

The effect of changing size on vergence is mediated by changing disparity

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In this study, we investigated the effect of changing size on vergence. Erkelens and Regan (1986) proposed that this cue to motion in depth affects vergence in a similar way as it affects perception. The measured effect on vergence was small and we wondered why the vergence system would use changing size as an additional cue to changing disparity. To elucidate the effect of changing size on vergence, we used an annulus carrying both changing size and changing disparity signals to motion in depth. The cues were either congruent or signaled a different depth. The results showed that vergence was affected by changing size, however in an opposite way than that perception was affected. These results were incongruent with those reported by Erkelens and Regan (1986). We therefore additionally measured the effects on vergence of the individual parameters associated with changing size, i.e., stimulus area, retinal eccentricity, and luminance. Stimulus (retinal) eccentricity was inversely related to vergence gain. Luminance, on the other hand, had a smaller but positive relation to vergence gain. Thus, changing size affected the disparity signal two-fold: it changed the retinal location of the disparity signal and it changed the strength of the disparity signal (luminance change). These effects of changing size on disparity can explain both our results (change in retinal location of the disparity signal) and those of Erkelens and Regan (1986; change in luminance). We thus conclude that changing size did not in itself contribute to vergence, rather its effect on vergence was mediated by disparity.

Keywords: motion in depth, vergence, disparity, changing size

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Introduction

Interaction effects between eye movements and perception of motion in depth have received little attention (Howard & Rogers, 2002). Recently, Howard (2008) summarized the effects of extra-retinal signals on the perception of motion in depth reported in several earlier studies. The compensation of eye movements using extra-retinal signals induces a perception of motion in depth only if the stimulus is unable to carry changing size (or looming) information (Brenner, Van Den Berg, & Van Damme, 1996; Nefs & Harris, 2007, 2008; Welchman, Harris, & Brenner, 2009). Otherwise, extra-retinal signals are ignored even if vergence amplitudes are large (Erkelens & Collewijn, 1985a, 1985b; Regan, Erkelens, & Collewijn, 1986). Studies on what drives eye movements while viewing 3D motion, however, are limited. One study that has addressed the issue (Erkelens & Regan, 1986) showed that vergence was more accurate in response to the simulation of 3D motion of a rigid object than in response to an identical disparity signal alone. In addition, they reported vergence responses to motion in depth simulated by changing size only. They concluded that

although changing disparity was the main source of information for vergence, changing size affected vergence in a similar way as it affected perception of motion in depth.

The effect of changing size on vergence reported by Erkelens and Regan (1986) was small (at maximum 10% of the total vergence response), and therefore, the added value of using changing size as an additional input for vergence is not self-evident. Moreover, Nefs and Harris (2008) showed that whereas a monocularly presented (small) looming target did induce vergence, that same target failed to do so (significantly), when presented binocularly. Therefore we address the issue whether changing size per se contributed to vergence or whether the effect reported by Erkelens and Regan (1986) was an epiphenomenon. For example, the changes in vergence could have been caused by a change of the effective disparity stimulus, i.e., the change in size displaced the stimulus disparity to another retinal position, increased the stimulus area, and increased stimulus luminance.

To elucidate the effect of changing size on vergence, we used congruent and incongruent combinations of both changing size and changing disparity cues to motion in depth. As changing size is a relatively weak cue for vergence, we sought to find a stimulus

for which the relative weight of (changing) disparity could be reduced. An annulus can carry both changing size and changing disparity information, but the effect of disparity on vergence is significantly reduced compared to stimuli that have foveal disparities (Howard, Fang, Allison, & Zacher, 2000). On the other hand, two metric properties play a role in defining the size of a stimulus, namely contour(s) and area. An annulus contains two radii (edges) that signal a change in size, whereas a filled disk has only one radius (edge). Thus, the strength of the changing size signal (based on the change in radius) is larger for an annulus than for a filled disk. Although the changing size signal related to a change in stimulus area is smaller for an annulus compared to a filled disk, Howard et al. (2000) have shown that stimulus area does not affect vergence. The changing size signal conveyed by an annulus should thus be equally strong, or even stronger, compared to that same signal conveyed by a filled disk. This suggests that the relative weight of the changing size signal in an annulus is enlarged compared to the relative weight of that same signal in a filled disk.

In a first set of two experiments, we assessed the efficacy of the stimulus in eliciting perception of motion in depth. To this end, we measured perception of motion in depth and eye movements separately. In addition, we compared the effect of changing size on perception to its effect on vergence.

The results showed that with an increase in size, vergence response (gain) decreased. In contrast, Erkelens and Regan (1986) reported a positive relation between vergence gain and increased size. Our incongruent results could have been due to the changing size stimulus. Therefore, we measured vergence in response to individual parameters associated with the changing size stimulus in a third experiment. Across trials, we varied stimulus area, stimulus radius, and luminance.

Results from this experiment showed that both the radius of the stimulus and luminance had an effect on vergence, although the effect of stimulus radius was more pronounced. Larger eccentricities resulted in a decrease in vergence gain. Luminance, on the other hand, was positively related to vergence. Our finding in the first experiment that vergence gain is inversely correlated with changing size can be explained by the combination of these effects, i.e., an increase in size (an increase in stimulus radius and a simultaneous decrease in luminance) effectively resulted in a decrease in vergence gain. The report by Erkelens and Regan (1986) of a positive relation between size and vergence can be attributed to a change in luminance.

We thus conclude that although changing size per se affects perception of motion in depth to a great extent, its effect on vergence is due to changes in the effective disparity stimulus. Under binocular viewing conditions, vergence is only determined by (absolute) disparity.

