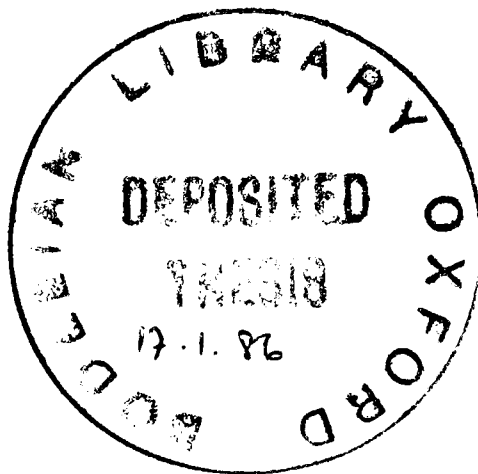


The Neural Control of Convergence Eye Movements and Accommodation

Thesis submitted for the degree of
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at the
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I performed the majority of the behavioural experiments and stimulation experiments myself, while Dr. Judge assisted me in the unit recording experiments. The data analysis for all experiments was carried out by me. No part of this thesis is being submitted, or has already been accepted, for any other degree at this or any other University.

B.G. Cumming,

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ABSTRACT

The Neural Control of Convergence Eye Movements and Accommodation.

B.G. Cumming, Magdalen College, D. Phil. Thesis, Trinity Term, 1985.

Vergence eye movements and ocular accommodation were measured in three monkeys (Macacca mulatta) trained to track a haploscopically presented target which appeared to move in depth. The dynamic performance of both vergence and accommodation were found to be much better during binocular viewing than during monocular viewing. Responses during binocular viewing in which blur stimuli were removed (AOL viewing) were comparable to those in normal binocular viewing. It was concluded that disparity stimuli were more effective in the dynamic control of accommodation than blur cues.

In two of the three monkeys extracellular recordings were made from cells in a midbrain region dorsal and dorso-lateral to the oculomotor nucleus, which modulated their firing rate when the awake animals tracked target motion in depth, but not during side-to-side target motion. The amplitude of this modulation was similar during monocular viewing, normal binocular viewing, and AOL viewing, demonstrating a relationship to the motor output of accommodation or vergence, rather than any relationship to the blur or disparity stimuli. When presented with conflicting accommodation and vergence stimuli the accommodation and vergence responses, which are normally tightly coupled, were partially dissociated. Comparing unit activity during this task with that during normal binocular viewing, it was possible to show that nineteen cells were related to the vergence response alone, and eight cells were related to the accommodation response alone. For cells related to the vergence response alone, the phase advance of the cells' activity over the vergence response was much larger than that of motoneurons recorded by others, suggesting that these cells may project (directly or indirectly) to motoneurons with time constants longer than the mean.

Extracellular microstimulation in the same midbrain area of one monkey evoked accommodation and vergence responses, confirming the motor nature of the cells recorded in this region. Stimulation over a wide area of the occipito-temporal cortex failed to evoke accommodation or vergence responses, calling into question the assertion of Jampel (1960) that this area of the macaque cortex contains a centre for co-ordinating accommodation, vergence, and pupil constriction.

CHAPTER ONE

INTRODUCTION

1.1 Introduction

Man and other primates are able to discern fine details in the three dimensional shape of objects, and are able to identify the position of objects in depth. These abilities are made possible by disjugate eye movements, which bring the images of a near object onto the foveae of both eyes. In order to make full use of the high visual acuity of foveal vision it is also necessary that the eyes accommodate to bring the images of an object into clear focus. Vergence eye movements must be controlled precisely in order to be effective in providing stereoscopic vision, since horizontal retinal disparities on the fovea of greater than 6 minutes of arc cannot be fused. Such precise control of the accommodation system would be superfluous since the human eye has a depth of focus of at least 0.1 dioptries, and other primates have a somewhat larger depth of focus (Green et al., 1980).

Although vergence and accommodation might be thought to be separate control systems regulating disparity and blur respectively, there are intimate links between the two systems. Accommodation to a monocularly viewed target produces convergence (accommodative-convergence, Mueller, 1842) and, in the absence of blur, vergence movements are associated with accommodation changes (vergence-accommodation, Fincham and Walton, 1957). This interrelationship makes sense functionally as there is a nearly linear relationship between the convergence angle and the accommodation required to maintain single clear vision. As a result of this

relationship it is possible to define commensurate units for measuring accommodation and vergence. The units used here are the dioptre (reciprocal of the viewing distance in metres, abbreviated as D) for accommodation, and the metre-angle (the vergence required to bring a target at a distance of one metre onto the foveae of both eyes, abbreviated as MA) for vergence. The relationship between MA and degrees is a simple function of a subject's inter-ocular separation: $1 \text{ MA} = \text{inter-ocular separation (in metres)} \times 180/\pi$ degrees. In addition to changes in vergence and accommodation, fixation of near objects is associated with pupil constriction (these three responses together are known as the near response). The magnitude of this pupil constriction is modest, typically producing a 5 - 10% decrease in pupil diameter per dioptre of accommodation (Roth, 1969; Semmlow and Stark, 1973; Semmlow et al., 1975). This is unlikely to effect any significant optical improvement by increasing the depth of focus of the eye, since the depth of focus is inversely proportional to pupil diameter (Green et al., 1980). As the functional importance of pupil constriction in the near response is small, I shall not consider it further.

The interactions of vergence and accommodation render the study of vergence eye movements more difficult than that of conjugate eye movements. This, coupled with the need to measure the position of both eyes, has resulted in slow progress in our understanding of the neurophysiological organization of vergence movements, especially when compared with the recent advances in describing how the brain controls saccadic and vestibular eye movements. Equally little progress has been made in understanding the neurophysiology of accommodation, which is more difficult to measure objectively than vergence.

This chapter describes first what is known about accommodation performance in human subjects in response to blur stimuli, and the associated accommodative-vergence responses. Next the performance of disparity-driven vergence responses are discussed, and the associated vergence-accommodation responses. Evidence for adaptive changes in the coupling between accommodation and vergence is described in section 1.4, and finally, section 1.5 describes what little is known about the neurophysiological processing of disparity and blur stimuli, and the organization of the motor output to the extra-ocular and intra-ocular muscles.

1.2 Accommodation performance

1.2.1 The stimulus to accommodation

Changes in a target's position in depth are accompanied by changes in its angular subtense at the eye (henceforth called its angular size) and, usually, in its luminance. In order to examine the responses of accommodation to blur (which I use to refer to all aspects of a monocular stimulus created by a discrepancy between the accommodative stimulus and the accommodation response) independently of these other distance cues, many studies have arranged for targets to be viewed through Badal lenses. A Badal lens is a positive lens arranged so that its near focal plane is coincident with the principal plane of the eye; targets viewed through such a lens do not change in angular size as they move in depth (to a high degree of approximation). In addition, the accommodative stimulus (in dioptries) produced by the target is linearly related to the displacement of the target from the far focal plane of the lens. All of the studies described in this section used targets viewed monocularly,

so that no disparity cues were available.

Although accommodation acts to reduce the blurring of retinal images, Fincham (1951) claimed that blur alone was insufficient to elicit accommodation responses. However, Phillips and Stark (1977), using a dynamic optometer, showed that defocusing a target projected onto a screen did produce transient accommodation changes. The accommodation response then settled down to that appropriate to the distance of the screen, since this was the position of minimum blur. The initial direction of the accommodation response was claimed to be random; this is not surprising since a defocused image on a screen contains no information concerning the direction of accommodation necessary to reduce blur. However, when the optical distance of a target changes, the initial direction of an accommodation response is usually correct, even when the target is viewed monocularly through a Badal lens. Several cues have been suggested as providing the accommodation system with information concerning the direction of blur. Fincham (1951) suggested that light vergence could be sensed directly by means of the Stiles-Crawford effect, but this has never been established. He also suggested that colour fringes resulting from the chromatic aberration of the eye, or asymmetries in the blur pattern resulting from spherical aberration or astigmatism, could provide information as to the direction (or sign) of blur. Campbell (1954) and Alpern (1958a) suggested that the fluctuations in accommodation which occur continuously (Campbell, Robson, and Westheimer, 1959) could be used to extract information about the sign of accommodation errors.

None of these cues is useful according to Troelstra et al. (1964),

who claimed that in Badal viewing changes of accommodation (indicated by measuring accommodative-vergence) were initially in the wrong direction in 50% of trials. This was true only when sufficient care was taken to remove cues derived from slight lateral or vertical changes in target position associated with target movement in depth. This claim was based on the results from a single subject, the other two subjects in this study having always accommodated in the correct direction (which the authors attribute to there being some extraneous cues still available!). From all the studies in which accommodation or accommodative vergence has been measured dynamically, this is the only subject whose initial direction of response was claimed to be random in response to step changes in the accommodative stimulus.

Two important studies concerning the nature of the accommodative stimulus have been made using homotropinized subjects instructed to bring out-of-focus targets into focus through manual adjustments of target position (Campbell and Westheimer, 1959; Stark and Takahashi, 1965). The initial direction in which subjects moved the targets was monitored to assess whether or not subjects were aware of the direction of blur. Stark and Takahashi found that even in polychromatic light, with a natural pupil and no correction for any astigmatism of subjects, the initial direction of response was random. Campbell and Westheimer (1959) found that the response was random only when the target was viewed through an annular pupil and in monochromatic light - when viewed with a natural pupil responses were usually correct in all three subjects. One subject responded accurately when the target was illuminated in polychromatic light, but when monochromatic green light was used the responses were random for a long period. These authors concluded that

chromatic aberration was used by some, but not all, subjects - in agreement with Fincham (1951) who found variation between individuals in their use of chromatic cues - and that spherical aberration or astigmatic cues could be used by all subjects. It is not at all easy to reconcile these conflicting results. Stark and Takahashi suggested that Campbell and Westheimer may have failed to eliminate cues derived from slight lateral target motion associated with changes in target depth, but if this were the explanation then Campbell and Westheimer's subjects would still have made correct responses consistently when viewing through annular pupils. The amplitudes of the stimuli used in the two studies were comparable (1.0 and 0.5 D changes in Campbell and Westheimer, 1.0 and 1.2 D in Stark and Takahashi) so the difference is not attributable to an amplitude non-linearity.

Stimuli other than blur associated with target nearness (especially angular size and luminance) have been claimed to increase the size of a response to a given blur stimulus (Ittelson and Ames, 1950) in addition to providing clues to the direction of blur. This effect, known as 'proximal accommodation', is very small, and neither Alpern (1958b) nor Morgan (1962) (cited by Hokoda and Cuiffreda, 1983) found any significant effect of target size or apparent distance on accommodation.

If 'proximal' cues are important for determining the direction of blur, one might expect that the addition of such information to a stimulus would improve the dynamic performance of accommodation. Although Campbell and Westheimer (1960) mentioned that accommodation responses to step changes in target distance seen through a Badal lens were frequently slower than those in response to targets viewed

directly, no systematic investigation of this effect was reported, and the observation has not been followed up in any subsequent publications.

1.2.2 Steady-state performance

Although the anatomical resting position of accommodation is at infinity, the system has a physiological resting position of 1.5 D or so, which is assumed in darkness (Rayleigh, 1883) or in featureless photopic environments (Whiteside, 1952 and 1957). The value of the 'night myopia' for an individual is correlated with the value of the 'empty field myopia' (Leibowitz and Owens, 1978). When presented with stimuli at positions other than this resting level, considerable steady state errors are observed (known as the 'lazy lag' of accommodation) which are often as large as 0.5 D for a stimulus 4 D away from the resting position (Alpern and David, 1958; Fincham and Walton, 1957; Heath, 1956; Johnson, 1976; Morgan, 1944a, 1944b, and 1968). The accommodative stimulus for which a subject has no accommodative error is very similar to the dark focus for the same subject (Johnson, 1976).

This lazy lag led Toates (1970 and 1972) to propose that the accommodation controller constitutes a proportional control system¹. However, from steady-state data alone it is not possible to exclude the possibility that the system is a leaky integrator, as suggested by Krishnan and Stark (1975). These authors noted that accommodation returned slowly

¹ A proportional control system is one in which the output is derived from the input by multiplication of the input by a constant. An integral controller is one in which the output is derived from mathematically integrating the input. A leaky integrator is a first order low-pass filter with a long time constant, described by the Laplace transform $k/(Ts + 1)$.

to its resting value in the absence of a target, although they gave no description of how eye position was maintained in the absence of a target, making the result difficult to interpret since the optometer used to measure accommodation was sensitive to eye position. Krishnan and Stark also arranged to introduce and maintain step changes in target blur by using the measured accommodation response to control the position of the stimulus. They claimed that linear ramps resulted (as one would expect if the open-loop transfer function¹ was that of an integrator). However, the only figure presented in the paper showed that this response saturated rapidly, and it is possible that the responses could equally well have been described by an exponential rise, as expected of a proportionally controlled system. Indeed, Van der Wildt et al. (1974), also using feedback to open the accommodation loop, reported exponential accommodation responses following blur steps. A second problem with the proposal of Krishnan and Stark (1975) is that an integrator with the gain and time constant used in their model would show much smaller steady-state errors than those usually observed for accommodation.

1.2.3 Dynamic accommodation performance

Any mathematical description of the accommodation system should also take account of its dynamic properties. Campbell and Westheimer

¹ The open-loop transfer function of a feedback system describes the relationship between the input to the system (the difference between the stimulus and the response - i.e. blur or disparity) and the output of the system (accommodation or vergence). A closed-loop transfer function describes the relationship between the stimulus (distance of the image or its binocular angular subtense) and the response of the system.

(1960), using pulse stimuli of different durations, showed that accommodation behaved as a continuously sampling system. The closed-loop step response has a long latency of about 360 msec (Campbell and Westheimer, 1960; O'Neill and Stark, 1968; Phillips et al., 1972; Smithline, 1974; Tucker and Charman, 1979) and is roughly exponential with a time constant of about 250 msec (Campbell and Westheimer, 1960; Tucker and Charman, 1979) although response times show some dependence on stimulus amplitude (Tucker and Charman, 1979). In some subjects responses are faster in response to far-to-near target movement than in response to near-to-far changes (Tucker and Charman, 1979), while in other subjects an asymmetry in the opposite direction has been reported (Campbell and Westheimer, 1960). Several studies have been made of the responses where the optical power required for the eye to maintain focus was modulated with a sinusoidal time course (henceforth referred to as a 'sinusoidal stimulus' to accommodation) at different frequencies (Campbell and Westheimer, 1960; Krishnan et al., 1973a; Stark et al., 1965). A feature common to all of these studies is that it was difficult to describe both the gain and phase of the responses with a simple transfer function which included the measured latency of the system. The phase lags were usually smaller than those of transfer functions which described the variation of gain with frequency. One explanation, proposed by Stark et al. (1965), is that the system is able to predict simple sinusoidal motion, and thus reduce delays in responding to the stimulus. However, there is little experimental evidence to support this view - Krishnan et al. (1973a) found little difference between accommodation responses to simple sinusoidal stimuli and responses to stimuli which were composed of multiple non-harmonic sinusoids. Van der Wildt et

al. (1974) found that accommodation responses to sinusoidal target motion were variable, and were dependent upon subject instruction and attention. Responses to stimuli composed of sinusoids masked by filtered Gaussian noise (with equal power in each of these two components) were within the range covered by responses to simple sinusoids. Although Phillips et al. (1972) claimed a significant difference between the latency of responses to repetitive step changes in target distance and the latency of responses to unpredictable step changes, the latency was much more variable in response to predictable changes than it was in the unpredictable case, so the predictive effects must have been variable. It is possible that if the subjects were not naive (two appear to have been the experimenters themselves) some voluntary accommodation responses were involved. In connection with this it is interesting to note that in other studies where predictable target motion was used (Campbell and Westheimer, 1960; Stark et al. 1965) the latency reported was similar to that reported by Phillips et al. for unpredictable stimuli.

Other than the suggestion of a prediction operator, no model has been proposed which accounts for the gain and phase of accommodative responses to sinusoidal stimuli over a range of frequencies.

1.2.4 Accommodative-vergence

The vergence associated with accommodation to a monocularly viewed target is linearly related to accommodation, at least over a moderate stimulus range (Alpern et al., 1959; Flom, 1960). The slope of this relationship defines the gain of accommodative-vergence. This is expressed in two ways: the stimulus AC/A ratio is the slope of the

relationship between the accommodative stimulus and the accommodative-vergence response, and the response AC/A ratio is defined as the slope of the relationship between the accommodative response and accommodative-vergence. If both vergence and accommodation (response or stimulus) are expressed in commensurate units (MA and D respectively) the AC/A ratio is a dimensionless quantity. In a clinical survey of large numbers of patients a population mean stimulus AC/A ratio of about 0.65 has been reported (Morgan, 1944b, 1968), although in young subjects this is usually larger (about 0.8 according to Alpern and Larson, 1960). Owing to the lazy lag of accommodation the response AC/A ratio is typically larger than the stimulus AC/A ratio by about 8% (Alpern et al., 1959; Alpern, 1969). The dynamic responses of accommodative-vergence are similar to those of accommodation (Brodkey and Stark, 1967; Yoshida and Watanabe, 1969), although the latency of the accommodative-vergence response is shorter than the latency for the accommodation response (Wilson, 1973).

1.3 Vergence performance

1.3.1 The stimulus for vergence

Although vergence eye movements usually occur in order to bring the images of an object onto the foveae of both eyes, Westheimer and Mitchell (1969) showed that the movements could equally well be initiated in response to quite different stimuli in the two eyes. Furthermore, Jones and Kerr (1971) showed that when there was a choice of two targets vergence was not preferentially initiated in the direction of the targets whose shape was the same in each eye. None the less, dissimilar targets cannot be fused, so that the vergence response was not

sustained when the targets were dissimilar. Consequently, two different systems in the control of vergence are now recognized - disparity vergence, which controls movements towards targets with large disparities, and fusional vergence, which controls vergence used to maintain fusion of images on the foveae. Where the boundary between these systems lies has not been clearly delineated.

In the steady state, errors in vergence (known as fixation disparities) are typically only a few minutes of arc (Rashbass and Westheimer, 1961a; Riggs and Niehl, 1960). These small disparities are presumably a necessary stimulus for the fusional vergence system to maintain the vergence output. Fixation disparities are also small (although somewhat larger than in normal viewing) if the vergence stimulus is not accompanied by an appropriate accommodation stimulus, as occurs when viewing through prisms (Mitchell and Ellerbrock, 1955; Ogle et al., 1967; Schor, 1979a), suggesting that the contribution of accommodative-vergence to the vergence response in binocular viewing is small. In fact, during prism viewing, the accommodation system is working to counteract the effect of vergence-accommodation (see below), so accommodative-vergence opposes the fusional vergence drive. Consequently, fixation disparities when wearing prisms are smaller if accommodation is open-loop than when there is an effective accommodation stimulus (Semmlow and Hung, 1979).

1.3.2 Dynamic vergence performance

Vergence eye movements are slow compared with conjugate eye movements, the response to a step change taking about 1 second to complete. This is composed of a reaction time of about 160 msec, followed by a roughly exponential response with a time constant in the region of 200

msec (Rashbass and Westheimer 1961a; Zuber and Stark, 1968). In some subjects convergence is achieved more rapidly than divergence (Zuber and Stark, 1968; Krishnan and Stark, 1977), but this is not always true (Rashbass and Westheimer, 1961a). Rashbass and Westheimer showed that the response to a step change in disparity (maintained by feeding back the measured vergence response to control the stimulus) was a linear ramp whose slope was proportional (with a slope of 10 degrees/sec per degree of disparity) to the size of the disparity step. In other words the open-loop step response was that of an integrator with delay.

