5

ACCOMMODATION DYNAMICS

Niall C. Strang, PhD, FCOptom and Mhairi Day, PhD, MCOptom

DYNAMIC ACCOMMODATION RESPONSE

In many practical situations, it is necessary to change accommodation rapidly as fixation moves between objects at differing distances. Alternatively, the object of interest may be approaching or receding. Thus, the dynamic, as well as the static, aspects of the accommodation system are of interest. As will be discussed below, it is striking that, although the amplitude of accommodation declines steadily with age, the dynamics of the responses within the available amplitude show only relatively minor changes until the accommodation breaks down completely at approximately age 50 years. It should be noted that most of the studies cited were carried out under monocular conditions of observation.

Although Collins[1] was able to continuously record the optical power of the eye as long ago as 1937, it was not until more than 2 decades later that a systematic investigation of the accommodation dynamics was carried out with the use of an infrared, continuously recording optometer.[2] The study by Campbell and Westheimer[2] and subsequent studies have allowed us to understand the major characteristics of the accommodation dynamics. Temporally changing stimuli used to explore accommodation include steps, sinusoids, pulses, and ramps (Figure 5-1). Some response characteristics to these stimuli have been found to vary significantly with direction of accommodation (near-to-far [N-F] or far-to-near [F-N]), response amplitude, and starting point. Most responses show some variation with the patient's age. A summary of the results is given in the sections that follow. The results will be interpreted on the assumption that the visual system contains some form of "controller," which continuously monitors the quality of the perceived image of the object of interest and uses this information to actively adjust the accommodation to an appropriate level.

ACCOMMODATION MICROFLUCTUATIONS

When Collins[1] built the first continuously recording, infrared optometer, he noticed fluctuations in the ocular power during nominally "steady-state" accommodation to an object at a constant distance. These fluctuations were of small amplitude and could not be attributed to imperfections of his recording apparatus. Collins thought that the fluctuations were "an abnormality or a physiological variation with no significant purpose," although he also recognized their potential for providing information about changes in image clarity to the accommodation controller. Later work found microfluctuation amplitudes of up to 0.50 D,[3,4] and a frequency spectrum with 2 distinct peaks—one

Pallikaris IG, Plainis S, Charman WN.
Presbyopia: Origins, Effects, and Treatment (pp. 41-50).

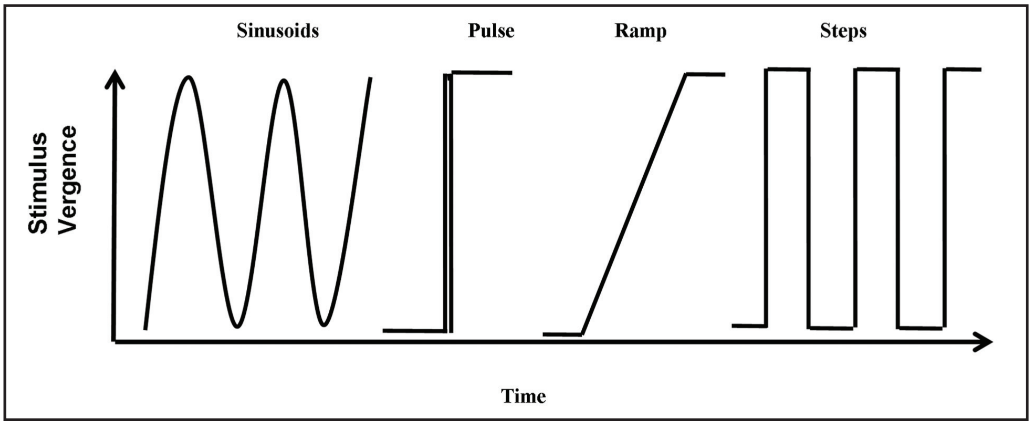


Figure 5-1. The changes in stimulus vergence with time in sinusoidal, pulse, ramp, and step stimuli.

below 0.6 Hz (the low-frequency component [LFC]) and a second between 1 to 2 Hz (the high-frequency component [HFC]).[3,5] The HFC has been linked to heartbeat and arterial pulse,[6] and the LFC has been linked to pulmonary responses.[7] Two mechanisms have been suggested to explain the origin of the HFC: (1) that the ciliary body changes according to its blood volume and thereby causes rhythmic shape changes in the crystalline lens or (2) that the pulse of the intraocular pressure generates forces that change the axial position of the lens.[8]

Both the LFC and the overall magnitude of the microfluctuations have been shown to change according to alterations in accommodation demand,[9] target spatial frequency (SF),[4] pupil size,[3,5,10,11] and target luminance[11,12] (Figure 5-2). The existence of systematic relationships between these stimulus characteristics and the magnitude of the accommodation microfluctuations suggest that the microfluctuations, specifically the LFC, play an active role in providing negative feedback for continuous control of the accommodation response amplitude.[5,9,12,13]

