The relationship between object spatial profile and accommodation microfluctuations in emmetropes and myopes

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The accommodation microfluctuations are thought to be used by the accommodation controller to obtain information about the direction and magnitude of the required response by monitoring changes in the contrast gradient of this image. The contrast gradient can be altered by presenting different spatial frequency (SF) targets to the eye. Twelve myopes (MYOs) and 12 emmetropes (EMMs) viewed sine and square wave targets of SF 0.5, 1, 2, 4, 8, 16 cpd in a Badal optical system. Accommodation responses were recorded continuously using the Shin-Nippon SRW-5000 autorefractor. There is no change in magnitude of the accommodation microfluctuations as the SF of square waves is altered. While viewing sine wave targets, the microfluctuations are smallest for mid (2, 4 cpd) SFs and increase for low (0.5 cpd) and high (16 cpd) SFs. MYOs show a significantly larger increase in the microfluctuations for the 16 cpd target compared to the EMMs. MYOs have significantly larger microfluctuations than the EMMs throughout. The microfluctuations seem to be monitoring the contrast gradient of the cortical image, which is likely to be used by the accommodation control system during error detection. The results indicate that MYO subjects may have a shallower contrast gradient and the potential reasons and implications of this are discussed.

Keywords: accommodation, ocular, adult, human, microfluctuations, myopia, spatial frequency, sine wave, square wave, contrast gradient

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Introduction

The accommodation error detector monitors and responds to the level of cortical image blur within a closed-loop negative feedback system. Previous work suggests that information regarding image blur may be provided by modulation of the cortical image by the accommodation microfluctuations, which are small variations in dioptric power (within an envelope of about 0.50D) of the crystalline lens (Campbell, Robson, & Westheimer, 1959; Charman & Heron, 1988; Collins, 1937; Collins, Davis, & Wood, 1995; Denieul, 1982; Kotulak & Schor, 1986a; Seidel, Gray, & Heron, 2003; Winn, Pugh, Gilmartin, & Owens, 1990a). Computational modeling of the accommodation error detector proposed that the accommodation controller compares changes in lens power with the cortical image contrast over time (Kotulak & Schor, 1986a). This is thought to provide essential odd-error information about the required direction of the accommodation response as well as even-error information about the magnitude of the required response. Specifically, the accommodation controller may monitor the contrast gradient of the cortical image. The contrast gradient is defined as the difference in luminance between two points in an image, which is the contrast amplitude, divided by the space between these two points. It is likely that the accommodation controller monitors the maximum gradient contained within this cortical image to optimize performance.

These theories are supported by findings showing that the magnitude of the accommodation microfluctuations vary systematically with target characteristics such as target luminance (Day, Seidel, Gray, & Strang, 2009a;



Figure 1. Examples of sine and square wave targets of three SF (approx. 0.5 cpd, 1 cpd and 2 cpd) are shown.

Gray, Winn, & Gilmartin, 1993b), the spatial frequency (SF) content of the stimulus (Niwa & Tokoro, 1998) as well as with variations in ocular depth of focus induced by alterations in pupil size (Campbell et al., 1959; Day et al., 2009a; Gray, Winn, & Gilmartin, 1993a; Stark & Atchison, 1997).

Under conditions where depth of focus is altered using artificial pupils, microfluctuations are seen to increase systematically when depth of focus is increased (Atchison, Charman, & Woods, 1997; Campbell, 1957; Charman & Whitefoot, 1977; Day et al., 2009a; Ogle & Schwartz, 1959; Stark & Atchison, 1997). The increase in depth of focus for pupils <2 mm in diameter is caused by restricting image formation to paraxial rays only, and it is thought that any changes in the contrast gradient of the image modulated by the microfluctuations cannot be detected by the accommodation controller (Day et al., 2009a). As a result, the magnitude of the microfluctuations increases in an attempt to produce a detectable change in the contrast gradient of the image (Day et al., 2009a).

Calculations of the contrast gradient of the cortical image formed when varying the luminance of a target containing a broad spectrum of SFs have been made previously (Day et al., 2009a). These calculations show that the contrast gradient remains steep as luminance is reduced to luminance levels of $\leq 0.002 \text{ cd/m}^2$, whereupon it becomes progressively shallower (Day et al., 2009a). The shallower contrast gradient available at luminances ≤ 0.002 cd/m² is caused by a reduction in the SF content available to the accommodation error detector (Day et al., 2009a). Accommodation microfluctuations are found to increase in magnitude at these lower luminance levels, and it is thought that the microfluctuations increase because larger changes in focus are required to produce alterations in the contrast gradient detectable by the accommodation controller (Day et al., 2009a; Gray et al., 1993b).

