Potential role for microfluctuations as a temporal directional cue to accommodation

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The goal was to revisit an important, yet unproven notion that accommodative microfluctuations facilitate the determination of direction (sign) of abrupt focus changes in the stimulus to accommodation. We contaminated the potential temporal cues from natural accommodative microfluctuations by presenting uncorrelated external (screen) temporal defocus noise that combined with the retinal image effects of natural microfluctuations. A polychromatic Maltese spoke pattern thus either modulated defocus at a combination of two temporal frequencies (on-screen noise condition) or was static (control condition). The on-screen conditions were combined with step changes in optical vergence that were randomized in direction and magnitude. Five subjects monocularly viewed stimuli through a Badal optical system in a Maxwellian view. An artificial 4-mm aperture was imaged at the entrance pupil of the eye. Wavefront aberrations were measured dynamically at 50 Hz using a custom Shack–Hartmann aberrometer. Dynamic changes in the Zernike defocus term with step changes in optical vergence were analyzed. We calculated the percentage of correct directional responses for 1, 2, and 3 D accommodative and disaccommodative step stimuli using preset criteria for latency, velocity, and persistence of the response. The on-screen noise condition reduced the percent-correct responses compared to the static stimulus, suggesting that this manipulation affected the detectability of the sign of the accommodative stimulus. Several possible reasons and implications of this result are discussed.

Introduction

Young prepresbyopic eyes can accommodate or disaccommodate to focus on objects at various distances within the far point. Autofocusing on targets that step nearer or further than the baseline, based only on the signals from retinal blur due to optical vergence, has generally been referred to as reflex accommodation. In the natural environment, combinations of several binocular, monocular, and other spatial cues like size, disparity, and chromatic and monochromatic aberrations might contribute to estimates of the sign of defocus of the object of interest.

Accommodative microfluctuations, commonly seen in prepresbyopes, have been hypothesized to play a potential role in extracting directional (or odd-error) information by acting as a temporal cue (Alpern, 1958; Charman & Heron, 1988, 2015; Crane, 1966; Kotulak & Schor, 1986a); however, that hypothesis is untested. Microfluctuations have also been proposed to maintain an optimal mean level of focus during accommodation (Charman & Heron, 1988, 2015; Winn, 2000). The suggested mechanism for both these potential roles for microfluctuations is to assess the contrast of the retinal image over time, and perform contrast discrimination between the peak and the trough of the micro-contrast fluctuations to direct the focus behavior of the system (Alpern, 1958; Kotulak & Schor, 1986a).

The nature and characteristics of microfluctuations have been studied for many decades (for detailed reviews, see Charman & Heron, 1988, 2015). Several factors affect microfluctuations including age (Ander-

son, Glasser, Manny, & Stuebing, 2010; Heron & Schor, 1995; Mordi & Ciuffreda, 2004; Toshida, Okuyama, & Tokoro, 1998), pupil size (Campbell, Robson, & Westheimer, 1959), mean focus state (Arnulf & Dupuy, 1960; Denieul, 1982; Kotulak & Schor, 1986b), monochromatic aberrations (Chen, Kruger, Hofer, Singer, & Williams, 2006; Chin, Hampson, & Mallen, 2009a, 2009b; Fernandez & Artal, 2005; Hampson, Chin, & Mallen, 2010; Metlapally, Tong, Tahir, & Schor, 2014; Wilson, Decker, & Roorda, 2002), the contrast and spatial frequency composition (Bour, 1981; Denieul, 1982; Denieul & Corno-Martin, 1994), color of the stimulus (Kruger, Aggarwala, Bean, & Mathews, 1997), ametropia (Harb, Thorn, & Troilo, 2006; Sreenivasan, Aslakson, Kornaus, & Thibos, 2013), nature of the task (Sreenivasan et al., 2013), and instructions (Ciuffreda & Hokoda, 1985; L. R. Stark & Atchison, 1994).

Fincham (1951) reported that microfluctuations were only observed in 10% of his subjects, perhaps since a high-resolution optometer was not used in this study. He considered a role for microfluctuations in the detection of stimulus direction by trial and error, but rejected it. Arguments for the even-error (or unsigned) nature of the accommodation system have come from Stark and Takahashi (1965), who found that their subjects responded at chance level to step stimuli in conditions with minimal binocular and monocular spatial cues. Additional support for the even-error theory comes from the work of Troelstra, Zuber, Miller, and Stark (1964) and Phillips and Stark (1977). The odd-error (or signed) theory has been discussed by others (Smithline, 1974), and the origin and role for high-temporal frequency (Campbell, Westheimer, & Robson, 1958) versus low-temporal frequency (Charman & Heron, 1988, 2015; Denieul & Corno-Martin, 1994; Winn, Charman, Pugh, Heron, & Eadie, 1989) components of microfluctuations have been investigated, discussed, and debated, but little has emerged in terms of their role in detection of direction.