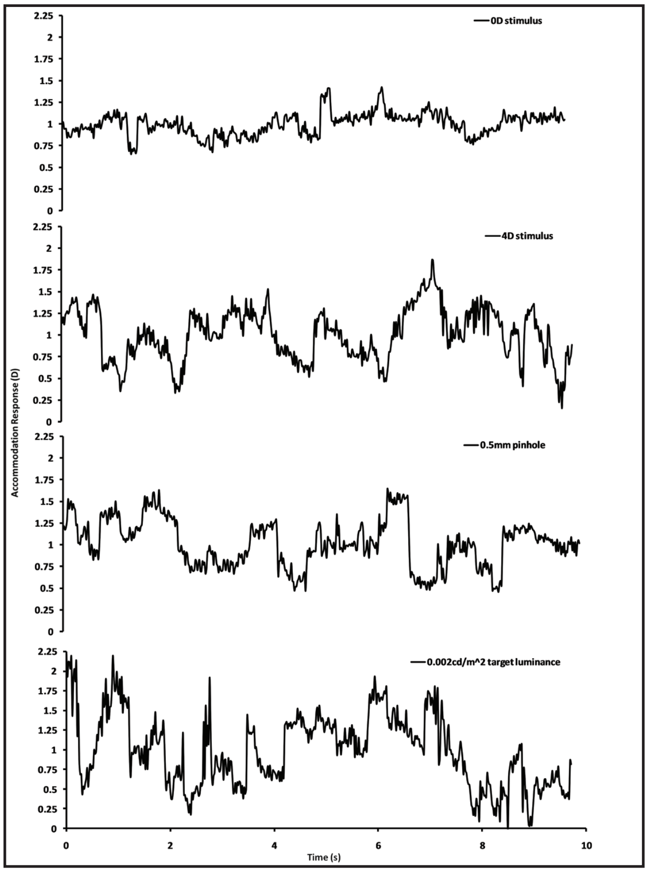


Figure 5-2. Continuous accommodation recordings while a patient viewed a Maltese cross target at 0.00 and 4.00 D target vergence[9] and when the target was placed at the resting state of the patient's accommodation and viewed through a 0.5-mm artificial pupil or at a target.

It is well established that the accommodation error detector uses image contrast to monitor the level of cortical image blur within a closed-loop, negative feedback system and responds to changes in the level of cortical image blur to maintain image clarity. Recent analysis suggests that the accommodation system monitors the maximum gradient of illuminance contained within the cortical image produced by a target and uses this information to determine the required direction of response.[4,11] This illuminance gradient is reduced in some conditions (eg, when viewing low luminance targets), where the high SF information contained within a target containing a broad bandwidth of SFs is filtered out by the neural system or when viewing a low (≤1 cpd) or a high (≥16 cpd) SF sine-wave target.[4] In all of these conditions, the maximum illuminance gradient contained within the cortical image is shallow, and it has been found that the microfluctuations increase in magnitude (see Figure 5-2).[4] Microfluctuations are thought to do this to provide a consistent error signal to the accommodation controller. In addition to a reduction in illuminance gradient, there is an increase in the depth of focus (DOF) when viewing these targets.

Some of the effects of different stimulus and viewing conditions are shown in Figure 5-2. The lower 2 traces show the waveforms produced when the microfluctuations were recorded while the patient observed a low luminance target and a target through a small pupil. In both cases, the target was placed at the resting state of the patient's accommodation (ie, his or her open-loop level), so that the response would not be influenced by the target vergence. Note the relatively unstable response, with low-frequency microfluctuations of large amplitude. Figure 5-2 also shows the "steady-state" accommodation response at 2 levels of accommodation demand (0.00 and 4.00 D, upper 2 traces). Microfluctuations are of small magnitude for the 0.00 D distant stimulus but increase at 4.00 D.

As mentioned previously, it is the LFC that is thought to contain the feedback information used by the accommodation control system.

In the case of small pupils, the microfluctuations appear to increase in magnitude solely in response to an increase in DOF.[5,11] In fact, the size of the microfluctuations is approximately equivalent to the DOF of the eye at any given time,[14] and as a result we are not perceptually aware of the presence of the microfluctuations.[15]

A general trend toward an increase in microfluctuation amplitude with increasing accommodation level is noted.[9,16,17] In this case, it is hypothesized that the increased magnitude of microfluctuations results from a greater movement of the lens as the lens zonules relax during accommodation.[9] It is not known whether this is noise or is under neurological control, because some studies report an increase in the LFC with increasing accommodation, and others report an increase in the HFC.

