LC and DOL conditions were statistically insignificantly different from each other (Figure 6, panel a; red histograms) while the mean stimulated vergence response in the PC condition was statistically significantly smaller than that in the BOL condition (Figure 6, panel b; blue histograms). This result indicates that the stimulated accommodative response is capable of achieving its open-loop performance even when there is a conflict between blur and disparity cues whereas the stimulated vergence response does not appear capable of doing so under cue-conflict conditions. With regard to the coupled responses, the size of the coupled vergence response in the LC condition was poorly correlated and significantly smaller than the size of the open-loop vergence response in the DOL condition (Figure 6, panel a; blue histograms). Similarly, the size of the coupled accommodative response in the PC condition was also poorly correlated with and statistically significantly smaller than that of the open-loop accommodative response in the BOL condition (Figure 6, panel b; red histograms). Overall, these results suggest that there is, if any, only a weak bias towards the retinal disparity cue in driving accommodative and vergence responses during normal visual development. The number of subjects in the youngest age group (<1 year old) was too small to perform a detailed analyses of the relative weighting of blur and disparity cues during the early phase of accommodative and vergence development. Experiments are currently being conducted to address this question in detail.

Another line of evidence for the lack of a significant bias towards either cue during development comes from the raw accommodation and vergence traces of 12 subjects in the PC condition of Experiment 1 (representative data from two subjects is shown in Figure 4). In these subjects, the prism stimulation elicited a stable change in vergence and a transient change in accommodation. These responses were qualitatively similar to those of adults when vergence was stimulated independently of accommodation in a stereoscopic display (Torii, Okada, Ukai, Wolffsohn, & Gilmartin, 2008). The initial change in accommodation associated with the vergence response can be attributed to the vergence-accommodation cross-coupling and then the return of accommodation to a new steady-state illustrates the relative compensation for the convergence induced accommodation, presumably through blur-driven feedback (Figure 4). These responses suggest that the developing visual system can use both blur and disparity cues to generate compensatory accommodation and vergence responses. These results also support the notion that the reduced coupled responses in the LC and PC conditions, when compared to those obtained in the DOL and BOL conditions (Figure 6),

resulted from a dynamic compensation of coupled vergence and accommodative responses by disparity and blur signals, respectively.

Transient changes in accommodation were observed only in 12 of the 89 subjects who gave usable data in the PC condition (Figure 4). Interestingly, the accommodative transients in these subjects were observed only when convergence was stimulated with prisms and not when the convergence stimulus ceased with the removal of the prisms (Figure 4). The cooperation level of these 12 subjects was comparable to those whose raw data did not show evidence of such accommodative transients. These observations might be related to the dynamic characteristics of stimulated and coupled accommodative and vergence responses. Typically, the speed of accommodation and vergence of adults is correlated with the response magnitude, with increased speed resulting in a larger change in accommodation and convergence within a given time frame (Hung, Ciuffreda, Semmlow, & Horng, 1994; Kasthurirangan, Vilupuru, & Glasser, 2003; Suryakumar, Meyers, Irving, & Bobier, 2007). Perhaps the coupled vergence accommodation responses of these 12 subjects were faster than those of others, thereby resulting in a larger and more detectable change in their accommodation. For comparable stimulus magnitude and response starting position, the speed of convergence and divergence responses of adults are comparable to each other (Alvarez, Semmlow, & Pedrono, 2005), while the speed of accommodative responses is much faster than that of disaccommodative responses in adults (Kasthurirangan & Glasser, 2005). Perhaps, the disaccommodative responses of these 12 children were also slower than their accommodative counterparts, thereby causing a gradual and sustained change in disaccommodation coupled with divergence (elicited upon removal of prisms) than a transient change in accommodation coupled with convergence (elicited upon placement of prisms). The dynamics of accommodative and vergence responses, however, cannot be assessed in detail from the current data set due to the limited temporal sampling frequency (25 Hz) of the PowerRefractor.

Transient changes in vergence were not observed in any subject in the LC condition (e.g., Figure 3). This is in contrast with the previous observation of vergence transients in adults in response to binocular lens stimulation (Semmlow & Venkiteswaran, 1976; Semmlow & Wetzel, 1979). The vergence transient during lens stimulation is expected to be somewhat smaller than the accommodative transient during prism stimulation in adults because the threshold for detecting disparity [sensory: 0.08 MA (Schor et al., 1984); motor: 0.01 MA (Duwaer & van den Brink, 1981)] is smaller than the threshold for detecting blur [sensory: 0.18–0.25 D (Charman & Whitefoot, 1977; Winn, Charman, Pugh, Heron, & Eadie, 1989); motor: 0.15 D (Kotulak & Schor, 1986)] and because vergence responds more rapidly to changes in disparity [the average latency and movement time for 1.1 MA near-to-far vergence step