The system cannot be described by a pure integrator, since an integrator in a feedback loop shows no steady state errors, but a 'leaky' integrator would produce very small steady-state errors, as observed for vergence. Krishnan and Stark (1977) estimated that the time constant for the vergence integrator was about 10 seconds, but it is far from clear that their method of measuring this parameter was not confounded by the effects of prism adaptation (see below).

The responses to sinusoidally modulated disparities resemble those of an integrator in so far as the gain rolls off with increasing frequency with a slope of -6 dB per octave; however, the phase lags of the responses are much smaller than those of an integrator with delay (Rashbass and Westheimer, 1961a; Zuber and Stark, 1968). Rashbass and Westheimer suggested that this may be explained by a sensitivity to finite rates of change of disparity, but they did not produce an exact mathematical description of this idea. Krishnan and Stark (1977) used a model including integrating and differentiating elements in parallel to describe the closed-loop step response of vergence, and found that the

same model provided a good description of the closed-loop frequency response. However, their model did not account for the lack of any noticeable derivative effect in responses to open-loop steps. The significance of the fit between the modelled and the measured responses to sinusoidal stimulation is unclear since the data were not presented with estimates of the variability of the measurements.

As with accommodation, it has been suggested that the small phase lags observed in vergence responses to sinusoidally modulating disparity could be the result of prediction. Again, experimental evidence in support of this is sketchy. Zuber and Stark (1968) found a small difference between the gain and phase of responses to simple sinusoids and those in response to unpredictable combinations of sinusoids. However, the difference was not greater than the variability of their measurements (estimated by comparing different figures in the paper), and in any case could be explained by an amplitude-dependent non-linearity which they demonstrated in response to predictable stimuli. Krishnan et al. (1973a) also found small differences in vergence responses to predictable as compared with unpredictable stimuli. Thus although Krishnan et al. (1973b) found a difference in the latency of vergence responses to predictable compared with unpredictable step changes in the vergence stimulus (contrary to the findings of Rashbass and Westheimer, 1961a), this does not seem to be the only factor responsible for the unexpectedly small phase lags observed in tracking of sinusoidal vergence stimuli.

1.3.3 Interaction of vergence and saccadic eye movements.

It has classically been believed that vergence and versional eye movements take place independently of one another. Simultaneous saccadic and vergence movements occur when changing fixation between targets differing both in depth and in eccentricity. Such saccades were believed not to influence the ongoing vergence movement. (Alpern and Ellen, 1956; Rashbass and Westheimer, 1961b; Westheimer and Mitchell, 1956; Yarbush, 1957). More recently, however, it has become clear that saccades occurring during vergence movements cause a transient increase in the rate of change of vergence angle - in other words the saccades are disconjugate (Enright, 1984a; Kenyon et al., 1980). Kenyon et al. modelled this effect by a non-linear interaction of muscle forces in the periphery, suggesting that the generation of saccadic and vergence commands were independent. Enright (1984a) favoured a similar explanation, but neither group presented conclusive evidence against the possibility of some central interaction.

1.3.4 Vergence-accommodation

When targets are viewed through pinholes they appear in focus independent of a subjects accommodative state. When viewing such targets binocularly, changes in vergence angle are accompanied by changes in accommodation (Fincham and Walton, 1957; Kent, 1958; Kersten and Legge, 1983; Morgan, 1954). Fincham and Walton (1957), in their classic study, found that the gain of this coupling (accommodation response divided by vergence response in commensurate units) was close to 1.0 in young subjects, and declined with age (presumably in proportion to the subject's presbyopia). In view of the fact that fusional vergence is much more

accurately controlled than blur-driven accommodation the vergence-accommodation response could be very important in controlling accommodation. In particular, the fact that vergence responses to disparity changes have shorter latencies and faster dynamics than accommodation responses to blur, suggests that vergence-accommodation could be useful in controlling the dynamic responses of accommodation in binocular viewing. A brief report has been published in which the dynamics of accommodation to binocularly viewed step changes in the vergence stimulus were measured (Krishnan et al., 1977). The latency was shorter than that of accommodation to monocularly viewed target steps, but no detailed comparison of response dynamics in the two conditions was made. Furthermore, such a comparison would have provided an incomplete description of the dynamic interaction of vergence-accommodation with blur-driven accommodation, since images away from the fovea are less effective stimuli to accommodation than foveal images (Campbell, 1954; Hennesy and Leibowitz, 1971; Whiteside, 1957). Semmlow and Tinor (1978) have shown that the same is true for accommodative-vergence responses. Thus, when the vergence stimulus is suddenly changed symmetrically, and a target is no longer on either fovea, blur-driven responses are reduced in their effectiveness until after vergence has brought the target onto the foveae. During tracking of an object moving in depth more gradually, so that the images are never far from the foveae, blur-driven components may play a greater part in controlling the responses of accommodation and vergence. Yoshida and Watanabe (1969) measured the responses of accommodation to monocularly viewed target motion producing a sinusoidal accommodation stimulus, and compared this with the vergence-accommodation responses to sinusoidal vergence stimuli at different fre-

quencies. Although the amplitude of vergence-accommodation responses were greater than those of blur-driven accommodation for frequencies up to 0.8 Hz, they reported large phase lags for vergence-accommodation (relative to the vergence stimulus) even at low frequencies (30 degrees phase lag at 0.2 Hz). In their study however, a pinhole was placed in front of one eye only, so that vergence-accommodation would have produced blurring of the image seen in the other eye (the target viewed by that eye was at a fixed distance from the eye). The responses to that blur would have opposed the vergence-accommodation response. A second difficulty with the study by Yoshida and Watanabe (1969) is that they only performed the experiment on one subject, who was 40 years old, so the general significance of these results is doubtful.

1.4 Adaptability of the relationship between accommodation and vergence

1.4.1 Prism adaptation

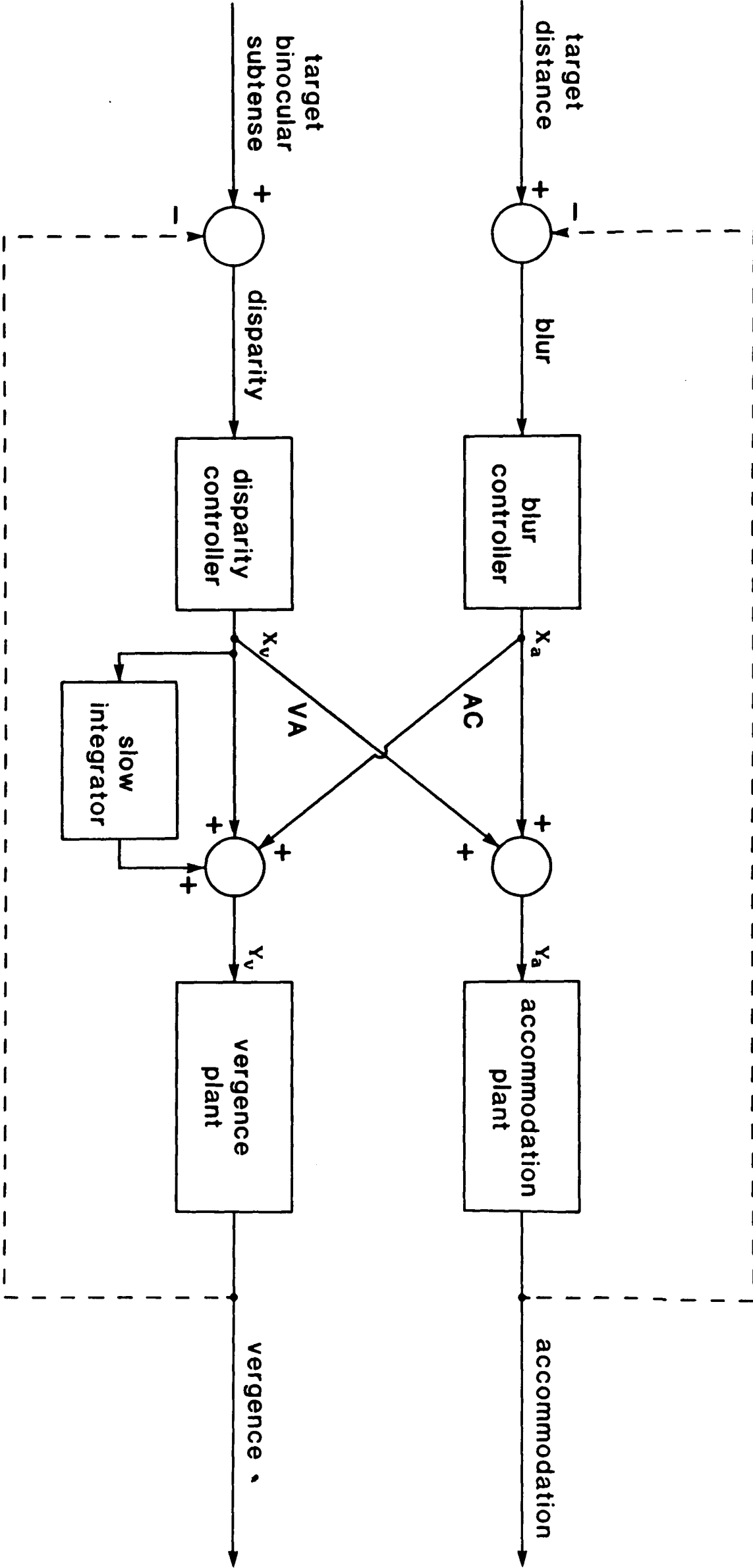
After a short period (e.g. 1 minute) of binocular viewing through base-out prisms¹ there is a persistent positive aftereffect: when tested monocularly subjects show more convergence than usual for the accommodation stimulus. Schor (1979b and 1983) has suggested that this prism adaptation can be described by a slow integrator in parallel with the basic (fast) integrator in the vergence pathway. This slow integrator has a time constant of about 30 - 60 seconds (Henson and North, 1980; Schor 1979b) in normal subjects, and often has sufficient gain to produce nearly complete adaptation. This slow integrator must be driven by

¹ A base-out prism is a wedge prism placed with its apex medial to the eye viewing through the prism.

the output from the fast integrator because accommodative-vergence does not produce prism adaptation in humans Schor (1979b), or in the monkey (Judge and Miles, unpublished observations). Schor (1983) argued that the vergence-accommodation drive must be derived from the output from the fast integrator (not the total vergence output) since prism adaptation does not alter the dark focus (Owens and Leibowitz, 1980). In accordance with this suggestion, Miles and Judge (unpublished observations) have shown that following prism adaptation the value of the vergence-accommodation associated with a given vergence response is reduced. The interactions of vergence and accommodation are summarized in the block diagram of Fig. 1.1, which is an elaboration of a diagram first used by Westheimer (1963), and subsequently elaborated by Semmlow and his associates. Semmlow (1981) argued that the elements in this scheme interact in a linear fashion, rather than in a hierarchical way. A hierarchical interaction was first proposed by Maddox (1893) in which he suggested that vergence was predominantly supported by accommodative and tonic vergence, fusional vergence acting only as a supplement. Although such a scheme does not account for the fact that the performance of the vergence system is accurate in the absence of accommodative stimuli, it has remained influential. An alternative hierarchical model, suggested by Fincham and Walton (1957), is that the disparity stimulus is the dominant factor in the control both of accommodation and of vergence, blur-driven responses serving only as a supplement. Neither of these hierarchical ideas have been modelled mathematically, whereas Hung and Semmlow (1980) have shown that a linear interaction of blur-driven and disparity-driven responses accounts for the observed steady state performance of accommodation and vergence under a variety of stimulus

Figure 1.1

Block diagram of accommodation and vergence control. Two feedback loops are shown - the dotted lines indicate the feedback by the outputs of the system (accommodation or vergence) reducing the inputs to the controllers (blur and disparity respectively). The two feedback loops are cross coupled by accommodative-vergence (AC) and vergence-accommodation (VA). The slow integrator produces prism adaptation. It is placed at the position shown in the diagram because it is known that accommodative-vergence does not produce prism adaptation, and also that dark focus does not change after prism adaptation (see text).



conditions. Little work has been done to elucidate whether a linear interaction can also account for the dynamic performance of the system, although there are data to suggest that the interaction of accommodative-vergence and disparity vergence is linear (Semmlow and Wetzell, 1979).

1.4.2 Periscope adaptation

It has usually been believed that the elements illustrated in Fig. 1.1 have fixed and stable properties, so that for example the AC/A ratio cannot be altered (Alpern, 1969). However, if the accommodative-vergence or vergence-accommodation cross-links serve an important functional role, it would certainly be advantageous if the possibility of adaptive regulation existed, in a way formally similar to the well known adaptive plasticity of the vestibulo-ocular reflex. Judge and Miles (1981 and 1985) showed that wearing periscopic spectacles (which displaced the effective position of each eye laterally) increased the stimulus AC/A ratio when subjects were instructed to exercise vergence and accommodation extensively while wearing the spectacles. The same effect has been demonstrated in monkeys (Judge and Miles, unpublished observations). Measuring accommodation and vergence objectively, the same authors demonstrated both a reduction in the gain of vergence-accommodation and an increase in the response AC/A ratio (Miles and Judge, 1982).

1.5 Neuroanatomy and neurophysiology

1.5.1 Disparity input

Barlow, Blakemore and Pettigrew (1967) and Pettigrew, Nikara and Bishop (1968) discovered that many cells in the striate cortex of the

cat strongly preferred binocular visual stimulation with a particular disparity, characteristic of each cell. Poggio and Fischer (1977) showed that such cells also existed in the monkey striate cortex, and that there were other classes of cells which were either inhibited by particular disparities, or responded to a range of either crossed or uncrossed disparities so that they could be said to be 'near' or 'far' cells respectively. All these types of cell have now also been reported in the cat (Ferster, 1981). Cynader and Regan (1978) reported that some cells in cat area 18 were selectively sensitive to the direction of movement in depth, and Poggio and Talbot (1981) have reported such cells in the monkey. A difficulty with Cynader and Regan's study, which both Poggio and Talbot (1981) and Maunsell and Van Essen (1983) pointed out, is that they failed to centre their moving-in-depth stimulus at the preferred static disparity of the cells and so the tuning for direction of movement in depth may have been artefactual.

Although it is clear that cortical cells exist which could supply disparity information useful in controlling vergence, it is not clear that any of the cells described to date are in fact the source of signals controlling vergence. Indeed, the fact that vergence movements are initiated in response to dissimilar stimuli in each eye (discussed above) suggests that they are not. It does at least seem to be clear that some area of the cortex is used in initiating vergence responses - Westheimer and Mitchell (1969) found that a patient whose corpus callosum had been sectioned (as part of a treatment for epilepsy) did not make vergence responses to targets near the midline (whose images from each eye would be processed in opposite hemispheres), but did initiate vergence movements to targets placed sufficiently lateral to ensure that

the two images would be represented in the same cerebral hemisphere.

It may be that the stimulus for vergence is detected not by typical striate cortex cells, but by cells in the prestriate cortex. Jampel (1960) claimed that stimulation of cortical areas 19 and 22 in the anaesthetised monkey produced all aspects of the near response, separately or in conjunction, but this study has not yet been replicated in alert monkeys, and there are a number of difficulties with Jampel's study (discussed in chapter 5) which leave his interpretation open to question. Zeki (1974) reported a small number of cells in the posterior bank of the Superior Temporal Sulcus with opposite direction selectivity in the two eyes, and also some cells sensitive to edges moving in opposite directions presented to one eye alone. Such cells must be rare because Maunsell and van Essen (1983) were unable to find such cells in a large sample of cells in the same area (now usually called 'MT').

Sakata et al. (1980) reported a category of cells in the posterior parietal cortex of the monkey whose activity was modulated according to the depth of fixation, and although they emphasized the possible sensory roles of such cells, they did not exclude the possibility that the cells had a motor function. Sakata et al. (1983) reported cells in the same area whose activity modulated during tracking of targets moving in depth, but did not modulate in relation to changes in the depth of static fixation. They suggested that these cells were involved in the motor control of accommodation or vergence. Some of these cells also modulated their activity during monocular tracking of targets moving in depth.

1.5.2 Blur input

Nearly nothing is known about the neural mechanisms that signal blur. Naturally, almost any contrast sensitive visual cell will modulate its firing as blur diminishes contrast: this principle is sometimes used by visual neurophysiologists to establish that an anaesthetised animal's refractive correction is optimal. There is no evidence that any particular group of visual cells actually signal blur. Bando et al. (1981a and 1984b) found cells in the Clare-Bishop area of the anaesthetized cat which fired prior to spontaneous fluctuations of accommodation in darkness, and they also showed that microstimulation in this area produced accommodation responses. It is not clear what part these cells play in the control of accommodation, i.e. whether they signal blur or are related to the magnitude of an accommodation response.

1.5.3 Accommodation output

As Gullstrand (1924) proposed, changes in accommodation of the human eye are brought about by the elastic property of the lens capsule, which is allowed to increase the lens curvature according to the degree by which the static tension on the lens equator is relieved by contraction of the ciliary muscle. This curious arrangement has the consequence that later in life a perfectly healthy ciliary muscle is unable to produce an accommodative change partly because of changes in the elastic property of the lens itself, but more especially of the lens capsule (Fisher, 1969a, 1969b and 1977). The ciliary muscle is innervated by fibres from the ciliary ganglion. The ciliary ganglion cells (of which there are about 3000 in each ganglion, judging from Warwick,

1954), are innervated by afferents from the Edinger-Westphal nucleus and possibly from contiguous cell groups i.e. the anteromedian nucleus and in the animals in which it exists, the nucleus of Perlia (Warwick, 1954; Akert et al., 1980; Burde and Loewy, 1980). Westheimer and Blair (1973) observed that painting the ciliary ganglion with nicotine abolished the pupil response, but not the accommodation response, to midbrain stimulation, and so suggested that some at least of the fibres innervating the ciliary muscle pass straight through the ganglion without synapsing there, but this was not rigorously proven. Bando et al. (1981b and 1984a) recorded from 30 cells in the midbrain of the anaesthetized cat related to spontaneous fluctuations of accommodation. Seventeen of these cells were identified as Edinger-Westphal neurones by antidromic activation from electrical stimulation in the ciliary ganglion. The onset of cell discharges preceded the onset of the accommodation response by 270 msec on average and they also found that the latency of accommodation responses to microstimulation in this region was 240 msec. In the monkey, Thompson (1975) reported a latency of 80 msec for accommodation responses to electrical stimulation of the ciliary nerve, which although shorter than the latency reported by Bando et al. (1984a) for the cat, is long compared to the latency of 8 msec or so between oculomotor motoneurone firing and eye movement (Fuchs and Luschei, 1970). Lovasik and Beauchamp (1982) recorded from ten cells in the midbrain of alert cats. These cells responded to accommodation induced by placing lenses in front of the right eye of the animal. Unfortunately, this study did not exclude the possibility that the cells were actually related to vergence.

In birds there is a clear segregation of the Edinger-Westphal

nucleus into three parts, subserving pupil constriction, accommodation, and modulation of choroidal blood flow (Reiner et al., 1983). In the monkey, it has been claimed on the basis of electrical stimulation and lesion experiments (Jampel and Mindel, 1967; Carpenter and Pierson, 1973; Pierson and Carpenter, 1974) that the anteromedian nucleus is related to the pupil and the Edinger-Westphal nucleus to accommodation, but Akert et al. (1980) failed to find any projection from the anteromedian nucleus to the ciliary ganglion. In the marmoset, Clarke et al. (1985) also failed to find any projection from the anteromedian nucleus to the ciliary ganglion, but claimed that electrical stimulation only in the ventral portion of the Edinger-Westphal nucleus produced pupil constriction.