Continuously recording aberrometers have recently been developed to measure microfluctuations of the different aberration components of the wavefront error. Results suggest that defocus is the largest component of the microfluctuation response but that other wavefront aberrations are also involved.[18] However, the contribution of dynamic ocular surface power changes to the overall microfluctuations is thought to be minimal.[19]

Under given stimulus conditions, aging appears to have the effect of reducing the amplitude of all frequency components within the power spectrum of the microfluctuations.[20,21] This reduction is thought to result from a reduced elasticity in the lens zonules and/or capsule.[20]

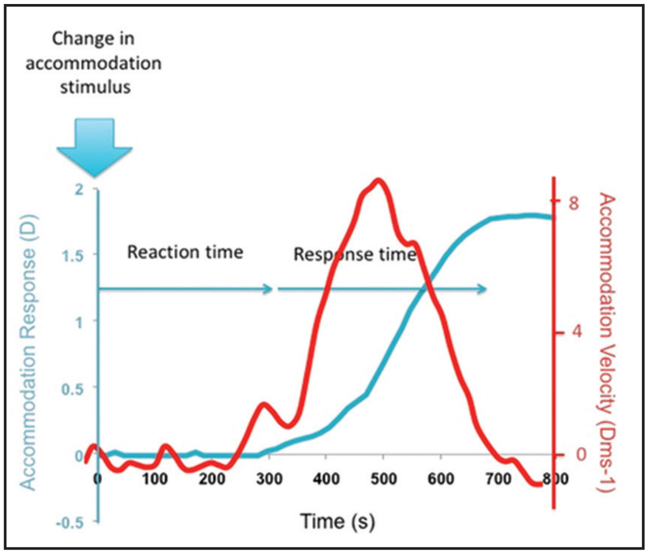


Figure 5-3. A typical dioptric accommodation response (blue curve) and the corresponding rate of change with time (ie, its velocity [red curve]) for a 2.00-D accommodation step stimulus, the onset of which occurs at zero seconds.

Accommodation Step Responses

A "step" change in the accommodation stimulus is a frequently encountered situation where accommodation must change abruptly to focus objects at different distances following a change in fixation. The typical characteristics of a 2.00-D accommodation step response are shown in Figure 5-3. Figure 5-3 shows a typical dioptric accommodation response (blue curve) and the corresponding rate of change with time (ie, its velocity [red curve] for a 2.00-D accommodation step stimulus), the onset of which occurs at zero seconds.

Accommodation Reaction Time

As shown in Figure 5-3, dynamic accommodation responses are executed after a reaction time, or latency period, which is approximately 300 ms.[22-24] Although reaction time does not appear to change systematically with changes in accommodation amplitude,[25] dioptric starting point, direction of accommodation,[25] and age,[26] considerable differences are found in the values reported in the literature (Table 5-1). These differences are thought to reflect several factors, such as the

TABLE 5-1. *REACTION AND RESPONSE TIMES OF DYNAMIC ACCOMMODATION*

AUTHORS	REACTION TIME (S)		RESPONSE TIME (S)	
	F-N	N-F	F-N	N-F
Campbell and Westheimer (1960)[2]	0.36±0.09	0.38±0.08	0.64	0.56
Shirachi et al (1978)[27]	0.36	0.40		
Beers and van der Heijde (1996)[28]			F-N>N-F both increasing with age	
Tucker and Charman (1979)[25]	0.29±0.07	0.34±0.13	0.75±0.31	1.18±0.54
			No age-related changes	
Heron et al (1999)[29]	0.34±0.1	0.35±0.1	0.53±0.18	0.56±0.24
Culhane and Winn (1999)[30]	0.25±0.15	0.24±0.15	1.06±0.32	1.44±0.44
Kasthurirangan et al (2003)[31]	0.2-0.5		F-N>N-F	
Rucker and Kruger (2004)[32]			F-N<N-F	
Blue	0.31	0.58		
Yellow	0.49	0.34		
Blue/Yellow	0.47	0.39		
Blue/Yellow/LCA	0.47	0.30		
Kasthurirangan and Glasser (2005)[33]	0.226	0.231	near range < far range	near range < far range
Bharadwaj & Schor (2006)[22]		0.28-0.43		near range < far range

Note: Reaction and response times are separated by direction of accommodation responses. Additional information relating to age and experimental conditions is provided where appropriate.

patient's level of alertness and the training received during experiments, differences in the visual stimuli used to elicit accommodation responses, instructions given to the patient, and the criterion used to define the onset of the response.[34] The reaction time of the pupil to a near target (0.32 s) is longer than that to light (0.24 s), reflecting the longer pathways of accommodation and near pupil responses compared to the light reflex. A more recent study comparing accommodation and near pupil latencies found that the accommodation reaction time (average 0.226 s) is also significantly shorter than the pupil response reaction time (average 0.311 s).[33]

Accommodation Response Time

Accommodation response time, or the time taken to execute a response and reach a new, stable response level (see Figure 5-3), has been shown to depend on the amplitude of the F-N accommodation response,[31] summarized in Table 5-1, but not the amplitude of the N-F response[35] or the dioptric starting point.[35-37] A number of studies reported that response time is unaffected by age, up to approximately 40, if the required response lies within the available accommodation range.[25]

