

Investigating the mechanisms that may underlie the reduction in contrast sensitivity during dynamic accommodation

Sven Mucke

Department of Vision Sciences, Glasgow Caledonian University, Cowcaddens Road, Glasgow, UK



Velitchko Manahilov

Department of Vision Sciences, Glasgow Caledonian University, Cowcaddens Road, Glasgow, UK



Niall C. Strang

Department of Vision Sciences, Glasgow Caledonian University, Cowcaddens Road, Glasgow, UK



Dirk Seidel

Department of Vision Sciences, Glasgow Caledonian University, Cowcaddens Road, Glasgow, UK



Lyle S. Gray

Department of Vision Sciences, Glasgow Caledonian University, Cowcaddens Road, Glasgow, UK



Uma Shahani

Department of Vision Sciences, Glasgow Caledonian University, Cowcaddens Road, Glasgow, UK



Head and eye movements, together with ocular accommodation enable us to explore our visual environment. The stability of this environment is maintained during saccadic and vergence eye movements due to reduced contrast sensitivity to low spatial frequency information. Our recent work has revealed a new type of selective reduction of contrast sensitivity to high spatial frequency patterns during the fast phase of dynamic accommodation responses compared with steady-state accommodation. Here we report data which show a strong correlation between the effects of reduced contrast sensitivity during dynamic accommodation and velocity of accommodation responses, elicited by ramp changes in accommodative demand. The results were accounted for by a contrast gain control model of a cortical mechanism for contrast detection during dynamic ocular accommodation. Sensitivity, however, was not altered during attempted accommodation responses in the absence of crystalline-lens changes due to cycloplegia. These findings suggest that contrast sensitivity reduction during dynamic accommodation may be a consequence of cortical inhibition driven by proprioceptive-like signals originating within the ciliary muscle, rather than by corollary discharge signals elicited simultaneously with the motor command to the ciliary muscle.

Keywords: accommodation, accommodative suppression, computational modeling, contrast sensitivity, eye movements, proprioception

Citation: Mucke, S., Manahilov, V., Strang, N. C., Seidel, D., Gray, L. S., & Shahani, U. (2010). Investigating the mechanisms that may underlie the reduction in contrast sensitivity during dynamic accommodation. *Journal of Vision*, 10(5):5, 1–14, <http://journalofvision.org/content/10/5/5>, doi:10.1167/10.5.5.

Introduction

We perceive the external world as a continuous three-dimensional visual scene in which objects are stable and clear. Our ability to process spatially detailed visual information is restricted to a small part of the retina, the fovea. Detailed processing of objects at different spatial locations in the visual scene is achieved by a combination of ocular movements: saccades place the retinal image of interest on the fovea; vergence eye movements minimize

retinal disparity to maintain binocular single vision; and ocular accommodation changes lens power to produce sharp retinal images. During these oculomotor movements remarkable transformations of the retinal representation of the external world occur, and yet, we generally perceive a sequence of sharp snapshots of different objects at different positions in the visual scene.

For hundreds of years, scientists have questioned why we do not perceive degraded images among the snapshots. The object of much of this work has been to investigate the neural mechanisms involved in maintaining stable

visual perception during eye movements (for a review see Wurtz, 2008). Reduced sensitivity of visual information processing during saccadic eye movement is selective for low-spatial frequency information and, as a result, alleviates anomalous motion perception, whereas contrast detection thresholds for high-spatial frequency patterns and detection thresholds for iso-luminant color stimuli remain normal (Burr, Morrone, & Ross, 1994, Latour, 1962, Volkman, 1986). This suggests that the sensitivity of the magnocellular pathway is being selectively reduced during saccadic eye movements (Burr et al., 1994). Saccadic suppression does not seem to remove visual information from awareness however, as a recent study found in which low spatial frequency information remained accessible to the visual system throughout the saccadic eye movement (Watson & Krekelberg, 2009). Spatial selectivity of reduced sensitivity during vergence eye movements has not been explored in detail, but studies have shown that vergence eye movements attenuate sensitivity to uniform flash stimuli, which represent low spatial frequency information (Manning, 1986, Manning & Riggs, 1984).

Recently, we have found reduced contrast sensitivity to patterns of higher spatial frequency during dynamic accommodation step responses (Mucke, Manahilov, Strang, Seidel, & Gray, 2008). Contrast sensitivity reduction during dynamic accommodation shows spatial-frequency selectivity, which differs from that of saccadic suppression and is not related to the predicted reduction in contrast sensitivity produced by optical factors (Fernández & Artal, 2005). Contrast sensitivity to patterns of higher spatial frequency was reduced significantly during dynamic accommodation compared with steady-state accommodation, whilst sensitivity to patterns of lower spatial frequency was not altered. This effect was maximal when the accommodation step response reached its peak velocity (350–400 ms after the accommodation target onset), with unaltered sensitivity being found around the starting (200 ms) and end points (500–600 ms) of the response.

Neural mechanisms underlying reduced contrast sensitivity during saccadic eye movements have been attributed mainly to extra-retinal signals, such as corollary discharge signals (Sperry, 1950) elicited simultaneously with the motor command to the extra-ocular muscles. These outflow signals precede the physical muscle response and cause maximal reduction in sensitivity around the response onset (for review see Wurtz, 2008). Such corollary discharge signals are also believed to be available for accommodation (Rosenbluth & Allman, 2002). However, the late onset of contrast sensitivity reduction during dynamic accommodation, as compared to saccadic suppression, suggests a different neural pathway. While afferents from mechanoreceptors within extra-ocular muscles have been rejected for saccadic suppression, because of their delayed availability (Wurtz, 2008), such neural input from the ciliary muscle could arrive

in time to reduce contrast sensitivity during dynamic accommodation. The existence of mechanoreceptors within the ciliary muscle has only recently been established (Flügel-Koch, Neuhuber, Kaufman, & Lütjen-Drecoll, 2009).

The aim of *this* study was to explore whether a proprioceptive-like (inflow) mechanism, a corollary discharge (outflow) mechanism or both contribute to the reduced sensitivity during dynamic accommodation. First, we investigated the correlation between the magnitude of contrast sensitivity reduction during dynamic accommodation and accommodation velocity for ramp changes in accommodative demand. The obtained results were accounted for by a contrast gain control model of a cortical mechanism for detecting patterns using divisive normalization, with the magnitude of contrast sensitivity reduction being proportional to the absolute value of accommodation velocity. The velocity of accommodation responses reflects the change in refractive power of the crystalline eye lens as a consequence of the change in ciliary muscle tone. Given that contrast sensitivity is reduced during the fast phase of the accommodation response and the magnitude of this effect is proportional to accommodation velocity, one could suggest that contrast sensitivity reduction during dynamic accommodation is determined by a cortical inhibitory mechanism controlled by proprioceptive-like feedback produced by mechanoreceptors of the ciliary muscle.

This hypothesis, however, does not reject the role of corollary discharge in regulating the observed reduction in contrast sensitivity. The outflow mechanism should reduce contrast sensitivity mainly during the onset of dynamic accommodation responses (following the logic of corollary discharge signals, reviewed in Wurtz, 2008), but it might also affect pattern detection during the fast accommodation phase. In order to test these possibilities, we examined whether contrast sensitivity was reduced when the ciliary muscle is paralyzed. We assumed that the proprioceptive inputs from within the paralyzed ciliary muscle would be eliminated in a similar way as the proprioceptive inputs from paralyzed extra-ocular muscles are greatly reduced or absent (for reviews see Donaldson, 2000 and Ruskell, 1999). Additionally, we assumed that attempted dynamic accommodation to a far-to-near accommodation target with paralyzed ciliary muscles should have elicited a corollary discharge signal together with the motor command (Rosenbluth & Allman, 2002; Sperry, 1950). If similar reduction in contrast sensitivity occurred during dynamic accommodation attempts, we could suggest that the corollary discharge from the motor command elicited in the midbrain areas would be its source. Alternatively, lack of contrast sensitivity reduction would support the hypothesis that proprioceptive-like signals from within the ciliary muscle would perhaps cause the loss in contrast sensitivity. If, however, contrast sensitivity reduction occurred with reduced magnitude,

then both corollary discharge and proprioceptive-like signals could be regarded as factors contributing to the loss in contrast sensitivity.