Methods

In the first and second experiments, we used an annulus with changing size and changing disparity cues to motion in depth. Perception and eye movements were measured in two separate sessions using identical stimuli but different presentation times. In a third experiment, we varied the parameters associated with the changing size stimulus, stimulus area, radius, and luminance, across trials. The changing disparity signal was identical for all trials in all experiments.

Stimuli and procedure

Binocular separation was achieved using red–green anaglyphs. The stimulus images consisted of an annulus surrounding fixation with an initial radius of 5° (inner radius of 4.25° and an outer radius of 5.75°). We refer to the position of the stimulus using the mean radius: halfway between the inner and outer radii. An annulus consisted of random dots ($N = 500$) and a dot size of 1.5 arcmin. Its inner and outer edges were jittered circles because of the random dot pattern (see Figure 2).

Motion in depth was induced by changing disparity and changing size. The changing disparity cue was constant across trials.¹ Changing disparity was induced by translating the eyes' images in opposite horizontal directions across the screen. It defined a sinusoidal movement in depth of the fused stimulus with an amplitude (A) of 150 mm and with a frequency of 0.25 Hz ($\omega = 2\pi 0.25$), see Equation 1. This means that the maximum amplitude of the target had a binocular disparity of 2.32° , for an assumed interocular distance of 65 mm and actual viewing distance of 57 cm:

$$\text{depth (relative to screen): } d(t) = A \sin(\omega t) \quad (1)$$

The resulting target vergence is described by Equation 2, where IOD is the interocular distance and $ScrD$ is the distance between the observer and the screen. The disparity defined movement always started at screen depth (Figure 1):

$$\text{changing target vergence: } dv(t) = \arctan\left(\frac{IOD}{ScrD d(t)}\right) \quad (2)$$

We simulated the change in retinal image size, based on a cyclopean viewpoint, using Equation 3. In Equation 3, motion in depth induced by changing size is defined relative to motion in depth induced by changing disparity. For a rigid object moving in depth, that is an object for

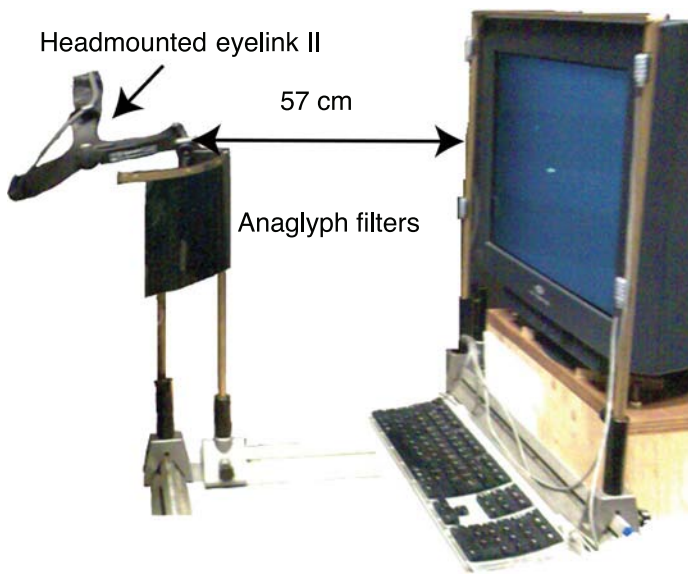


Figure 1. Setup. Data were collected using the head-mounted EyeLink II using head correction. Subjects were seated 57 cm from the CRT screen. A whole field anaglyph setup was used. The cameras of the EyeLink were in front of the filters (subject's viewpoint).

which a change in depth is accompanied by a change in retinal image size, the simulated change in retinal image size is produced by Equation 3 with a unity *scale factor*. A negative *scale factor* simulates a stimulus that decreases in size (contraction) while target vergence defines motion in depth toward the observer. The *scale factors* used to simulate size changes were identical for left and right eye images. We tested five different changing size conditions

(with *scale factors* of -2 , -1 , 0 , 1 , and 2) and kept the initial stimulus size constant across conditions:

$$\text{changing size: } dsize(t) = 1.0 + \left(\frac{d(t)}{ScrD} \right) * \text{scale factor} \quad (3)$$

Sketches of two of the stimuli are depicted in Figure 2. The left panel shows a stimulus in which changing disparity and changing size defined the same motion direction and the right panel shows the change in stimulus when the cues defined opposite motion-in-depth directions. Only the diameter and area of the stimulus changed. The dot size (of one pixel) remained constant, because with the scale factors used the change in size always rounded to 1 pixel. Stevenson, Reed, and Yang (1999) have shown that changing element size in the periphery does not change perceived motion in depth, but only the total area over which there is binocular correspondence between the two eyes. Thus, keeping the single element size constant should not influence perceived motion in depth.

Before stimulus onset, a fixation mark was presented to redirect the observers' eyes to focus at screen depth. After each trial, the screen was blanked until observers indicated that they were ready for the next trial by pressing the space bar.

In all experiments, observers were instructed to track the perceived motion in depth of the center of the annulus and were asked to refrain from making eye movements toward the annulus itself.

In the perceptual experiment, observers were asked to report the perceived end position of the stimulus (the result of the amplitude and direction of perceived motion in depth).