Peak Velocity of Accommodation

The peak velocity of the accommodation response depends primarily on the dioptric starting point, the direction (F-N versus N-F) of accommodation,[26,33] and to a lesser degree on the amplitude of the accommodation response.[31]

Age-related changes in accommodation velocity appear to be a more complicated topic than one would predict.[31] Although Heron et al[26,29,38] reported that the peak accommodation velocity remains almost unaffected by age, it has also been shown to decline with age under some conditions.[35,39] These differences in conclusions seem to be due to methodological differences, where Heron et al[26,32,33] studied relatively small responses within the patient's existing amplitude of accommodation, whereas Beers and van der Heijde[28] used patients up to 55 years old and Schaeffel et al[39] used 5.00 D stimuli. Beers and van der Heijde[28] suggested that the reduction of accommodation velocity with age is due to a reduction in the viscoelastic properties of the lens itself, rather than the elastic properties of the lens zonules or choroid because the velocity of F-N and N-F steps were similarly affected by age.

Acceleration

Unlike step duration and maximum velocity, the acceleration characteristics have been found by Bharadwaj and Schor[40] to be independent of step size for F-N steps. When investigating solely N-F accommodation dynamics, Bharadwaj and Schor[22] demonstrated that, for a constant near-target vergence, the peak acceleration was independent of step magnitude, although the peak acceleration became larger if the near target was closer, regardless of whether it was a larger or same-sized step. The time to peak acceleration was independent of all parameters. Bharadwaj and Schor[40] found that peak acceleration in 40 year olds was only about half that of 20 year olds.

Direction

With monocular viewing, monochromatic light, and pure defocus, the blurred retinal image is similar under both positive defocus (where the light is focused in front of the retina) and negative defocus (where the light is focused behind the retina). Thus, the defocus image blur provides no cue to the direction of accommodation response required (ie, it is an even-error cue). When only this even-error or magnitude information is provided, accommodation step responses start in the wrong direction 50% of the time.[41] Bour[42] found that more than 50% of steps were in the correct direction, but suggested that the presence of errors gives weight to the idea of the accommodation step response being primarily even-error, with secondary cues providing odd-error, or directional, information. Odd-error cues to direction may be given both by monochromatic ocular wavefront aberration and by chromatic aberration (see Chapter 6). Under binocular conditions, disparity provides a further cue. Overshoots and oscillations in the response have been noted to be larger for smaller-amplitude accommodation steps—the former are thought to be bigger and more frequent as the near target gets closer.[22]

SINUSOIDAL ACCOMMODATION RESPONSES

When a dioptric stimulus changes sinusoidally with time, the accommodation system responds in a similar fashion as the stimulus, at the same frequency.[2] The gain of the response (ie, the dioptric amplitude of the response divided by that of the stimulus) decreases linearly with increases in temporal frequency, while the phase lag (ie, the fraction of the temporal period by which the response lags behind the stimulus, multiplied by 360 degrees), increases linearly.[2,34,43] The reduction in gain with increasing temporal frequency for ages 20 to 50 years is replotted from Heron et al[29] in Figure 5-4. It can be seen that the rate of change in gain with temporal frequency decreases approximately 0.2 units/Hz for each decade of life between 20 and 50 years.

For slow sinusoids (ie, low temporal frequency), the response occurs in a series of steps rather than following a smooth curve.[2] The maximum frequency of oscillation for which any kind of a response is obtained is 2 to 4 Hz, which is essentially independent of age.[2,38]

Sinusoidal responses have been found to be most accurate to mid-SF targets (between 3 and 5 cpd)[44]—adding a 3-cpd harmonic increases accommodation accuracy to a 1-cpd sinusoidally moving grating, although there is no change in accommodation accuracy when adding 9 cpd to a 3-cpd target nor 15 cpd to a 5-cpd grating.[45] These results add weight to the contrast control hypothesis, where the accommodation system responds to changes in perceived retinal image contrast.

Manipulation of ocular chromatic aberrations produces changes in the accommodation response to a sinusoidally moving stimulus over a 1.00-D range.[46] This supports the view that chromatic aberration provides an odd-error cue to guide the direction of the accommodation response (see Chapter 6).