The subject of this paper was thus the longstanding broad question of whether the accommodation system derives a temporal directional cue from accommodative microfluctuations in young prepresbyopic subjects. The practicality of the possibility that the system might be sampling focus state to direct focusing behavior is attractive. However, it is interwoven with the difficulty of controlling factors that control either microfluctuations (see above) or accommodation, while studying the influence of one over the other. Earlier studies on accommodative microfluctuations in the detection of accommodation direction or control generally eliminated feedback using an empty field or opened the accommodative control loop using a pinhole (Campbell & Westheimer, 1959; Phillips & Stark, 1977; Westheimer, 1957), or through cycloplegia while external

fluctuations were introduced (Walsh & Charman, 1988) or electro-optical open loop systems (Kruger, Mathews, Katz, Aggarwala, & Nowbotsing, 1997; Phillips & Stark, 1977). Kruger et al. (1997) suggested that feedback from microfluctuations was not required for tracking a monochromatic sine target, but indicated that feedback may not have been fully eliminated at the higher frequencies, and it was unclear whether other residual monochromatic cues were present.

Considering these issues, we chose the less complicated approach of introducing uncorrelated extrinsic defocus noise, by way of screen-rendered temporally varying retinal image blur that exaggerated blur fluctuations caused by natural microfluctuations. Accommodation responds to on-screen defocus just as it responds to optical defocus stimuli (Phillips & Stark, 1977; Smithline, 1974). This assured us that our on-screen defocus movie would be akin to delivering defocused images over time on the retina much like microfluctuations, except exaggerated. Our hypothesis was that if the eye were using the sign information extracted from natural accommodative microfluctuations, then external uncorrelated defocus noise would obscure the temporal signal, reducing the percentage correct responses to unpredictable step stimuli.

Methods

Subjects

The inclusion criteria for subjects and some of the general procedures and apparatus were similar to Metlapally et al. (2014) and are described briefly here. We screened prepresbyopic subjects with normal general and ocular health, low refractive errors, and astigmatism correctable to within 0.5 D, in the age range 18–25 years (average: 23 years). Only those who showed accommodation responses when viewing the stimulus through a Badal imaging system were recruited. Our experience was similar to observations by other groups regarding intersubject variability in accommodative responses (Fincham, 1951; Kruger, Mathews, Aggarwala, & Sanchez, 1993; Kruger, Stark, & Nguyen, 2004; Lee, Stark, Cohen, & Kruger, 1999; Metlapally et al., 2014; Schaeffel, Wilhelm, & Zrenner, 1993; L. R. Stark & Atchison, 1994), where a number of subjects had sluggish or no reflex accommodation responses through the Badal imaging system, possibly due to the potential lack of the size or binocular disparity cues that normally accompany changes in viewing conditions. Twenty-five subjects were screened to obtain the final sample ($n = 5$) for the study. The study procedures followed the tenets of the declaration of Helsinki.
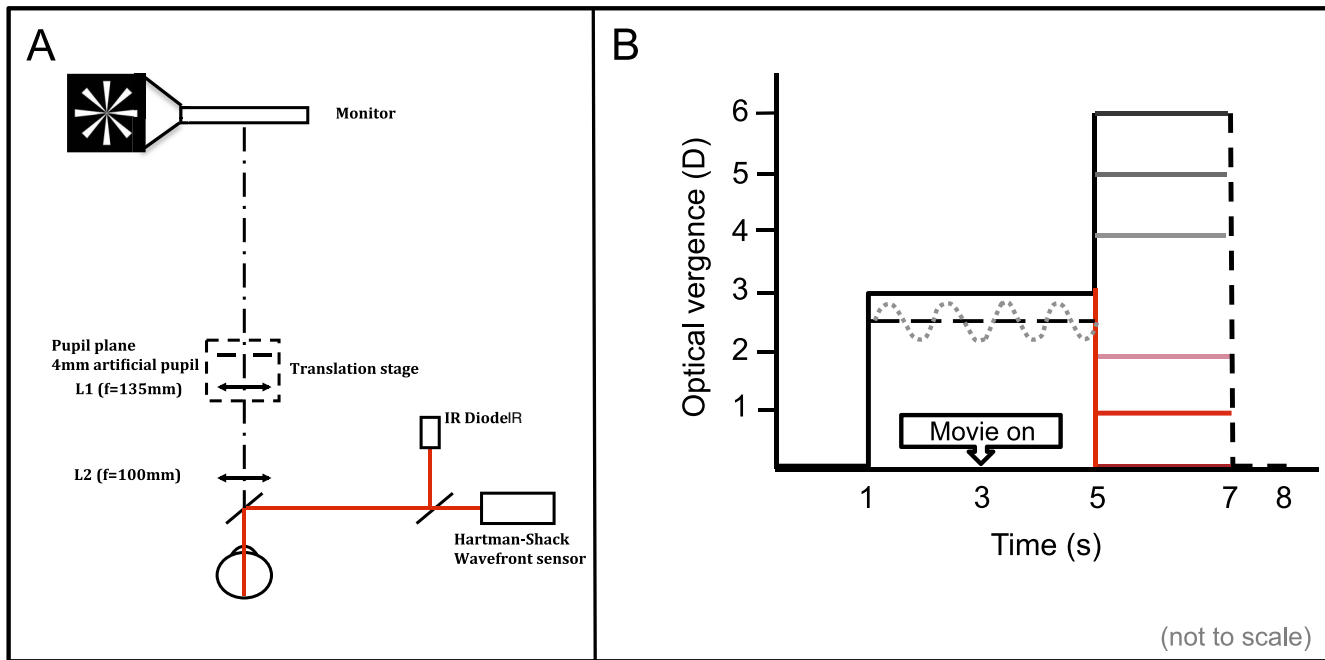
Figure 1. Schematic representations of the set up and time sequence used in the study. (A) Plan view of the arrangement of the apparatus used in the experiments and the static broadband Maltese spoke stimulus displayed on the monitor; (B) Time sequence of the experiment showing the change of the baseline from far to 3-D at 1 s. The wide dashed lines indicate the mean response level showing a lag of accommodation. Natural accommodative microfluctuations about the mean are schematized as a simple sinusoidal fluctuation. A second step occurred 4 s later to one of the six levels shown. For the on-screen stimulus condition showing the defocus blur noise, the movie was turned on 2 s after the first step as we expected a near complete response to the first step by then, and before the second step occurred.