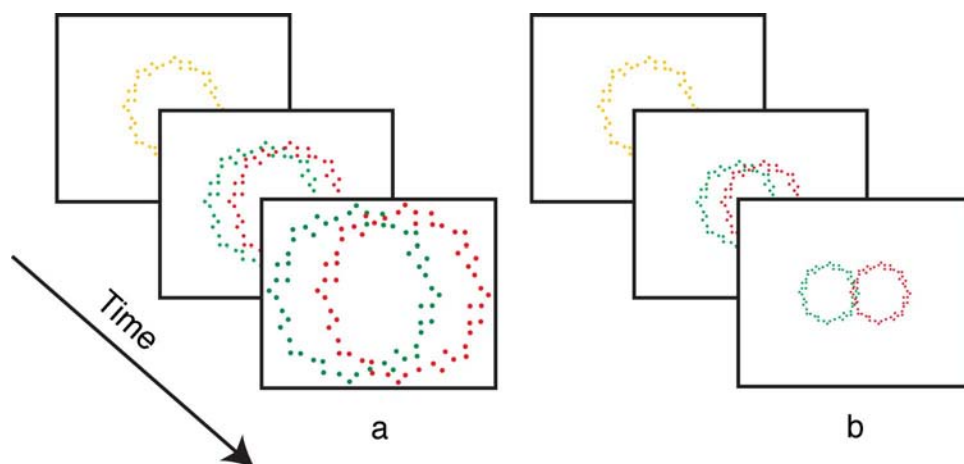


Figure 2. Stimulus. The sketches of the stimuli are shown. The first quarter of the sinusoidal movement in depth is depicted. The stimuli were initially displayed at screen depth (panels at the back of the sequence). Motion in depth of the stimulus defined by changing disparity always started toward the observer. In panel (a), changing size defines the same motion-in-depth direction as changing disparity, whereas changing size is pitted against changing disparity in panel (b).

Because the perceptual experiment mainly served to measure the effectiveness of the implemented changing size cue to induce a sensation of motion in depth, we kept the task as simple as possible by only asking for a judgment on an ordinal scale from 1 (greatest distance toward the observer) to 9 (greatest distance away from the observer) with 5 used to indicate no motion in depth at all. In this experiment, we showed exactly the same stimuli as in the original experiment, thus there was no fixation point during stimulus presentation. Beside the instruction to report the perceived end position of the stimulus, observers were instructed to fixate the center of the annulus during presentation. However, we only showed the stimulus for 1 s (one fourth of the complete cycle) to keep the experiment and task as short and simple as possible. Note that observers were instructed to follow the center of the annulus and that they could make vergence eye movements.

In eye movement recording trials, the stimuli were displayed for 2 s (half of the full cycle). Presentation times needed to be longer here, because vergence can have a large onset latency (up to 400 ms for annuli; Howard et al., 2000) and we did not want the stimulus to disappear before the largest peak amplitude would have occurred. Conditions were randomly repeated ten times.

In the third experiment, the procedure was identical. Stimuli varied in area, radius, and number of dots across trials but remained constant during a single trial, for the values of the used parameters (see the Results section, Table 1). Each condition was randomly repeated four times (divided over two experimental sessions). Only changing disparity could induce a perception of motion in depth in this experiment. It is known that changing absolute disparity does not induce motion in depth for the stimuli used in this study (Erkelens & Collewyn, 1985b, 1985c; Howard, 2008; Regan et al., 1986), therefore there was no additional psychophysical experiment.²

Experimental setup

Subjects were seated 57 cm in front of a CRT screen (LaCie PhotonVision IV, 1600 × 1200 pixels at 75 Hz) on which the stimulus images were displayed. Chin and headrests were used to stabilize the head. The experimental room was completely darkened. Eye movements were recorded using a head-mounted EyeLink II system with head tracking.

Using anaglyph filters in combination with the infrared (IR) sensitive cameras of the EyeLink system decreases the signal-to-noise ratio of the EyeLink significantly, because

of the reduced transmission through the green anaglyph filter of IR light is reflected by the pupil. We therefore created a filter setup (see Figure 1) in which the cameras of the head-mounted system could be positioned nearer to the eye than the anaglyph filters.

Luminance values for each phosphor were adjusted to minimize bleeding and background illumination. Luminance values are given as follows: for red: 15.2 cd/m² without filter, 2.60 cd/m² through red filter, and 0.12 cd/m² through green filter and for green: 35.2 cd/m² without filter, 1.85 cd/m² through green filter, and 0.14 cd/m² through red filter. Michelson's contrast for green/red through green filter was 88% and for red/green through red filter it was 90%. Background illumination through the filters was 0.01 cd/m².

Under the condition that a subject's head was vertically aligned with the screen, there was no binocular reference frame. Due to the separator of the filter setup, the vertical (left and right) edges of the screen were only monocularly visible. Depending on interocular distance, 85–100% of the contralateral side of the screen was visible (FOV was 33.0°–38.5° or 34–40 cm). The horizontal (top and bottom) edges of the screen, although binocularly visible, would only result in relative disparities if a subject's head would have been tilted, an almost impossible condition in our setup.

Data analysis

Perceptual data were normalized by rescaling the range of perceived amplitudes and directions of motion in depth per observer between 0 (greatest distance toward the observer) and 1 (greatest distance away from the observer).

Eye movement data were analyzed offline. Trials with blinks or saccades with a version amplitude greater than 2° were removed from further analysis. We analyzed relative vergence (right eye–left eye gaze direction), peak amplitude (relative to vergence at stimulus onset), and vergence onset latency. Onset latency was defined as the difference in time between stimulus onset and onset of vergence, with vergence onset defined by a vergence change of more than 0.1°. Additionally, we analyzed gain and phase lag of the vergence movement by fitting the vergence traces with the movement predicted for vergence (see Equation 4) with gain (G) and phase lag (ϕ) as variables. Offset and (interocular distance) IOD are subject dependent parameters:

$$f(t, G, \phi) = offset - 2.0G \arctan\left(\frac{0.5IOD}{ScrD - A \sin(\omega t + \phi)}\right) \quad (4)$$

Observers

All observers (3 females and 3 males aged between 24 and 40) participated in the perceptual as well as the eye

| Parameter | V1 | V2 | V3 |
|--------------------------|------|------|-------|
| Radial eccentricity | 2.5° | 5.0° | 10.0° |
| Area (deg ²) | 23.5 | 47 | 94 |
| Number of dots | 125 | 500 | 2000 |

Table 1. Changing size parameter values.