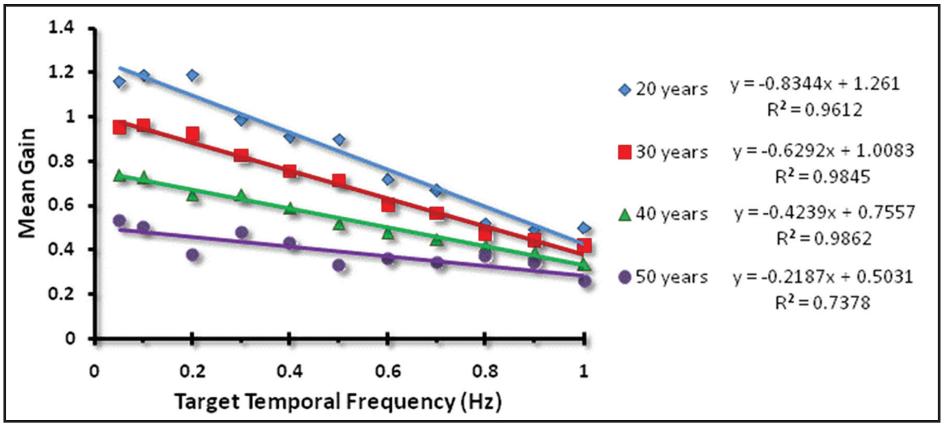


Figure 5-4. The mean gain as a function of temporal frequency of a sinusoidally moving target for patients aged 20, 30, 40, and 50 years. (Based on data compiled and replotted from Heron G, Charman WN, Gray LS. Accommodation responses and ageing. *Invest Ophthalmol Vis Sci.* 1999;40(12):2872-2883.)

PULSES

Campbell and Westheimer[2] elicited dynamic accommodation responses in their patients with pulse stimuli as short as 100 ms in duration, although the accommodation target had returned to its starting position within reaction time of accommodation. The authors[2] concluded that accommodation employs "a continuous monitoring system and that an accommodation movement can be halted during its progress." More recent computational models of dynamic accommodation[24,47] generally agree with these conclusions, although preprogrammed steps elicited in all the models cannot be stopped. It appears that pulse stimuli of amplitude higher than 2.00 D would need to be tested to find operating ranges of continuous visual feedback and response amplitudes of preprogrammed step responses.

RAMPS

Focus must sometimes be maintained on an object moving continuously in depth. Ramp stimuli are those in which the dioptric stimulus changes linearly with time (see Figure 5-1). Slow ramp stimuli produce smooth ramp responses, but fast ramp stimuli produce accommodation step responses, and intermediate velocity stimuli result in a mixture of the two.[47] This suggests that the accommodation system is composed of a fast component with an element of preprogramming and a second slower element, which may utilize feedback.[47] Recently, Mucke et al[48] have shown that high-SF information is suppressed during fast accommodation ramp responses >3 ms (effectively step responses) but not during slower ramp responses where active feedback is likely.

MECHANISMS OF DYNAMIC ACCOMMODATION RESPONSES

Feedback During a Dynamic Accommodation Response

Several studies examining the accommodation step response have modeled it with a single-step input into the system.[28,49,50] This basic model suggests that, as the accommodation response becomes larger, there is a proportional increase in peak velocity and acceleration. This theory was highly regarded until recently, when acceleration was measured. It was found that, as response increased, there was an increase in peak velocity but not acceleration.[40] Therefore, an opposing theory of dual-innervation input has been hypothesized, where there is an initial open-loop component that is independent of response magnitude, combined with a second closed-loop component that is in proportion to the size of response.[40] The results of the responses to ramp stimuli also suggest a 2-component system—a fast, preprogrammed component combined with a slower one, utilizing continuous feedback.[47]

Considering the influence of different SF components in the spatial target, step responses to targets of varying SF content were recorded in an early study.[42] A reduction in dynamic accommodation responses to low and high SF targets were observed.[42] The small reduction in response for the 1-cpd target compared to 4 cpd was explained by increased DOF for the lower SF target.[42] The reduction in accuracy for the high SF targets was consolidated by a reduction in the magnitude of the step response as step size increased, which was explained by the fact that patients were not able to see the higher SF information due to the amount of defocus present in the larger steps.[42,51] In a different study, responses to 4.00-D steps of ≤4 cpd sinusoidal grating targets were reasonably accurate, but as SF increased, they became less accurate until they were random at 16 cpd.[52]

From these results, it is thought that the accommodation system uses low SF information to guide that initial response and then higher SFs for accurate focusing.[42,52,53] In addition, the accuracy of the dynamic response can be increased by having chromatic aberration in the correct direction[32,46] and reduced by having no chromatic aberration[32] or chromatic aberration in which the colors are reversed.[46] Monochromatic aberrations also appear to be helpful, as they result in the blur of the retinal image no longer being the same for equal amounts of positive and negative defocus and hence provide an odd-error cue to the correct direction of accommodation (see Chapter 6).

Recently, it was demonstrated that dynamic ocular accommodation reduces visual sensitivity to fine image detail.[54] Reduced visual sensitivity during dynamic accommodation does not occur around the onset of a dynamic accommodation response, but rather it reduces visual sensitivity as soon as a critical accommodation velocity is exceeded.[48] 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. In the future, it will be interesting to see whether changes in response produced by accommodating IOLs will provide appropriate signals to enable neural changes to occur.