The studies described above, which manipulate the contrast gradient by altering target luminance, each have only 2 conditions where there is a significant alteration in the contrast gradient of the cortical image. An alternative method by which the contrast gradient can be manipulated more directly and over a greater range is to use sine wave targets of varying SF. Only a limited number of studies have measured accommodation microfluctuations for targets of varying SF. Bour (1981) measured the magnitude of the microfluctuations while subjects viewed sine waves of low (1 cpd), mid (4 cpd) and high (16 cpd) SFs, and found that the microfluctuations were smallest when subjects viewed the mid (4 cpd) SF target and increased for both the low and high SF targets (Bour, 1981). Niwa and Tokoro (1998) used a larger range of SFs (0.85–15 cpd), and reported a similar finding with the smallest microfluctuations occurring for the mid SF targets. Although the authors likened their results to those using sine waves, they used square wave targets, which have an edge profile and contrast gradient which is not proportional to SF, unlike sine wave targets.

Sine and square wave targets of varying SFs are shown in Figure 1. Square wave targets are produced by adding odd integer harmonic sine waves to a sine wave with a SF equal to the fundamental frequency of the square wave being produced. The contrast gradient of all square wave targets is infinitely large, irrespective of the SF. In comparison, the contrast gradient of sine wave targets gets steeper as the SF increases, as shown in Figure 2.

The cortical image refers to the image created once the retinal image has been transmitted by the neurons in the visual pathway to the visual cortex. The cortical image is therefore influenced by optical aberrations degrading the retinal image, and the internal neural noise of the visual pathway. The combined modulation transfer function (MTF) describes the ability of the combined optical and neural system to transmit accurately the contrast ampli-



Figure 2. Maximum contrast gradient of sine wave targets (80% contrast) of varying SF.



Figure 3. Modulation transfer functions when no blur is present as measured by interferometry (Campbell & Gubisch, 1966), and calculated from an ideal eye with 0.5D and 1D blur (Charman, 1983).

tude of various SFs within an object, and allows the calculation of the edge profile within the cortical image. Three MTFs are shown in Figure 3. The MTF obtained by Campbell and Gubish (1966) was measured using psychophysical techniques and therefore describes the degradation of SFs by the effects of both optical and neural transmission. The MTFs labeled "Charman (1983; 0.5D blur)" and "Charman (1983; 1D blur)" show the effect of induced optical blur, which reduces the transmission of high SF components to both the retinal image and subsequently the cortical image (Charman, 1983). These calculations are account only for the optical effect of blur and do not include any neuronal effects which may exist. However, when blur is induced, optical factors are likely to become the limiting factor in image creation. Figures 4 and 5 show the estimated maximum contrast gradient contained within the cortical image for square and sine waves respectively as a function of SF, taking into account the effect of the combined MTF on the target. All of these MTFs were measured under photopic conditions (Campbell & Gubish, 1966; Charman, 1983)

and therefore any luminance effects producing a reduction in the contrast gradient, which occur at luminances $\leq 0.002 \text{ cd/m}^2$, can be ignored (Day et al., 2009a).

Figure 5 shows that the cortical image of the low SF sine waves contains a relatively shallow contrast gradient, which is due to the shallow gradient contained within the target itself (Figure 2). The contrast amplitude of low SF targets is transmitted well by the visual system (Figure 3) and therefore the contrast gradient of the cortical image is similar to that of the target. With increasing SF the contrast gradient of the target becomes steeper (Figure 2) and, since the modulation transfer is high for mid SF targets, the corresponding cortical image has a steep contrast gradient (Figure 5). When considering high SFs, the contrast gradient within the target is attenuated by the visual system (Figure 3) and this produces a relatively shallow contrast gradient within the cortical image for these SFs (Figure 5).

Figure 4 shows the contrast gradient of the cortical image formed when viewing square wave targets, which is steep and constant for low and mid SF targets, and



Figure 4. Contrast gradients of the cortical image formed by square wave targets of varying SF. The contrast gradient of the cortical image was calculated from square wave targets (80% contrast) with an infinitely large contrast gradient and using the MFTs shown in Figure 3, as measured by interferometry (Campbell & Gubisch, 1966), and calculated from an ideal eye with 0.5D and 1D blur (Charman, 1983).