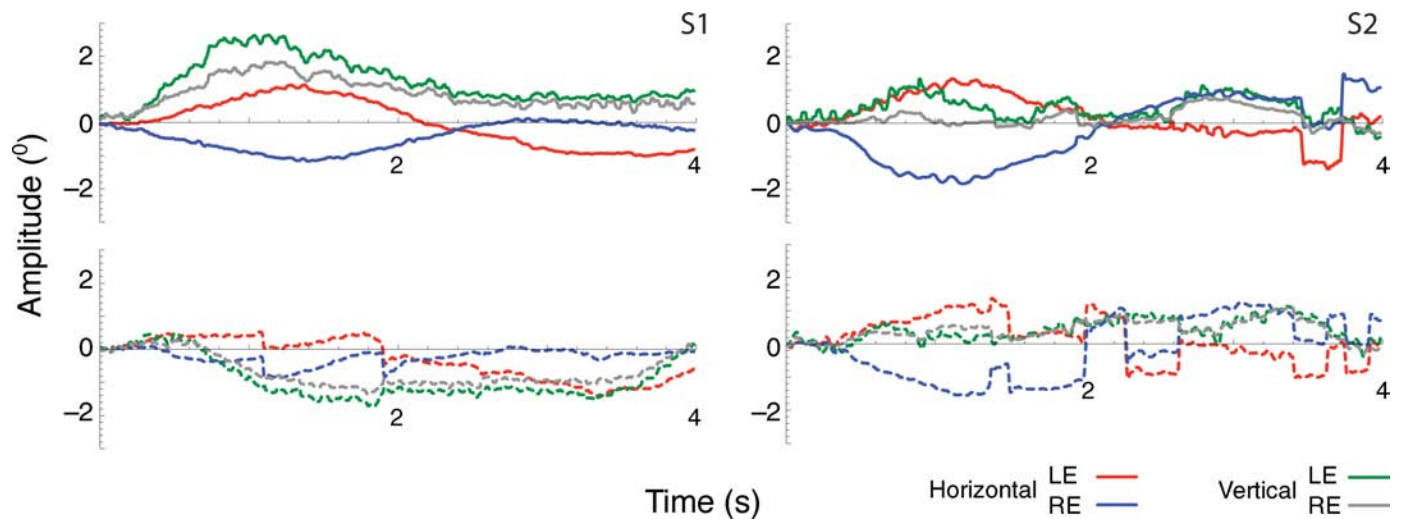


Figure 3. Eye movement traces of two subjects. Traces of horizontal and vertical eye movements in time (horizontal axis) of both left and right eyes are shown for two subjects. The data are smoothed with a moving average filter with a 20-ms (10 data points) kernel and depicted in degrees amplitude (vertical axis) relative to the gaze direction at stimulus onset. The upper panels show data from clean trials, i.e., almost no saccades were present. The stimulus conditions were scale factor -1 (S2) and scale factor 0 (S1). The lower two panels show data from trials with a lot of small saccades (S2, stimulus condition scale factor -2) or hardly any horizontal vergence (S1, both left and right eye gaze directions are similar, stimulus condition was scale factor 1). Note that stimulus was always at least at 2° radial eccentricity.

movement experiment. All had good stereoacuity (TNO test) of at least 45 arcsec and normal or corrected-to-normal vision.

Results

In both experiments, observers were instructed to track the imaginary center of the stimulus, to which they

obliged quite well. In the first experiment, 3.8% of the 360 trials were removed due to blinks and 3.6% due to saccades. In the second experiment, 5.2% of the 648 trials were removed due to blinks and 4.3% due to saccades. In Figure 3, horizontal and vertical eye movements of both eyes of two observers are shown. In the top two panels, two clean traces are depicted, whereas the bottom two panels show eye movements from relatively noisy trials, the left one showing almost no vergence movement, i.e., left and right eye horizontal movements are almost identical and the right one showing a lot of small saccades