Methods

Subjects

Four subjects, three naïve to the aims of the experiment and one of the authors, participated with informed consent in this study. All participants were young emmetropes (aged 19–34) with good ocular and general health, vision of 6/6 or better and a near point of accommodation closer than 30 cm. The latter was measured during eye examination and confirmed during practice runs of the experiment.

Apparatus

Accommodation step responses were induced by mounting an accommodation target on a linear actuator (Movopart M 55, Tollo linear AB, Kristianstad, Sweden), powered by a servo drive and run by a NextMove ESB motion controller. The system had a non-linearity of 0.39% and maximum speed of 5 meters per second, which allowed the accommodation target to travel from 1 m to 33 cm in about 180 ms. The actuator was programmed to perform a non-linear movement to generate a constant accommodation target speed in dioptres per second (D/s). Initiation of movement of the accommodation target was randomized to suppress any temporal frequency pattern.

Ocular accommodation was monitored and recorded with a modified infra-red open-field autorefractor (Shin-Nippon SRW-5000) and data acquisition software (LabView 7) which allowed a sampling rate of 60 Hz, well above the Nyquist frequency for accommodation (Denieul, 1982), with a resolution of <0.001 D (Wolffsohn, Gilmartin, Mallen, & Tsujimura, 2001). Continuous accommodation recordings were smoothed with a low-pass filter at 10 Hz, and blinks removed using an algorithm described previously by Day, Strang, Seidel, Gray, and Mallen (2006). However, blinks were rare during trials, which lasted between 3 and 5 seconds depending on the random time delay for initiation of the accommodation target movement. Accommodation velocity was calculated for each subject and each target speed individually, and used to determine the onset of the dynamic accommodation response (Suryakumar, Meyers, Irving, & Bobier, 2007). The experiment took place in a dimmed room to allow for pupil sizes >3 mm. A smaller pupil would result in signal loss from the autorefractor. Head and eye movements were minimized by using a chin and forehead rest and the eye under test was carefully aligned with the

accommodation target and center of the test monitor. Pupil sizes were monitored and recorded in *Experiment 2* utilizing an EyeLink I video eye tracker with a sampling rate of 250 Hz (SR Research Ltd., Mississauga, Ontario, Canada). Recordings were smoothed offline with a sliding 100 ms window.

Visual stimuli

The test stimulus was generated by a Pentium 3 computer on a 19" RGB monitor (Vision Master Pro 450, Iiyama Electronics America, Inc.) at a screen resolution of 1024×768 pixels and a frame rate of 75 Hz. The stimulus was displayed using a 256-color look-up table and a 12-bit gray-scale resolution obtained by a custom video summation device (Pelli & Zhang, 1991). The distance between the screen (angular size of 19×14.4 deg) and the subject was 1 m. The mean luminance was 30 cd/m^2 . The monitor's gamma non-linearity was corrected carefully using an OptiCal photometer (Cambridge Research System Ltd.) interfaced to the PC. The 90% decay of the monitor phosphor signal (using white color and an image formed by 1 line) was about 1 ms.

The test stimulus was a 4-deg diameter circular patch of a horizontal square-wave grating with a fundamental frequency of 9 c/deg. The effects of spatial transients at the stimulus edges were reduced by dumping the contrast of the outer area (0.5 deg) with a linear function. In dynamic conditions, the test stimulus was presented at different time lags (to an accuracy of 1 screen frame), which were triggered by the onset of the accommodation target movement. Stimulus duration was about 5 ms ($1/3$ screen frame of 13.3 ms plus phosphor decay) for the majority of conditions and about 18 ms ($1/3$ screen frames plus phosphor decay) for the highest defocus condition.

Experimental design

This study compared contrast sensitivity measures between conditions with steady-state and dynamic accommodation. For the static condition (steady-state accommodation), subjects were instructed to focus monocularly (dominant eye) on a Snellen E (angular letter size 10 arcmin at 1 m) at five individual distances ranging from 1 m to 33 cm, whilst the fellow eye was occluded. For the dynamic condition, two-dioptre (1–3 D) far-to-near accommodation ramp responses with different velocities were induced. A valid dynamic accommodation response was performed after a reasonable reaction time (~ 200 ms), with a consistent dioptrical increase, and with an amplitude >1 D. Individual continuous recordings of 100 accommodation responses following each target speed (10, 3, 2, 1 D/s) were obtained prior to the experiment and averaged. From the

mean accommodation response profile of the 10 D/s target speed individual accommodation velocity profiles were computed by differentiating the averaged accommodation responses using a 2-point-difference algorithm, and subsequently smoothing the data, using a 100 ms window. Three points of interest (B, C, D) were chosen around accommodation peak velocity, one point (A) before accommodation response onset, and a further point (E) near the final steady-state response level (Figure 1). Each point of interest in the dynamic condition had a time lag, which had a distinct accommodation response level. The five accommodation response levels (A–E) were converted into five static viewing distances between 1 m (1 D) and 33 cm (3 D) (Figure 1). Hence, accommodation amplitudes were always matched between static and dynamic conditions. Viewing conditions following accommodation target speeds of 3, 2 and 1 D/s were also matched with the same accommodation response levels (Figure 1), and each accommodation target speed was given its separate set of five dynamic time lags. Due to the individual accommodation dynamics of the four subjects, time lags and accommodation response levels differed slightly amongst subjects, and are therefore shown as arbitrary points of interest A–E (Figure 1).

During the first experimental session for each participant, the accommodation target was positioned at 1 m and ten measures of steady-state accommodation were taken. The same procedure was repeated for 33 cm, calibrating the continuous recording of dynamic accommodation. In dynamic mode the accommodation target was moving at four different speeds (1, 2, 3 and 10 D/s) from 1 m to 33 cm. Participants were instructed to “focus carefully on the accommodation object” (Stark & Atchison,

1994), and to regain focus as fast as possible after the initiation of an accommodation ramp response.

The test stimulus was presented randomly 2 deg above or below the accommodation target, for the duration of 5 ms (points of interest A–D), or 18 ms (point of interest E, Figure 1) on the monitor at 1 m distance. As the subject accommodated from 1 m to 33 cm the test stimulus became increasingly blurred. This expected reduction in contrast sensitivity made it necessary to use a longer test stimulus duration at the highest level of defocus. Participants used mouse buttons to indicate the perceived position of the grating. Negative feedback was given for mismatches. Detection thresholds were measured using a staircase method and a two-alternative-forced-choice procedure designed to determine 79% correct responses (Levitt, 1971). Each staircase started at a supra-threshold contrast level of the test stimulus with a contrast step of 0.2 log units. After each staircase reversal, the step size was halved and this process continued until the step size became 0.05 log units. The subsequent six staircase reversals were collected and the threshold measure was the geometric mean of these estimates. If the subject was not able to accommodate accurately (extremely short reaction time, slow or inconsistent response, low response amplitude), or blinked, the experimenter would reject the trial from the staircase procedure.