Figure 5. Contrast gradients of the cortical image of sine wave targets of varying SF calculated using the target contrast gradients in Figure 2 and the MFTs in Figure 3, as measured by interferometry (Campbell & Gubisch, 1966), and calculated from an ideal eye with 0.5D and 1D blur (Charman, 1983).

becomes shallower for high SFs. The maximum contrast gradient contained within the cortical image of low and mid SF square wave targets is steep because these targets contain mid SF sine waves, which produce a cortical image with a steep contrast gradient. High SF square wave targets contain only high SF information and therefore the contrast gradient of the cortical image is shallow, as for the high SF sine wave targets.

The magnitude of the microfluctuations measured while viewing sine wave targets of 1, 4 and 16 cpd (Bour, 1981) compares well with the calculated maximum contrast gradients found within the cortical image of these targets as shown in Figure 5. The smallest microfluctuations were found for the mid SF target, which corresponds to a steep contrast gradient. If the accommodation controller is monitoring a change in the contrast gradient over time and the contrast gradient is steep then only a small change in the dioptric power of the crystalline lens would be needed to gain the relevant information. The contrast gradient is shallower when the SF is low or high and larger microfluctuations are measured because larger changes in the lens are needed before the same change in the contrast gradient is produced.

Niwa and Tokoro (1998) found similar results using square wave targets, which the authors felt were comparable to using sine waves. However, the contrast gradient in the cortical image produced by square wave targets (Figure 4) will be different to that of sine waves, as explained above. Increases in the magnitude of the microfluctuations for low SF square wave targets reported in this study cannot be explained by a shallow contrast gradient since the low SF square waves produce a cortical image with a steep contrast gradient.

In a second experiment, Niwa and Tokoro (1998) added Gaussian blur to square wave targets, altering the SF content of the target and producing a shallower contrast gradient in the target (Niwa & Tokoro, 1998). Increases in the magnitude of microfluctuations were found with increasing blur, supporting the hypothesis that the accommodation controller can use feedback information through the effect of the microfluctuations upon the contrast gradient of the cortical image, and any decrease in the contrast gradient will produce corresponding increases in the magnitude of accommodation microfluctuations. As this study altered the contrast gradient by adding Gaussian blur to square wave targets, it is difficult to quantify the contrast gradient of the cortical image used by the accommodation controller.

A previous report suggested that myopic subjects may be less sensitive to high SF (≥ 8 cpd) targets compared to non-myopic observers (Radhakrishnan, Pardhan, Calver, & O'Leary, 2004). If high SFs are below the detection threshold of the accommodation controller in myopes (MYOs), the contrast gradient available in the cortical image would be shallower than that found in non-myopic observers. This finding could explain the higher magnitude microfluctuations that have been reported in myopic observers (Day et al., 2009a; Day, Strang, Seidel, Gray, & Mallen, 2006; Seidel et al., 2003). In addition, a shallower perceptual contrast gradient would lead to a larger ocular depth of focus (Day et al., 2009a), which has also been reported in MYOs (Collins, Buehren, & Iskander, 2006; Rosenfield & Abraham-Cohen, 1999; Vasudevan, Ciuffreda, & Wang, 2006).

In summary, no study has comprehensively investigated the type of feedback used by the accommodation controller in myopic and emmetropic subjects. Two studies have investigated the effect of SF on the microfluctuations (Bour, 1981; Niwa & Tokoro, 1998), but neither of these have calculated the cortical image produced by their targets and related this to the information used by the accommodation controller in order to gain information about feedback. This is either because the targets used in the studies make this difficult (Niwa & Tokoro, 1998), or a limited number of targets and subjects have been used (Bour, 1981). Additionally, the results from previous studies are conflicting. Differences in the magnitude of the accommodation microfluctuations have been found between MYOs and EMMs have been found (Day et al., 2009a; Day et al., 2006; Seidel et al., 2003), but none of the studies have made a detailed investigation of the effect of altering the contrast gradient in these subject groups. There is a suggestion from a recent paper that MYOs may be less sensitive to high SFs than EMMs (Radhakrishnan et al., 2004), and this needs to be investigated further. Therefore this paper aims to extend on existing knowledge of the information used by the accommodation system in MYOs and EMMs and this may provide further insight into the underlying mechanism of myopia development.

This study will comprehensively investigate the effect of varying target SF on the magnitude of the accommodation microfluctuations while viewing both sine and square wave targets in myopic and emmetropic subject groups.

Methods

Subjects

Twenty four young (mean $\pm SD$ age: 21 ± 2.12 years) adult volunteers participated in the study. All subjects had ≤ 0.50 D of astigmatism, no ocular or systemic disease and 0.0 logMAR visual acuity or better. All subjects gave informed consent and the study was approved by the Glasgow Caledonian University, School of Life Sciences ethics committee and was conducted in accordance with the Declaration of Helsinki.