1.5.4 Vergence output

Keller and Robinson (1972) and Keller (1973) claimed that all oculomotor motoneurones modulate their firing rates during vergence eye movements, and that no motoneurones modulated only in relation to vergence movements. Furthermore, Keller (1973) claimed that the sensitivities of motoneurones' discharges to vergence and version eye movements were not significantly different. However, Mays and Porter (1984) pointed out that Keller's test would have failed to detect even quite large differences in sensitivity to the different types of eye movement, and consequently they repeated the experiment with more precise tests. Mays and Porter found that the version and vergence sensitivities of individual motoneurones were usually not identical. They therefore suggested that version and vergence signals were combined at the level of the motoneurone, and not at some higher level as was suggested earlier

(Keller, 1973).

The results of Mays and Porter (1984) also differed from those of Keller (1973) in their description of the dynamic relationship between motoneurone firing and vergence movement. Keller claimed that the step response of vergence was achieved by a step change in motoneurone firing, the dynamics of the movement therefore being determined by the oculomotor plant. Mays and Porter reported that the step response was associated with slow ramp changes in motoneurone firing lasting 100 - 200 msec. Mays and Porter attributed the difference to the fact that the stimulus used by Keller moved directly towards the viewing eye, and since vergence movements are symmetrical, this stimulus contained a conjugate component. However, since the animals in Keller's study were viewing monocularly, there was no stimulus for conjugate eye movements until after the vergence movement started to displace the viewing eye (as shown by Kenyon et al. (1978) in humans). Since the change in motoneurone firing reported by Keller was completed before the vergence movement began, Mays's explanation does not seem to be adequate. Keller's result was obtained using accommodative-vergence to bring about the change in vergence, while Mays and Porter used binocular viewing, yet in humans accommodative-vergence has poorer dynamics than disparity vergence, and comparing the figure presented by Keller (1973) to those presented by Mays and Porter (1984), this also seems to be true in the monkey. It is curious, therefore, that Mays and Porter reported a slower change in motoneurone firing than did Keller.

An additional reason to believe that the combination of version and vergence signals takes place at the level of motoneurons is the obser-

vation that damage to the medial longitudinal fasciculus (MLF) can cause a deficit in adduction of the eyes for versional movements while adduction during vergence is normal, a condition called inter-nuclear ophthalmoplegia (Smith and Cogan, 1959). Recent anatomical (Carpenter and Batton, 1980; Graybiel and Hartweg, 1974) and stimulation (Baker and Highstein, 1975; Highstein and Baker, 1978) studies have shown that there is a projection from each abducens nucleus to the contralateral oculomotor nucleus complex, which travels in the MLF. The cells which make up this projection are known as abducens internuclear neurones. The suggestion that this projection carried signals co-ordinating the activity of the medial rectus and lateral rectus muscles during conjugate horizontal eye movements was confirmed by extracellular recording of fibre activity in the MLF (King et al., 1976). Fibres were reported that discharged with a burst-tonic relationship to the horizontal component of eye movements during saccades, the vestibulo-ocular reflex, and smooth pursuit movements. Internuclear ophthalmoplegia is believed to result from damage to these fibres, and the sparing of adduction in vergence movements suggests that there is a separate pathway carrying vergence signals alone to the oculomotor nucleus, which does not travel in the MLF.

Robinson (1970) noted two cells dorsal to the OMN that discharged in relation to the near response, and Schiller (1970) mentioned a small number of cells in the dorso-lateral region of the caudal part of the OMN that seemed to be related to convergence. Mays (1981 and 1984) has made a thorough study of these types of neurone in awake trained monkeys. He showed that the firing rate was linearly related to the convergence angle, and that most cells increased their firing with increased

convergence, but a few increased their discharge rate during divergence. The cells discharged in a similar (but not always identical) way when the vergence angle was produced by accommodative-vergence as when it was achieved in binocular viewing. No conclusive evidence was presented to exclude the possibility that some at least of these cells were related to aspects of the near response other than vergence.

1.5.5 Prism adaptation

Milder and Reinecke (1983) claimed that some patients with cerebellar degeneration had very little capacity for prism adaptation. Judge and Miles (unpublished observations) tested two monkeys with lesions of the flocculus of the cerebellum, a structure which is known to be critical for some (but not all) types of oculomotor plasticity (Zee et al., 1981). The monkeys showed prism adaptation after 30 minutes of prism wearing, and the effects were similar in two control monkeys.

1.6 Conclusions

Although the static and dynamic performance of the human accommodation and vergence systems considered separately have received considerable attention, the interaction of blur-driven and disparity-driven responses has not been well described, especially for dynamic stimuli. Consequently, the investigation of accommodation and vergence behaviour in this study concentrates on describing the dynamic responses to blur and disparity stimuli, presented separately and together, in natural and artificial combinations.

In order to investigate the neurophysiological organization of these interactions the activity of cells in the midbrain was recorded

while awake monkeys tracked targets moving in depth. The activity was recorded while a variety of different stimuli for accommodation and vergence were presented, in an attempt to demonstrate whether or not the cells were simply related to the motor output of accommodation or vergence (corresponding to points Y_a or Y_v in Fig. 1.1), or whether these cells carried sensory or sensorimotor signals (corresponding to points X_a or X_v on the diagram).

CHAPTER TWO

APPARATUS AND METHODS

2.1 Monkey preparation and training

Monkeys were trained according to the method described by Wurtz (1969). Operant conditioning (under the control of a microcomputer) was used to train the monkeys to fixate targets. The monkeys pressed a lever to switch on a small spot target. After a variable interval (0.5 to 3.5 sec) the spot dimmed slightly and the monkey was rewarded with a drop of water if he/she promptly released the lever. The monkeys worked for their daily fluid requirements. In order to help ensure that the monkeys had adequate water intake, they were accurately weighed (to the nearest 20 gm) each working day and their eating habits were carefully observed. At no time were the monkeys deprived of water for more than 24 hours. In addition, they never worked for more than five consecutive days and were always given generous fluid and fruit at the weekends. Every six weeks the monkeys had at least one week in which they had generous fluid and fruit supplies. Once trained, each monkey was implanted (under general anaesthesia) with scleral magnetic search coils in both eyes, a head holder, and a recording chamber. The coils were implanted using the technique of Judge et al. (1980) in which the coil was placed underneath the conjunctiva, and the lead taken out to an incision in the skin over the zygomatic process of the frontal bone, via a pouch made between Tenon's capsule and the conjunctiva. The lead was then threaded underneath the skin to emerge on top of the skull where a plug was fitted and cemented to the skull above the orbit with acrylic dental cement. The coils themselves consisted of three turns (16 mm in

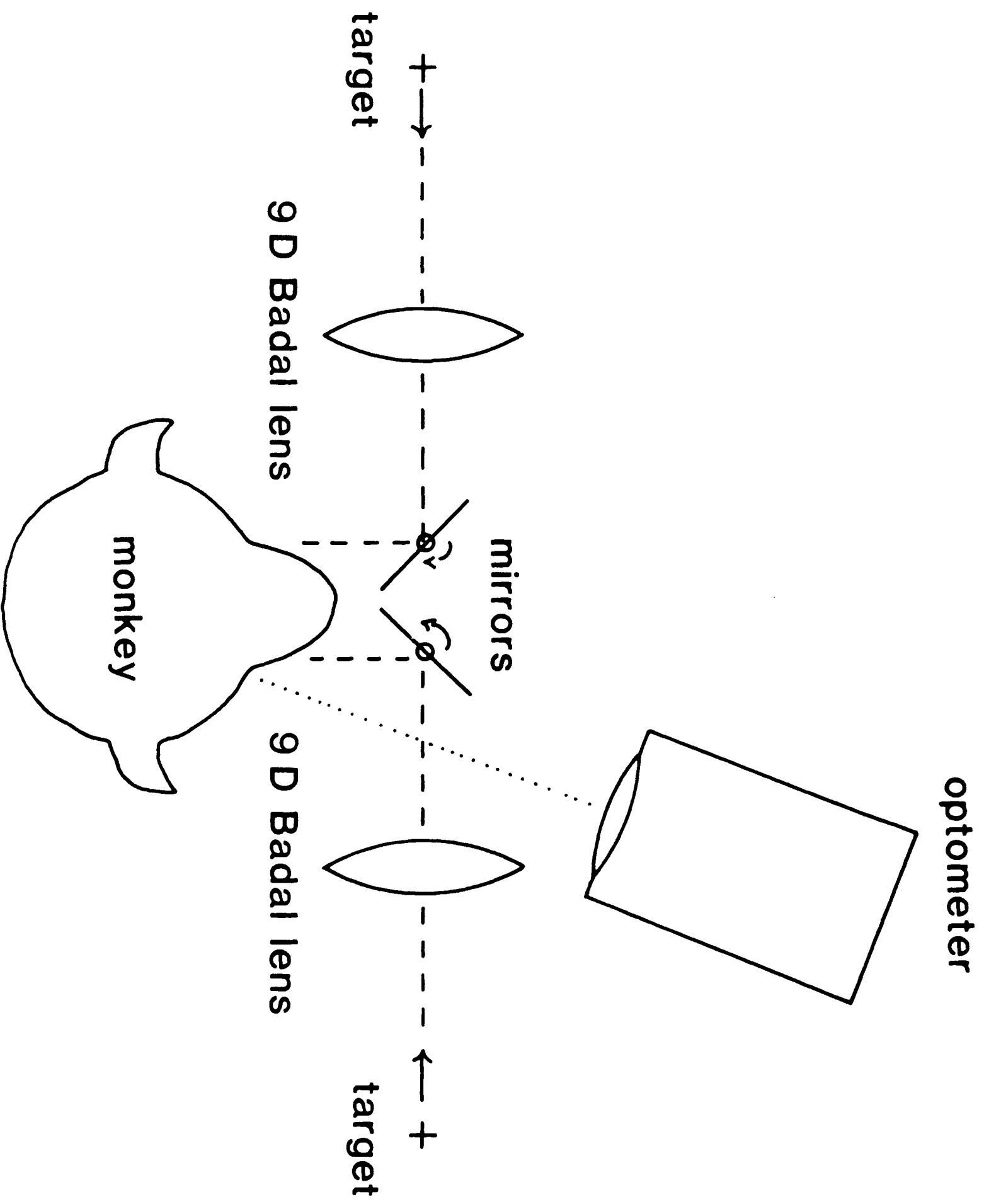
diameter) of Cooner type AS632 multistrand stainless steel wire. The head holder was of the modified Evarts (1966) type, developed by Miles et al. (1980). It consisted of a pedestal in the vertical stereotaxic plane, fixed with acrylic cement to four short aluminium bars. These bars were secured to the skull via four implanted bolts. The pedestal was used each day to attach the head holder to a large bolt fixed to a perspex chair in which the animal sat. The recording chamber was placed over the midline, so that its axis was aimed at a point 8 mm anterior and 5.5 mm superior to stereotaxic zero. The axis of the cylinder was tilted 26 degrees back from stereotaxic vertical. After a recovery period of at least six days the monkeys were further trained to track a haploscopically-presented target (seen monocularly or binocularly) moving in depth. During this further training and for the duration of the experiments the monkeys were rewarded for accurate eye movement and accommodation performance. They were trained for at least two weeks in this apparatus before any of the data presented here were collected.

2.2 Stimulus presentation

In order to investigate interactions of accommodation and vergence, both neurophysiologically and behaviourally, it was necessary to build an apparatus for presenting accommodation and vergence stimuli independently of one another. The general features of this apparatus are illustrated in Fig. 2.1: two identical targets were presented, one to each eye, via mirrors which could be rotated independent of the motion of the targets in depth. The stimulus to accommodation was determined by the distance of each target from the principal planes of the monkey's eyes, while the vergence stimulus was determined by the mirror angle,

Figure 2.1.

Experimental set-up. The target was presented haploscopically. The two eyes viewed identical targets via mirrors mounted on servo motors and 9 D Badal lenses (positive lenses placed so that their near focal planes were at the principal planes of each eye). The targets were mounted on linear servos. The position of the targets and the angles of the mirrors were controlled by a PDP 11/34 computer. The accommodation of the right eye was measured with a Scheiner principle infra-red optometer and the position of each eye was measured using implanted magnetic search coils (not shown).



the target position, and the distance of the mirrors from the centres of rotation of the eyes. The positions of the centre of rotation and principal plane of each eye were estimated on the assumption of Rolls and Cowey (1970) that a monkey schematic eye can be obtained by linearly scaling the reduced human eye. This suggested that the principal plane of the monkey eye was 1.15 mm behind the cornea, while the centre of rotation was 10.3 mm behind the cornea.

The targets were viewed through 9 D positive lenses (measured focal length 109 mm) placed with their near focal point at the estimated position of the principal plane of the monkeys eyes (Badal lenses). The targets consisted of a black cross hairs (hairs 3 min. arc wide) on a yellow circular background 0.5 degrees in diameter (produced by illumination with red and green light from a dual light emitting diode). This target was at the centre of a white cross whose arms spanned a black background 26 degrees by 26 degrees. The whole assembly was illuminated in one of two ways: either with a small 6 volt bicycle bulb mounted underneath the Badal lenses, or by diffuse illumination from an angle poise lamp shining against the back wall of the box in which the monkey and apparatus were enclosed. This Badal viewing system allowed accommodative stimuli up to 8.5 D to be produced (higher values being prevented by the target assembly running into the lens mounting). The luminance of the targets was measured with a photometer (Salford Electrical Instruments). At 0 D, the luminance of the centre of the target illuminated by the L.E.D. from behind was approximately $0.5 \log \text{cd/m}^2$, while the dark part of the surround had a luminance of $-0.5 \log \text{cd/m}^2$. For accommodative stimuli between 0 and 6 D the luminance was constant to within $\pm 0.05 \log$ units. As the target moved between 6 D

and 8D its luminance was reduced by 0.5 log units. The Badal lenses could be removed to allow direct viewing of the target, when changes in the angular subtense of the target at the eye accompanied changes in its distance. In direct viewing the range of the accommodation stimuli available was 2.5 - 8.5 D. Although the luminance of the target centre was similar in Badal viewing and in direct viewing, the luminance of the surround was 0.65 log units lower during direct viewing of the target. During direct viewing, the luminance of the surround was constant to within ± 0.06 log units for target movements between 3 D and 7 D.

The targets were mounted on linear servos constructed from the 'Y' movements of Gould Bryans 50000 series chart recorders and RS components servo motor kits. These are referred to below as the 'accommodation stimulus servos'. The servos had a slew rate limit of 103 cm/second, which corresponded to 87 dioptres/second when the targets were viewed through the Badal lenses, and 25 dioptres/second in direct viewing of a target at 20 cm. Over the range of frequencies used in this study, the gain of this accommodation stimulus servo system was within 0.5% of unity, although small phase lags occurred at higher frequencies (see Appendix 1).

The mirrors of the haploscope were mounted on angular servo motors (General Scanning G-300 PD) with a -3 dB bandwidth of 120 Hz and negligible phase lags in sinusoidal motion over the frequency range used here (see Appendix 1). The mirrors were mounted with the axis of rotation 50 mm in front of, and 3 mm medial to, the centre of rotation of each eye. The medial displacement increased the range of convergent stimuli which could be produced, since as either mirror rotated to

produce a convergence stimulus, the image of the target moved towards the medial edge of the mirror. Since the mirrors did not rotate about the centre of rotation of the eyes, unless the vergence demand was zero, movement of the accommodation stimulus servos would have produced a stimulus which had both an accommodative and a vergence component. The appropriate compensatory mirror rotations were calculated by the method described in Appendix 2, and applied on-line to the mirrors so that movements of the accommodation stimulus servos produced no change in vergence stimulus. The compensation signals were calculated on the basis of the instantaneous measured position of the left accommodation stimulus servo, so that when the target position was not at its desired value (e.g. in the period before the completion of a step response) the compensation signals were still appropriately calculated.

Lateral to each mirror shutters were mounted, which could be moved to cover either eye (or neither), to allow monocular (or binocular) stimulation. The accommodation stimulus servos, the mirrors and their servos, and these shutters were all mounted on a rigid board which could be slid smoothly towards and away from the animal.

2.3 Eye movement and accommodation recording

Eye movements were recorded by means of a magnetic search coil system, similar to that first used by Robinson (1963) in humans, and Fuchs and Robinson (1966) in the monkey. In the system used here, the animal (with coils implanted as described above) was placed in oscillating magnetic fields produced by two sets of Helmholtz coils, one pair above and below the animal, creating a vertical field, and the other pair to the right and left of the animal, creating a horizontal

field. The field coils were driven at 35 KHz by a Quad 405 stereo amplifier, which delivered approximately 1 ampere r.m.s. currents. The currents in the two sets of coils were 90 degrees out of phase with one another, so that phase-sensitive detection (using E.G. and G. Brookdeal 9503 and 9505C lock-in analysers) measured the vertical and horizontal components of eye movements independently. The strength and phase of the fields were controlled by the circuit described by Optican et al. (1982) which used sense coils near the monkey to monitor the field strength and correct for perturbations which could arise if, for example, metal objects were placed in or near the field coils.

The field coils had 16 turns and were nearly square, approximately 1.6 metres across. This large coil size was useful both to allow space to put the haploscope and the optometer close to the monkey and to provide a volume at the centre of the coils within which the field is close to uniform, large enough to allow precise recording of the position of both eyes. (According to Robinson (1963) the area bounded by edges one tenth the size of the coils has a field constant to within 1%.)

The gain of the eye recording system was adjusted by changes in the field strength. This was set initially to give an appropriate gain using a coil with the same nominal dimensions as those implanted in the monkeys, rotated upon a plastic gimbal. With each monkey the phase of the fields relative to one another were adjusted so that when the monkey transferred gaze between two L.E.D's which were vertically displaced from one another there was no eye movement recorded on the horizontal channel, and during horizontal eye movement there was no recorded

vertical movement. The final calibration of the gain of the eye coil system was made while the animal fixated targets presented monocularly in the haploscope. The signal from one eye coil was shunted through a variable resistance to ground to allow the gains of the signals from the two eyes to be matched.

Accommodation was recorded by a purpose made dynamic infra-red-optometer. It had an r.m.s. noise level of ± 0.06 dioptres, and a -3 dB bandwidth of 15 Hz. Details of the design and calibration procedures used are given in Appendix 4. The optometer was aligned on an axis approximately 32 degrees lateral to 'straight ahead', and the input beams (whose alignment was checked with an infra-red TV camera) entered the pupil somewhat below the centre in order to avoid corneal reflections of the infra-red sources entering the optometer. Each day one or two drops of phenylephrine were instilled into the animal's right eye in order to dilate the pupil (for reasons discussed in Appendix 4). Although it is usually believed that phenylephrine has little effect on accommodation, Chin et al. (1968) disputed this. Evidence is presented in Chapter 3 suggesting that the phenylephrine had little effect on accommodation in these monkeys.