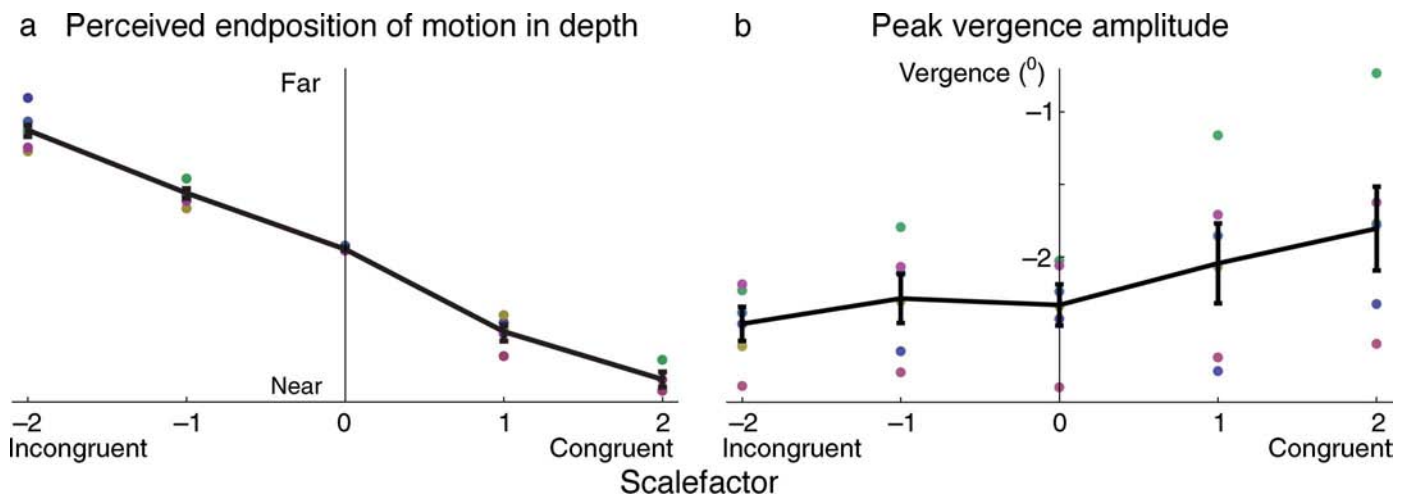


Figure 4. Influence of changing size on perceptual and vergence peak amplitudes. Individual subject peak amplitudes for both (a) perception and (b) vergence are depicted by the single dots for each condition. Mean peak amplitudes and 95% confidence interval (perceptual data) or standard error (vergence data) across subjects are depicted by the joined black error bars (errors were very small for the perceptual data). Both perceptual and vergence data vary with changing size. The direction of the slope, however, is opposite.

but none greater than 2° (the minimum inner radius of the stimulus).

In the perceptual experiment, we investigated the effectiveness of the changing size stimulus to induce perceived motion in depth, by asking the observers to judge the perceived end position of the stimulus relative to starting position. Figure 4 (left panel) shows the mean normalized perceived end position of the targets' motion in depth of individual observers (circles) and the mean and 95% confidence interval across observers (black joined error bars, calculated using a bootstrap procedure). Judgments across observers were similar and perceived end positions were mainly based on the direction and amplitude of motion in depth induced by changing size. The changing size cue was efficient in eliciting motion-in-depth sensations (two-way ANOVA $F_{2,241} = 942, p = 0.0$), whereas the absolute disparity signal hardly influenced perception of motion in depth. The absence of a contribution of (absolute) disparity to perceived motion in depth is most clearly visible in the condition without a changing size signal. There was only one single response indicating some perceived motion (in the receding direction), all other responses were equal to no perceived motion in depth at all (see the Discussion section for a more in-depth discussion of the various cues inducing motion-in-depth perception in our experiment).

Figures 5a and 5b show mean vergence traces of the different changing size conditions of two observers.

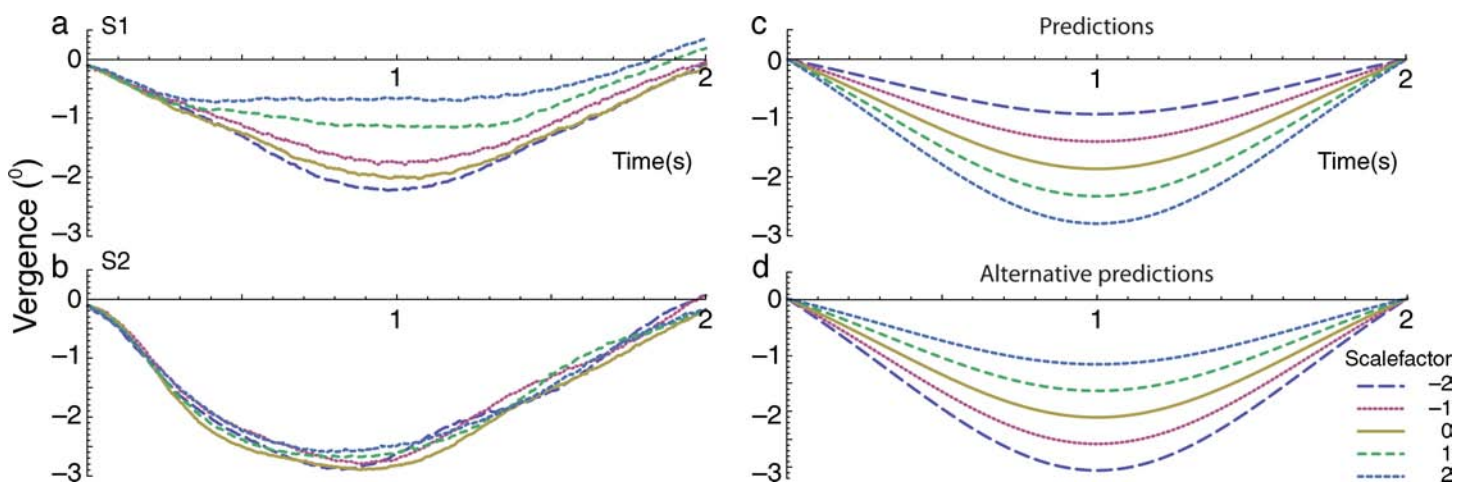


Figure 5. Data of single subjects: mean vergence traces per stimulus condition. (a, b) Mean changes in vergence relative to the vergence angle at stimulus onset in time (horizontal axis) of two subjects. Onset latency (around 300 ms) present in the data in Figure 3 is similar across stimulus conditions and is removed in these traces for better visualization. Even after removal of onset latency (vergence onset was defined when vergence became less than -0.1°) it still takes about another 250 ms before vergence starts to differ between the various stimulus conditions. (c) Predictive vergence traces based on an 80/20 contribution of changing disparity and changing size to vergence gain. Changing disparity was constant across trials and changing size is defined relative to changing disparity, using a scale factor (see main text for more details). Only the gain was assumed to vary across stimulus conditions and a correction for onset latency is not included. Notice that although the effect is less pronounced for S2 (b), the change in gain across conditions is opposite from that predicted in (c). (d) Modified predictions using the fitted gain parameters based on the data of the second experiment. These modified predictions resemble the data in (a) and (b) much better than the predictions presented in (c).