The subjects completed a questionnaire regarding their refractive history before taking part in the experiment. The subjects were then sub-divided into two groups, dependent upon their refractive error. Emmetropia (EMM) was defined as a mean spherical equivalent refractive error (MSE; sphere + 0.5*cyl) between -0.25 and +0.75 D and myopia as a MSE Rx ≤ -0.75 D. Table 1 gives the mean age and refractive error of each subject group. There was no significant difference in age between the EMMs and MYOs (t-test, $t_{22} = -1.693$, p = 0.120) and there was a significant difference in MSE between the two groups (t-test $t_{22} = 5.812$, p < 0.001).

Refractive Group	EMMs	MYOs
Number of subjects	12	12
Age (years)	20.6 ± 1.9	21.4 ± 2.4
Age of myopia onset (years)	N/A	11.6 ± 3.7
MSE (D)	-0.08 ± 0.59	-3.27 ± 1.72

Table 1. Details of the subject groups. Age and refractive error rows show mean \pm *SD*. Refractive errors are calculated as the MSE (sphere + 0.5*cyl).

Accommodation measurement and analysis

Static and dynamic accommodation responses of the right eye were recorded using a specially modified, commercial, open field, infrared autorefractor (Shin-Nippon SRW-5000, Shin-Nippon, Japan). This instrument has been found to be repeatable and accurate in both children (Chat & Edwards, 2001) and adults (Mallen, Wolffsohn, Gilmartin, & Tsujimura, 2001) and the operation of the Shin-Nippon in both static and continuous modes has been previously described (Mallen et al., 2001; Wolffsohn, Gilmartin, Mallen, & Tsujimura, 2001).

Throughout the experiment, all myopic subjects were fully corrected with mid-water content (58%) thin soft contact lenses (Acuvue, Johnson & Johnson, UK) which they adapted to for at least 30 mins before any measurements were taken. Contact lenses have been shown not to affect the measurement of the accommodation microfluctuations with the Shin-Nippon SRW-5000 (Day, Strang, Seidel, & Gray, 2008). Subjects viewed the target monocularly using the right eye through a +5D Badal lens at a stimulus vergence adjusted to produce a static accommodation response equal to their individual dark focus level, which was measured at the start of the experiment as an average of 10 static measures after 3 minutes in the dark.

Targets were sine and square wave gratings (angular subtense: 15.8° ; 80% contrast; maximum luminance: 600 cd/m^2) with SFs of 0.5, 1, 2, 4, 8 and 16 cpd (Figure 1). Targets were presented to the subjects in a random order with a break of at least 3 minutes between conditions so that retinal adaptation effects were minimized. Ten static measurements were taken for each condition and an average of these was used to plot the accommodation response function.

The autorefractor was then used in dynamic mode (Wolffsohn et al., 2001) to record 2 minutes of continuous accommodation response for each target SF at a sampling rate of 52 Hz. During recording the subjects were instructed to fixate the center of the target and to keep it as clear as possible. In dynamic mode, the instrument was calibrated for each individual subject while they were viewing a 0.0 logMAR letter at a distance of 6 m. Ten repeatable measures of the dimensions of the measurement ring in pixels were made and the average of these was used as the calibration value (Wolffsohn et al., 2001).

One hundred seconds of data containing not more than 2 blinks every 20 seconds were selected for data analysis. Blinks were removed from the data automatically using Microsoft Excel macro capabilities as described previously (Day et al., 2006). The average root mean square (rms) value of these recordings was calculated and used as a measure of the magnitude of the accommodation microfluctuations.

The data were filtered with a 10 Hz low pass filter since useful frequencies in the accommodation response occur at a frequency less than this (Pugh, Eadie, Winn, & Heron, 1987). A Fast Fourier Transform was then applied to each 10 s segment of data, producing 10 individual power spectra which were then averaged to give a mean power spectrum with a frequency resolution of 0.1 Hz (Pugh et al., 1987). This method has been used to analyze the frequency components previously (Day et al., 2006). In accordance with previous classifications (Charman & Heron, 1988; Day et al., 2006; Denieul, 1982; Gray, Gilmartin, & Winn, 2000; Gray et al., 1993a, 1993b; Heron & Schor, 1995; Kotulak & Schor, 1986a; 1986b; van der Heijde, Beers, & Dubbelman, 1996; Winn et al., 1990a, 1990b), the power in each of the following areas of the power spectrum was calculated for each subject, giving the overall power for each component: low frequency component (LFC, 0.0–0.6 Hz); mid frequency component (MFC, 0.6–0.9 Hz); high frequency component (HFC, 1.0–1.4 Hz).