2.4 Data collection

A PDP 11/34 computer with a Cambridge Electronic design model 502 interface controlled stimulus presentation and sampled the horizontal position of both eyes, the position of the left hand side accommodation stimulus servo, the accommodation response, and (in unit recording studies) pulses derived from nerve cell discharges. The program, written in the C programming language, also provided an on-line display of the

signals sampled and allowed on-line calculation of the fundamental component of the responses. A variety of stimuli could be delivered: the waveform and frequency of the stimulus were controlled by a Wavetek model 162 signal generator, whose output was sampled by the computer. The vergence stimulus was delivered asymmetrically (apparent target motion directly towards one eye or the other). The vergence and accommodation stimuli could be combined in a ratio simulating natural target motion, or in any other ratio from zero to infinity - producing accommodation and vergence stimuli in conflict. The combination of stimuli used to simulate natural viewing differed slightly from the stimuli associated with the movement of a real object in two ways. Firstly, the relationship between the dioptric power required to bring an object into focus and the vergence angle required to fixate it is only approximately linear, and the program controlling the stimuli assumed that the relationship was exactly linear. Secondly, the dynamic performance of the accommodation stimulus servo system was poorer than that of mirror rotation, so at high frequencies the accommodative stimulus lagged the vergence stimulus by a few degrees. The magnitude of these imperfections is discussed in Appendix 1, and was small enough not to affect the animal's performance significantly.

In addition to combining the stimuli to accommodation and vergence in arbitrary ratios, the program also allowed the measured responses of accommodation and/or vergence to be used to drive the appropriate stimulus - opening the control loops by feedback. When one control loop was opened in this way, it was still possible to deliver time-varying stimuli to the other system. Thus, when the measured accommodation response was used to position the accommodation stimulus servos (AOL

viewing), it was still possible to deliver a sinusoidally varying vergence stimulus. This allowed dynamic measures of vergence-accommodation to be made. The chief limitation of this technique was that as a result of delays in the measurement of accommodation and delays in the response of the accommodation stimulus servos to control signals, blur stimuli were not accurately removed when accommodation was changing rapidly. Provided that the dynamic response of the feedback loop was good compared with that of the animal's blur-driven responses, this effect should not have greatly compromised the measurement of vergence-accommodation performance. A method is presented in Appendix 3 for estimating the effect of any residual blur on the measurements, and this suggested that the effects were small. The direction of target motion was usually directly towards the right eye, since the optometer recorded the accommodation response of this eye, and the output of the instrument was affected by large eye movements.

Finally, the program allowed both mirrors to be rotated in the same direction, to produce a conjugate eye movement stimulus with no change in the accommodation stimulus.

The rate at which the sampling and stimulus output were performed changed during the course of this study owing to the installation of an FP11A floating-point processing unit in the midst of the project. For monkeys A and H the sampling of behavioural responses and the output of control signals to the stimulus apparatus was performed every 12.5 msec, while for monkey M it was performed every 4 msec. Although the signals were sampled at this rate, not every sample was stored on disk for off-line analysis. For example, at a stimulus frequency of 0.2 Hz and

sampling every 4 msec, every ninth sample was stored, and at other frequencies the rate was adjusted so that the same number of samples (approximately 135) were recorded in a complete cycle (thus at 0.6 Hz every third sample was stored).

The input from the signal generator could be replaced by the output from a Gaussian random noise generator (Cambridge Electronic Design 502-25), filtered with a Rockland model 452 dual high-pass/low-pass filter, to produce pseudo-random target motion. In order to permit spectral analysis of responses to pseudo-random stimuli, it was necessary to ensure that the stimuli and the responses had the same value at the beginning and the end of data collection. In order to achieve this the amplitude of the stimulus movement was attenuated gradually (with a cosinusoidal time course) during the first and last 500 msec of data collection. The movement of the stimulus was sufficiently gradual to allow the animal's responses to return to their initial values.

A second program, similar to the one described above in other respects, sampled and recorded the vertical position of both eyes (in addition to the horizontal signals) but did not record the vergence stimulus or the position of the accommodation stimulus servo. This program was developed in order to record responses to electrical stimulation, so that any vertical eye movements that resulted could be recorded. The program was also used to record spontaneous eye movements while recording from cells in and around the oculomotor nucleus, facilitating the identification of cells related to vertical eye movements.

In addition to the computer display, the vertical and horizontal positions of each eye were displayed on two Gould OS 255 oscilloscopes operating in 'X-Y' mode.

2.5 Unit recording and microstimulation

Two techniques were employed in investigating the neurophysiological organization of the system: extracellular unit recording and microstimulation. In both cases tungsten in glass recording electrodes, modified after Merrill and Ainsworth (1972), were lowered through the chronically implanted chamber. The electrodes had steeper tapers at the tip than those described by Merrill and Ainsworth, and were mounted in rigid stainless steel tubing after the manner of platinum-iridium electrodes (Wolbarsht et al., 1980). These two features made the electrodes mechanically strong enough to be lowered through the dura without damage to the electrode, and stiff enough to allow them to be lowered to the region of interest reliably, without bending. After long periods the dura exposed at the bottom of the chamber thickened considerably and frequently damaged electrodes. It was possible to alleviate this problem by removing some of the new growth on the dura, using a sharp bone scraper and a pair of forceps to peel off layers. This was done while the animal was tranquillized with ketamine. This solution was sometimes only effective for a short while, so in order to avoid scraping the dura too frequently, a guide tube was sometimes used to penetrate the dura before lowering an electrode.

The electrodes were mounted in a Narishige MO-9 hydraulic microdrive, which clamped onto the chronically implanted chamber. During recording experiments, the signal from the microelectrode was amplified

by a W.P.I. DAM-5 A preamplifier (bandpass 10 Hz to 30 KHz), low-pass filtered (12 KHz, 48 dB/octave) to remove interference from the magnetic fields produced by the eye monitor, delayed by a purpose-made digital delay line, and discriminated by means of a W.P.I. Model 121 window discriminator. The delayed signal, along with the levels at which the discriminator was triggered, was displayed on an oscilloscope, and pulses corresponding to the discriminated action potentials were collected by a PDP/11-34 computer, which recorded the total number of impulses in each sampling period (37.5 msec for target motion at 0.2 Hz).

Microstimulation experiments were performed only on monkey H. Stimulus pulse trains were passed through the electrode using a Grass S88 stimulator with PSIU6 constant current isolation units. The actual current passed during stimulation was monitored on a Tektronix 5440 oscilloscope. Two regions of the brain were investigated - the midbrain area in which unit recordings were made, and an area of the occipito-temporal cortex on either side of the Superior Temporal Sulcus, for which a second electrode chamber was implanted.

2.6 Data Analysis

Spectral analysis was used to calculate the gain, phase, and total harmonic distortion of the fundamental component of the responses to sinusoidal stimuli, as described in Appendix 5. The gain of an accommodation or accommodative-vergence response was defined as the ratio of the amplitude of the response modulation to that of the accommodation stimulus (the reciprocal of the target image distance from the principal plane of the eye). The phase of the response refers to

the phase angle between the modulation of the stimulus and that of the response. Similarly, the gain of a vergence or vergence-accommodation response refers to the ratio of the amplitude of the response modulation to that of the vergence stimulus (the angle subtended by the centres of rotation of the eyes at the target), and the phase refers to the phase difference between the response and the vergence stimulus.

This analysis was performed on all complete cycles of data where the animal's fixation was never interrupted for more than 250 msec. Artefacts in the accommodation and vergence signals, introduced by blinks or brief periods of inaccurate fixation, were removed from the data by a routine which detected rates of change of accommodation (vergence) greater than 20 D(MA)/sec and replaced the measured response for the following 250 msec with a linear interpolation to the measured response at a point 250 msec after the blink was detected. For data collected at frequencies above 0.6 Hz, only cycles without blinks were used, as 250 msec formed a significant portion of the whole cycle. This analysis was performed by a program written in the 'C' programming language, using the algorithms described in Appendix 5. The same program also provided a display on an Electrochrome V10 video monitor of the data used in calculations.

Although spectral analysis has frequently been used to analyse the responses of accommodation and vergence to sinusoidal stimuli, none of the earlier reports provided any method for estimating the variability of the responses. In order to extract this information here, the spectral analysis was performed separately on each complete cycle of data, and the results from all the cycles averaged vectorially.

Variances of the components of the responses in phase and in quadrature with the stimulus were calculated separately, and then combined to give an estimate of the variance of the mean gain and phase. The method for doing this vector averaging is described fully in Appendix 5.

The responses to pseudo-random target motion were analysed by a similar technique, the gain and phase of the fundamental component and of a number of harmonics being calculated by spectral analysis. The analysis was done both for the stimulus and the response variables, so that the response relative to the stimulus for each harmonic could be obtained. When averaging the results from several different runs of random target motion, the data were weighted according to the calculated power in the stimulus, as described in Appendix 5.

The mean values for the phase lags of the accommodation responses (relative to the stimulus) were adjusted to take account of the delays introduced by the optometer (described in Appendix 4).

For spectral analysis of modulations in unit discharge rate, spikes were grouped into bins of width 225 msec for data collected at 0.2 Hz 450 msec for data collected at 0.1 Hz, and so on. These bin sizes were selected to allow a reasonably felicitous representation of discharge rate without introducing too much quantization noise (important for the calculation of total harmonic distortion).

Latencies of responses to step changes were determined by hand, counting sample points up to the point where a response had a value outside the range covered by the variations immediately before the target moved.

CHAPTER THREE
BEHAVIOURAL EXPERIMENTS

3.1 Introduction

As discussed in Chapter 1, several studies in human subjects have described the dynamic properties of disparity-driven vergence and of blur-driven accommodation, but very little work has been published exploring the dynamic interactions of the blur-driven and disparity-driven responses. In particular, very little is known about the dynamic performance of accommodation during binocular viewing. One of the reasons why this has not been studied is that vergence stimuli usually produce movements of both eyes, and many devices used for measuring accommodation dynamically do not tolerate movements of the eye being observed. In this study, this difficulty has been avoided by presenting stimuli which moved directly towards the right eye, in which accommodation was measured. During target motion in which the target vergence (in both senses)¹ modulated with a sinusoidal time course, smooth pursuit movements combined with vergence movements to maintain the position of the right eye nearly constant (during high frequency target motion there was some movement of the right eye). Using such stimuli, the performance of accommodation and vergence were systematically investigated in three conditions: 1) normal binocular viewing (where both blur and disparity cues were present); 2) monocular viewing (where only blur cues were present); and 3) accommodation-open-

¹I.e. convergence of the eyes and vergence of the light from the target (Davson, 1972; p. 556).

loop binocular viewing (where only disparity cues were present).

3.2 Results

These experiments were performed on three adult monkeys (Macacca mulatta). Two were female (monkeys A and H) and one was male (monkey M). Monkeys A and H had inter-ocular separations of 30 mm (1 MA corresponded to 1.71 degrees) while monkey M had an inter-ocular separation of 40 mm (1 MA corresponded to 2.29 degrees). Each monkey received extensive training in the haploscope (for at least 2 weeks) before any of the data presented below were collected. The data were collected over a period of two weeks in monkey A, five weeks in monkey M, and in four separate periods of a few days spread over 3 months in monkey H.

Monkey M was approximately six dioptres myopic, and also esotropic when viewing distant targets. In addition he had a leftward beating nystagmus when left in darkness, and showed a tendency to produce convergence predominantly by moving the left eye alone. These oculomotor abnormalities are discussed in more detail in Appendix 6. When his refractive error was corrected his accommodation and vergence responses were similar to those recorded in monkeys A and H, so results from all three monkeys will be presented together.

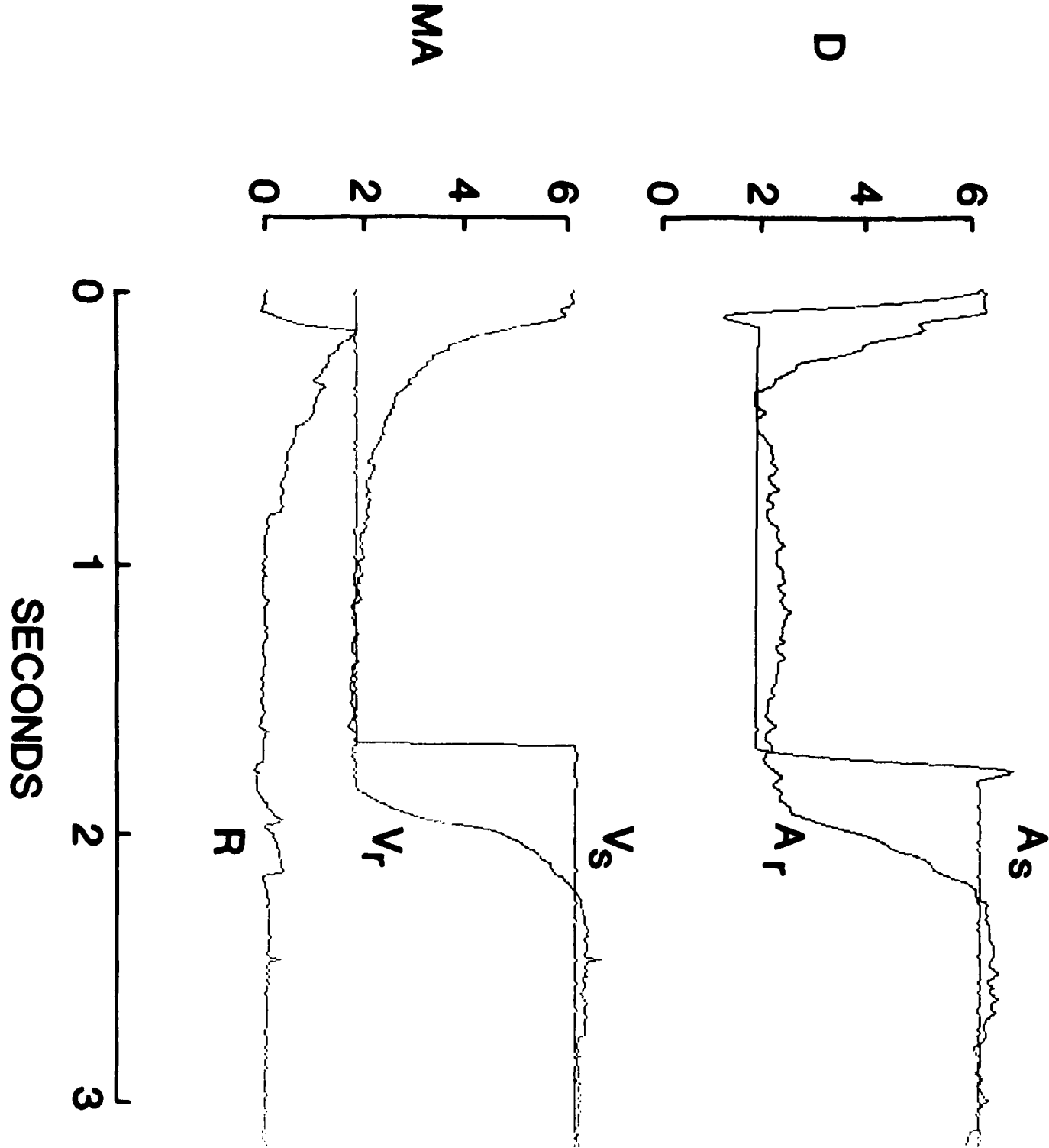
3.2.1 Responses to step changes in target position

Fig. 3.1 shows examples of the responses made by monkey H to step changes in target position in two conditions: Fig. 3.1A shows the responses to binocularly viewed target motion, while Fig. 3.1B shows the

Figure 3.1.

Accommodation stimulus (A_s) and response (A_r), vergence stimulus (V_s) and response (V_r) and horizontal position of the right eye (R) in response to steps (from 6 D to 2 D and back) of a target moving directly towards and away from the right eye in a plane parallel to the midline. A) shows the responses during binocular viewing, B) shows the responses during monocular viewing. Vergence and right eye position are plotted in metre-angles (MA) so as to be commensurate with accommodation (in dioptries). Monkey H.

A) Binocular



B) Monocular



responses to monocularly viewed target motion. The movement of the right eye in this task was usually small enough not to interfere with the operation of the optometer. Data from trials in which the right eye deviated by more than 2 MA from 'straight ahead' were discarded. In monkeys A and M the step changes in stimuli were half the size of those used in monkey H, so that the movement of the right eye was much smaller than that shown in Fig. 3.1. The mean latencies of accommodation and vergence responses in both conditions are shown in Table 3.1 for all 3 monkeys. In monocular viewing, the latencies of accommodation and accommodative-vergence were considerably shorter than those of humans (370 msec for accommodation in Tucker and Charman, 1979; 250 msec for accommodative-vergence according to Wilson, 1973). In binocular viewing the latency of the vergence response was very similar to the 160 msec reported for human subjects (Rashbass and Westheimer, 1961a; Zuber and Stark, 1968). The latency of accommodation to a given stimulus was always longer than that of vergence to the same stimulus. This was true in all three monkeys, in both monocular and binocular viewing. This strongly suggests that transport delays in the accommodation plant are longer than those for the vergence plant. Averaging the latency difference from all conditions for all 3 monkeys, the mean value of the latency difference was 66 msec ($\pm$ 31 msec S.D.). Wilson (1973) reported a similar result in human subjects, although the magnitude of the latency difference was larger (120 msec) than reported here for the monkey.

Although there was little difference between the latency of responses to binocularly or monocularly viewed target motion, the responses to binocularly viewed target motion were executed more rapidly

TABLE 3.1

Latencies (in milliseconds) of accommodation and vergence (all figures based on at least 25 samples). Steps towards the animal are called positive and steps away are called negative.