Predictions for vergence given a 20/80 contribution of changing size and changing disparity to vergence are depicted in Figure 5c. We predict that changing size, if it affects vergence, should have a similar effect on vergence as in the study of Erkelens and Regan (1986). Thus vergence gain should increase with increasing size. This means that in the present case vergence amplitude should be larger for positive scale factors (motion in depth induced by changing size and changing disparity in the same direction) than for negative scale factors (changing size induces motion in depth in a direction opposite to the one induced by changing disparity).

However, the data show the opposite effect, i.e., for changing size opposing changing disparity vergence following was very accurate and the gain was close to one. However, when changing size defined the same motion-in-depth direction as changing disparity, vergence following was less accurate and the gain was less than one.

We quantified the effect of changing size on vergence using the vergence peak amplitude shown in the right panel of Figure 4. The mean peak values of individual subjects are displayed for each stimulus condition (filled circles) as well as the mean and standard error across subjects (black joined error bars). The peak values show the same trend as the single subject data presented in Figure 5. For changing size opposing changing disparity or no changing size cue at all, peak amplitudes are similar

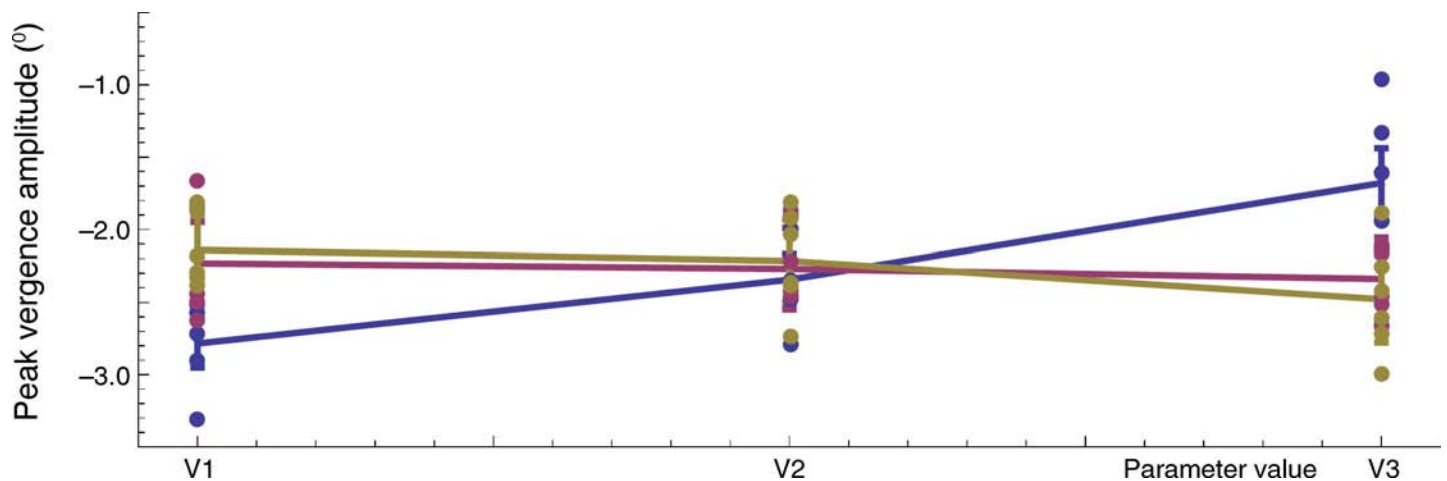


Figure 6. Peak vergence amplitude depending on various changing size parameters. The parameters defining changing size as a cue to motion in depth are individually varied to assess their contribution to vergence. Parameters varied were stimulus/retinal eccentricity, (stimulated retinal) area, and the number of dots. Values for these parameters are given in Table 1. Mean changes in gain across different values for the parameters (denoted by V1...V3) of all subjects are depicted by the joined error bars (blue: eccentricity, yellow: area, red: number of dots). The dots define individual subject data. There is a main effect of eccentricity on vergence and an, albeit smaller, effect of the number of dots. There were no interaction effects. For details, see Table 2 and main text.

and close to unity. However for changing size congruent with changing disparity peak values drop significantly and vergence following becomes much less accurate (two-way ANOVA $F_{4,327} = 5$, $p < 0.001$, main effect between scale factors 2 and -2 , -1 and between scale factors 1 and -2 , Tukey HSD). Comparing the slopes in the graphs in the left and right panels of Figure 4 shows that the effect of changing size on vergence is opposite to its effect on perceived end position in depth.

Although changing size showed a pronounced effect on vergence gain, there was no significant effect of changing size on onset latency (ANOVA). Mean value of onset latency of all observers was 270 ms (with a standard deviation of 47 ms). Our data showed an inverse relation between vergence gain and changing size. This effect is incongruent with that reported by Erkelens and Regan (1986). This could be caused by the implementation of the changing size cue. Therefore, we investigated the effects on vergence of the individual parameters defining changing size. In this experiment, we varied stimulus radius, stimulus area, and the number of dots across trials. For each of these parameters, we tested three different values, which were based on (but not identical to) the two extremes and the midway value occurring in the original stimulus presentation, see Table 1 for the used values.

We measured the effect of each of these parameters on vergence by calculating the peak vergence amplitude, as in the first experiment. Figure 6 shows the dependency of peak vergence amplitude on each of the parameters. Mean values per condition were obtained by averaging across the other parameter conditions, the exact values are given in Table 2. There is a main effect of stimulus radius on vergence ($F_{2,567} = 100$, $p = 0.0$, each condition was significantly different from the two others, Tukey HSD). The number of dots, i.e., luminance, had some effect on peak vergence amplitude as well ($F_{2,567} = 12$, $p < 0.001$, main effect due to the $N = 2000$ condition being significantly different from the two other conditions, Tukey HSD). There were no significant interaction effects.