Mechanisms Underlying Directional Accommodation Response Differences

As both biochemical and neurophysiological features of the accommodation response are different during F-N and N-F accommodation, either could be responsible for the directional differences that exist.[31] During F-N accommodation, the ciliary body actively moves inward, reducing tension on the zonules and allowing the lens to change in shape. In N-F accommodation, the ciliary muscle reverts to its original position, causing an increase in zonular tension and tightening on the lens, pulling it back to a more flattened shape. Near-to-far accommodation relies on a more passive innervational process consisting of a reduction in parasympathetic innervation, which is accompanied by an increase in sympathetic innervation in 25% to 30% of individuals.[55] It is possible that, in an F-N step, there is a set amount of innervation reaching the ciliary muscle that causes a consistent acceleration, the velocity of the response increasing with larger step sizes. Another possible explanation is neurophysiological. Near-to-far changes in the accommodation response may not use negative feedback, as the accommodation system travels back to an unaccommodated or tonic accommodation level; in contrast, feedback is crucial to allow an accurate response in an F-N step.[31]

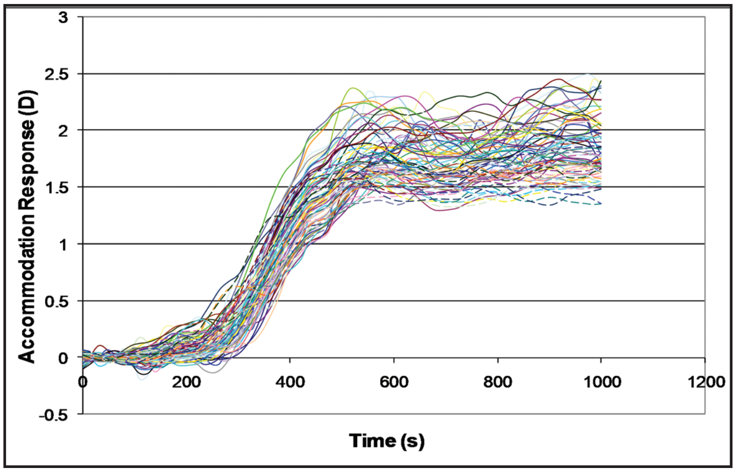
INTRAPATIENT AND INTERPATIENT VARIABILITY

As alluded to earlier in this chapter, various characteristics of the accommodation response have marked intrapatient (Figure 5-5) and interpatient variability. Kasthurirangan et al[31] found such variations in dynamic step responses, and between-subject differences have been found in one of the fundamental elements of the accommodation system, the sympathetic innervation.[56] Variations in accommodation lags[57] and steps,[31] as well as errors and microfluctuations at all levels of accommodative reading demand, have been found between patients.[58] The interpatient variabilities probably result because the main driver of accommodation response varies between individuals. For example, interindividual variations in the ocular aberrations and their changes with accommodation have been reported.[59] Patients also differ in their use of chromatic aberration as a cue.[60,61]

SUMMARY OF THE DYNAMIC ACCOMMODATION SYSTEM

When viewing a stationary target, accommodation microfluctuations occur. The accommodation system can respond within approximately 1 second to abrupt or other changes in stimulus vergence. Step changes have been studied in most detail, as they occur most frequently in everyday life. Step responses are thought

Figure 5-5. The variability of the accommodation response dynamics. The figure shows 100 measures of a 2.00-D step response taken in one 32-year-old individual over a short time period.



to be composed of 2 components. The first occurs when there is a large accommodation error and is a fast, open-loop, intermittently sampling response. The response is then refined using the slower, continuously sampling, closed-loop retinotopic system.

Although, as age increases, the objective amplitude of accommodation declines to reach essentially zero by the approximate age of 50 years; within the available, increasingly limited amplitude of accommodation, the speed of the response is quite well maintained, and the response to a step is usually completed within approximately 2 seconds. This sets a goal for the dynamic characteristics of any "active" correction for presbyopes, such as accommodating IOLs. This information needs to be considered when different mechanisms for producing accommodating IOLs are developed.