Monkey	Sense	Accommodation				Vergence			
		Monocular		Binocular		Monocular		Binocular	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
H	+	263	28	240	19	170	27	166	14
	-	228	59	173	35	168	35	135	24
A	+	177	28	179	29	157	24	159	30
	-	196	30	214	51	129	28	177	22
M	+	266	61	234	31	157	33	138	24
	-	254	52	280	23	186	50	184	19

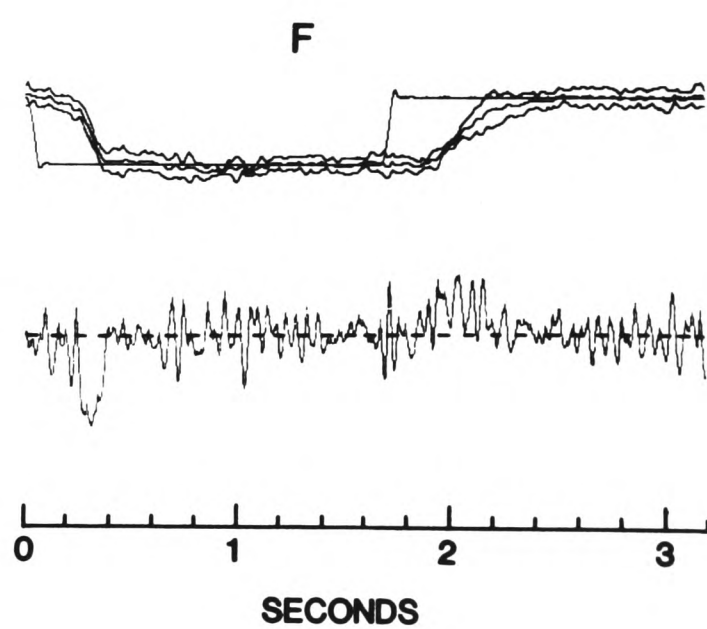
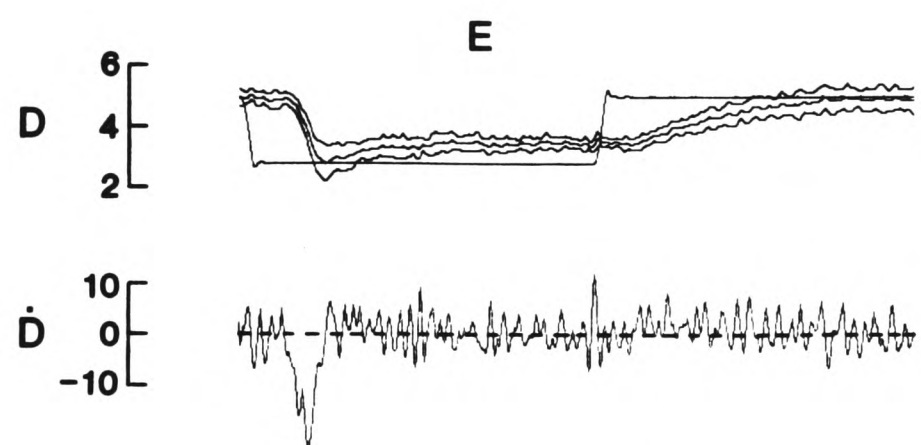
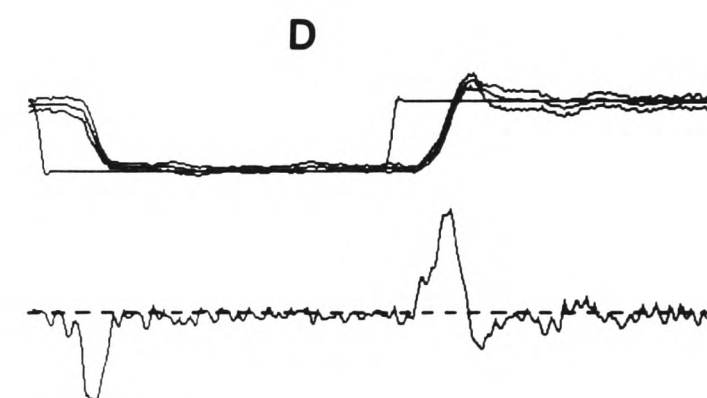
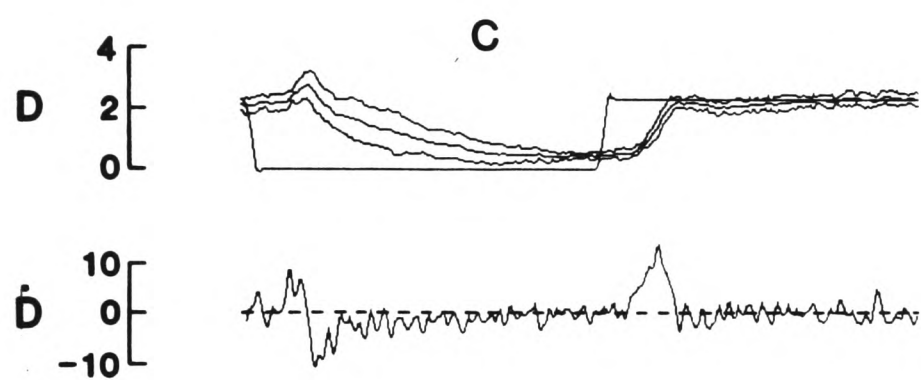
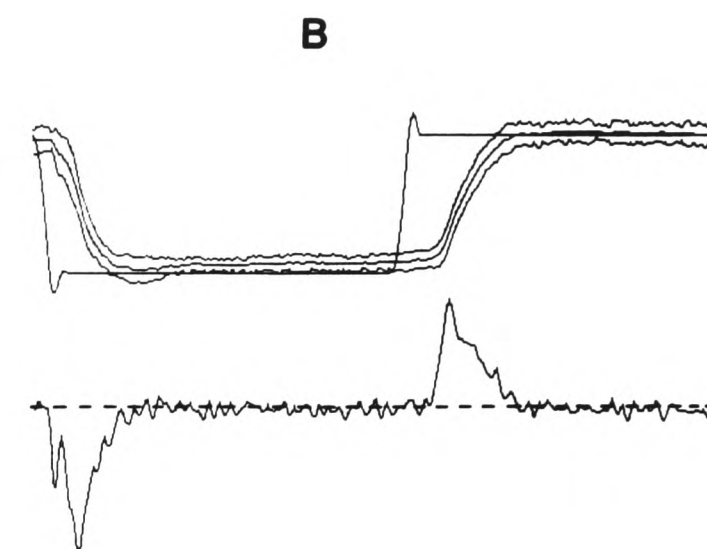
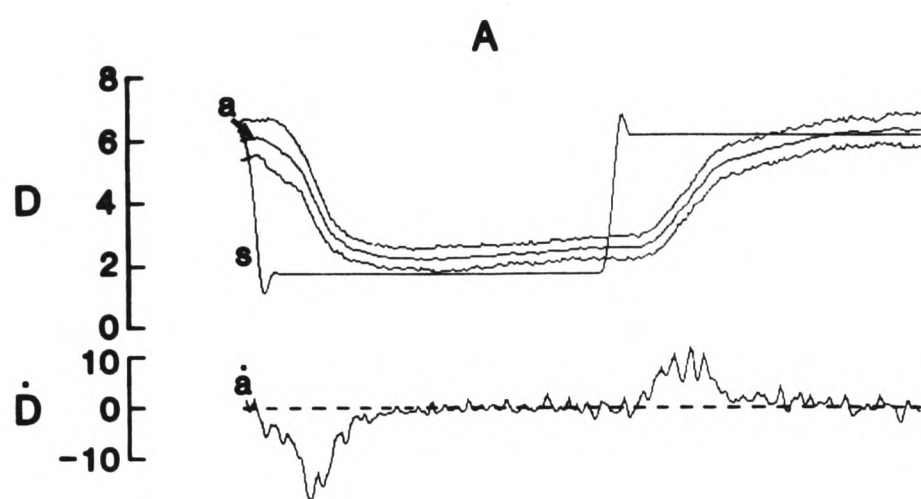
than responses to monocularly viewed target motion. Fig. 3.2 compares the dynamics of accommodation changes in monocular and binocular viewing for all 3 monkeys. It is clear in most cases that the responses were executed more rapidly in binocular viewing. The only exception is in the responses to target steps away from monkey M, where the behaviour is similar in monocular and binocular viewing. During monocular viewing monkey A systematically responded to target steps away from her by an accommodation response which was initially in the wrong direction (Fig. 3.2c). The latency in this case was defined as the latency of onset of the initial (albeit incorrect) response.

The responses to target motion in opposite directions were not usually symmetrical. In monkeys H and M the responses to target steps from near to far were accomplished more rapidly than the responses to steps from far to near. In monkey A the opposite asymmetry was observed. In all three monkeys the asymmetry was more marked in monocular viewing than in binocular viewing (see Fig. 3.2).

In Fig. 3.1 it can be seen that in both monocular and binocular viewing the right eye made saccades to keep on target. Although it was once believed that the viewing eye did not move during accommodative-vergence, it has recently become clear that in human observers (Kenyon et al., 1978) the viewing eye does move. It has also recently been demonstrated that in human subjects saccades occurring during vergence movements produce a transient increase in vergence velocity (Kenyon et al., 1980 and Enright, 1984a). In the monkey, the saccades which occurred in response to binocularly viewed target motion were either larger than those which occurred during monocular viewing or else more

Figure 3.2

Mean accommodation responses in three monkeys (monkey H in A and B, monkey A in C and D, monkey M in E and F) to target steps presented monocularly (A, C and E) and binocularly (B, D and F). In each section of the figure, the five traces are: the accommodation stimulus (s), the mean accommodation response ($a \pm$ S.D.), and the time derivative of the mean response ($\dot{a}$) - the response velocity. Monocular accommodation is slower than binocular in all cases excepting the responses of monkey M to target steps from near to far. For each monkey, all the responses were obtained in a single session. In A, $n = 19$; in B, $n = 19$; in C, $n = 6$; in D, $n = 10$; in E, $n = 9$; and in F, $n = 7$.



frequent (see Fig. 3.1). It is therefore possible that the improvement in vergence dynamics during binocular viewing resulted from the acceleration of vergence during saccades. Fig. 3.3 shows (for monkey H) that in the monkey vergence velocity did increase during saccades, both in monocular and in binocular viewing. However, as Fig. 3.3 shows, the difference between vergence velocity in the monocular and binocular cases was evident before the first saccades occurred (indicated by the arrows). The same was true for monkey A, and for monkey M following target steps from near to far. Monkey M rarely made saccades following target steps from far to near towards the right eye (see Appendix 6) so saccades could not have accelerated the vergence responses. Therefore the more rapid vergence responses observed during binocular viewing (compared with monocular viewing) in all three monkeys cannot be accounted for by an interaction between vergence and saccades.

3.2.2 Responses to sinusoidal target motion

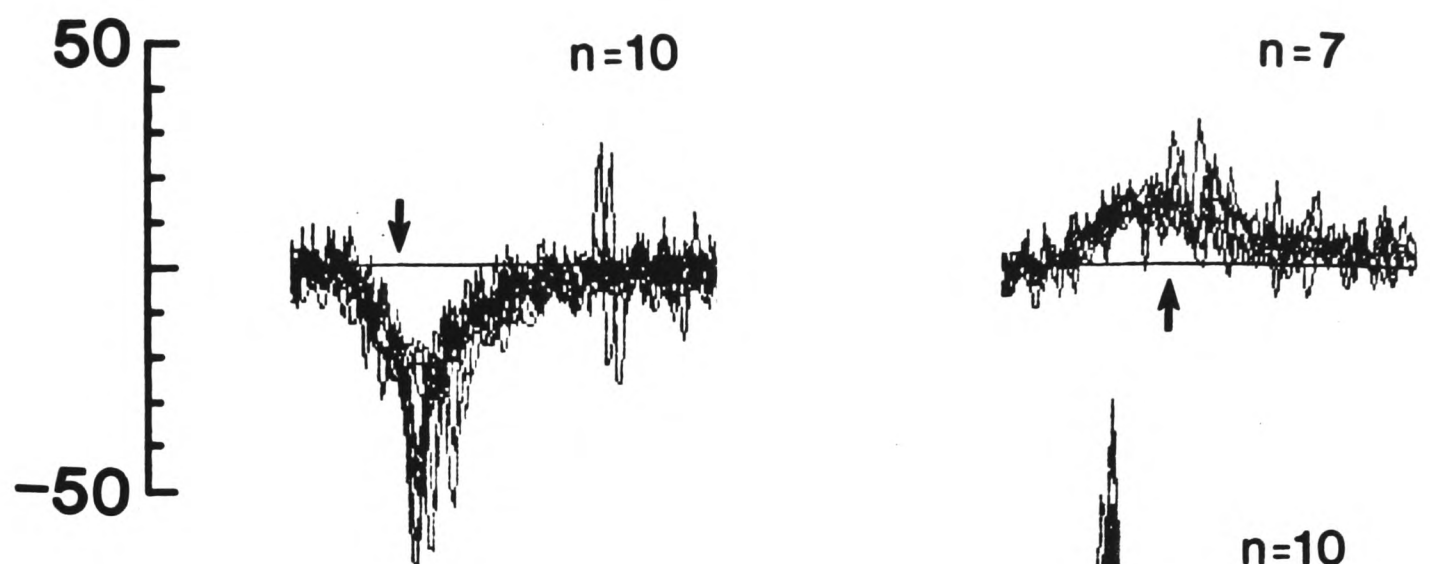
In order to avoid the complications introduced by the interaction between vergence and saccades, and in order to describe more fully the improvement of accommodation dynamics during binocular viewing, the monkeys' responses were measured during tracking of targets producing accommodation and vergence stimuli which modulated with a sinusoidal time course. The responses were analysed by spectral analysis, performed separately for each cycle of target motion. The results were then averaged vectorially, as described in Appendix 5.

The gain of an accommodation (or vergence) response is defined as the ratio of the amplitude of the modulation in the accommodation (or

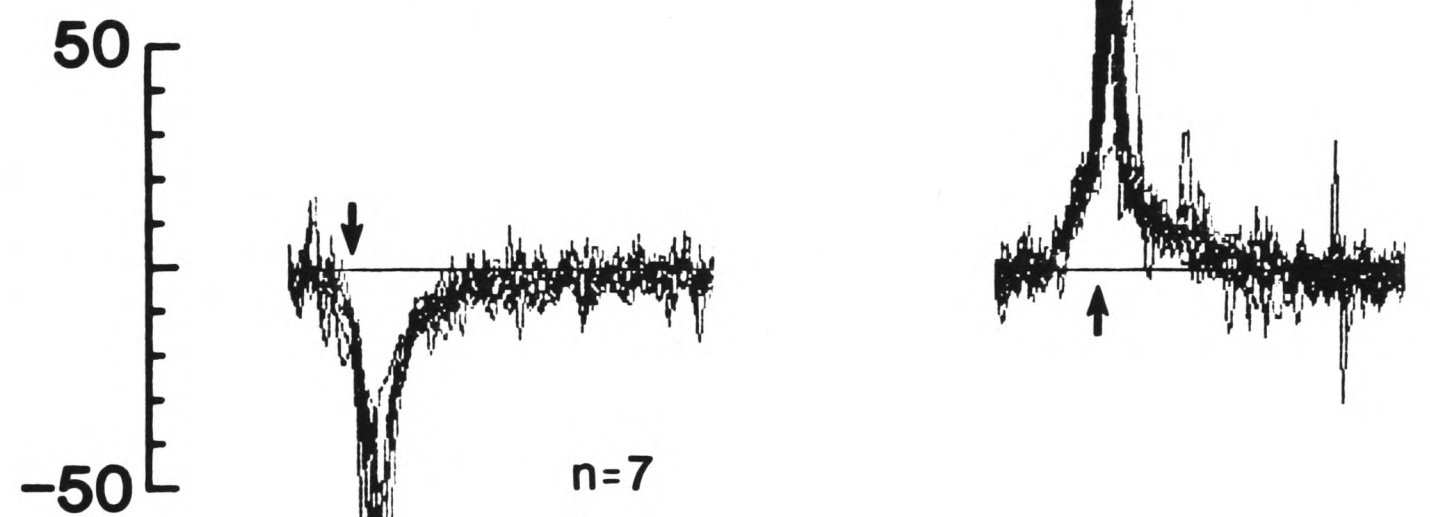
Figure 3.3

Velocity of individual vergence responses of one monkey (H) to 4 D target steps viewed monocularly (A) or binocularly (B). Asymmetrical vergence in which the target moved directly away from and towards the right eye. The left side of the figure shows responses to target steps away from the animal, the right side to target steps towards the animal. The arrows mark the latency of onset of the earliest saccade in each condition. C) The mean velocity of vergence in binocular (b) and monocular (m) viewing. Note that the vergence velocity is clearly higher in binocular viewing, even in the period before the first saccade.

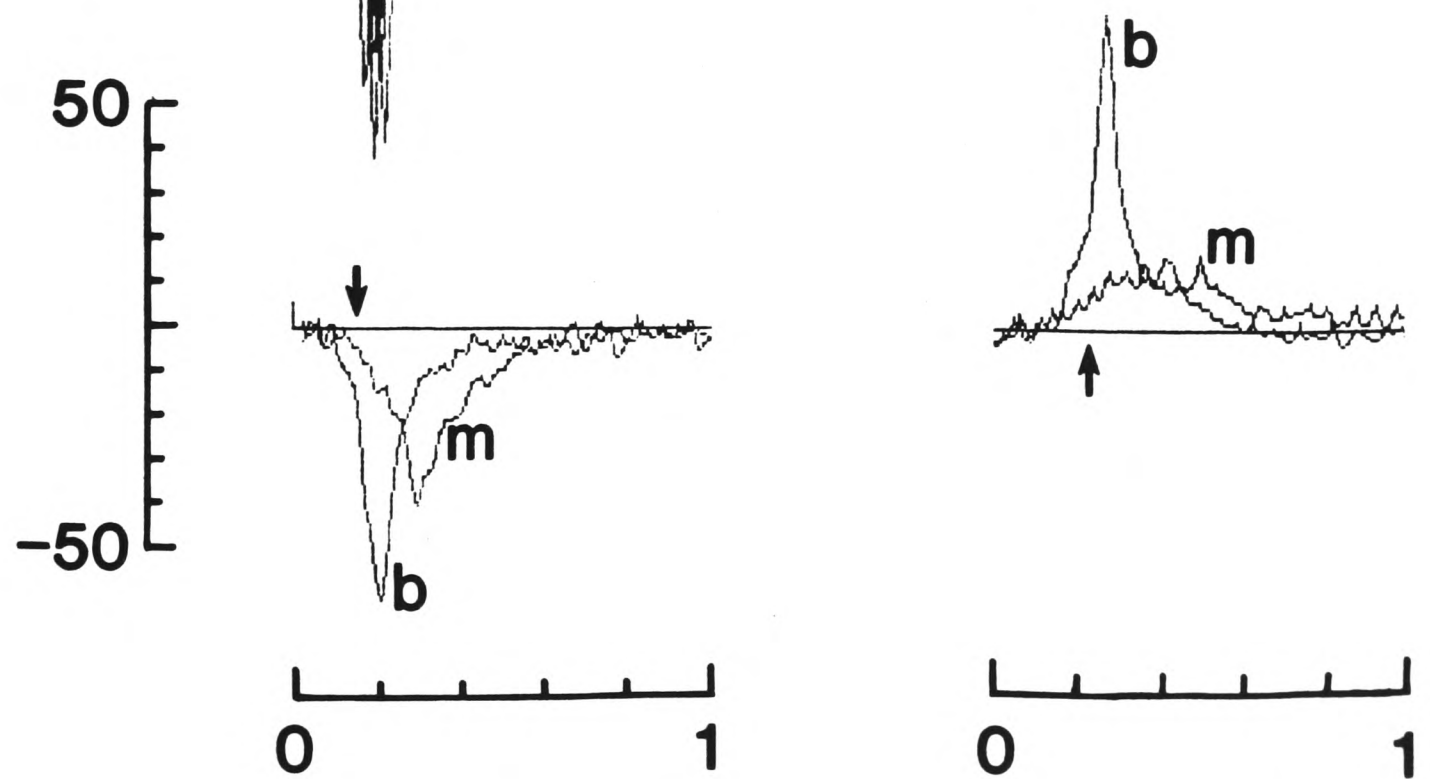
A)



B)



C)



SECONDS

vergence) response to the amplitude of the stimulus modulation. Note that 'stimulus' is used to describe the dioptric power of the eye (or the vergence angle) necessary to maintain clear (or single) vision, as distinct from the blur (or disparity) produced by any difference between the accommodation (or vergence) stimulus and response.

Before the results were averaged, they were examined for evidence that the responses did not alter from one cycle to the next. For each stimulus frequency, the gain and phase of the responses averaged from the first cycle of each set of data was compared with the average of the responses to all cycles. If the gains were the same to within 5%, and the two phases differed by less than 5 degrees, the data from all cycles were used to calculate the mean response. This condition was satisfied in binocular viewing for responses to stimuli of frequencies lower than 0.6 Hz. When this condition was not satisfied, the gain and phase of the responses were examined cycle by cycle and only cycles after the steady state had been reached were used to estimate the overall mean responses. At stimulus frequencies of 0.9 and 1.2 Hz this involved discarding data from the first two or three cycles of the responses. At these frequencies the gain of the responses was larger in the first few cycles than in later cycles, although the phase lags were similar in all cycles. Fig. 3.4A shows an example of the responses to a binocularly viewed stimulus with a frequency of 0.6 Hz. Fig. 3.4B shows the responses to the same stimulus viewed monocularly. Note that the responses to monocularly viewed target motion had smaller gains and larger phase lags than the responses to a binocularly viewed stimulus.