Results

Accommodation responses

Mean static accommodation responses for EMMs and MYOs viewing both square and sine wave targets are shown in Figures 6 and 7. There was no significant variation in the static accommodation response with changes in SF for either sine or square waves in either of the subject groups (Sin, EMMs: ANOVA, $F_{5, 66} = 0.421$, p = 0.832; Sin, MYOs: ANOVA, $F_{5, 66} = 0.300$, p = 0.911; Square, EMMs: ANOVA, $F_{5, 66} = 0.278$, p = 0.923; Square, MYOs: ANOVA, $F_{5, 66} = 0.293$, p = 0.915). Additionally there was no significant difference in static accommodation response between sine and square wave targets of the same SF (ANOVA, $F_{1, 264} = 0.170$, p = 0.681), nor between refractive groups (ANOVA, $F_{1, 264} = 1.102$, p = 0.295).



Figure 6. Accommodation responses for EMMs and MYOs while viewing square wave gratings with SF 0.5, 1, 2, 4, 8 and 16 cpd. Error bars are standard errors of the mean.



Figure 7. Accommodation responses for EMMs and MYOs while viewing sine wave gratings with SF 0.5, 1, 2, 4, 8 and 16 cpd. Error bars are standard errors of the mean.

Accommodation microfluctuations

RMS values

Square waves

Figure 8 shows the mean rms value of the accommodation microfluctuations for the EMMs and MYOs while viewing the square wave targets. No significant variation in the rms is found as SF changes in either of the refractive groups (EMMs: ANOVA, $F_{5, 72} = 1.301$, p =0.277; MYOs: ANOVA, $F_{5, 72} = 0.413$, p = 0.838). The rms values are significantly larger in the MYOs than the EMMs (ANOVA, $F_{51, 144} = 42.160$, p < 0.001).

Sine waves

For all subjects viewing the sine wave targets, there is a significant variation in the size of the accommodation



Figure 8. Magnitude of the accommodation microfluctuations in MYOs and EMMs while viewing square wave targets of different target SFs (0.5, 1, 2, 4, 8, 16 cpd). Error bars are standard errors of the mean.



Figure 9. Magnitude of the accommodation microfluctuations in MYOs and EMMs while viewing sine waves of different SFs (0.5, 1, 2, 4, 8, 16, 32 cpd). Error bars are standard errors of the mean.

microfluctuations as the SF of the sine waves changes (ANOVA, $F_{5, 144} = 7.528$, p < 0.001). The microfluctuations are significantly larger while viewing both the 0.5 and 16 cpd targets than when viewing the 2 and 4 cpd targets (Scheffe post hoc, p < 0.015 for all comparisons).

Figure 9 shows the size of the accommodation microfluctuations in both refractive groups for all sine wave targets. The MYOs have significantly larger microfluctuations than the EMMs (ANOVA, $F_{1, 144} = 99.683$, p < 0.001). Both refractive groups have a significant variation in the size of the microfluctuations as SF changes (EMMs: ANOVA, $F_{5, 72} = 5.919$, p < 0.001; MYOs: ANOVA, $F_{5, 72}$ = 5.663, p < 0.001). EMMs have significantly larger microfluctuations when the target SF is 0.5 cpd compared to the 2, 4 and 8 cpd targets (Scheffe post hoc, p < 0.02 for all three comparisons). MYOs have significantly larger microfluctuations when viewing the 0.5 cpd target than viewing the 4 cpd target, while the 16 cpd target results in significantly larger microfluctuations than the 2 and 4 cpd targets (Scheffe post hoc, p < 0.04 for all 3 comparisons). For each target SF, the increase in the microfluctuations compared to that while viewing the 4 cpd target was calculated, since this SF produced the smallest microfluctuations. MYOs have a significantly larger increase in the magnitude of the microfluctuations than the EMMs when viewing the 16 cpd target (t-test, $t_{22} = -2.259$, p < -2.2590.05), while there is no significant difference between the refractive groups for the other SFs.

Frequency components

Square waves

Figure 10 shows the power of the LFC (0.0–0.6 Hz), MFC (0.6–0.9 Hz) and HFC (1.0–1.4 Hz) for the EMMs and MYOs while viewing the square wave targets. Statistics show that, as with the accommodation microfluctuations, there was no significant change in the power of any of these components in either refractive group as the SF of the square wave targets altered (LFC, EMMs: ANOVA, $F_{5, 72} = 0.730$, p = 0.604; LFC, MYOs: ANOVA, $F_{5, 72} =$



Figure 10. Power of the LFC (0.0–0.6Hz), MFC (0.6–0.9 Hz) and HFC (1.0–1.4 Hz) for the EMMs and MYOs while viewing square wave targets of different target SFs (0.5, 1, 2, 4, 8, 16 cpd).

p = 0.327).