Within one experimental session contrast thresholds were measured during one static and four dynamic conditions of equal accommodation response level, following different accommodation target speeds. Dynamic accommodation was monitored throughout the whole experiment. Approximately six sessions were necessary to collect all data for each participant, including practice

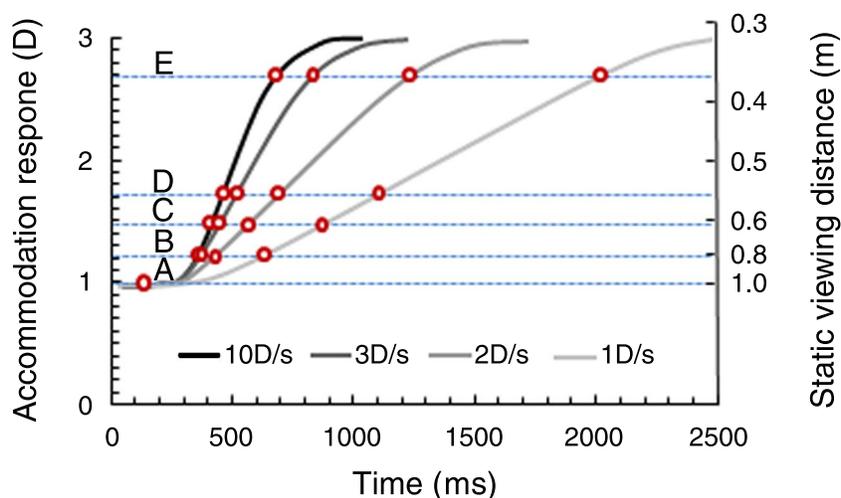


Figure 1. Examples of dynamic accommodation ramp responses following target speeds of 10, 3, 2 and 1 D/s as a function of time after the accommodation target onset. Horizontal, dashed lines mark equal accommodation response levels across all dynamic accommodation ramp responses elicited during the experiment, and also connect the time domain via accommodation response amplitude with static viewing distances for steady-state accommodation. Points of interest (A–E) chosen from the 10 D/s response profile [1× pre-ramp (200 ms), 3× fast phase (300, 350, 400 ms), 1× slow phase (500 ms for LM, CM; 600 ms for KP, SM)] are highlighted across all dynamic conditions.

runs, and initial dynamic accommodation recordings at all four target speeds for reaction and response time assessment. One session lasted approximately one hour including small breaks between trials.

Results

Figure 2 shows examples of typical dynamic accommodation responses and their velocities following accommodation target speeds of 10, 3, 2 and 1 D/s. Accommodation peak velocity decreased, as expected, following slower accommodation target speeds, while time-to-peak velocity remained similar for all target speeds (Table 1).

Figure 3 shows contrast sensitivity (the reciprocal of contrast threshold) as a function of defocus levels during dynamic accommodation (Figure 3, markers) and steady-state accommodation (Figure 3, dashed lines) for each subject. Using SPSS version 16 we conducted a repeated-measures ANOVA [4 (subject) \times 5 (accommodation

velocity, including zero velocity (steady-state accommodation) \times 5 (defocus level)]. As expected, the results showed a main effect of defocus level [$F_{(1.8,40.4)} = 199$, $P < 0.001$, Huynh-Feldt correction]. The type of accommodation had also a main effect on contrast sensitivity [$F_{(2.9,66.7)} = 57.3$, $P < 0.001$, Huynh-Feldt correction]. Statistical analysis showed a significant interaction between defocus level and type of accommodation [$F_{(7.3,168)} = 24.3$, $P < 0.001$, Huynh-Feldt correction]. Because the important comparisons were those between contrast sensitivity in steady-state accommodation and those in dynamic accommodation following a 1, 2, 3, 10 D/s target, we conducted multiple comparisons [$N = 80$; t -tests using a Holm-Bonferroni correction (Holm, 1979)] between contrast sensitivity measurements in steady-state and all four dynamic conditions for each point of interest. The results showed that contrast sensitivities measured during steady-state accommodation and dynamic accommodation following the 1 D/s target were not significantly different. Dynamic conditions following the 2 D/s target speed had significantly ($P < 0.05$) reduced contrast sensitivity in two subjects (LM: point B; SM: points B and D), possibly due to higher than expected accommodation velocities at these

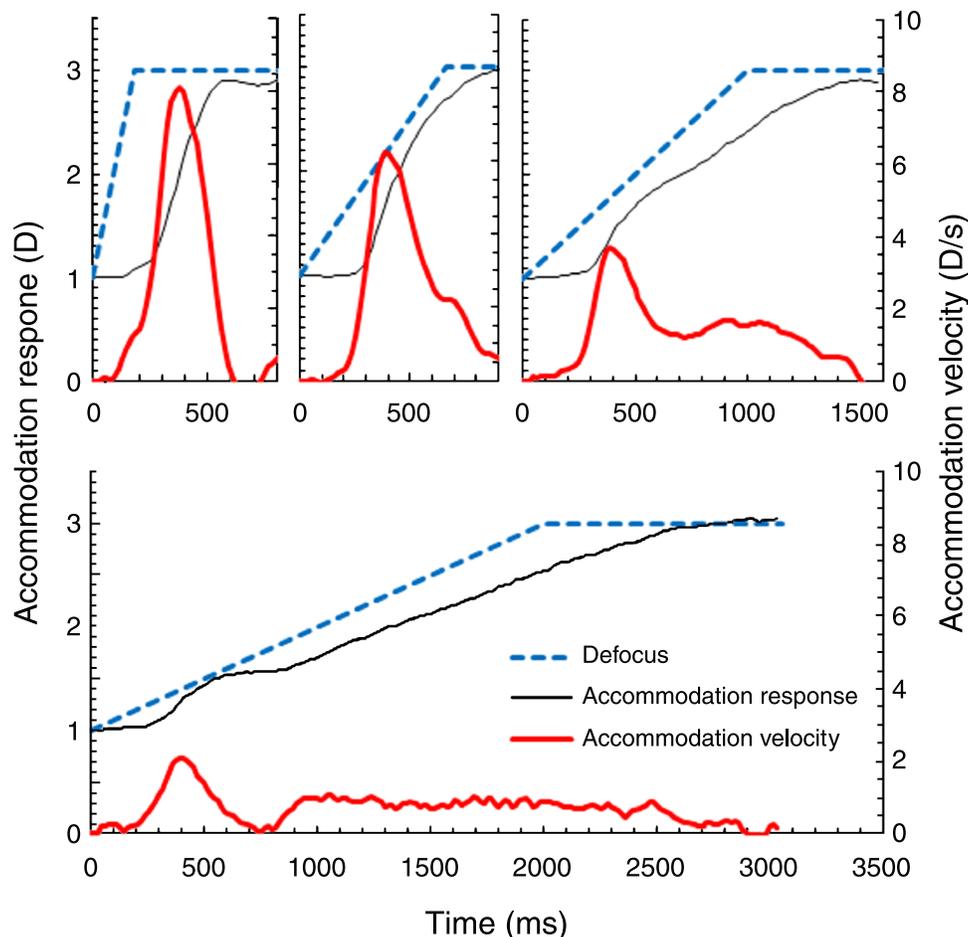


Figure 2. Dynamic accommodation responses (black lines) and their velocity traces (red lines) following accommodation targets (blue dashed lines) at speeds of 10 (A), 3 (B), 2 (C) and 1 (D) D/s. The graphs show data of subject LM.

accommodation target velocity (D/s)	10	3	2	1
peak velocity (D/s)	6.75 ± 3.0	4.92 ± 1.0	3.13 ± 0.6	1.99 ± 0.5
time-to-peak velocity (ms)	367 ± 16	391 ± 22	379 ± 23	395 ± 23

Table 1. Mean values (\pm SD) for reaction time, peak velocity and time-to-peak velocity for dynamic accommodation, tracking the accommodation target with speeds of 10, 3, 2 and 1 D/s.

points (LM: 3.69 D/s; SM: 2.56 D/s). Dynamic conditions following the 3 and 10 D/s targets reduced significantly ($P < 0.05$) contrast sensitivities during the fast phase of the dynamic accommodation response (around peak velocity, points of interest B, C and D) following 10 D/s target (all subjects) and 3 D/s target (KP, LM, SM). The mean value and 95% confidence interval of the differences between the contrast sensitivities in steady-state and dynamic conditions during the fast phase was 0.27 ± 0.08 log units (following the 10 D/s target speed) and 0.21 ± 0.08 log units (following the 3 D/s target speed). It should be noted that the test grating has a limited range of contrast levels whose maximum is 100%. In order to measure contrast sensitivity to the test stimulus within the available contrast levels, the test stimulus at the highest defocus had a longer duration (18 ms) than that at the lower defocus levels (5 ms). This resulted in higher contrast sensitivity compared to the sensitivity level at the shorter stimulus duration. The difference in stimulus duration cannot influence the estimation of suppressive effects because the measurements in both static and dynamic conditions for each defocus level were carried out at the same stimulus duration. The ceiling effects of stimulus contrast did not allow the correct measurement of contrast sensitivity in some subjects at lower defocus levels (CM and LM; Figures 3A and 3C, empty diamonds). In cases of this type, the difference between contrast sensitivity in static and dynamic conditions is underestimated.