responses are 192 ± 42 ms and 575 ± 270 ms, respectively (Suryakumar et al., 2007)] than accommodation responds to changes in retinal blur [the average latency and movement time for 1.0 D near-to-far accommodative step responses are 248 ± 81 and 1017 ± 280 ms, respectively (Suryakumar et al., 2007)] (Heron, Charman, & Schor, 2001). It is therefore possible that the transient changes in vergence during lens stimulation were too small and too fast to be detected by the PowerRefractor. The eye tracker used by Semmlow and colleagues to measure vergence responses had a resolution of 0.17° and a temporal sampling rate of 200 Hz, both of which are superior to that of the PowerRefractor (resolution: approximately 2.2°; temporal sampling: 25 Hz) (Schaeffel et al., 1993; Semmlow & Venkiteswaran, 1976; Semmlow & Wetzel, 1979).

Taken together, these data suggest that, when in conflict, blur and disparity cues might have approximately equal importance in typically developing infants and children and that the developing visual system possesses the ability to actively eliminate blur and diplopia to achieve the final steady-state responses. Interestingly, some infants and children did exhibit a strong preference for either blur or disparity stimuli in the current study (Figure 2, panel b and Figure 8, panel b). This preference does not appear to be related to the cycloplegic refractive error of the subject, at least within the range studied (+2.8 D to −0.12 D) (Figure 8, panel b). Alternative explanations for such strong preferences need to be explored.

The adult data compare well with earlier studies (Fincham & Walton, 1957; Jaschinski, 1997; Ogle et al., 1949; Ramsdale & Charman, 1988; Semmlow & Hung, 1979) and computer simulations (Hung & Ciuffreda, 1994; Schor, 1999) that have assessed accommodative and vergence performance under similar cue-conflict viewing conditions. For example, Ramsdale and Charman (1988) obtained a mean accommodative response of 1.42 ± 0.14 D (mean ± 1 *SEM*) for a 2-D lens stimulus when fixation was held at 33 cm in their two subjects (see their Table 1). This compares well with the mean adult accommodative response of 1.39 ± 0.09 D for a 2-D lens stimulus in the current LC experiment (Figure 4, panel a). Similarly, Fincham and Walton (1957) and Ramsdale and Charman (1988) observed mean coupled accommodative responses of 0.34 ± 0.06 and 0.72 ± 0.16 D (estimated from visual inspection of Figures 7 and 8 in Fincham & Walton, 1957), respectively, when prisms were introduced and fixation was held at 100 and 33 cm, respectively. These values compare well with the corresponding adult mean accommodative gain of 0.48 ± 0.07 D obtained in the PC condition (Figure 4, panel b). Unfortunately, Ramsdale and Charman and Fincham and Walton did not measure vergence responses in order for us to quantitatively compare the vergence gains obtained in their studies with the current one.

The design of the current study can be used to examine ways in which the developing visual system might compensate for conflicting accommodative and vergence demands experienced in habitual viewing conditions. When compared to adults, infants experience a larger accommodative demand due to their typical hyperopia (Mayer et al., 2001) (Figure 8, panel a) and a smaller vergence demand due to their narrow IPD (MacLachlan & Howland, 2002). If the gain of the accommodative-vergence coupling (AC/A ratio) is adult-like from birth, a hyperopic infant is at risk of generating an over-convergence to their reduced vergence demand if they accommodate accurately to compensate for their hyperopia. This over-convergence would need to be compensated for using fusional divergence. The results of this study suggest that the typically developing visual system is capable of making compensatory relative responses (Figures 2–6). The range over which the visual system can perform this compensation needs to be determined, but the current data suggest that the accuracy of this compensation decreases with increasing demand—both with experimentally imposed additional stimuli (Figure 7) and with increasing baseline refractive error (Figure 8, panel b). Perhaps, the exaggerated levels of conflict between blur and disparity stimuli resulting from high AC/A ratios and the inability to generate fusional divergence to compensate for excessive accommodative-convergence precipitates binocular anomalies like refractive esotropia and convergence excess in some children (Anker et al., 2003; Campos, 2008; Chin & Breinin, 1967; Ingram et al., 1994; Parks, 1958; Scheiman & Wick, 2002; von Noorden & Avilla, 1990). Compensation for conflicting accommodative and vergence demands through relative responses causes visual fatigue and reduced binocular sensory visual performance (e.g., reduced stereo acuity and increased depth distortions) in adults (Hoffman, Girshick, Akeley, & Banks, 2008; Sheedy & Saladin, 1977), suggesting that this might not be a viable long-term solution during development.