General methods

The stimulus was a polychromatic (black and white), spatially broadband, high-contrast Maltese spoke pattern shown on a high resolution LCD screen (Totoku Electric Co., Ltd., Tokyo, Japan) in a dimly lit room (4.5 cd/m^2). Subjects were stabilized with a headrest and chin cup to minimize head movements and viewed visual stimuli through a Maxwellian view system (Westheimer, 1966; Figure 1A). The Badal system ensured that there were no size changes with the step changes in optical vergence. The steps were produced by translating a collimating lens that imaged the stimulus screen at or within the anterior focal point of the Badal lens. The collimating lens was mounted on an x–y plotter that was driven with analog signals controlled by a computer. A 4-mm artificial pupil was imaged at the entrance pupil of the eye to eliminate variations in pupil size. We also minimized the convergence cue by having subjects view monocularly, and ensured the best alignment of the apparatus possible to minimize lateral movement of the stimulus with step changes. Chromatic cues were available with the polychromatic target. Pharmacological agents were not used to dilate the pupil. Subjects were instructed to pay active attention to the stimulus to keep it as clear as possible.

Wavefront aberrations were measured using a custom built Shack–Hartmann wavefront sensor, using custom written programs. They were sampled dynamically over each 8-s trial at 50 Hz, with custom pupil tracking software to center the measurements during micro eye movements. The high sampling rate ensured that we obtained dynamic estimates of wavefront aberrations at high temporal resolution. The data were fitted with Zernike polynomials up to the sixth order, and for purposes of this paper, we directed most attention to changes in the Zernike defocus term (Z4 or C_2^0).

Refractive errors were corrected so that all the spokes of our stimulus were focused at the beginning of the trial. The accommodative stimulus consisted of two step stimuli. The first step stimulus was introduced 1 s after trial initiation, and changed the baseline from far (infinity) to 33 cm, (a 3 D accommodative step stimulus) and stayed for 4 s. We then presented either accommodative or disaccommodative step stimuli of magnitudes 1, 2, and 3 D lasting 2 s before returning to the original far position (Figure 1B). The trial time sequence and step magnitudes were under computer control, and were completed 125 ms after the trigger.
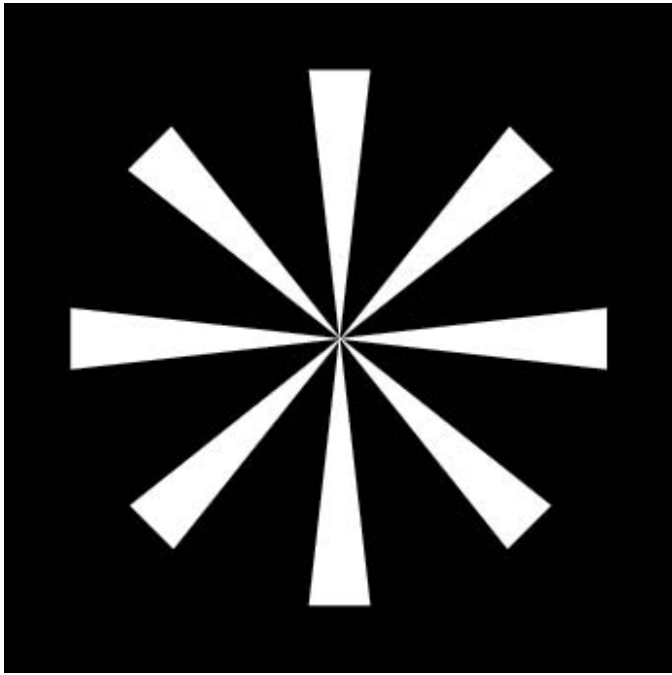
Movie 1. Demonstration of the on-screen defocus fluctuation movie stimulus. This is illustrative, and does not represent the actual resolution or temporal characteristics of the movie used in the experiments.