Model

To describe quantitatively the results obtained, we propose a computational model for visual responses incorporating contrast sensitivity reduction during ocular accommodation. Models for contrast gain control (Albrecht & Geisler, 1991; Heeger, 1992) assume that the responses of cells of primary visual cortex are determined by two main mechanisms: linear feed-forward excitation from lateral geniculate nucleus (LGN) neurons, and a non-linear normalization mechanism which divides the linear response by a quantity proportional to the pooled activity of a large number of neurons with a wide variety of tuning properties. The divisive inhibition increases with stimulus contrast, which results in response magnitude saturation.

Models for pattern detection (Foley, 1994; Watson & Solomon, 1997) assume that the response of a spatial

channel to an optimal sinusoidal grating during steady-state accommodation could be determined by two components, which are proportional to stimulus contrast: an

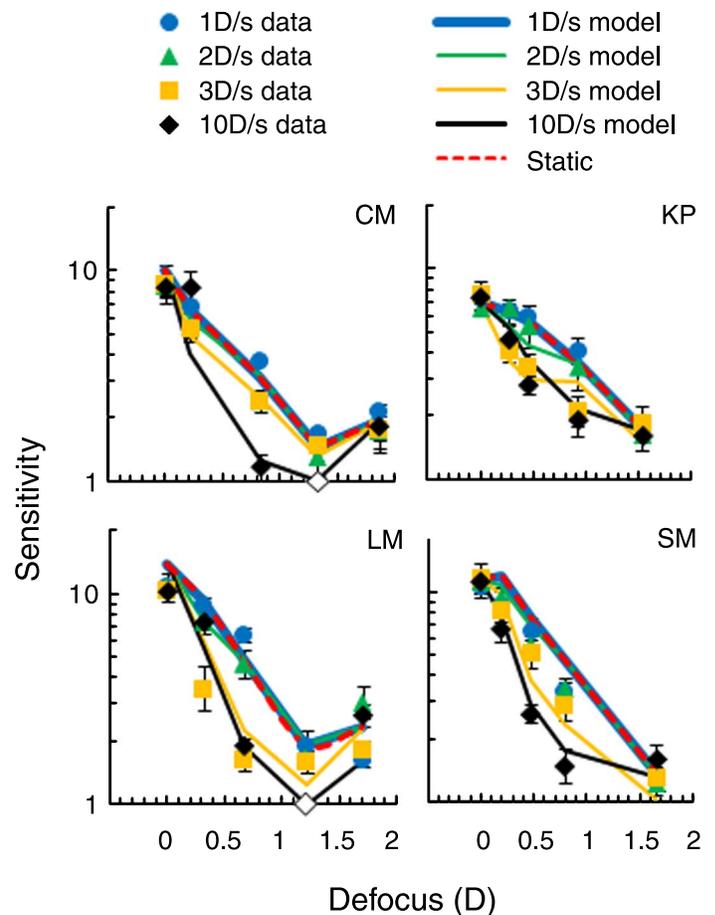


Figure 3. Contrast sensitivity for detecting gratings of 9 cpd in static (red dashed line) and dynamic [target speeds of 10 (black diamonds), 3 (orange squares), 2 (green triangles) and 1 D/s (blue circles)] conditions as a function of defocus of the test stimulus. Error bars denote 95% confidence intervals and are smaller than symbols when not seen. Static data points with error bars have been removed from the graphs for clarity. Note, that measurements marked with empty diamonds (graphs A, C) were restricted by the highest available grating contrast. Measurements at the highest level of defocus were carried out with stimulus duration of 18 ms, and therefore can return higher sensitivity than measurements at lower defocus levels. Solid lines represent model predictions using Equation 5 and the best-fitted values of the free parameters (Table 2). Data of four subjects (CM, KP, LM and SM) are shown.

Subjects

Model parameters	CM	SM	KP	LM	Mean ± SE
m	0.050	0.325	0.398	0.125	0.224 ± 0.0820
p	2.545	2.525	2.030	2.541	2.410 ± 0.1267
V_0	1.541	1.494	1.036	1.529	1.400 ± 0.1216
R^2	0.921	0.942	0.932	0.886	0.920 ± 0.0122

Table 2. Best-fitted values of the free model parameters (Equation 5) for each subject and the average across all subjects' data. R^2 values represent the proportion of variability in a data set that is accounted for by the model.

excitatory component (aC_s^p) and a divisive inhibitory component (bC_s^p). The response magnitude (R_{stat}) could be written as follows:

$$R_{stat} = \frac{aC_s^p}{1 + bC_s^p}, \quad (1)$$

where a and b are constants and p is a power coefficient.

We propose that during dynamic accommodation, the response (R_{dyn}) of the same spatial channel would have an additional inhibitory component whose strength is proportional to the velocity of the dynamic accommodation response when it exceeds a threshold value of V_0 as follows:

$$R_{dyn} = \frac{aC_d^p}{1 + bC_d^p + m[|V| - V_0]_+^p}, \quad (2)$$

where V is the velocity of the dynamic accommodation response, V_0 is a parameter representing a threshold velocity, $[|V| - V_0]_+ = |V| - V_0$ if $|V| > V_0$, else = 0, m is a coefficient. The contrast sensitivity reduction depends on the absolute value of the accommodation velocity, because in a previous study (Mucke et al., 2008) we found that both far-to-near (positive velocity) and near-to-far (negative velocity) accommodation step responses reduced sensitivity to high spatial frequency information.

At threshold, the responses approach a fixed level. Therefore, the responses in both conditions could be regarded as equal:

$$\frac{aC_d^p}{1 + bC_d^p + m[|V| - V_0]_+^p} = \frac{aC_s^p}{1 + bC_s^p}. \quad (3)$$

Equation 3 can be simplified as follows:

$$C_d = C_s(1 + m[|V| - V_0]_+^p)^{1/p}. \quad (4)$$

Noting that sensitivity is inversely proportional to threshold contrast, Equation 4 can be re-written as follows:

$$S_d = \frac{S_s}{(1 + m[|V| - V_0]_+^p)^{1/p}}. \quad (5)$$

It should be noted that in the standard models for contrast detection (Foley, 1994), the power coefficients in the numerator and denominator of Equation 1 are different (usually the first > the second). Here we assumed that they are equal which allowed Equation 5 to be derived exactly. The best-fitted values of the free model parameters (m , p and V_0) were obtained using the least square method implemented by Microsoft Excel solver (Table 2). The model predictions using these values are shown in Figure 3 (solid lines).

The ratios of contrast sensitivity in static and dynamic conditions as a function of accommodation velocity are plotted in Figure 4 (markers) for each subject. The red lines represent model calculations of the sensitivity ratio using Equation 5 and the best-fitted values of the free parameters. The results show clearly that the sensitivity ratio decreases due to reduction of contrast sensitivity when the accommodation velocity exceeds a threshold value.

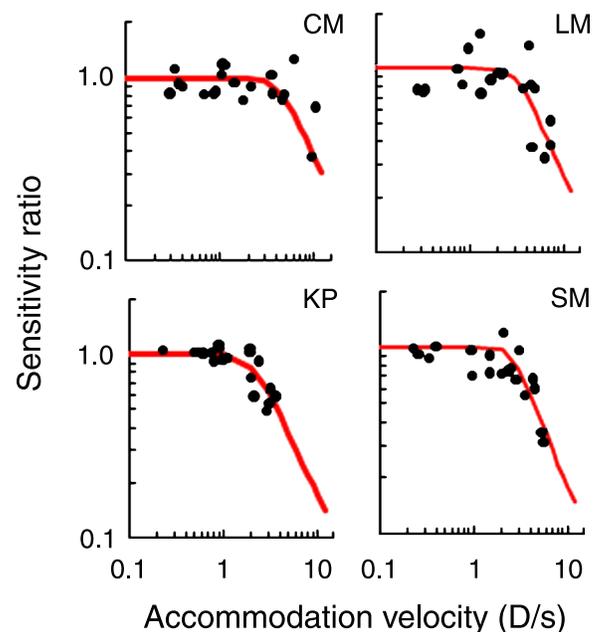


Figure 4. Relative sensitivity expressed as the ratio between contrast sensitivity measurements during dynamic and steady-state accommodation as a function of accommodation velocity. Red lines illustrate model predictions using Equation 5 and the best-fitted values of the free parameters (Table 2). Data of four subjects (CM, KP, LM and SM) are shown.