Onset latency was affected by stimulus radius ($F_{2,567} = 4$, $p < 0.05$) and the number of dots ($F_{2,567} = 4$, $p < 0.05$), but the difference was only significant between the two extreme values of these parameters (Tukey HSD), see Table 2 for the values per condition. There were no significant interaction effects on onset latency.

We extended our analysis by using the effect of stimulus radius on vergence to make alternative predictions for the first experiment. To quantify the dependence of vergence gain on stimulus radius, we fitted mean vergence traces per condition as explained in the Data analysis section (Equation 4). Only

| Parameter | Peak vergence amplitude (°) | | | Onset latency (ms) | | |
|----------------|-----------------------------|------------------|------------------|--------------------|-------------|--------------|
| | V1 | V2 | V3 | V1 | V2 | V3 |
| Radius | -2.84 ± 0.03 | -2.47 ± 0.04 | -1.83 ± 0.08 | 218 ± 8 | 231 ± 8 | 258 ± 12 |
| Area | -2.25 ± 0.05 | -2.35 ± 0.07 | -2.59 ± 0.05 | 245 ± 10 | 234 ± 8 | 227 ± 9 |
| Number of dots | -2.34 ± 0.05 | -2.35 ± 0.05 | -2.50 ± 0.07 | 250 ± 11 | 240 ± 8 | 214 ± 8 |

Table 2. Mean peak vergence amplitude and onset latency and SE.

data with fit residuals ($\frac{1}{T} \int_{t=0}^{t=T} (v_{\text{fit}}(t) - v_{\text{data}}(t))^2 dt$, i.e., the mean squared error summed over all data points in time) that were less than one standard deviation from the mean of all fits were used in further analysis.

The vergence gains that were obtained by the fit procedure showed a linear decrease with an increase in radius, similar to the peak amplitudes depicted in Figure 6. We described this linear change in vergence gain depending on stimulus radius ($G(r)$, with the stimulus radius defined as r) using a linear function: $G(r) = G_0 + ar$ (where G_0 is the intercept with the vertical axis, i.e., vergence gain for a single dot and a is the slope of the curve). We calculated alternative predictions by replacing the constant gain (G) in Equation 4 with the function $G(r)$. These alternative vergence predictions, with vergence depending linearly on stimulus radius, are depicted in Figure 5d. These predictions describe the results found much more accurately than our original predictions (Figure 5c). Thus, in the first experiment it was not changing size but changing disparity and the location of the stimulus on the retina that determined vergence.

Discussion

In the present study, we investigated whether changing size affects vergence. Results of the study of Erkelens and Regan (1986) reported that changing size had an, albeit small, effect on vergence. On the other hand, Nefs and Harris (2008) showed that a monocularly presented looming target did induce vergence, while that same target failed to do so (significantly) when presented binocularly. Here we addressed the issue whether the vergence system would use changing size under binocular viewing conditions or whether the effect noted by Erkelens and Regan (1986) should be attributed to a change in the effective disparity stimulus. We used an annulus conveying both changing disparity and changing size cues to motion in depth, in which the relative strength of changing disparity to induce vergence is reduced (Howard et al., 2000). Although there was no (stationary or moving) fixation point, observer's performance in tracking the center of the annulus moving in depth was quite good. Less than 4% of all trials had to be removed due to saccades larger than 2° (the smallest inner radius of the annulus).

Results from the first two experiments showed that perceived end position varied with the changing size cue. The effect of changing size on vergence, however, was opposite to that predicted based on the results from Erkelens and Regan (1986). As the annulus expanded, vergence peak amplitude reduced and as the annulus contracted, vergence peak amplitude increased. Although we used an annulus to reduce the relative strength of changing (absolute) disparity on vergence, the effect of changing size was still small compared to the effect of changing (absolute) disparity on vergence.

Two other cues could have contributed to the motion-in-depth percept, namely changing absolute disparity and extra-retinal signals related to vergence movements. To what extent extra-retinal signals influenced motion-in-depth perception depends on the vergence movements made by the observer. Because the stimuli and task were identical in the perceptual and the (first) eye movement experiment, we can infer from the (first) eye movement experiment whether or not observers made vergence movements, and it is very likely that they did (see Figure 5). Vergence movements affect perception, because they counteract the disparity signal of the stimulus. In the present experiments, a substantial amount of disparity was still present due to the vergence onset latency and the (sometimes) insufficient vergence gain (vergence gain was modulated by changing size). For the sake of brevity, we assume here that the variation in vergence gain had less influence on the amount of disparity than the onset latency (which was similar across stimulus conditions). If we assume that Bayesian theories on cue combination hold for perception of motion in depth, a contribution of disparity to motion-in-depth perception can be described as follows. In the cue conflict condition, the absolute disparity signal counteracted the changing size signals, leading to less perceived motion in depth. In the extreme case, no motion would be perceived at all, for instance if both cues were weighted equally and defined exactly opposite motion directions. In the cue congruent condition, the combination of disparity and changing size signals would result in a smaller variance (in Bayesian theories of cue combination). Both these effects were not observed in the data. The fact that absolute disparity and extra-retinal signals did not contribute to perception in our experiment is similar to earlier reported results on perceived motion in depth (Brenner et al., 1996; Harris, 2006; Harris & Drga, 2005; Harris, McKee, & Watamaniuk, 1998; Regan & Beverley, 1979; Regan et al., 1986). Other studies have shown that if retinal signals are not adequately compensated by vergence, they induce a percept of motion in depth (Howard, 2008; Nefs & Harris, 2007, 2008; Welchman et al., 2009). Howard (2008) recently showed that the differences reported on the effects of extra-retinal signals and absolute disparity on perception can be accounted for by the various types of stimuli used. He showed that for stimuli that did convey changing size information, changing (absolute) disparity or changing vergence did not induce perception of motion in depth, whereas they did, if stimuli (such as small dots) could not convey looming information. Our stimuli did convey looming information and that may explain the absence of an influence of disparity and eye movement signals on perception. However, we should note that our measurement paradigm was mainly focussed on estimating the effect of changing size of an annulus on perception and not to fully recover the contribution of individual cues to motion-in-depth perception and we should be prudent about generalizing our results.