Visual stimuli used in experiments

Experimental procedures were divided into two sets, based on the on-screen condition. In the first set of experiments, the Maltese spoke target was static. In this control condition, the eye had information available from chromatic aberration, monochromatic higher order aberrations (HOAs) for a 4-mm pupil, and from natural accommodative microfluctuations representing the most number of uncontaminated cues available to subjects in our experiments overall. The natural micro-contrast fluctuations reduced contrast in one direction and increased contrast in the other direction from the mean response level.

In the second set of experiments, we presented a screen-generated defocus noise stimulus that was temporally independent of the natural accommodative fluctuations, and that had contrast fluctuations consistent with a well-focused eye. This noise was presented in the form of an on-screen polychromatic Maltese spoke movie (see Movie 1 for a demonstration). Matlab (The MathWorks, Inc., Natick, MA) and PsychToolBox 3 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997) were used to generate the individual frames of the movie by convolving the Maltese spoke pattern with a temporal defocus noise sequence. Cycling through the frames resulted in simulating defocus blur magnitudes that exaggerated the changes in retinal image quality produced by natural accommodative microfluctuations. The timing in the final movie represented a combination of two component temporal frequencies. The first component had a simulated defocus blur magnitude of 0.5 D and a temporal frequency of 0.5 Hz, and the second component, a simulated defocus blur magnitude of 0.25 D at a temporal frequency 2 Hz. The choices of defocus blur magnitudes and temporal frequencies in the individual components were based on the amplitudes at the respective dominant temporal frequencies of accommodative microfluctuations from power spectrum analyses (Campbell et al., 1959; Kotulak & Schor, 1986b). The screen rendered contrast changes for the noise stimulus fluctuated at twice the frequency of the dioptric fluctuations of the same stimulus. In this condition, over- and under-accommodation from the mean response level caused uncorrelated changes in the contrast of the stimulus. The images simulated 0–0.75 D defocus due to constructive and destructive interference between the two noise frequencies.

All trials started with a static Maltese spoke and had a common first step magnitude of 3 D to change the baseline from far. In the control condition, the Maltese spoke remained unchanged and static throughout the 8-s trial. In the noise condition, the fluctuating stimulus was introduced 2 s after the 3 D step to ensure that accommodation to that step was completed (see time sequence in Figure 1B). Data was collected over several experimental sessions, each lasting no more than 1–1.5 hours to minimize subject fatigue. Seven to nine unique sets comprising 20 eight-second trials (10 accommodation and 10 disaccommodation) were performed twice for each of the two on-screen stimulus types (i.e., static and defocus blur fluctuations). All experimental sets were randomized for sign and magnitudes by intermixing two step magnitudes for accommodation and disaccommodation in each set to minimize predictability.

Analyses

We used a custom Matlab program to visualize the recorded change in the Zernike defocus term over an 8-s trial and to compute the first derivative, the accommodative velocity in D/s. We assigned "yes" (i.e., correct) or "no" (i.e., incorrect) to the initial accommodative responses following presentation of the second step in each trial to compute the percentage of correct responses for the direction of accommodation. A response was expected and usually seen within a latency period of 175–375 ms. We assigned "yes" only if the initial deflection of dioptric change was in the correct direction to compensate for the step change in vergence, and if it satisfied the following
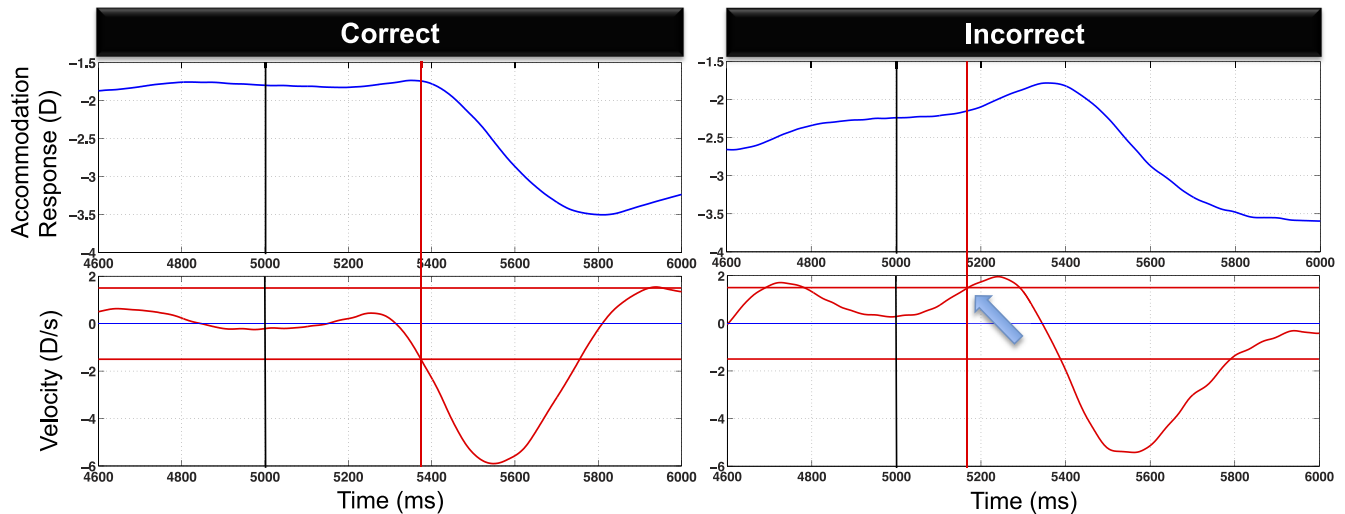
Figure 2. Example correct (left) and incorrect (right) accommodation responses are shown. Top blue traces show dioptric changes over time, and bottom red traces the corresponding changes in accommodative velocity over time for one subject. Two horizontal red straight lines in the bottom traces mark our velocity threshold of 1.5 D/s in either direction. Vertical black lines mark onset of the second step stimulus and vertical red lines mark response onset. The time duration between these two vertical lines represents the response latency. Arrow on the right velocity trace marks both a shorter latency for the subject and an initial response in the wrong direction.