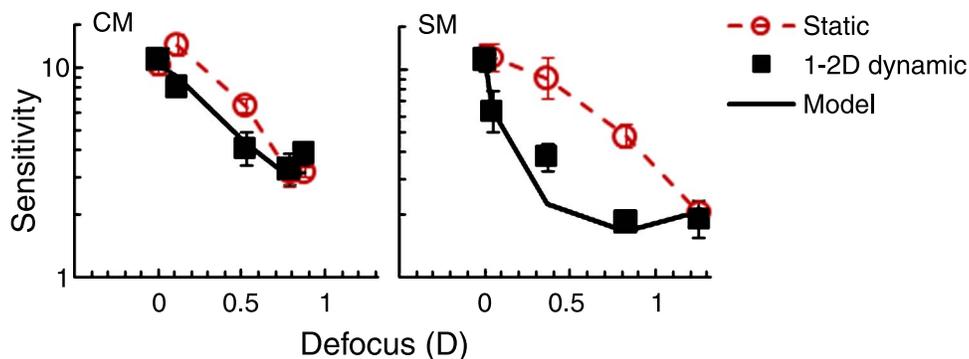


Figure 5. Contrast sensitivity for detecting gratings of 9 cpd in static (open circles) and dynamic (black squares) conditions as a function of defocus of the test stimulus for 1–2 D accommodation responses. Black lines show model fit to dynamic data using Equation 5 and the best-fitted values of the free parameters (Table 2). Data of two subjects (CM, SM) are shown.

Control Experiment 1

The robustness of our model was tested with data obtained from an additional experimental condition with reduced accommodation amplitude (1 D) following 10 D/s target speed. We found that subjects CM's and SM's accommodation step responses of 1 D and 2 D amplitude had peak velocities (1 D: 5.8 ± 1.7 D/s; 2 D: 6.8 ± 3.0 D/s) and time-to-peak velocities which were not significantly different (1 D: 337 ± 33 ms; 2 D: and 367 ± 16 ms). Pairwise comparison (paired t-tests, Bonferroni correction) between sensitivity measures in static and dynamic conditions showed significantly reduced ($P < 0.05$) sensitivity during dynamic accommodation for defocus levels of 0.11, 0.52 D (CM) and 0.05, 0.36, 0.82 D (SM). The black lines in Figure 5 represent the model calculations of sensitivity (Equation 5) using the parameters obtained in the main experiment (Table 2). The quality of fit was good in both subjects ($R^2 = 0.937$, CM; 0.878 , SM)

suggesting that accommodation amplitude did not affect the magnitude of reduction of contrast sensitivity. Rather it was determined by accommodation velocity.

Experiment 2

In order to determine whether corollary discharge or proprioceptive-like signals are the source of the observed contrast sensitivity reduction we tested subjects CM, SM and KP under the 1–3 D step response condition (10 D/s target speed), after paralyzing their ciliary muscles binocularly with two drops of 0.5% Cyclopentolate Hydrochloride (Chauvin Pharmaceuticals Ltd., UK) administered topically 20 minutes before the start of the experiment. Cyclopentolate Hydrochloride blocks muscarinic receptors receiving parasympathetic innervation, thereby relaxing the iris sphincter muscle and the ciliary muscle, causing mydriasis and cycloplegia (Frazier &

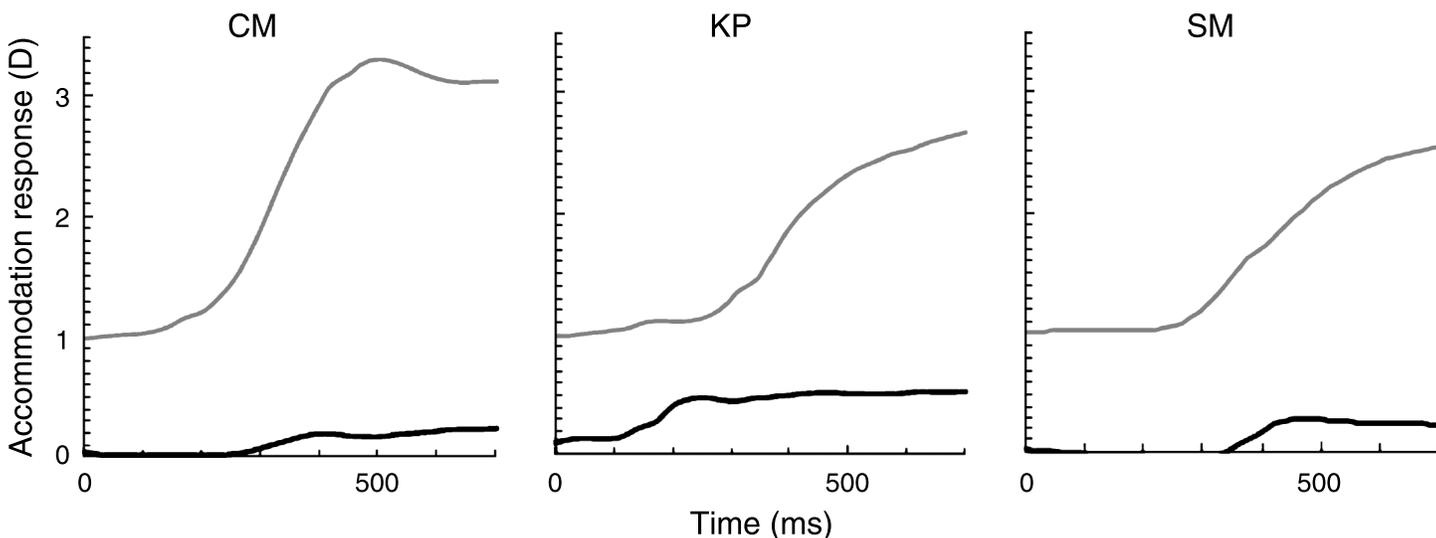


Figure 6. Mean accommodation response before (gray line) and after (black line) administration of Cyclopentolate Hydrochloride as a function of time after the onset of a 10 D/s accommodation target. Data of subjects CM, KP and SM are shown.

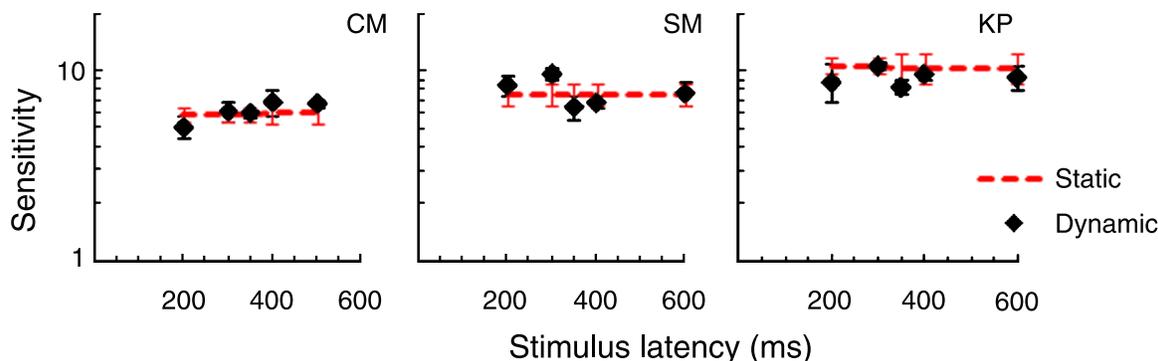


Figure 7. Contrast sensitivity for attempted 1–3 D accommodation responses in static (red, dashed lines) and dynamic conditions (black diamonds) under cycloplegia as a function of time after the accommodation target onset. Error bars denote 95% confidence intervals and are smaller than symbols when not seen. Data of subjects CM, SM and KP are shown.