Sine waves

0.601, p = 0.699; MFC, EMMs: ANOVA, $F_{5, 72} = 0.500$,

p = 0.775; MFC, MYOs: ANOVA, $F_{5, 72} = 0.824$, p = 0.538; HFC, EMMs: ANOVA, $F_{5, 72} = 0.331$, p = 0.892; HFC, MYOs: ANOVA, $F_{5, 72} = 1.050$, p = 0.398). There

was a significant difference in power between the fre-

quency components (ANOVA, $F_{2, 432} = 102.539$, p < 0.001), with the LFC having significantly greater power

than the MFC and HFC (Scheffe post hoc, p < 0.001 for

both comparisons). There was no significant difference

in power between the MFC and HFC (Scheffe post hoc,

Figure 11 shows the power of the LFC (0.0–0.6 Hz),

MFC (0.6-0.9 Hz) and HFC (1.0-1.4 Hz) for the EMMs

and MYOs while viewing the sine wave targets. There

was a significant alteration in the power of the LFC in

both the EMMs (ANOVA, $F_{5, 72} = 3.595$, p < 0.01) and

the MYOs (ANOVA, $F_{5, 72} = 3.478$, p < 0.01) with

varying SF, but no significant change in the MFC (EMMs:

ANOVA, $F_{5, 72} = 2.055$, p = 0.085; MYOs: ANOVA,

 $F_{5, 72} = 0.616, p = 0.688$) or HFC (EMMs: ANOVA,

 $F_{5, 72} = 1.447, p = 0.222;$ MYOs: ANOVA, $F_{5, 72} =$

1.027, p = 0.411). There was a significant difference

in power between the frequency components (ANOVA,

 $F_{2, 432} = 102.141, p < 0.001$, with the LFC having sig-

nificantly greater power than the MFC and HFC (Scheffe

post hoc, p < 0.001 for both comparisons). There was no

significant difference in power between the MFC and HFC

(Scheffe post hoc, p = 0.134).

Discussion

Changes in microfluctuations with variations in SF

This study measures the magnitude of the accommodation microfluctuations while subjects view sine and square wave targets of varying SFs, to identify the stimulus information used by the accommodation control system. We use a range of sine wave SFs to alter the contrast gradient of the cortical image that is thought to be used by the accommodation error detector. The edge profile of the cortical images produced when viewing these targets (Figures 4 and 5) can be estimated by calculating the effect of the optical and neural MTFs, in Figure 3, upon the target. Figure 3 shows 3 functions: the function plotted after Campbell and Gubish (1966) is a combined MTF, which describes the cortical sensitivity to SF after the effects of both optical and neural processing; the functions labeled "Charman (1983; 0.5D blur)" and "Charman (1983; 1D blur)" show the effect of blur in the optical system, which reduces the transmission of high SFs. It is likely that there was only a small amount of blur present during this experiment, therefore the values of cortical SF sensitivity most applicable to this experiment are likely to lie between the functions of Campbell and Gubish (1966) and Charman (1983; 0.5D blur).

The magnitude of the microfluctuations measured while subjects view the square and sine wave targets with



Figure 11. Power of the LFC (0.0–0.6Hz), MFC (0.6–0.9 Hz) and HFC (1.0–1.4 Hz) for the EMMs and MYOs while viewing sine wave targets of different target SFs (0.5, 1, 2, 4, 8, 16 cpd).

varying SF (Figures 8 and 9) compares well with the predicted variation of the contrast gradient of the cortical image (Figures 4 and 5) for the range of SFs used in this experiment. For all SF square wave targets, the microfluctuations are small and constant (Figure 8). As the contrast gradient remains steep for all square wave SFs used in the experiment (Figure 4), small changes in focus will produce large changes in contrast due to the steep contrast gradient, which will be sufficient to provide the necessary feedback information for the accommodation controller. The results of this study do not agree with those reported by Niwa and Tokoro (1998), who described an increase in the magnitude of the microfluctuations for low SF square wave targets. However, the authors likened their results to those using sine waves, and our discussions show that the edge profile of both sets of targets are very different.