As an alternative strategy, the developing visual system might recalibrate the strengths of the neural cross-coupling between accommodation and vergence (AC/A and CA/C ratios) to overcome conflicting stimulus demands. Computer simulations logically indicate that the amount of accommodation and vergence generated by adults in the presence of conflicting stimuli might depend on the strengths of the AC/A and CA/C ratios, with higher AC/A and CA/C ratios leading to larger errors in steady-state accommodation and vergence (Hung & Ciuffreda, 1994; Schor, 1999). Recent empirical evidence suggests that the response AC/A ratio is smaller in infants (4.1 ΔD/D for 4.4 cm IPD) than adults (5.7 ΔD/D for 6.4 cm IPD) (Bharadwaj & Candy, 2008; Turner et al., 2002) while the response CA/C ratio is higher in infants (0.18 D/ΔD) than adults (0.04 D/ΔD) (Bobier et al., 2000). The response AC/A ratio (in units of ΔD/D) also increases gradually with age (Bharadwaj & Candy, 2008), suggesting that neural recalibration of cross-coupling might accompany the decrease in accommodative demand with the growth

of the eye (loss of hyperopia) and increase in vergence demand with the growth of the head (widening of IPD). The stimulus CA/C ratio reaches adult-like levels by 3–5 years (0.11 D/ΔD) (Suryakumar & Bobier, 2004), suggesting that the age-related recalibration of the convergence-accommodation coupling might have a shorter time course than that of the accommodative-convergence coupling. Changes in the stimulus CA/C ratios are however harder to interpret because of their inherent ambiguity about the amount of convergence response generated to the stimulus. On a related note, the response AC/A ratios of non-strabismic hyperopic children (6 to 14 years) have been found to be significantly lower (3.40 ΔD/D) than age-matched emmetropes (3.94 ΔD/D) (Mutti, Jones, Moeschberger, & Zadnik, 2000). Perhaps, the lower AC/A ratio of hyperopic children reflects an attempt by the developing visual system to minimize the amount of over-convergence accompanying the increased accommodative response.

The developing visual system could also overcome the conflicting accommodative and vergence demands by employing the tonic accommodative and vergence controllers to drive their respective motor responses (Hung & Semmlow, 1982; Schor, 1992, 1999). Accommodative and vergence motor responses of adults have been modeled using phasic and tonic integral controllers, with the phasic controller eliciting a rapid stimulated and cross-coupled response and the tonic controller eliciting a gradual stimulated response, with no cross-coupled response (Jiang, 1996; Schor, 1992, 1999). The activity of the tonic controller is slow and therefore it could not respond rapidly to transient stimuli (Hung & Semmlow, 1982; Schor, 1992). However, its activity is central to maintaining responses in the presence of sustained accommodative and vergence demands (Hung & Semmlow, 1982; Schor, 1992). Computer simulations indicate that the increased activity of the tonic accommodative and vergence controllers of adults reduces the lag of accommodation in the presence of uncorrected hyperopia (Schor, 1999). The tonic controllers of the developing visual system could therefore compensate for underlying hyperopia (sustained increase in accommodative demand) and narrow IPD (sustained reduction in vergence demand) and bring other faster compensatory mechanisms into their limited operating ranges. The tonic accommodative and vergence states, measured as the location in space where accommodation and vergence settle in the absence of any visual stimulus, have been found to be 1.43 D (*SD* = 0.25 D) for accommodation and 0.98 MA (*SD* = 0.52 MA) for vergence in 3- to 12-month-old infants and 1.14 D (*SD* = 0.04 D) for accommodation and 0.43 MA (*SD* = 0.16 MA) for vergence in adults (Aslin & Dobson, 1983). The small difference between infant and adult tonic accommodative states (approximately 0.3 D) may suggest that the infant tonic accommodative system has adapted to the sustained accommodative demand created by the hyperopic refractive error (Mayer et al., 2001). The difference in infant and adult tonic vergence states (approximately 0.5 MA) is harder to interpret because the vergence demands are determined by both IPD and horizontal phoria of the subject. While the IPD of typically developing infants and children is known (MacLachlan & Howland, 2002), the horizontal phoria is poorly understood.

Conclusions

The relative importance of blur and disparity cues in generating accommodative and vergence responses was assessed in the typically developing visual system by placing the two cues in conflict with each other. The results demonstrated that the developing accommodative and vergence responses are capable of at least partially compensating for conflicting blur and disparity stimuli, without exhibiting a strong preference towards either cue or system. The accuracy of this compensation decreases with an increase in the amplitude of cue-conflict, both with experimentally induced stimuli and with the underlying cycloplegic refractive error.

Acknowledgments

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