Jaanus, 2008). The residual accommodation response amplitude of around 0.5 D (Figure 6) lagged considerably behind the accommodative demand of 3 D. We assumed that by paralyzing the ciliary muscle proprioceptive-like feedback from within the ciliary muscle would be greatly reduced and may not suffice to cause a reduction of contrast sensitivity.

There were no significant (paired t-test, Bonferroni correction) differences between contrast sensitivity measurements during steady-state and attempted dynamic accommodation (Figure 7).

Control Experiment 2

Changes in pupil size during dynamic accommodation modify the amount of retinal illumination which could

influence contrast sensitivity to the test grating. To distinguish between reduction in contrast sensitivity caused by changes in pupil size and dynamic accommodation, we tested subjects LM and SM using a 10 D/s accommodation target after they had one drop of Phenylephrine hydrochloride 2.5% (Chauvin Pharmaceuticals Ltd. UK) administered in each eye. Phenylephrine hydrochloride 2.5% is a sympathomimetic drug, which causes the iris dilator muscle to contract, thereby inducing mydriasis, while minimally affecting the accommodation response amplitude (Portello, 2008).

Pupil size changes during the 1–3 D accommodation step response before administering Phenylephrine hydrochloride were executed with an average latency across subjects of 488 ± 34 ms after the accommodation target onset (Figures 8A and 8B). Mean reduction in pupil diameter across both subjects was 0.31 ± 0.11 mm per

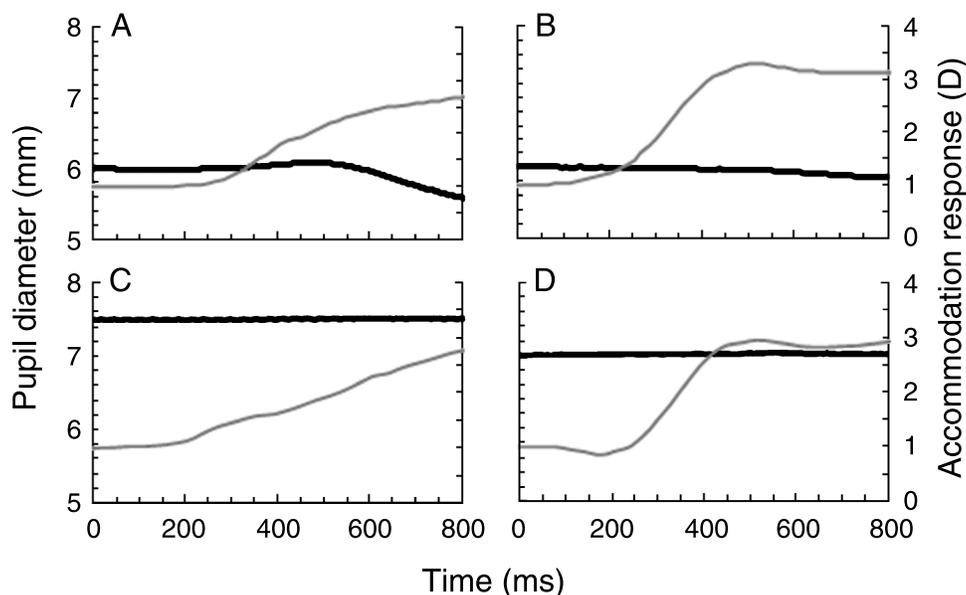


Figure 8. Average pupil diameter (black lines) and accommodation step response (gray lines) as a function of time before Phenylephrine hydrochloride administration (A, subject SM; B, subject LM) and 40 minutes later (C, subject SM; D, subject LM).

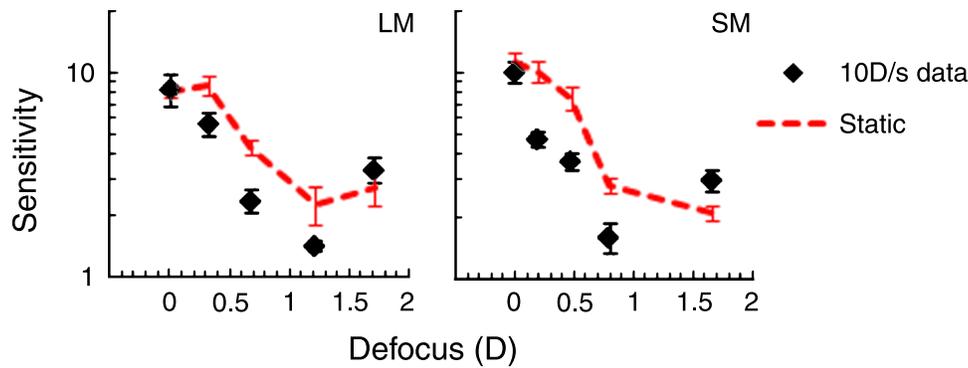


Figure 9. Contrast sensitivities for static (red dashed line) and dynamic (black diamonds) conditions as a function of defocus of the test stimulus, for subjects LM and SM. Error bars denote 95% confidence intervals. Measurements at the highest level of defocus were taken with a stimulus-duration of 18 ms, and therefore can return higher sensitivity than measurements at lower defocus levels.

dioptric accommodation response. Following administration, pupil diameters remained larger than 7 mm in both subjects. No changes in pupil diameter were observed during dynamic accommodation responses after administration of Phenylephrine hydrochloride (Figures 8C and 8D). Phenylephrine hydrochloride did not significantly (paired *t*-test) affect accommodation velocity in the two subjects.

In order to ensure constant pupil-sizes a 5 mm artificial pupil was used at 10 mm in front of the eye under test, with the fellow eye occluded. Contrast threshold measurements (Figure 9) with fixed pupil size revealed significantly (paired *t*-tests, Bonferroni correction) reduced sensitivity during dynamic accommodation for defocus levels of 0.32, 0.67, 1.21 D (LM) and 0.19, 0.47, 0.79 D (SM). The mean reduction in contrast sensitivity of 0.27 log units around the time of peak accommodation velocity was similar to the results in *Experiment 1*.

Discussion

This study has shown that reduction of contrast sensitivity to high spatial-frequency patterns during dynamic accommodation was strongly determined by the velocity of dynamic accommodation responses to changes of accommodative demand.

The effects of accommodation velocity on the magnitude of reduction of contrast sensitivity were modeled using a normalization model for contrast processing during dynamic accommodation. Divisive normalization models have been proposed to describe quantitatively contrast gain control of cells in visual cortex (Albrecht & Geisler, 1991; Heeger, 1992) and pattern masking phenomena (Foley, 1994; Watson & Solomon, 1997). These models assume that the responses of cortical mechanisms are determined by excitatory inputs from mechanisms sensitive to the stimulus and divisive inhibitory inputs

from mechanisms with a wide variety of tuning properties. An important feature of these models is that they provide an algorithm for describing reduced sensitivity, which is driven by signals within the visual pathway. The reduction in sensitivity during dynamic accommodation responses as compared to that in steady-state accommodation conditions could be explained by a normalization model assuming that the pool of inhibitory mechanisms included inputs from extra-retinal oculomotor mechanisms. This additional suppressive input was a divisive component, which was proportional to the velocity of dynamic accommodation responses when it exceeded a threshold velocity level. R^2 values were in the range of 0.886–0.942 (Table 2) indicating a good fit between model predictions (Equation 5) and experimental data. The results showed that only the fast component of the accommodation response, whose velocity was larger than a threshold of 1.4 D/s (Table 2), produced reduction in contrast sensitivity. The power coefficient values (range of 2.03–2.54) were similar to those obtained in standard detection tasks (Foley, 1994).