objective criteria based on the laboratory's previous experience.

- Latency criterion: The start of an accommodative response was defined as the instant when the accommodation velocity reached 1.5 D/s, and latency computed as the time elapsed from the presentation of the stimulus to the start of this response. We generated a histogram of the response latencies for individual subjects from the first set of experiments using the static Maltese spoke. The range of latencies about the mode was noted, and responses were assessed as correct only if they occurred within this range. This minimized counting responses as correct if they were predetermined before stimulus presentation (early) due to potential subject bias, or were contaminated by other factors such as a voluntary effort (late).
- Velocity criterion: Responses were only included when there was a systematic change in the direction of accommodation and the response velocity reached at least 1.5 D/s. This minimized including occasional small changes in accommodative velocity that did not become a full-fledged accommodative response.
- Duration criterion: This criterion dictated that the initial deflection should be sustained for at least 150 ms to be included as an actual response in order to avoid including random transient fluctuations.

Example correct and incorrect responses for accommodation and disaccommodation are shown in Figures 2 and 3, respectively. Percentage of correct responses for accommodation and disaccommodation stimuli for step magnitudes of 1, 2, and 3 D were computed separately. When no measurable responses occurred within the latency range for a subject, they were assigned a "yes" or "no" by a coin toss to ensure that chance responses were represented by proportion correct of 0.5 or 50%. These ~3% no-response trials were included because they were valid trials that represent the system's indecision, similar to responses at the chance level. We pooled the percent-correct data for all our subjects for each of the on-screen stimulus conditions separately for accommodation and disaccommodation and analyzed the differences between averaged data using Microsoft® Excel and SPSS software (IBM SPSS® statistics for Macintosh, Version 23, IBM Corp., Armonk, NY).

Results

The mean response level was 2.3 D for the first 3 D step stimulus across all our subjects. The changes in the Zernike defocus term (Z4 or C_2^0) over time at the 3 D baseline were extracted with the goal of documenting the micro-oscillation frequency characteristics of the natural accommodative microfluctuations prior to the second step. They were obtained from two randomly chosen trials over 6 s (~300 samples) in each of our subjects. Fourier amplitude spectra were then obtained and amplitudes were averaged within 0.5 Hz temporal frequency bins. Within this small sample, Figure 4 shows the beginnings of lower (~0.5 Hz) and higher (~2 Hz) frequency peaks as documented previously
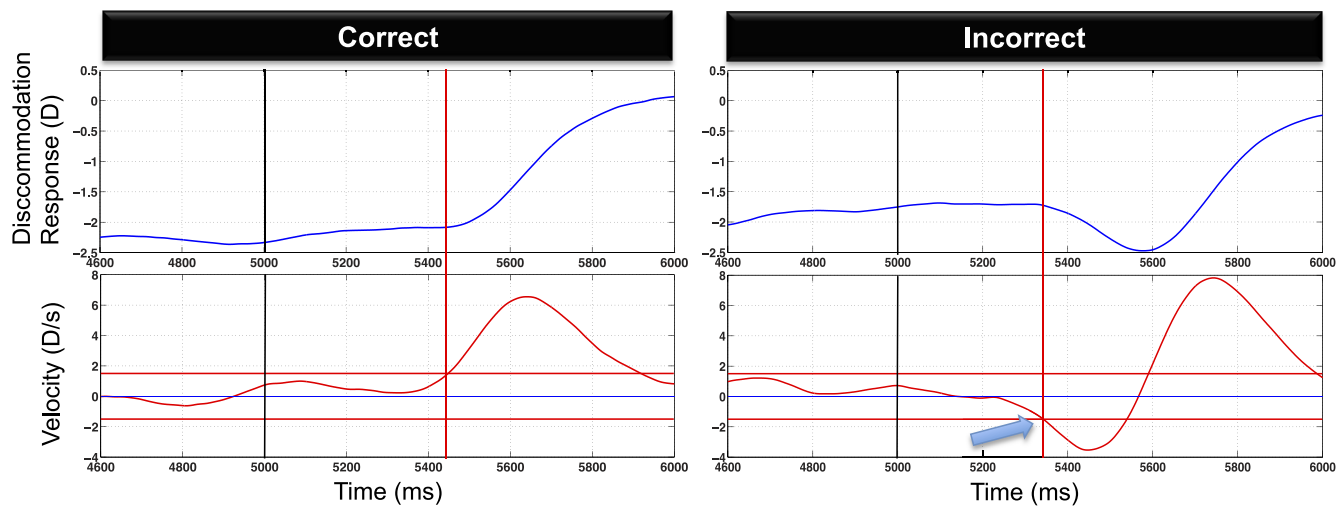
Figure 3. Example correct (left) and incorrect (right) disaccommodation responses are shown. Top blue traces show dioptric changes over time, and bottom red traces the corresponding changes in disaccommodative velocity over time. Arrow on the right velocity trace marks an initial response in the wrong direction. The meanings of the other markers are the same as Figure 2.