Niwa and Tokoro (1998) added Gaussian blur to the square wave targets used, making the edge profile progressively more similar to a that of a single sine wave target. An increase in the magnitude of the microfluctuations was found with increasing blur, which does support the theory that the accommodation microfluctuations increase as the contrast gradient in the cortical image becomes shallower. These results are comparable to those of Bour (1981), who reported larger microfluctuations when viewing sine wave targets of low and high SF, where the contrast gradient is shallower. Bour (1981) used sine wave targets, which allows accurate calculation of the contrast gradient in the cortical image, however, measurements were obtained from only 2 subjects.

Our results extend those of previous studies by reporting the magnitude of the microfluctuations in 24 subjects, who viewed both sine and square wave targets with a wide range of SFs. While viewing the square wave targets of all SFs, the microfluctuations remained small (Figure 7). The contrast gradient of the cortical image formed by these targets is steep (Figure 4) and therefore the small microfluctuations seem to provide enough information to the accommodation controller. For the sine wave targets our results agree with previous studies that the microfluctuations are smallest for mid SF sine wave targets (2 and 4 cpd) and increase in magnitude when viewing low (0.5 cpd) and high (16 cpd) SF sine waves (Figure 9). As the contrast gradient of mid SFs is steep, small microfluctuations should be sufficient to provide the required feedback for the accommodation controller. However, the contrast gradient is shallower for low and high SF targets (Figure 5), leading to increases in the magnitude of the microfluctuations because larger changes in focus are required to produce equivalent changes in contrast due to the shallower contrast gradient.

The results suggest that in the conditions of this experiment it is the alteration in the contrast gradient of the cortical image which seems to drive the magnitude of the accommodation microfluctuations and be used during feedback. As discussed, the contrast gradient of the cortical image results from changes in the target by both optical and neural processes. The change in ocular aberrations over time has been suggested as a potential input to the accommodation controller during feedback, since neutralization of these may alter the accuracy of the some aspects accommodation response (Fernandez & Artal, 2005). However, these temporal changes in the aberrations are thought not to be correlated with the accommodation microfluctuations (Hofer, Artal, Singer, Aragon, & Williams, 2001), and their origin (Fernandez & Artal, 2005) and role in the feedback process (Hofer et al., 2001) is not yet understood.

The systematic alteration of the magnitude of the microfluctuations with SF, which seemingly reflects a change in the contrast gradient of the cortical image, supports the hypothesis that the microfluctuations are under neurological control. While we cannot rule out that the microfluctuations, at least in part, may be a result of anatomical plant noise (Day et al., 2006; Kotulak & Schor, 1986b), the findings that the magnitude of the microfluctuations alter with changing pupil size (Atchison et al., 1997; Campbell, 1957; Charman & Whitefoot, 1977; Day et al., 2009a; Ogle & Schwartz, 1959; Stark & Atchison, 1997), luminance (Day et al., 2009a; Gray et al., 1993b) and SF (Bour, 1981; Niwa & Tokoro, 1998), provides a strong indication that the magnitude of these microfluctuations can be altered by neurological signals.

This study shows that the alterations in the magnitude of the microfluctuations while subjects viewed the sine wave targets are reflected by an alteration in the LFC but not the MFC or HFC. The results substantiate findings that the HFC does not appear to respond to changes in stimulus conditions (Day et al., 2006; Gray et al., 1993a, 1993b) and it is thought to be a physiological rhythmic variation as the components of the eye change shape in accordance with the heartbeat (Charman & Heron, 1988; Winn et al., 1990a; Zhu, Collins, & Iskander, 2004). In contrast, the LFC has repeatedly been shown to alter as the microfluctuations change (Day et al., 2006; Gray et al., 1993a, 1993b; Miege & Denieul, 1988; Stark & Atchison, 1997) and is therefore thought to reflect the neurological part of the signal.

Differences between refractive groups

The results of the present study show differences in accommodation microfluctuations between the MYO and EMM groups. Firstly, there is a difference in the variation of microfluctuation size while viewing the sine wave gratings. EMM subjects have significantly larger microfluctuations at 0.5 cpd compared with 2, 4 and 8 cpd, whereas the MYO group have significantly larger microfluctuations at 16 cpd compared to 4 cpd. For each target SF, the increase in the microfluctuations compared to that while viewing the 4 cpd target was calculated and it was found that MYOs have a significantly larger increase in

the magnitude of the microfluctuations than the EMMs when viewing the 16 cpd target. There are a number of possible reasons why the MYOs have a larger increase in the size of microfluctuations while viewing high SF sine wave targets.