REFERENCES

1. Collins M. The electronic refractometer. *Br J Physiol Opt*. 1937;1(1):30-42.
2. Campbell FW, Westheimer G. Dynamics of accommodation responses of the human eye. *J Physiol*. 1960;151:285-295.
3. Campbell FW, Robson JG, Westheimer G. Fluctuations of accommodation under steady viewing conditions. *J Physiol*. 1959;145(3):579-594.
4. Day M, Gray LS, Seidel D, Strang NC. The relationship between object spatial profile and accommodation microfluctuations in emmetropes and myopes. *J Vis*. 2009;9(10):5.1-5.13.
5. Gray LS, Winn B, Gilmartin B. Accommodative microfluctuations and pupil diameter. *Vision Res*. 1993;33(15):2083-2090.
6. Winn B, Pugh JR, Gilmartin B, Owens H. Arterial pulse modulates steady-state ocular accommodation. *Curr Eye Res*. 1990;9(10):971-975.
7. Collins M, Davis B, Wood J. Microfluctuations of steady-state accommodation and the cardiopulmonary system. *Vision Res*. 1995;35(17):2491-2502.
8. Owens H, Winn B, Gilmartin B, Pugh JR. Effect of a topical beta-adrenergic receptor antagonist on the dynamics of steady-state accommodation. *Ophthalmic Physiol Opt*. 1991;11(2):99-104.
9. Day M, Strang NC, Seidel D, Gray LS, Mallen EA. Refractive group differences in accommodation microfluctuations with changing accommodation stimulus. *Ophthalmic Physiol Opt*. 2006;26(1):88-96.
10. Stark LR, Atchison DA. Pupil size, mean accommodation response and the fluctuations of accommodation. *Ophthalmic Physiol Opt*. 1997;17(4):316-323.
11. Day M, Seidel D, Gray LS, Strang NC. The effect of modulating ocular depth of focus upon accommodation microfluctuations in myopic and emmetropic subjects. *Vision Res*. 2009;49(2):211-218.
12. Gray LS, Winn B, Gilmartin B. Effect of target luminance on microfluctuations of accommodation. *Ophthalmic Physiol Opt*. 1993;13(3):258-265.
13. Charman WN, Heron G. Fluctuations in accommodation: a review. *Ophthalmic Physiol Opt*. 1988;8(2):153-164.
14. Winn B, Charman WN, Pugh JR, Heron G, Eadie AS. Perceptual detectability of ocular accommodation microfluctuations. *J Opt Soc Am A*. 1989;6(3):459-462.
15. Kotulak JC, Schor CM. The accommodative response to subthreshold blur and to perceptual fading during the Troxler phenomenon. *Perception*. 1986;15(1):7-15.
16. Leahy C, Leroux C, Dainty C, Diaz-Santana L. Temporal dynamics and statistical characteristics of the microfluctuations of accommodation: dependence on the mean accommodative effort. *Opt Express*. 2010;18(3):2668-2681.
17. Miege C, Denieul P. Mean response and oscillations of accommodation for various stimulus vergences in relation to accommodation feedback control. *Ophthalmic Physiol Opt*. 1988;8(2):165-171.
18. Hofer H, Artal P, Singer B, Aragon JL, Williams DR. Dynamics of the eye's wave aberration. *J Opt Soc Am A Opt Image Sci Vis*. 2001;18(3):497-506.
19. Zhu M, Collins MJ, Iskander DR. The contribution of accommodation and the ocular surface to the microfluctuations of wavefront aberrations of the eye. *Ophthalmic Physiol Opt*. 2006;26(5):439-446.
20. Heron G, Schor C. The fluctuations of accommodation and ageing. *Ophthalmic Physiol Opt*. 1995;15(5):445-459.
21. Mordi JA, Ciuffreda KJ. Dynamic aspects of accommodation: age and presbyopia. *Vision Res*. 2004;44(6):591-601.