(Campbell et al., 1959; Charman & Heron, 1988; Kotulak & Schor, 1986b). The power spectrum characteristics following the introduction of the on-screen noise were investigated in two subjects where enough data was available. The trend (not shown) was of a change in the power spectrum characteristics, with loss of the peak present around 1–2 Hz in the static condition in each of these subjects.

Comparisons between static and fluctuating stimuli

The average percentage of correct responses for five subjects for the static and noise on-screen stimulus conditions and step sizes are plotted in Figure 5. A three-way repeated measures analysis of variance was conducted to examine any interactions between the effects of the on-screen conditions (static and defocus fluctuations), the direction of the step stimuli (accommodation and disaccommodation), and magnitude of the step sizes (1, 2, and 3 D) on percentage of correct directional responses. There were no significant three-way interactions, and a statistically significant interaction was only found between the on-screen conditions and the magnitude of the step sizes on the percent-correct, $F(2, 3) = 12.36$, $p = 0.04$. Importantly, comparisons revealed that the mean percent-correct for the two on-screen conditions were significantly different, $F(1, 4) = 25.52$, $p < 0.01$, where on average, defocus fluctuation noise decreased the percent-correct responses compared to the static stimulus. There was a trend toward increase in the variability of responses amongst subjects for the 3 D accommodative step, particularly for accommodative step stimuli, when the

on-screen stimulus was simulated defocus noise. However, this was not significant on the Levene's test for unequal variances.

For the static Maltese spoke stimulus, two individual subjects demonstrated a trend towards a decrease in the percent-correct responses for accommodation and disaccommodation with increasing step sizes, while three others did not (data not shown). Overall, the group results did not show a fall in the percentage of correct responses with increasing step sizes up to 3 D (i.e., the existence of an "upper defocus limit" in this subject population as proposed by Fincham, 1951).

In addition, we tested if the percent-correct responses were significantly different from chance level, in either direction (above or below chance level). If
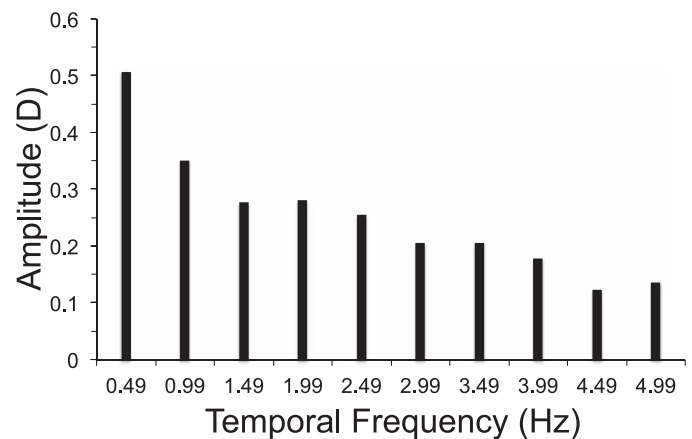