The eye movement data clearly showed that vergence always followed the disparity signal, albeit with a gain that was modulated by the changing size signal. These variations in vergence gain were contradictory to what one would predict if perceived depth contributed to vergence. In that case, vergence gain would have been greater in cue congruent conditions (that is when the stimulus appeared to approach) compared to cue conflict conditions (that is when the stimulus appeared to recede). Our results show the exact opposite effect. It thus seems unlikely that perceived depth contributed to vergence. The fact that vergence gain varied across stimulus conditions suggests that the changing size signal in itself modulated vergence gain. Our results seem to contradict those of Erkelens and Regan (1986), who reported a positive relation between size and vergence. However, as we showed in the third experiment, this apparent contradiction can be explained by the fact that a changing size stimulus changes the effective disparity stimulus.

In the third experiment, we measured the effects on vergence of individual parameters used to define changing size, namely changing stimulus radius, changing stimulus area, and changing luminance. Here, stimulus radius had a pronounced effect on vergence gain and onset latency. Stimulus area and the interaction between stimulus area and stimulus radius had no influence on vergence. Our results are in agreement with data presented by Howard et al. (2000) who showed that vergence gain significantly decreased with an increase of inner stimulus radius. He proposed that vergence gain depends on eccentricity in a similar way as stereopsis is related to eccentricity, namely that Panum's area increases with increasing retinal eccentricity. A similar mechanism for vergence would predict that vergence gain decreases with increasing retinal eccentricity. Although our results indeed show a decrease in vergence gain (from unity gain for small inner radii to about 0.8 for larger inner radii) similar to that reported by Howard et al. (2000), there are subtle differences that cannot be explained by Howard's theory. First, vergence gain for our stimulus with an inner radius of 8.7° was about 0.8, whereas for a stimulus with approximately the same size (inner radius of 10°) in the study of Howard et al. (2000) vergence gain was close to unity. Second, we used much larger disparities (maximum of 2.3° vs. 0.25° (Howard)) and measured smaller vergence gain. Third, the total stimulus area was very different (maximum of 94 deg^2 in this study and around 3000 deg^2 in the study of Howard et al., 2000). The first two differences together show that the reported changes in vergence gain cannot be explained by assuming that vergence gain depends on stimulus eccentricity in a similar way as stereopsis does. Rather, it suggests that other stimulus factors, such as stimulated retinal area, may also be of importance in driving vergence. Although neither we, nor Howard, found an influence of area on vergence, it is possible that in both studies the range of areas tested fell short of the range needed to observe a

significant change in vergence. If so, the vergence is not only modulated by stimulus eccentricity (but not similar to stereopsis) but also by total stimulus area. We believe that more work is needed to ascertain the exact relationship between stimulus properties and vergence.

Howard et al. (2000) reported a much larger vergence onset latency of 400 ms (inferred from their data for a stimulus with an inner radius of 10° moving at 0.25 Hz) than we did (± 250 ms for both experiments). Both these values are significantly higher than those found for stimulation with filled central disks (Erkelens & Collewijn, 1991; Howard et al., 2000; Rashbass & Westheimer, 1961). As the stimuli used by Howard et al. (2000) had a much larger area, the total area of the disparity stimulus had no influence on onset latency. Non-foveal presented changing disparities are able to induce vergence but apparently need more time to initiate vergence than foveal presented disparities.

In the third experiment, we also found an effect of the amount of dots in the stimulus on vergence. Changing the amount of dots effectively means changing the luminance of the stimulus. This had a positive effect on vergence peak amplitude, i.e., higher luminance resulted in higher vergence gain. It also had a small effect on onset latency, i.e., latency decreased as luminance increased. We did not find an interaction effect between stimulus area and number of dots, which means that dot density did not have an effect on vergence. The effects of changing size on vergence reported by Erkelens and Regan (1986) could be attributed to a change in luminance of the stimulus. They did consider this explanation and tested it using a flickering stimulus with a changing luminance, which failed to induce vergence. They thus concluded that luminance per se does not influence vergence. However, based on our results, this conclusion could be refined: if changing disparity is present, changing luminance positively influences vergence. Such a conclusion is supported by the recent report of Nefs and Harris (2008) that showed that changing size is not sufficient to induce a significant amount of vergence under binocular viewing conditions. Under monocular viewing conditions, however, loom is a sufficient cue to induce vergence. This effect of loom on vergence could be attributed to a change in perceived depth or a change in luminance. Our results suggest that the effect of loom on vergence should be attributed to a change in luminance rather than perceived depth of the stimulus.

The vast body of research on perception of motion in depth has shown that for perception of motion in depth the brain uses many diverse resources. Both monocular (changing size, looming) and binocular (changing relative and absolute disparities) visual cues and extra-retinal signals (changing vergence) can be employed for perception (Brenner et al., 1996; Howard, 2008; Nefs & Harris, 2007, 2008; Regan & Beverley, 1979; Regan et al., 1986; Welchman et al., 2009). It seems, however, that for eye movements only one source of information is relevant, namely absolute disparity.

Conclusion

In a set of three experiments, using perceptual and eye movement measurements, we show that changing disparity determines vergence under binocular viewing conditions. Other cues inducing motion in depth only affect vergence because they change the disparity signal's strength and/or location.

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Footnotes

¹Pilot data showed that reversing the motion defined by changing disparity did not influence the effects presented here.

²None of the observers reported perceiving motion in depth in this experiment.

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