There is a possibility that the MYO subjects have a larger accommodation error during the experiment. If defocus is greater, the contrast gradient of the cortical image produced when viewing the high SF targets would be shallower (see Charman, 1983 functions in Figure 5) causing an increase in the magnitude of the microfluctuations. Since the stimulus vergence was adjusted to produce a static accommodation response equal to each subject's dark focus level, the amount of error during the experiment is not known. However, some previous studies report larger microfluctuations (Day et al., 2009a; Day et al., 2006; Seidel et al., 2003) and increased blur (Abbott, Schmid, & Strang, 1998; Gwiazda, Bauer, Thorn, & Held, 1995; Gwiazda, Thorn, Bauer, & Held, 1993; McBrien & Millodot, 1986) in myopic subjects. MYOs have also been reported to have a larger depth of focus compared to the EMMs (Collins et al., 2006; Rosenfield & Abraham-Cohen, 1999; Vasudevan et al., 2006), which could result in less accurate accommodation responses.

MYOs are known to have larger eyes (Atchison et al., 2004; Strang, Schmid, & Carney, 1998). The expansion of the globe and the resultant stretching is thought to result in reduced visual performance limited by neural factors (Atchison, Schmid, & Pritchard, 2006). This will cause a reduction in the neural MTF which is likely to selectively affect high SFs and therefore produce a shallower contrast gradient in the cortical image of the MYO subjects.

A recent study has found that MYOs have reduced contrast sensitivity than non-MYOs for SFs \geq 8 cpd (Radhakrishnan et al., 2004). While this study does not differentiate whether this reduction in contrast sensitivity is due to optical or neural differences in MYO subjects, the effect of such a reduction in contrast sensitivity would be to produce a shallower contrast gradient within the cortical image. It is possible that the reduced contrast sensitivity for high SF targets results from neural deficits previously identified due to retinal stretching (Atchison et al., 2006). Furthermore such a reduction in contrast sensitivity could explain previous findings of a larger DoF in MYO subjects (Collins et al., 2006; Rosenfield & Abraham-Cohen, 1999; Vasudevan et al., 2006).

All of the theories outlined above are proposed mechanisms as to how the contrast gradient of the cortical image may become shallower in MYO subjects, producing the larger increase in the microfluctuations while viewing high SF sine wave targets. They could also explain the second difference in the accommodation microfluctuations between the refractive groups found in the present study: the MYOs have consistently larger microfluctuations than the EMMs. A shallower contrast gradient would produce larger microfluctuations for all conditions throughout the experiment. Equally, this could account for the larger microfluctuations in MYOs reported previously (Day et al., 2009a; Day et al., 2006; Seidel et al., 2003, 2005) and could be the cause of the larger DoF found in these subjects (Collins et al., 2006; Rosenfield & Abraham-Cohen, 1999; Vasudevan et al., 2006).

A second possible cause of the larger microfluctuations in MYOs found throughout this and other experiments (Day et al., 2009a; Day et al., 2006; Seidel et al., 2003, 2005) could be the known anatomical differences between the refractive groups. Myopic eyes are larger (Atchison et al., 2004; Strang et al., 1998), which could allow increased room for the lens to move. However, a recent study has shown no correlation between eye size and the magnitude of the accommodation microfluctuations (Day, Seidel, Gray, & Strang, 2009b). The ciliary body is thicker in MYOs (Bailey, Sinnott, & Mutti, 2008; Oliveira, Tello, Liebmann, & Ritch, 2005) and the reduced zonular tension produced by this could result in larger microfluctuations. However the regions of the ciliary body that are found to be thicker in MYOs are those that contain the ciliary muscle which has been proposed to be due to muscular hypertrophy (Bailey et al., 2008). If anything, this would presumably produce a reduction in function and therefore smaller microfluctuations. From these findings it seems unlikely that the larger microfluctuations in MYOs are a result of anatomical differences between the refractive groups, and the results and calculations within this study suggest that instead it may be due to a shallower contrast gradient contained within the cortical image.

Conclusions

There is no change in the magnitude of the accommodation microfluctuations as the SF of a square wave grating is altered between 0.5 and 16 cpd, but while viewing sine wave targets the microfluctuations are smallest for mid (4 cpd) SF targets, and increase for both low (0.5 cpd) and high (16 cpd) SFs. By considering the maximum contrast gradient of the cortical image produced by different SF sine and square wave targets in comparison with the microfluctuations measured, we conclude that the accommodation microfluctuations seem to be monitoring this contrast gradient, which is likely to be used by the accommodation control system during error detection. The larger microfluctuations in MYOs across the conditions together with the larger increase in the microfluctuations evident at 16 cpd indicate that these subjects may have a shallower contrast gradient and the potential reasons and implications of this have been discussed.

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