Figure 4. Fourier amplitude spectra of natural accommodative fluctuations of our subjects ($n = 5$) at the 3 D baseline. Amplitudes were averaged in temporal frequency bins and show emergence of peaks at ~0.5 Hz and 2 Hz. The mean (DC) response level was 2.3 D on average.
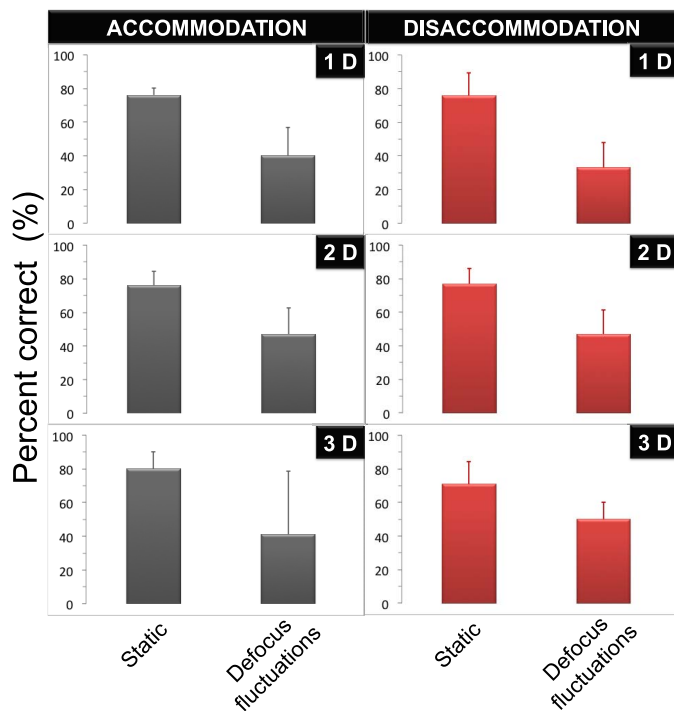
Figure 5. Average percent-correct for *n* = 5 subjects for the two on-screen stimulus conditions and three step sizes used in the experiments. Defocus fluctuations reduced the mean percentage of correct responses for all accommodative and disaccommodative step stimuli of 1, 2, and 3 D. Error bars represent standard deviation.

responses were above chance levels, then the signal (for accommodation or disaccommodation) was perceived and the response was in the intended direction. If the percent-correct responses were found to be significantly below chance, this might mean that a bias caused subjects to perform better than chance without the signal than with it, and responses were in the wrong direction. The static stimulus caused responses above chance level in all the tested conditions ($p \leq 0.05$), while the defocus noise condition caused responses not to differ significantly from chance level, except where it was below chance level for the 1 D disaccommodation condition ($p = 0.03$). We propose that this may have been due to a random variation due to the small sample size, and would expect this to converge to ~50% with additional subjects.

Discussion

We investigated the question of whether the addition of on-screen noise that was exaggerated, but uncorrelated with natural accommodative microfluctuations, would reduce correct responses for accommodative and disaccommodative step stimuli. Our hypothesis was

that if the eye were indeed using the temporal directional information contained in natural microfluctuations, uncorrelated noise would reduce correct performance.

We established that the static on-screen condition caused the responses to be significantly better than chance level for accommodative and disaccommodative step stimuli of 1, 2, and 3 D, implying that the system was able to compute the sign and respond correctly most of the time with the available cues. Stark and Takahashi (1965) suggested several interpretations for the occurrence of greater than chance responses to accommodative stimuli (static on-screen condition in this instance)—first, that accommodative microfluctuations were used to decipher direction, that some other cue such as lateral movement was available (caused by stage translation of the *x–y* plotter in this instance), that the sequence was learned, or that chromatic aberration was used. Accommodative microfluctuations were naturally available uncontaminated to potentially decipher direction. We ensured that lateral movement was minimized, and the presentation sequence of the step stimuli was randomized to avoid learning. Our pilot experiments with monochromatic stimuli (data not shown) largely reduced the percent-correct to chance levels for the static condition, and results were inconsistent among three subjects. Several others have shown that chromaticity of stimuli affect accommodative responses (Kruger, Aggarwala et al., 1997; Kruger et al., 1993; Kruger & Pola, 1986). While some subjects respond or learn to respond in the correct direction for monochromatic signals (e.g., Fincham, 1951), we did not pursue this further. Our design relied on adding defocus noise to investigate any reduction in percent-correct responses, and it would not enable this pursuit if responses were inconsistent or already at chance levels. We also did not attempt to negate native HOAs, which have more recently been investigated as potential cues (Chen et al., 2006; Chin et al., 2009a, 2009b; Fernandez & Artal, 2005; Hampson et al., 2010; Metlapally et al., 2014; Wilson et al., 2002). In particular, spherical aberration, a HOA which generally changes sign from a positive (at far) to a negative value (at near) with accommodation, has been examined for its role in discerning the sign of defocus (Campbell & Westheimer, 1959; Fincham, 1951; Thibos, Bradley, Liu, & Lopez-Gil, 2013). Thibos et al. (2013) have shown that with reducing pupil diameters from 6 to 3 mm, the *effective* spherical aberration changes so that the contrast cue of high contrast for hyperopic blur and low contrast for myopic blur vanishes, as does the strength of the sign of defocus contrast cue. We used 4-mm pupils, and step stimuli were presented at the 3 D baseline where spherical aberration was minimal, largely reducing its

effectiveness as a cue. The contribution of spherical aberration to the strength of contrast increments due to microfluctuations is also negligible at this baseline level (Metlapally et al., 2014). The eye may thus have used signals largely from accommodative microfluctuations and/or chromatic aberration to decipher direction with the static stimulus.