What could be the neural mechanisms underlying reduced contrast sensitivity during ocular accommodation? Reduced sensitivity of the magnocellular pathway during eye-blink, saccades and binocular vergence is believed to result from a centrally originating corollary discharge signals (for reviews see Volkman, 1986; Wurtz, 2008). These signals are elicited by innervations of external eye muscles or the eyelids, precede the actual muscle response and produce maximal reduction in sensitivity around response onset. It is possible that a similar extra-retinal mechanism operates during dynamic accommodation. In such a case contrast sensitivity would be reduced around the onset of the dynamic accommodation response (in our experiments ~200 ms). This prediction, however, was not supported by our experimental data showing that the contrast sensitivity reduction occurs during the fast phase of the dynamic accommodation responses.

The correlation between the effects of reduction of visual sensitivity and the magnitude of the accommodation velocity could be due to extra-retinal signals originating within the ciliary muscle. Free sensory nerve endings within the ciliary muscles have previously been associated with a mechanoreceptor function (Agababow, 1893; Ishikawa, 1962; Tamm & Lütjen-Drecoll, 1996), but only a recent study has revealed that proprioceptors are present in ciliary muscles (Flügel-Koch et al., 2009). We propose that these proprioceptors are able to provide extra-retinal signals which determine the reduction in contrast sensitivity during dynamic accommodation. We assumed that signals from proprioceptors could be eliminated by paralyzing the ciliary muscles having in mind that proprioceptive inputs from paralyzed extra-ocular muscles are greatly reduced or absent (for reviews see Donaldson, 2000 and Ruskell, 1999). The results showed that contrast sensitivity during dynamic accommodation remained unaffected. Since we encouraged subjects to execute accommodation responses, we assumed that the attempted accommodation which was accompanied by convergence eye movements of the occluded eye should have elicited a corollary discharge signal. Under these assumptions, if the reduction of contrast sensitivity was caused by this corollary discharge signal, reduced contrast sensitivity would have been observed in *Experiment 2*. Our proposition about the underlying neural mechanisms of reduced contrast sensitivity during dynamic accommodation points to encourage further neuro-anatomical research into feedback loops within the accommodation plant and its controller, as well as additional brain imaging studies providing independent evidence for the observed reduction of contrast sensitivity.

Are there other factors that could contribute to the observed reduction in contrast sensitivity to high spatial frequency patterns during dynamic accommodation? Dynamic accommodation is one of three components of the near response (Weber, 1851). Vergence eye movements and changes in pupil diameter generally accompany dynamic accommodation. For a far-to-near accommodation response convergence and pupil constriction can be observed (Weber, 1851). Convergence eye movements in the occluded eye do not influence sensitivity to high spatial frequency patterns (Mucke et al., 2008; Supplemental Data). The changes in pupil diameter before instilling Phenyelphrine Hydrochloride in *Control Experiment 2* are similar to previously reported values (0.48 mm/D, Kasthurirangan & Glasser, 2005; 0.26 mm/D, Charman & Radhakrishnan, 2009, 0.25 mm/D, Schaeffel, Wilhelm, & Zrenner, 1993). The pupil response latencies (490 ms) measured in *Control Experiment 2* are at the higher end of previously reported values (187–500 ms, Hunter, Milton, Ludtke, Wilhelm, & Wilhelm, 2000; Kasthurirangan & Glasser, 2005), which makes it unlikely that pupil size changes will have contributed to the loss of contrast sensitivity in our experiments. Furthermore,

contrast sensitivity reduction persists even when the optical effects of pupil size changes are abolished.

The observed loss of contrast sensitivity during dynamic accommodation could be due to temporal changes in retinal image quality during dynamic accommodation. The maintenance of contrast sensitivity with cycloplegia could be related to the lack of such temporal variations of retinal image quality. In our experiments observers viewed a uniform field at 1 m that was not affected by changes of retinal image blur. Blur would only reduce the contrast of the test stimulus. However, the test stimulus had a very short duration, within which retinal image defocus changes little. Therefore, temporal changes of retinal image blur in these experiments might not have played a significant role in determining sensitivity to the test stimuli.

We also tested whether attention could have an effect on contrast sensitivity measurements at longer test stimulus presentation lags as compared to short presentation lags. Three subjects (DS, MD and SM) were presented with a static accommodation target at an individual test distance [67 cm (DS), 64 cm (MD), 68 cm (SM)], matching the 350 ms dynamic condition. Under this condition, sensitivity was maximally reduced during accommodation step responses. The test stimulus was then presented at various presentation lags (200, 300, 350, 400 and 800 ms) and contrast sensitivity was measured in this static condition (data are not shown). There was no significant difference in contrast sensitivity for the five measurements at different presentation time lags. Hence, attention does not seem to affect contrast sensitivity during longer test stimulus presentation lags as compared to short presentation lags.

What is the role of contrast sensitivity reduction during dynamic accommodation in visual information processing? When a target moves from far to near its retinal image becomes blurred. Blur is the principal stimulus available from the retinal image to produce small (<1.5 D) dynamic accommodation responses (Fincham, 1951; Schor, Alexander, Cormack, & Stevenson, 1992). For large target movements (>2 D) additional cues to accommodation become available, including proximity (Schor et al., 1992). Large dynamic accommodation responses have been modeled with two distinct phases: a fast phase during the initial part of the response, and a slow phase during the final response stage (Hung & Ciuffreda, 1988; Khosroyani & Hung, 2002; Schor & Bharadwaj, 2006). The fast phase is executed on the basis of proximal information gathered prior to the onset of the response and does not use visual feedback. The slow phase, on the other hand, relies on visual feedback from the target enabling the accommodative system to focus accurately on the target and maintain steady-state accommodation. High spatial frequency information within the target is believed to play a vital role in focusing on objects (Charman & Tucker, 1977; Heath, 1956; Kotulak &

Schor, 1987). 3 D visual scenes contain various objects at different viewing distances which act as distracters for the object we fixate upon. Our ability to focus on objects of interest could be severely impaired because patterns from distracters may mask high-frequency selective spatial channels processing the accommodation target (Mitov, Vassilev, & Manahilov, 1981, for a review see Breitmeyer & Ogmen, 2006). Hence, reduction of sensitivity to higher spatial frequencies during the fast phase of the accommodation responses could be the mechanism which helps us to perceive sharp targets of interest at the final accommodation stage. Additionally, the clarity of the accommodation target at the final stage of dynamic accommodation could be enhanced by effects which are similar to previously reported effects of blur adaptation on image sharpness (Webster, Georgeson, & Websster, 2002). Retinal image defocus and reduced contrast sensitivity during dynamic accommodation blur visual objects lying between the far and near accommodation targets producing blur adaption which may enhance the clarity of the accommodation target at the final stage of the dynamic accommodation response. This suggestion requires experimental verification, which we are planning to carry out in future studies.

Conclusions

The present results show that the reduction of contrast sensitivity to stimuli of higher spatial frequencies during dynamic ocular accommodation depends on accommodation response velocity. Sensitivity, however, was not altered during attempted accommodation responses in the absence of crystalline-lens changes due to cycloplegia. These findings suggest that sensitivity reduction may be a consequence of cortical inhibition driven by proprioceptive-like signals originating within the ciliary muscle. A computational model, based on an inhibitory component with an extra-retinal origin, has been developed which explains adequately the detection of spatial patterns during dynamic ocular accommodation. The model could be implemented in a holistic computational model of human vision for incorporation in economical artificial network systems for robots to provide efficient performance in 3 D environments.

Acknowledgments

We would like to thank James Wolffsohn for providing software for recording dynamic accommodation responses. Further, we would like to thank the anonymous reviewers for their critical comments and suggestions for *Control Experiment 2*.

Commercial relationships: none.

Corresponding author: Sven Mucke.

Email: Sven.Mucke@gcal.ac.uk.

Address: Cowcaddens Road, Glasgow, G4 0BA, UK.