Fig. 3.5 is a Bode plot comparing the responses of monkey H to

Figure 3.4

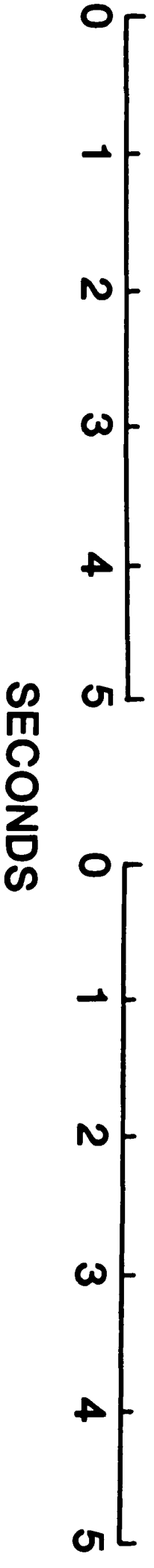
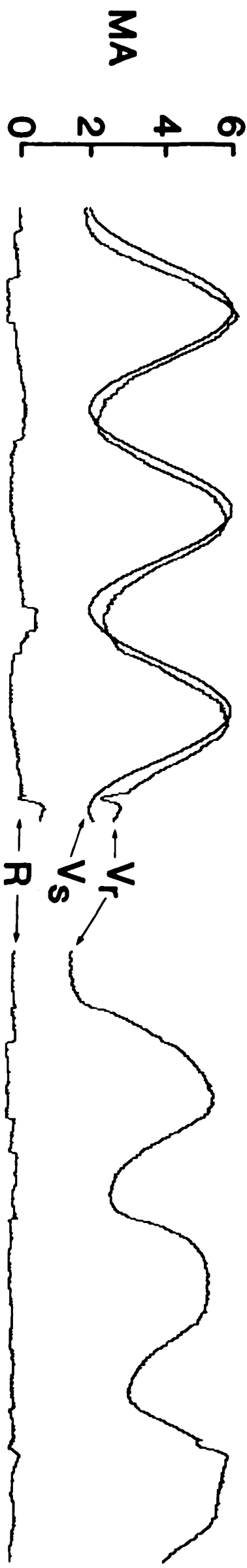
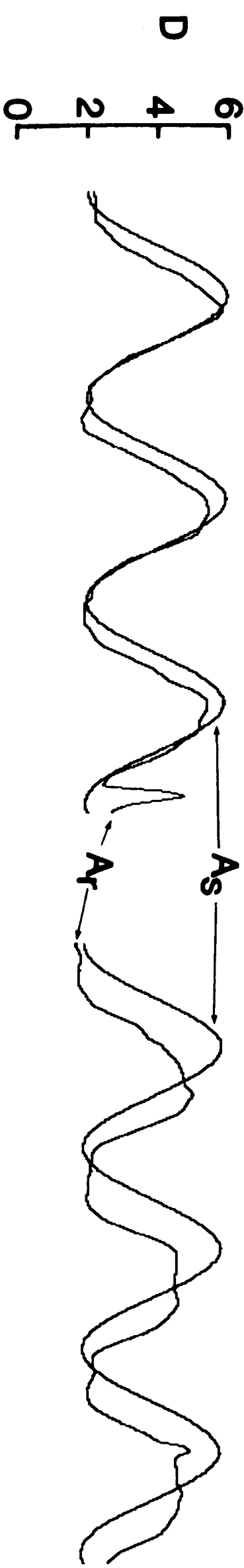
Accommodation stimulus (A_s) and response (A_r), vergence stimulus (V_s) and response (V_r) and horizontal position of the right eye (R), during sinusoidal modulation (at a frequency of 0.6 Hz) of the accommodation and vergence stimuli. Target motion was viewed binocularly in A) and monocularly in B). At the end of the third cycle of target motion in A) the effects of a blink on the accommodation recording can be seen.

A)

0.6 Hz binoc

B)

0.6 Hz monoc



monocularly viewed stimuli with those to binocularly viewed stimuli. Figs. 3.6 and 3.7 show the equivalent data for monkeys A and M respectively. In all cases the accommodation stimulus had a peak-to-peak amplitude of 4 D (accompanied by a vergence stimulus of 4 MA peak-to-peak in binocular viewing)¹. The phase lags of accommodation have been adjusted to account for the delays introduced by the optometer in measuring the accommodation changes. For data taken from monocular viewing the phase lags are expressed relative to the phase of the accommodation stimulus modulation, while for the data collected during binocular viewing the phases are expressed relative to the phase of the vergence stimulus modulation. As explained in Appendix 1, the movement of the accommodation stimulus lagged behind that of the vergence stimulus by a small amount (3 degrees at 1.2 Hz).

In each of Figs. 3.5, 3.6, and 3.7 it can be seen that the phase lags of the accommodation and vergence responses (relative to the stimulus) were much smaller during binocular viewing than in monocular viewing. The amplitude of responses were larger in binocular viewing than in monocular viewing. These results confirm the above finding that the dynamic performance of accommodation and vergence are enhanced during binocular viewing. It seemed most likely that the enhancement of

¹In monkey M the binocular stimulus was presented over the range 1 - 5 D. The monocular performance over this range was non-linear (the responses were not sinusoidal) and poor. Monocular responses to stimuli in the range 3 - 7 D were more nearly sinusoidal and at all frequencies tested showed smaller phase lags and larger gains than the responses to stimuli in the range 1 - 5 D. The monocular data presented are responses to stimuli over the range 3 - 7 D. It was not possible to present binocular stimuli over this range because the spectacle correction worn by monkey M limited the range of available vergence stimuli (as discussed in Appendix 6).

Figure 3.5

Bode plots of accommodation and vergence performance for monkey H in response to 4 D peak-to-peak sinusoidal accommodation and vergence stimuli at frequencies from 0.1 to 1.2 Hz. Open circles show responses during monocular viewing, filled circles show responses during binocular viewing. Each point is based on at least 9 cycles of data (average 11 cycles). Standard errors are smaller than the data points (typically ± 0.02 for gain, ± 2 degrees for phase) unless explicitly shown. Note that the phase lags of the accommodation and vergence responses are much smaller, and the response gains are larger, in binocular viewing than in monocular viewing.

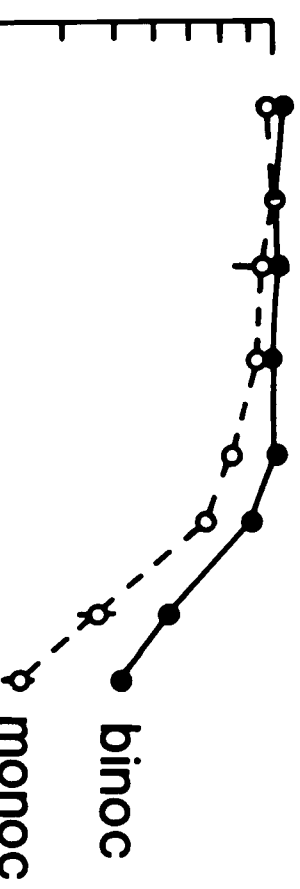
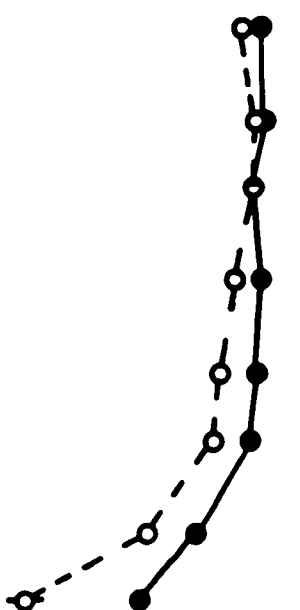
Accommodation

Monkey H

Vergence

gain

1.0
0.1



phase

0°
-100°

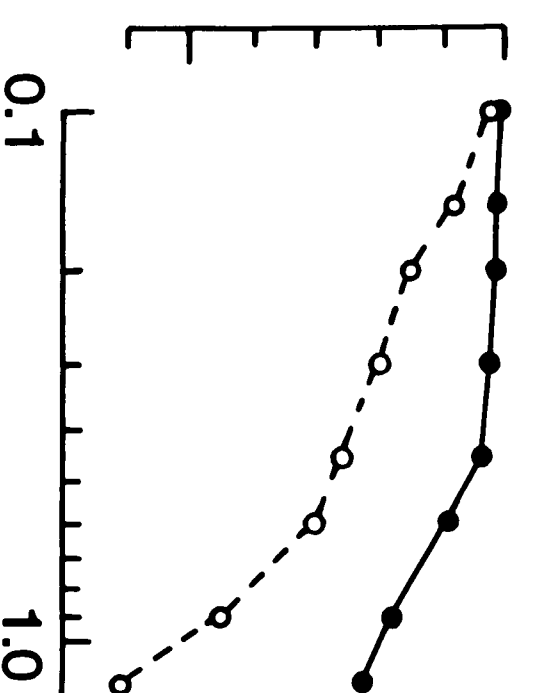
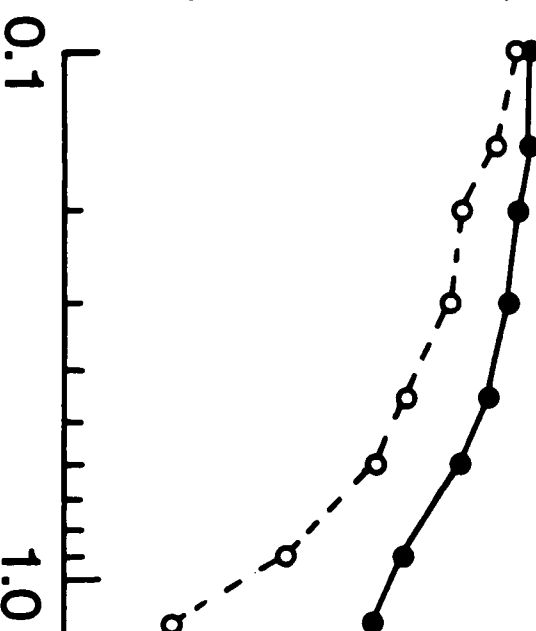


Figure 3.6

Bode plots of accommodation and vergence performance for monkey A in response to 4 D peak-to-peak sinusoidal accommodation and vergence stimuli at frequencies from 0.1 to 1.2 Hz. Open circles show responses during monocular viewing, filled circles show responses during binocular viewing. Each point is based on at least 10 cycles of data (average 18 cycles). Standard errors are smaller than the data points (typically ± 0.02 for gain, ± 2 degrees for phase) unless explicitly shown. Note that the phase lags of the accommodation and vergence responses are much smaller, and the response gains are larger, in binocular viewing than in monocular viewing.

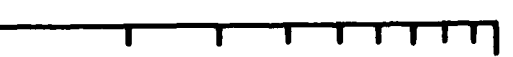
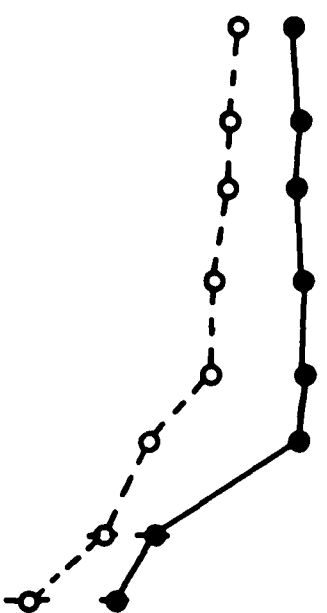
Accommodation

Monkey A

Vergence

gain

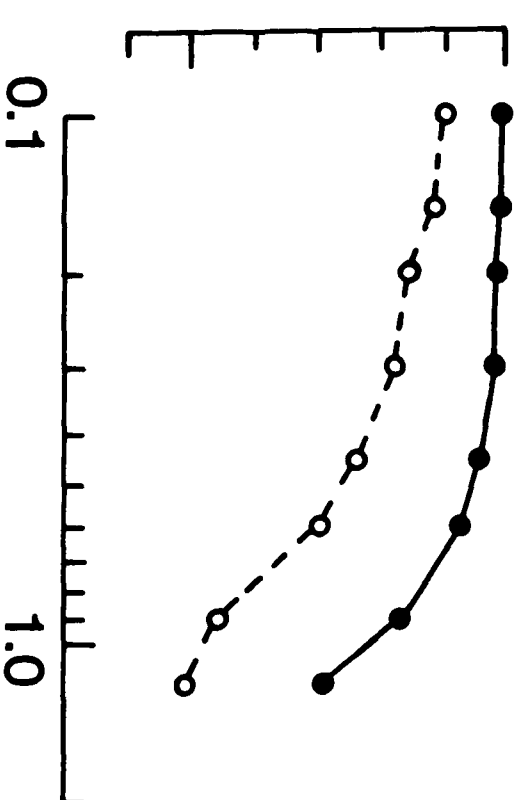
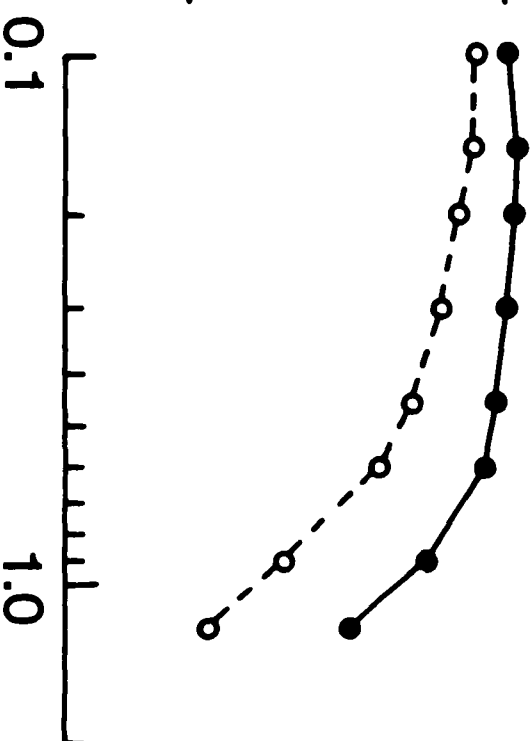
1.0
0.1



binoc
monoc

phase

0°
-100°



Hz

Hz

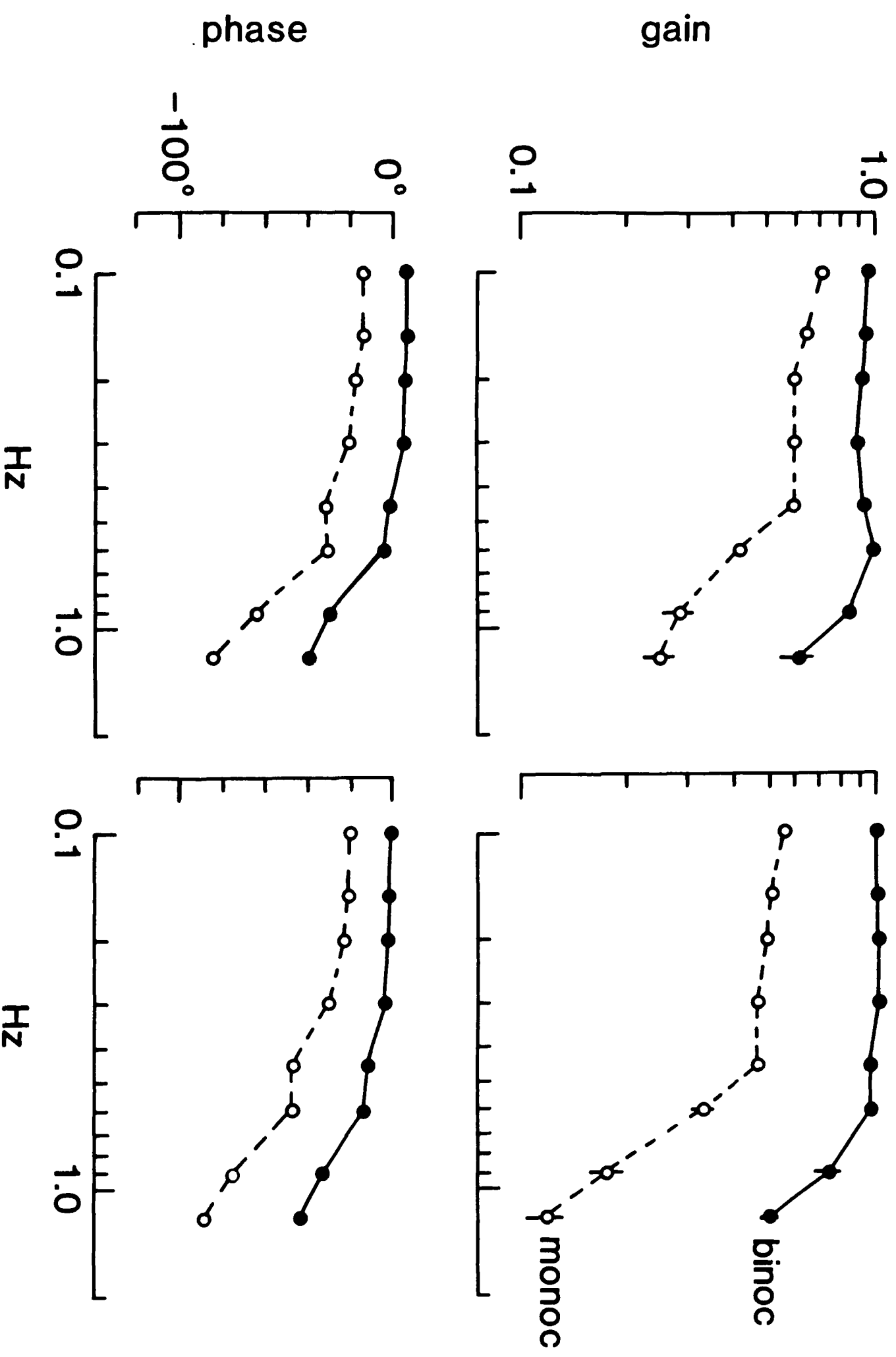
Figure 3.7

Bode plots of accommodation and vergence performance for monkey M in response to 4 D peak-to-peak sinusoidal accommodation and vergence stimuli at frequencies from 0.1 to 1.2 Hz. Open circles show responses during monocular viewing, filled circles show responses during binocular viewing. Each point is based on at least 8 cycles of data (average 13 cycles). Standard errors are smaller than the data points (typically ± 0.02 for gain, ± 2 degrees for phase) unless explicitly shown. Note that the phase lags of the accommodation and vergence responses are much smaller, and the response gains are larger, in binocular viewing than in monocular viewing.

Accommodation

Monkey M

Vergence



accommodation dynamics was the result of vergence-accommodation. In order to examine this possibility, the responses to vergence stimuli were measured with accommodation-open-loop. In this condition (henceforth termed AOL viewing) the measured accommodation response of the monkey's right eye was used to drive the position of the accommodation stimulus servos controlling the accommodation stimulus to both eyes. This arrangement largely deprived the monkey of blur cues, although the phase lags introduced by the dynamic properties of the optometer and the accommodation stimulus servos resulted in some small residual blur stimuli. The effects of this limitation on the measurement of dynamic vergence-accommodation were small, and are discussed in Appendix 3. It is important to note that since the changes in the accommodation stimulus lagged the accommodation response, the resulting blur tended to produce responses opposing vergence-accommodation, so that this method underestimated the gain of vergence-accommodation.