22. Bharadwaj SR, Schor CM. Dynamic control of ocular disaccommodation: first and second-order dynamics. *Vision Res*. 2006;46(6-7):1019-1037.
23. Schor CM, Bharadwaj SR. A pulse-step model of accommodation dynamics in the aging eye. *Vision Res*. 2005;45(10):1237-1254.
24. Schor CM, Bharadwaj SR. Pulse-step models of control strategies for dynamic ocular accommodation and disaccommodation. *Vision Res*. 2006;46(1-2):242-258.
25. Tucker J, Charman WN. Reaction and response times for accommodation. *Am J Optom Physiol Opt*. 1979;56(8):490-503.
26. Heron G, Charman WN, Schor C. Dynamics of the accommodation response to abrupt changes in target vergence as a function of age. *Vision Res*. 2001;41(4):507-519.
27. Shirachi D, Liu J, Lee M, Jang J, Wong J, Stark L. Accommodation dynamics: I. range non-linearity. *Am J Optom Physiol Opt*. 1978;55(9):631-641.
28. Beers AP, van der Heijde GL. Age-related changes in the accommodation mechanism. *Optom Vis Sci*. 1996;73:235-242.
29. Heron G, Charman WN, Gray LS. Accommodation responses and ageing. *Invest Ophthalmol Vis Sci*. 1999;40(12):2872-2883.
30. Culhane HM, Winn B. Dynamic accommodation and myopia. *Invest Ophthalmol Vis Sci*. 1999;40(9):1968-1974.
31. Kasthurirangan S, Vilupuru AS, Glasser A. Amplitude dependent accommodative dynamics in humans. *Vision Res*. 2003;43(27):2945-2956.
32. Rucker FJ, Kruger PB. The role of short-wavelength sensitive cones and chromatic aberration in the response to stationary and step accommodation stimuli. *Vision Res*. 2004;44(2):197-208.
33. Kasthurirangan S, Glasser A. Characteristics of pupil responses during far-to-near and near-to-far accommodation. *Ophthalmic Physiol Opt*. 2005;25(4):328-339.
34. Charman WN, Heron G. On the linearity of accommodation dynamics. *Vision Res*. 2000;40(15):2057-2066.
35. van der Heijde GL, Beers AP, Dubbelman M. Microfluctuations of steady-state accommodation measured with ultrasonography. *Ophthalmic Physiol Opt*. 1996;16(3):216-221.
36. Phillips S, Shirachi D, Stark L. Analysis of accommodative response times using histogram information. *Am J Optom Arch Am Acad Optom*. 1972;49(5):389-400.
37. Kasthurirangan S, Glasser A. Influence of amplitude and starting point on accommodative dynamics in humans. *Invest Ophthalmol Vis Sci*. 2005;46(9):3463-3472.
38. Heron G, Charman WN, Gray LS. Accommodation dynamics as a function of age. *Ophthalmic Physiol Opt*. 2002;22(5):389-396.
39. Schaeffel F, Wilhelm H, Zrenner E. Inter-individual variability in the dynamics of natural accommodation in humans: relation to age and refractive errors. *J Physiol*. 1993;46(1):301-320.
40. Bharadwaj SR, Schor CM. Acceleration characteristics of human ocular accommodation. *Vision Res*. 2005;45(1):17-28.
41. Stark L, Takahashi Y. Absence of an odd-error signal mechanism in human accommodation. *IEEE Trans Biomed Eng*. 1965;12(3):138-146.
42. Bour LJ. The influence of the spatial distribution of a target on the dynamic response and fluctuations of the accommodation of the human eye. *Vision Res*. 1981;21(8):1287-1296.
43. Heron G, Charman WN. Accommodation as a function of age and the linearity of the response dynamics. *Vision Res*. 2004;44(27):3119-3130.
44. Mathews S, Kruger PB. Spatiotemporal transfer function of human accommodation. *Vision Res*. 1994;34(15):1965-1980.
45. Mathews S. Accommodation and the third spatial harmonic. *Optom Vis Sci*. 1998;75(6):450-458.
46. Kruger PB, Nowbotsing S, Aggarwala KR, Mathews S. Small amounts of chromatic aberration influence dynamic accommodation. *Optom Vis Sci*. 1995;72(9):656-666.
47. Hung GK, Ciuffreda KJ. Dual-mode behaviour in the human accommodation system. *Ophthalmic Physiol Opt*. 1988;8(3):327-332.
48. Mucke S, Manahilov V, Strang NC, Seidel D, Gray LS, Shahani U. Investigating the mechanisms that may underlie the reduction in contrast sensitivity during dynamic accommodation. *J Vis*. 2010;10(5):5.
49. Vilupuru AS, Glasser A. Dynamic accommodation in rhesus monkeys. *Vision Res*. 2002;42(1):125-141.
50. Beers AP, van der Heijde GL. In vivo determination of the biochemical properties of the component elements of the accommodation mechanism. *Vision Res*. 1994;34:2897-2905.
51. Strang NC, Day M, Seidel D, Gray LS. Accommodation steps, target spatial frequency and refractive error. *Ophthalmic and Physiological Optics*. 2011;31(5):444-455.
52. Charman WN, Heron G. Spatial frequency and the dynamics of the accommodation response. *Optica Acta*. 1979;26(2):217-228.
53. Charman WN, Tucker J. Dependence of accommodation response on the spatial frequency spectrum of the observed object. *Vision Res*. 1977;17(1):129-139.
54. Mucke S, Manahilov V, Strang NC, Seidel D, Gray LS. New type of perceptual suppression during dynamic ocular accommodation. *Curr Biol*. 2008;18(13):R555-R556.
55. Mallen EA, Gilmartin B, Wolffsohn JS. Sympathetic innervation of ciliary muscle and oculomotor function in emmetropic and myopic young adults. *Vision Res*. 2005;45(13):1641-1651.
56. Gilmartin B, Mallen EA, Wolffsohn JS. Sympathetic control of accommodation: evidence for inter-subject variation. *Ophthalmic Physiol Opt*. 2002;22(5):366-371.
57. Plainis S, Ginis HS, Pallikaris A. The effect of ocular aberrations on steady-state errors of accommodative response. *J Vis*. 2005;5(5):466-477.
58. Harb E, Thorn F, Troilo D. Characteristics of accommodative behavior during sustained reading in emmetropes and myopes. *Vision Res*. 2006;46(16):2581-2592.
59. Cheng H, Barnett JK, Vilupuru AS, et al. A population study on changes in wave aberrations with accommodation. *J Vis*. 2004;4(4):272-280.
60. Kruger PB, Mathews S, Aggarwala KR, Sanchez N. Chromatic aberration and ocular focus: Fincham revisited. *Vision Res*. 1993;33(10):1397-1411.
61. Fincham EF. The accommodation reflex and its stimulus. *Br J Ophthalmol*. 1951;35(7):381-393.