Of more relevance is our finding that extrinsic uncorrelated on-screen defocus noise reduced performance for accommodative and disaccommodative step stimuli of 1, 2, and 3 D. Reduced performance with on-screen noise that was designed to contaminate the signal from microfluctuations suggests that microfluctuations were likely used to extract directional information. Based simply on the nature of on-screen defocus fluctuations, it is conceivable that one spatial cue from natural microfluctuations could be micro-contrast variations at certain mid-to-high spatial frequencies, detectable within the upper defocus limit (Metlapally et al., 2014). These micro-contrast signals are unavailable or unreliable during presentation of the on-screen defocus noise. Further, computation of the variations in contrast between low versus high spatial frequencies is likely to occur at edges of the spokes and their spacing of the Maltese spoke pattern. This is because it has the profile of a square-wave grating, whose fundamental frequency gradually decreases radially from the center to the periphery of the pattern, with the highest contrast gradient at the edge of the spokes against the background. This computation may have been hampered by the on-screen defocus noise. Additionally, contrast gradients contained within small visual angles are crucial for the perception of low-frequency components of stimuli (Campbell, Johnstone, & Ross, 1981). We speculate that defocus from the second step stimulus, in addition to natural and on-screen microfluctuations, might not have produced sufficient contrast gradients for detection of low-frequency information immediately following its presentation.

A second spatial cue that could be misleading the system in this condition is phase alignment. Simulated defocus together with the eye's natural HOAs cause lateral phase shifts (Walsh & Charman, 1989) that cannot be corrected by refocusing in the noise condition. Information from chromatic and monochromatic aberrations is a third spatial cue regarding the sign of defocus of the step stimulus that may have been obscured during presentation of the on-screen noise, whose chromatic aberration did not vary with changes in rendered blur. This could have reduced the response rates. Our results do not distinguish whether the noise hampered the signal contained in microfluctuations or signals from other spatial cues like chromatic or monochromatic aberrations.

In addition to spatial attributes, there were clear differences in the temporal characteristics of the retinal image quality changes between the two on-screen conditions. During the presentation of the static step stimulus, micro-contrast fluctuations produced by natural accommodative microfluctuations were the same temporal frequency as the natural dioptric fluctuations. Over- or underaccommodation in this condition reduced or improved the contrast in one direction as opposed to the other. In contrast, the competing noise created by the on-screen defocus blur fluctuation was temporally independent of natural accommodation fluctuations. Over- and underaccommodation always blurred the stimulus independent of the simulated sign of defocus, impairing responses to the step stimuli in this condition. Also, the on-screen contrast fluctuations were at twice the temporal frequency as the dioptric fluctuations of the same stimulus, at the frequency that would signal an in-focus image. This temporal frequency characteristic would have minimized any interactions between the on-screen and natural accommodative microfluctuations and prevented any spurious signals that increased or decreased the rate of correct directional responses to our step stimulus. Concurrently, this attribute of the noise stimulus could have been responsible for the reduced response rate in this condition. While we did not examine this in detail, if the power spectrum characteristics of natural microfluctuations were altered due to the on-screen noise as seen in two subjects, or were a phase-lagged mimicry of the on-screen noise as shown by Mathews and Kruger (1994), we might have contaminated a potential signal from microfluctuations by altering its innate temporal characteristics.

It is not clear whether or how the eye distinguished between screen-rendered blur fluctuations (extrinsic) from natural microfluctuations (intrinsic noise from the eye's motor apparatus). We know that temporal changes in defocus during natural microfluctuations would be accompanied by changes in axial (longitudinal) chromatic aberration, but temporal changes in rendered defocus would not change chromatic aberration. It is possible that the system perceived the subtle changes in chromatic aberration with natural microfluctuations, which was obscured by or in conflict with screen-rendered fluctuations. Our premise was that if accommodation used intrinsic blur fluctuations, the extrinsic noise would make it especially hard, suggesting a potential role for them. On the other hand, due to the combined spatial and temporal attributes of the on-screen stimulus, or the exaggerated blur magnitude in the noise condition (extrinsic + intrinsic noise), the task might simply have been difficult. Thus reduced performance might have occurred even when natural microfluctuations poten-

tially had no role in detection of direction. If the addition of extrinsic noise had not changed performance, we could have perhaps concluded more definitively that natural microfluctuations were not used. Our result thus leaves the possibility open that microfluctuations could be used to determine accommodation direction, but not conclusively.

In summary, our experiments took a novel, uncomplicated approach for studying the role of accommodative microfluctuations in determining the direction of responses, and since our subjects responded at consistently low rates to screen-rendered defocus fluctuations, it is possible that this condition affected one or more cues our subjects used in their natural environment. This is despite different internal (optical and neural) profiles, criteria, preferences, or weights for different directional cues, which could all potentially vary their accommodative responses in impoverished conditions (Kruger, Mathews et al., 1997; Metlapally et al., 2014). We conclude that a role for microfluctuations in determining accommodation direction is still worthy of consideration while the field awaits other controlled approaches to tease out the specific contributions of each of the related and confounding factors.

Keywords: accommodation, microfluctuations, accommodation control, aberration

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