References

- Agababow, A. (1893). Die Innervation des Ciliarkörpers. *Anatomischer Anzeiger*, 8, 555–561.
- Albrecht, D. G., & Geisler, W. S. (1991). Motion selectivity and the contrast-response function of simple cells in the visual cortex. *Visual Neuroscience*, 7, 531–546. [[PubMed](#)]
- Breitmeyer, B., & Ogmen, H. (2006). *Visual masking: Time slices through conscious and unconscious vision* (2nd ed.). Oxford: Oxford Physics Series.
- Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, 371, 511–513. [[PubMed](#)]
- Charman, W. N., & Radhakrishnan, H. (2009). Accommodation, pupil diameter and myopia. *Ophthalmic & Physiological Optics*, 29, 72–79. [[PubMed](#)]
- Charman, W. N., & Tucker, J. (1977). Dependence of accommodation response on the spatial frequency spectrum of the observed object. *Vision Research*, 17, 129–139. [[PubMed](#)]
- Day, M., Strang, N. C., Seidel, D., Gray, L. S., & Mallen, E. A. (2006). Refractive group differences in accommodation microfluctuations with changing accommodation stimulus. *Ophthalmic & Physiological Optics*, 26, 88–96. [[PubMed](#)]
- Denieul, P. (1982). Effects of stimulus vergence on mean accommodation response, microfluctuations of accommodation and optical quality of the human eye. *Vision Research*, 22, 561–569. [[PubMed](#)]
- Donaldson, I. M. (2000). The functions of the proprioceptors of the eye muscles. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 355, 1685–1754. [[PubMed](#)] [[Article](#)]
- Fernández, E. J., & Artal, P. (2005). Study on the effects of monochromatic aberrations in the accommodation response by using adaptive optics. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, 22, 1732–1738. [[PubMed](#)]
- Fincham, E. F. (1951). The accommodation reflex and its stimulus. *British Journal of Ophthalmology*, 35, 381–393. [[PubMed](#)]
- Flügel-Koch, C. M., Neuhuber, W., Kaufman, P. L., & Lütjen-Drecoll, E. (2009). Morphological indication for proprioception in the human ciliary muscle.

- Investigative Ophthalmology and Visual Science*, 50, 5529–5536.
- Foley, J. M. (1994). Human luminance pattern-vision mechanisms: Masking experiments require a new model. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, 11, 1710–1719. [PubMed]
- Frazier, M., & Jaanus, S. D. (2008). Cycloplegics. In J. D. Bartlett & S. D. Jaanus (Eds.), *Clinical ocular pharmacology* (5th ed., pp. 130–133). Boston: Butterworth-Heinemann.
- Heath, G. G. (1956). The influence of visual acuity on accommodative responses of the eye. *American Journal of Optometry and Archives of American Academy of Optometry*, 33, 513–524. [PubMed]
- Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience*, 9, 181–197. [PubMed]
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65–70.
- Hung, G. K., & Ciuffreda, K. J. (1988). Dual-mode behaviour in the human accommodation system. *Ophthalmic & Physiological Optics*, 8, 327–332. [PubMed]
- Hunter, J. D., Milton, J. G., Ludtke, H., Wilhelm, B., & Wilhelm, H. (2000). Spontaneous fluctuations in pupil size are not triggered by lens accommodation. *Vision Research*, 40, 567–573. [PubMed]
- Ishikawa, T. (1962). Fine structure of the human ciliary muscle. *Investigative Ophthalmology*, 1, 587–608.
- Kasthurirangan, S., & Glasser, A. (2005). Characteristics of pupil responses during far-to-near and near-to-far accommodation. *Ophthalmic & Physiological Optics*, 25, 328–339. [PubMed]
- Khosroyani, M., & Hung, G. K. (2002). A dual-mode dynamic model of the human accommodation system. *Bulletin of Mathematical Biology*, 64, 285–299. [PubMed]
- Kotulak, J. C., & Schor, C. M. (1987). The effects of optical vergence, contrast, and luminance on the accommodative response to spatially bandpass filtered targets. *Vision Research*, 27, 1797–1806. [PubMed]
- Latour, P. L. (1962). Visual threshold during eye movements. *Vision Research*, 2, 261–262.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *Journal of the Acoustical Society of America*, 49, 467–477. [PubMed]
- Manning, K. A. (1986). Eye-movement-dependent loss in vision and its time course during vergence. *Journal of Neuroscience*, 6, 1976–1982. [PubMed] [Article]
- Manning, K. A., & Riggs, L. A. (1984). Vergence eye movements and visual suppression. *Vision Research*, 24, 521–526. [PubMed]
- Mitov, D., Vassilev, A., & Manahilov, V. (1981). Transient and sustained masking. *Perception & Psychophysics*, 30, 205–210.
- Mucke, S., Manahilov, V., Strang, N. C., Seidel, D., & Gray, L. S. (2008). New type of perceptual suppression during dynamic ocular accommodation. *Current Biology*, 18, R555–R556. [PubMed]
- Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, 31, 1337–1350. [PubMed]
- Portello, J. K. (2008). Mydriatics and mydriolytics. In J. D. Bartlett & S. D. Jaanus (Eds.), *Clinical ocular pharmacology* (5th ed., pp. 114–117). Boston: Butterworth-Heinemann.
- Rosenbluth, D., & Allman, J. M. (2002). The effect of gaze angle and fixation distance on the responses of neurons in V1, V2, and V4. *Neuron*, 33, 143–149. [PubMed]
- Ruskell, G. L. (1999). Extraocular muscle proprioceptors and proprioception. *Progress in Retinal and Eye Research*, 18, 269–291. [PubMed]
- Schaeffel, F., Wilhelm, H., & Zrenner, E. (1993). Inter-individual variability in the dynamics of natural accommodation in humans: Relation to age and refractive errors. *The Journal of Physiology*, 461, 301–320. [PubMed] [Article]
- Schor, C. M., Alexander, J., Cormack, L., & Stevenson, S. (1992). Negative feedback control model of proximal convergence and accommodation. *Ophthalmic & Physiological Optics*, 12, 307–318. [PubMed]
- Schor, C. M., & Bharadwaj, S. R. (2006). Pulse-step models of control strategies for dynamic ocular accommodation and disaccommodation. *Vision Research*, 46, 242–258. [PubMed]
- Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology*, 43, 482–489. [PubMed]
- Stark, L. R., & Atchison, D. A. (1994). Subject instructions and methods of target presentation in accommodation research. *Investigative Ophthalmology and Visual Science*, 35, 528–537. [PubMed]
- Suryakumar, R., Meyers, J. P., Irving, E. L., & Bobier, W. R. (2007). Application of video-based technology for the simultaneous measurement of accommodation and vergence. *Vision Research*, 47, 260–268. [PubMed]
- Tamm, E. R., & Lütjen-Drecoll, E. (1996). Ciliary body. *Microscopy Research and Technique*, 33, 390–439. [PubMed]

- Volkman, F. C. (1986). Human visual suppression. *Vision Research*, *26*, 1401–1416. [[PubMed](#)]
- Watson, A. B., & Solomon, J. A. (1997). Model of visual contrast gain control and pattern masking. *Journal of the Optical Society of America A, Optics, Image Science, and Vision*, *14*, 2379–2391. [[PubMed](#)]
- Watson, T. L., & Krekelberg, B. (2009). The relationship between saccadic suppression and perceptual stability. *Current Biology*, *19*, 1040–1043. [[PubMed](#)]
- Weber, E. W. (1851) in Donders, F.C. (1864). *Anomalies of accommodation and refraction of the eyes* (pp. 573–575). London: New Sydenham Society.
- Webster, M. A., Georgeson, M. A., & Webster, S. M. (2002). Neural adjustment to image blur. *Nature Neuroscience*, *5*, 839–840. [[PubMed](#)]
- Wolffsohn, J. S., Gilmartin, B., Mallen, E. A., & Tsujimura, S. (2001). Continuous recording of accommodation and pupil size using the Shin-Nippon SRW-5000 autorefractor. *Ophthalmic & Physiological Optics*, *21*, 108–113. [[PubMed](#)]
- Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*, 2070–2089. [[PubMed](#)]