Fig. 3.8 shows an example of the responses of monkey A during binocular AOL viewing. It can be seen that disparity stimuli alone have a powerful influence upon accommodation in the monkey. This is the first demonstration of a vergence-accommodation cross-link in any species other than man. Figs. 3.9, 3.10, and 3.11 show Bode plots for vergence and vergence-accommodation in monkeys H, A, and M respectively. In each figure the results are compared with the monocular performance of the same animal, replotted from Figs. 3.5, 3.6, and 3.7. It can be seen immediately that the phase lags of vergence-accommodation were much smaller than those of blur-driven accommodation for all three monkeys. It can also be seen that the amplitude of the vergence-accommodation

Figure 3.8

Accommodation response (A_r), vergence stimulus (V_s) and response (V_r), and horizontal position of the right eye (R) during binocular viewing with accommodation-open-loop (AOL) viewing. In this condition, the measured accommodation response of the right eye was used to control the position of the accommodation targets, minimizing blur cues. There was a delay introduced in this feedback loop by the dynamic properties of the optometer and the accommodation stimulus servos, but the dynamics of responses to blur were sufficiently poor that the effects of this delay were negligible (see Appendix 3). Note that the movement of the accommodation stimulus (A_s) lags the accommodation response, so that the small residual blur cues opposed the vergence-accommodation response. At the beginning of the third cycle the effects of a blink on the optometer signal, and hence on the accommodation stimulus, are shown. Monkey A.

0.6 Hz VA

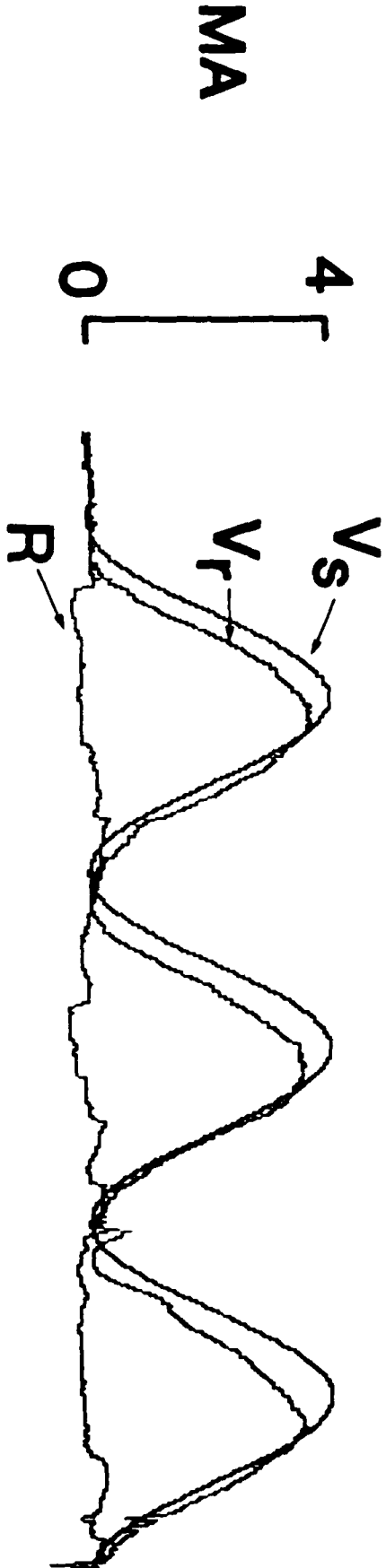
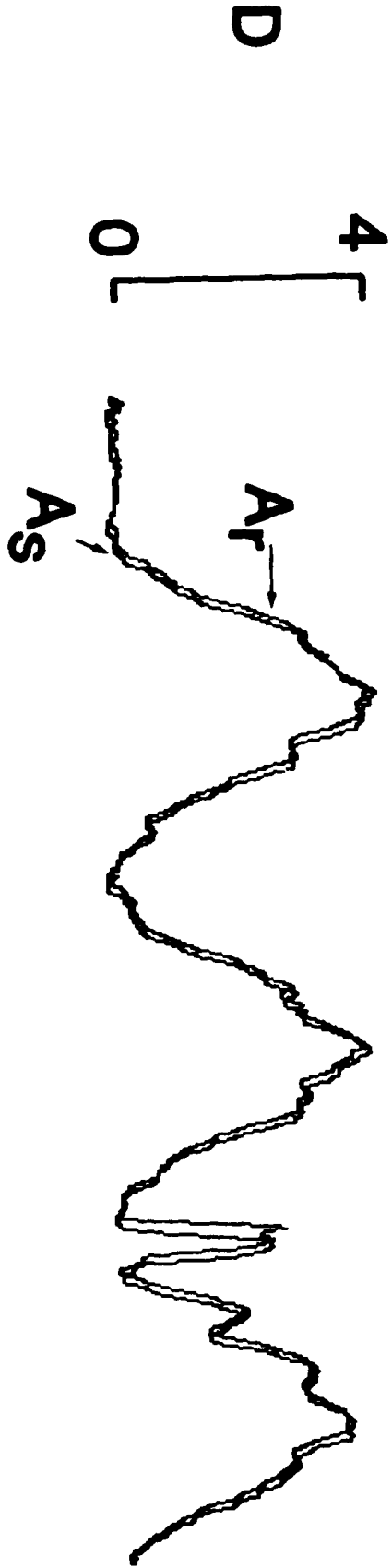


Figure 3.9

Bode plots of accommodation and vergence performance for monkey H in response to 4 D (MA) peak-to-peak sinusoidal accommodation and vergence stimuli at frequencies from 0.1 to 1.2 Hz. Open circles show responses during monocular viewing, filled circles show responses during binocular viewing with accommodation-open-loop (AOL). Each point is based on at least 3 cycles of data (average 9 cycles). Standard errors are smaller than the data points (typically ± 0.03 for gain, ± 2 degrees for phase) unless explicitly shown. Note that the accommodation and vergence responses show better dynamics in binocular AOL viewing than in monocular viewing, and that the performance in binocular AOL viewing is similar to that in normal binocular viewing (Fig. 3.5).

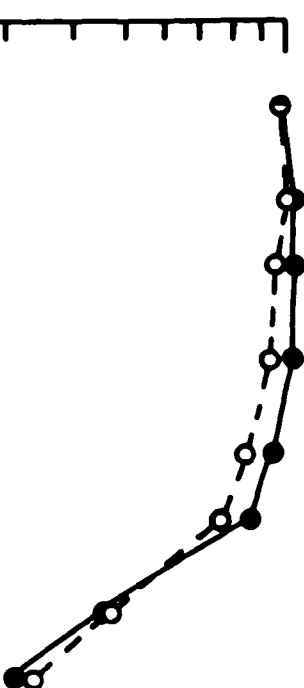
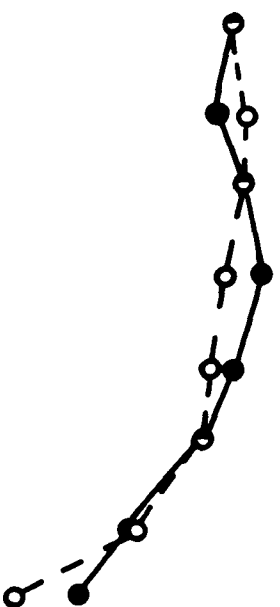
Accommodation

Monkey H

Vergence

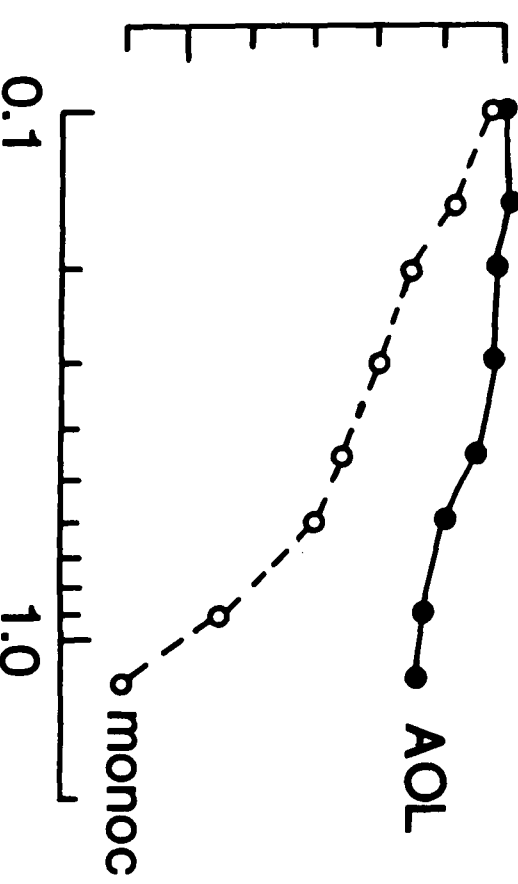
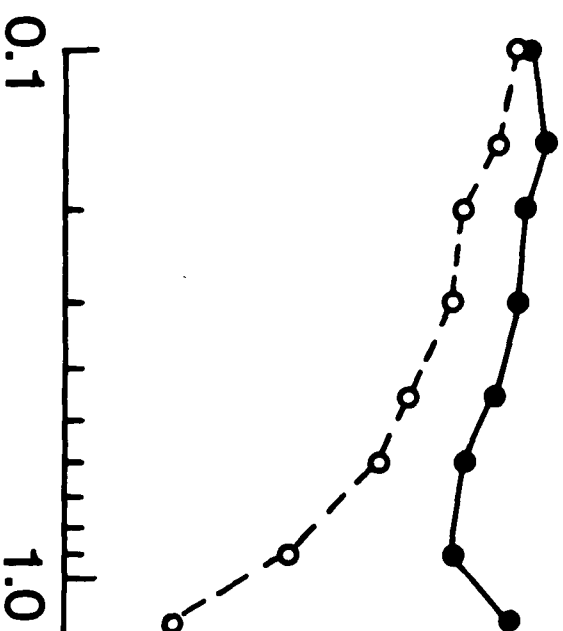
gain

1.0
0.1



phase

0°
-100°



Hz

Hz

AOL

monoc

Figure 3.10

Bode plots of accommodation and vergence performance for monkey A in response to 4 D (MA) peak-to-peak sinusoidal accommodation and vergence stimuli at frequencies from 0.1 to 1.2 Hz. Open circles show responses during monocular viewing, filled circles show responses during binocular viewing with accommodation-open-loop (AOL). Each point is based on at least 11 cycles of data (average 17 cycles). Standard errors are smaller than the data points (typically ± 0.02 for gain, ± 2 degrees for phase) unless explicitly shown. Note that the accommodation and vergence responses show better dynamics in binocular AOL viewing than in monocular viewing, and that the performance in binocular AOL viewing is similar to that in normal binocular viewing (Fig. 3.6). For stimulus frequencies of 0.9 and 1.2 Hz the amplitude of the accommodation response was greater in monocular viewing than the vergence-accommodation response, a difference significant at the 5% level (t-test). However, since the phase lags of the monocular responses were much greater than those of vergence-accommodation, the overall dynamic performance (judged from the magnitude of the error signals) was still superior in AOL viewing.

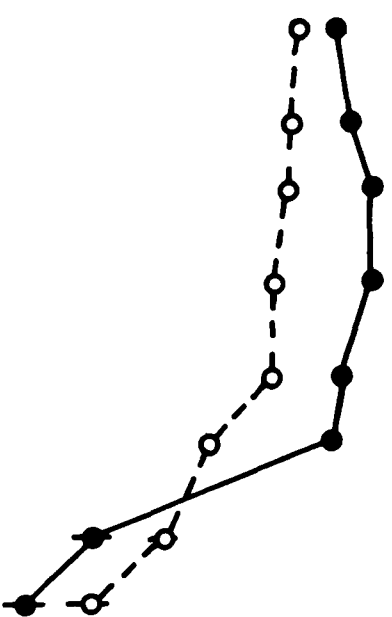
Accommodation

Monkey A

Vergence

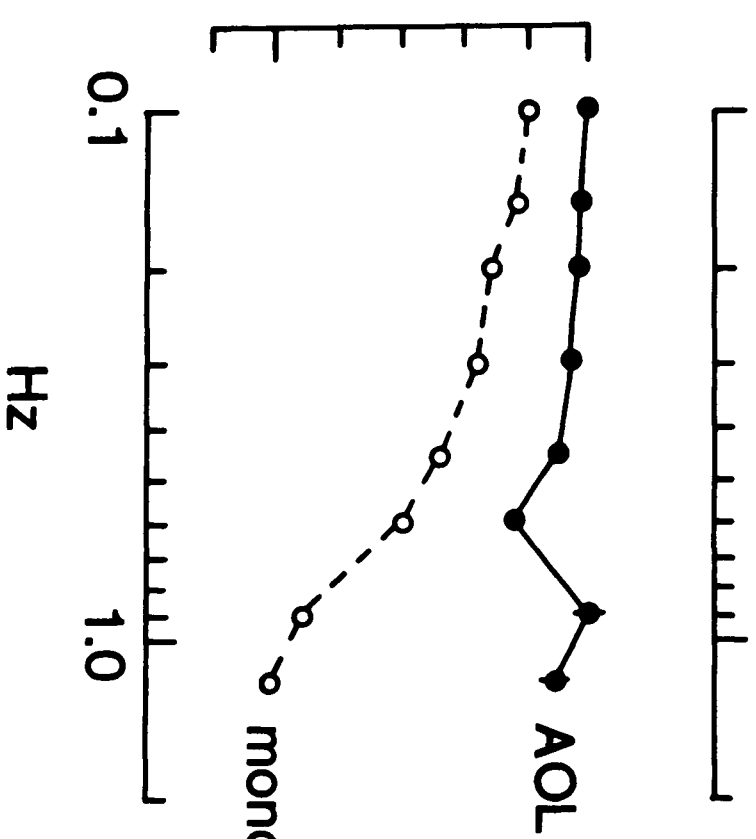
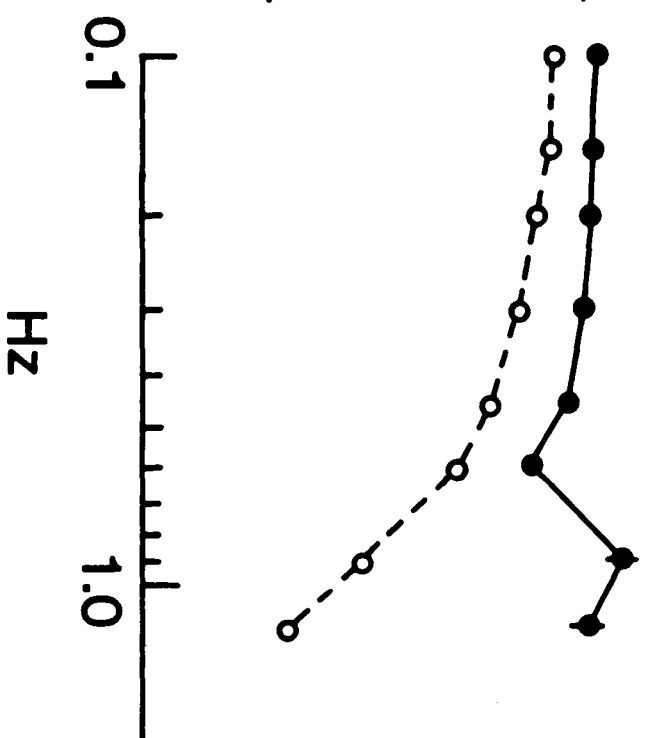
gain

1.0
0.1



phase

0°
-100°



AOL

monoc

Hz

Hz

Figure 3.11

Bode plots of accommodation and vergence performance for monkey M in response to 4 D (MA) peak-to-peak sinusoidal accommodation and vergence stimuli at frequencies from 0.1 to 1.2 Hz. Open circles show responses during monocular viewing, filled circles show responses during binocular viewing with accommodation-open-loop (AOL). Each point is based on at least 8 cycles of data (average 15 cycles). Standard errors are smaller than the data points (typically ± 0.02 for gain, ± 2 degrees for phase) unless explicitly shown. Note that the accommodation and vergence responses show better dynamics in binocular AOL viewing than in monocular viewing, and that the performance in binocular AOL viewing is similar to that in normal binocular viewing (Fig. 3.7). Data from AOL viewing for stimulus frequencies of 0.1 and 0.15 Hz were not available for this monkey since he tended to blink (terminating the trial) at least once in each cycle of tracking at these low frequencies.

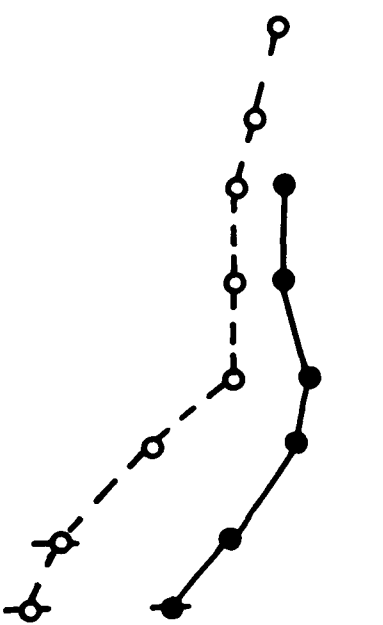
Accommodation

Monkey M

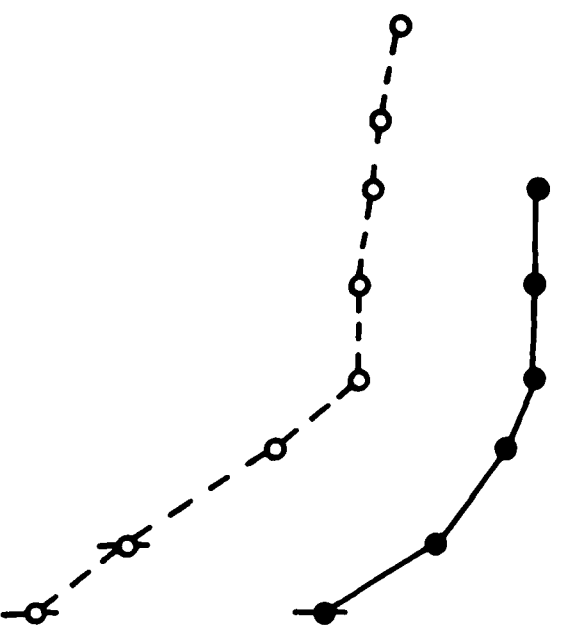
Vergence

gain

1.0
0.1

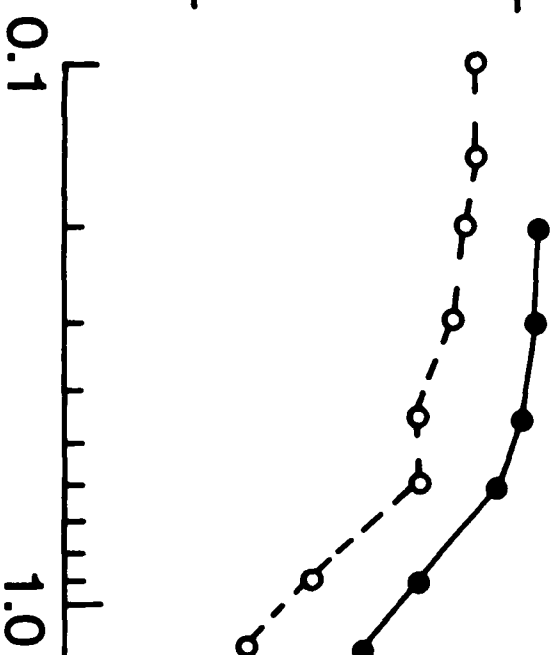


1.0
0.1

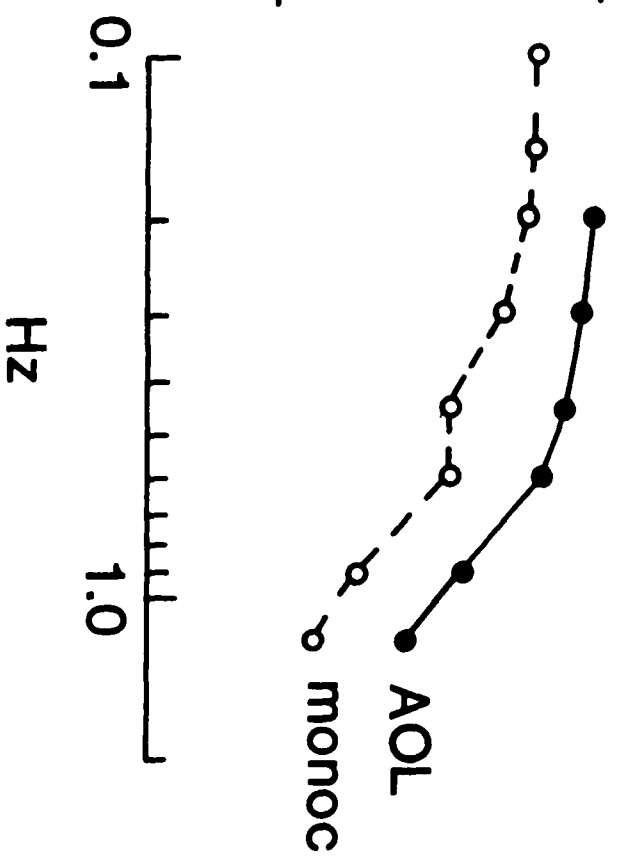


phase

0°
-100°



1.0
0.1



responses were usually greater than those of the blur-driven accommodation responses. For monkey A at stimulus frequencies of 0.9 and 1.2 Hz, and for monkey H at a stimulus frequency of 0.15 Hz, the amplitude of the monocular accommodation response was slightly larger than the amplitude of the vergence-accommodation response, differences significant at the 5% level (t-test). The phase lags of the monocular responses were, however, much larger than the vergence-accommodation responses.

In order to examine whether the performance of vergence-accommodation was sufficient to account for the performance of accommodation in normal binocular viewing, the measured responses to blur and disparity cues separately were used to calculate (on the assumption of linear interaction) the responses in normal binocular viewing (by the method described in Appendix 7). The calculated responses were in close agreement with those observed for frequencies up to 0.6 Hz. For stimulus frequencies of 0.9 and 1.2 Hz the calculated and observed responses were not in very good agreement - the observed response gains of accommodation and of vergence were usually larger than those expected (by 24% on average). There was no simple pattern describing the differences between the expected and observed phases - the mean phase difference was -1.7 degrees with a standard deviation of 13.1 degrees.

3.2.3 Do different stimulus conditions improve blur-driven responses?

The data presented above suggest that disparity-driven responses are more effective in the dynamic control of accommodation and vergence than blur-driven responses. Before drawing such a conclusion it is

important to be sure that these measurements have not underestimated the dynamic capabilities of blur-driven responses. Perhaps, for example, the dynamics of responses in monocular viewing with the left eye were better than the performance in monocular viewing with the right eye. To test this hypothesis the accommodative-vergence responses in monkeys A and M were recorded during monocular viewing with the left eye. Fig. 3.12 is a Bode plot of these responses, compared with the accommodative-vergence responses during monocular viewing with the right eye (replotted from Figs. 3.6 and 3.7). For monkey A the responses were very similar, while for monkey M the accommodative-vergence responses were somewhat poorer during monocular viewing with the left eye than with the right eye. Therefore blur stimuli in the left eye were no more effective in the dynamic control of accommodation and vergence than blur stimuli in the right eye. The poorer performance during viewing with the left eye probably resulted from monkey M's tendency to produce convergence by movements of the left eye alone (discussed in Appendix 6). This resulted in movements of the left eye even during monocular viewing with that eye, moving the image of the target away from the fovea. In human subjects it is known that stimuli away from the fovea are less effective in producing accommodative-vergence than stimuli on the fovea (Semmlow and Tinor, 1978).

It might be argued that a blur cue available to both eyes is a more effective stimulus to accommodation than a blur cue available to only one eye. This could explain the improvement in the dynamic performance of accommodation during binocular viewing. In monkey A this possibility was examined by using the measured vergence response to control the rotation of the mirrors in the haploscope (opening the disparity

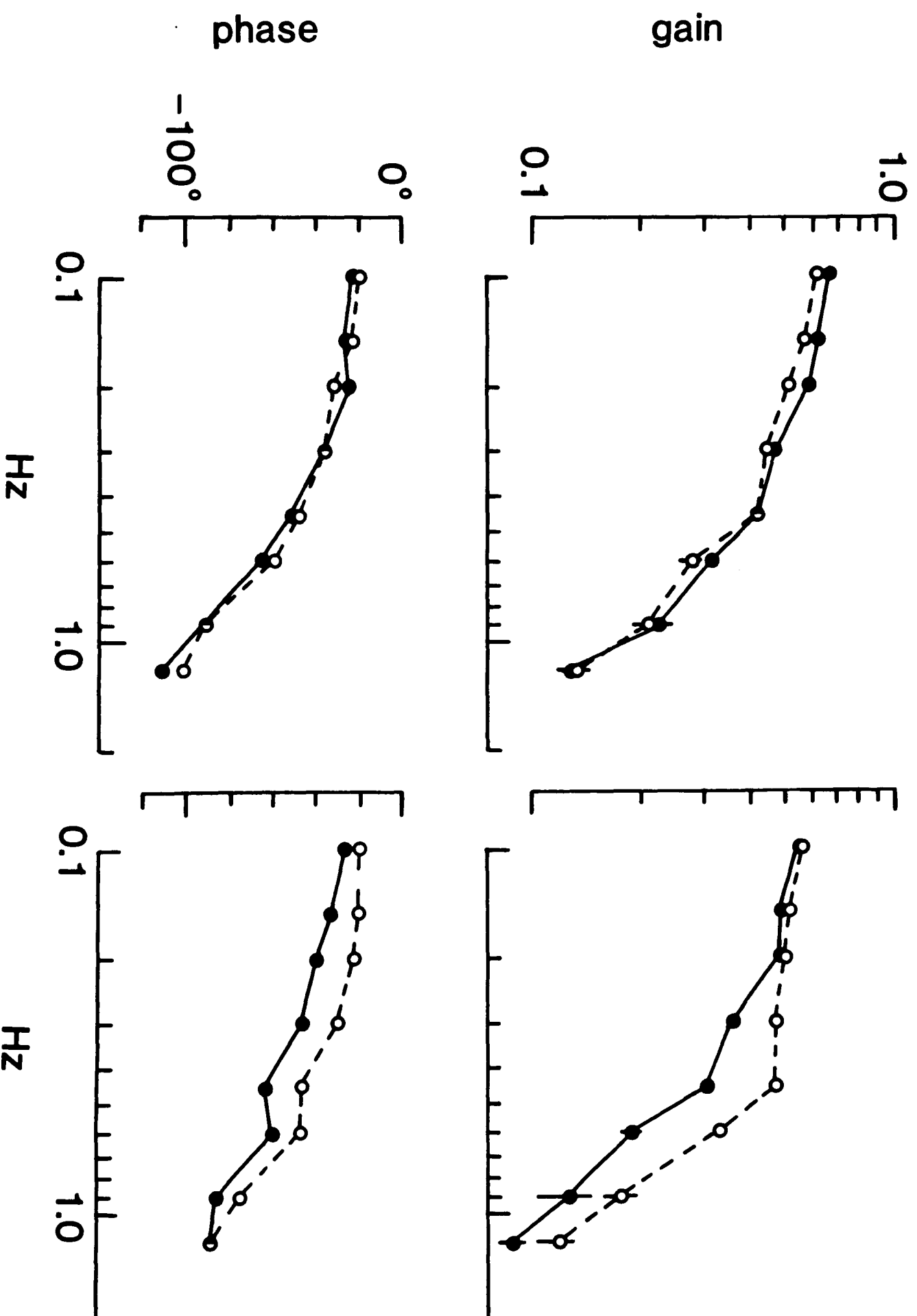
Figure 3.12

Bode plots of accommodative-vergence performance obtained in monocular viewing with the right eye (open circles) and monocular viewing with the left eye (filled circles). In each case the target moved directly towards the viewing eye in a plane parallel to the midline. Each point is based on at least 6 cycles of data (average 14 cycles). Standard errors are smaller than the data points (typically ± 0.03 for gain, ± 2 degrees for phase) unless explicitly shown. Data from monkey A on the left, and from monkey M on the right.

Accommodative-vergence

Monkey A

Monkey M



feedback loop). This viewing condition I call 'disparity-open-loop' (DOL) viewing. An accommodation stimulus was then presented binocularly without any disparity stimuli being produced. This experiment has not been performed before on human subjects or any other animal, probably because of the technical difficulties involved (the technique requires a signal with a low noise level which is linearly related to vergence, and the ability to control dynamic accommodation and vergence stimuli independently). Fig. 3.13 compares the responses to sinusoidally modulating accommodation stimuli during DOL viewing to those during monocular viewing (replotted from Fig. 3.6). The gains of both accommodation and accommodative-vergence are generally smaller with the binocular cue, but the phase lags are somewhat smaller. There was little overall improvement in the dynamic performance (the blur errors tolerated are similar in each case). The gains of the binocular blur-driven responses are smaller, and the phase lags greater, than the responses in normal binocular viewing (Fig. 3.6) or the vergence-accommodation responses (Fig. 3.10). The only exception to this rule is that for a stimulus frequency of 1.2 Hz the amplitude of the blur-driven accommodation response was slightly larger than that of the vergence-accommodation response. This difference was not significant at the 5% level (t-test). Thus the presence of a binocular blur cue is not adequate to account for the improvement in accommodation dynamics in normal binocular viewing compared with monocular viewing.

It should also be considered whether the phenylephrine, used to dilate the pupil to allow the recording of accommodation, compromised the performance of accommodation. Although it is usually believed that phenylephrine has little effect on accommodation (Biggs et al., 1959;

Figure 3.13

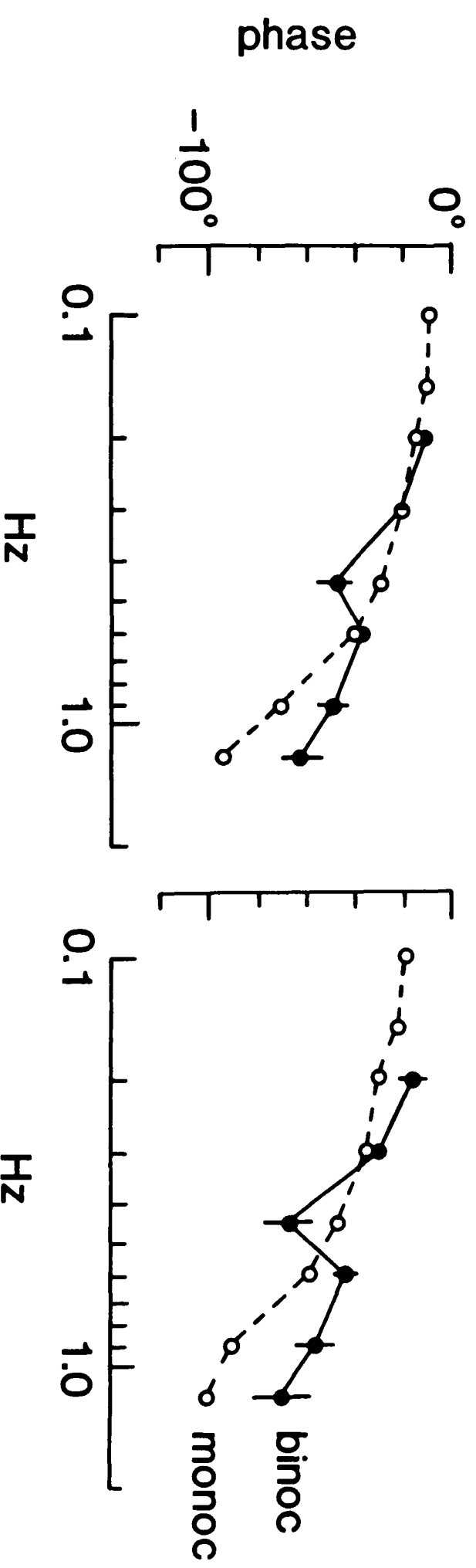
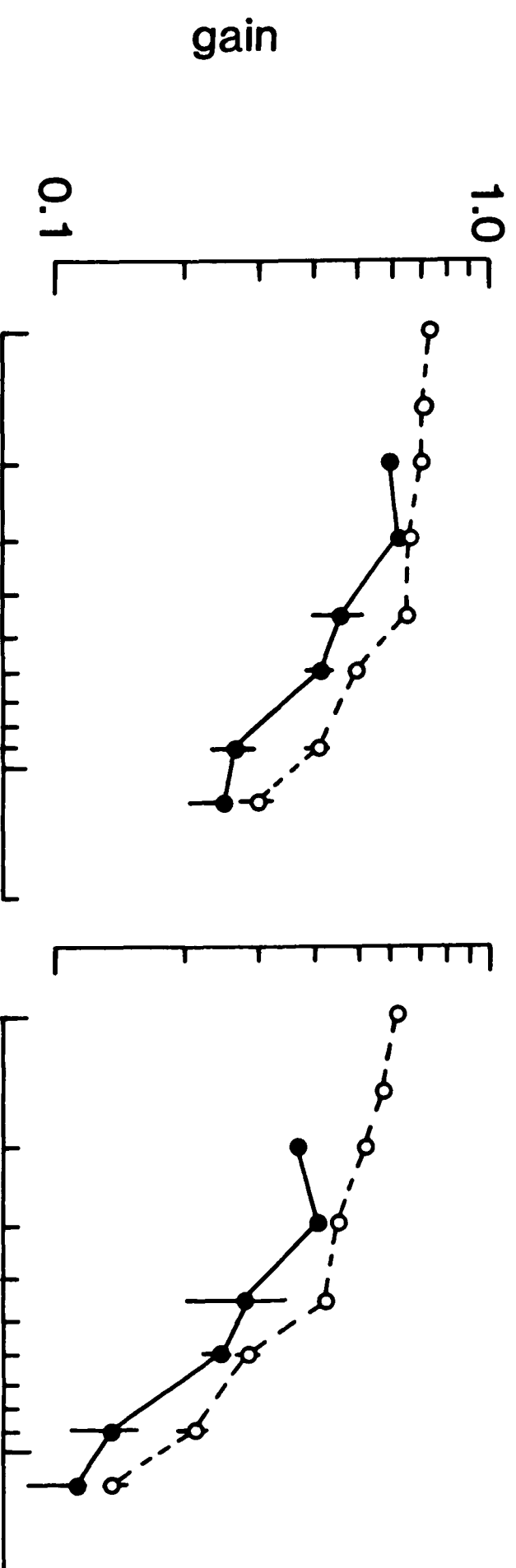
Bode plots for accommodation and accommodative vergence obtained for monkey A from monocular viewing with the right eye (open circles) and in DOL binocular viewing, in which the measured vergence response was used to control the vergence stimulus (filled circles). The dynamic performance was comparable in the two conditions, and it is clearly poorer in both of these conditions than in normal binocular viewing (Fig. 3.6). Each data point is based on at least 2 cycles (average 12 cycles). Standard errors are smaller than the data points (typically ± 0.03 for gain, ± 4 degrees for phase) unless explicitly shown.

Accommodation

Monkey A

Accommodative-

vergence



Ripps et al., 1962), Chin et al. (1968) found that phenylephrine reduced the size of accommodation responses evoked by electrical stimulation in the midbrain of anaesthetized monkeys. If the phenylephrine dose used in this study affected the accommodation responses in the same way, it should have produced an increase in the gain of accommodative-vergence. In monkey A, the gain of accommodative-vergence (during low frequency dynamic tracking) was slightly smaller on the first day when phenylephrine was used than the gain measured on the previous day, when no phenylephrine had been used. In monkey M, accommodative-vergence was measured on the first day on which phenylephrine was applied both before and after administration of the drug. The accommodative-vergence responses were measured during viewing of a stationary target at different distances from the animal, and the stimulus AC/A ratio was determined by linear regression of the accommodative-vergence response on the accommodation stimulus. The stimulus AC/A ratio was found to have increased by 11% following administration of phenylephrine. These observations suggest that the effect of phenylephrine on accommodation was small, a conclusion also supported by the observation that the accommodative-vergence responses when viewing monocularly with the left eye (in which no phenylephrine had been added) were similar to those when viewing monocularly with the right eye (Fig. 3.12). Any effect of phenylephrine on the accommodation plant should affect both the blur-driven accommodation responses and the vergence-accommodation responses, so the use of the drug cannot explain the superior performance of accommodation during binocular viewing relative to that in monocular viewing.

3.2.4 Responses to stimuli of different amplitudes

All the results described in section 3.2.2 were obtained with accommodation stimuli whose peak-to-peak amplitude was 4 D (note that this refers to the amplitude of the target motion, not to the amplitude of the blur stimuli). It is possible that the blur produced by these stimuli saturated the input to the accommodation controller. Accordingly, the responses to monocularly viewed target motion with a peak-to-peak amplitude of 1 D were examined in monkeys H and M. Fig. 3.14 shows a Bode plot of these responses for monkey M compared with the responses to stimuli with a peak-to-peak amplitude of 4 D for the same monkey replotted from Fig. 3.7. Although the gain of the responses were somewhat larger in response to the smaller stimuli, the phase lags were greater. A similar result was observed for monkey H over the frequency range 0.3-1.2 Hz, and also for monkey A at 0.2 Hz (the only frequency where the monocular responses to small stimuli were examined).

The responses in normal binocular viewing of stimuli with a peak-to-peak amplitude of 1 MA were examined in monkeys M and H. In monkey A the responses to stimuli with a peak-to-peak amplitude of 0.5 MA were examined. In monkey M the responses to stimuli with a peak-to-peak amplitude of 0.25 MA were also measured. The results for monkey M are shown in Fig. 3.15. The responses to the smaller amplitude vergence stimuli had phase lags which were very similar to those observed in response to the larger stimuli, while the gain of the responses at high frequencies was higher in response to smaller amplitude stimuli. One consequence of this non-linearity was that the animal was able to follow the smaller stimuli at higher frequencies than when a larger stimulus

Figure 3.14

Bode plots for accommodation and accommodative-vergence for monkey M obtained during monocular viewing with 4 D peak-to-peak stimuli (open circles) and 1 D peak-to-peak stimuli (filled circles). Each point is based on at least 8 cycles of data (average 14 cycles). Standard errors are smaller than the data points unless explicitly shown.

Accommodation

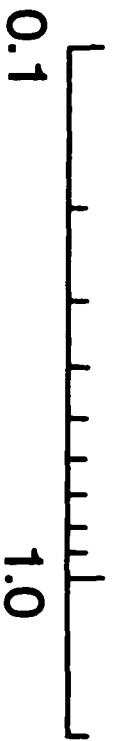
Monkey M

Accommodative-
vergence

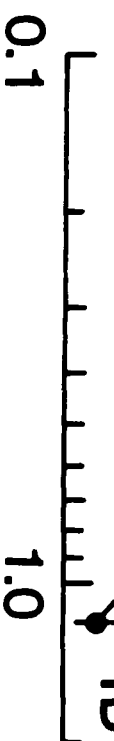
gain



phase



Hz



Hz

1D
4D

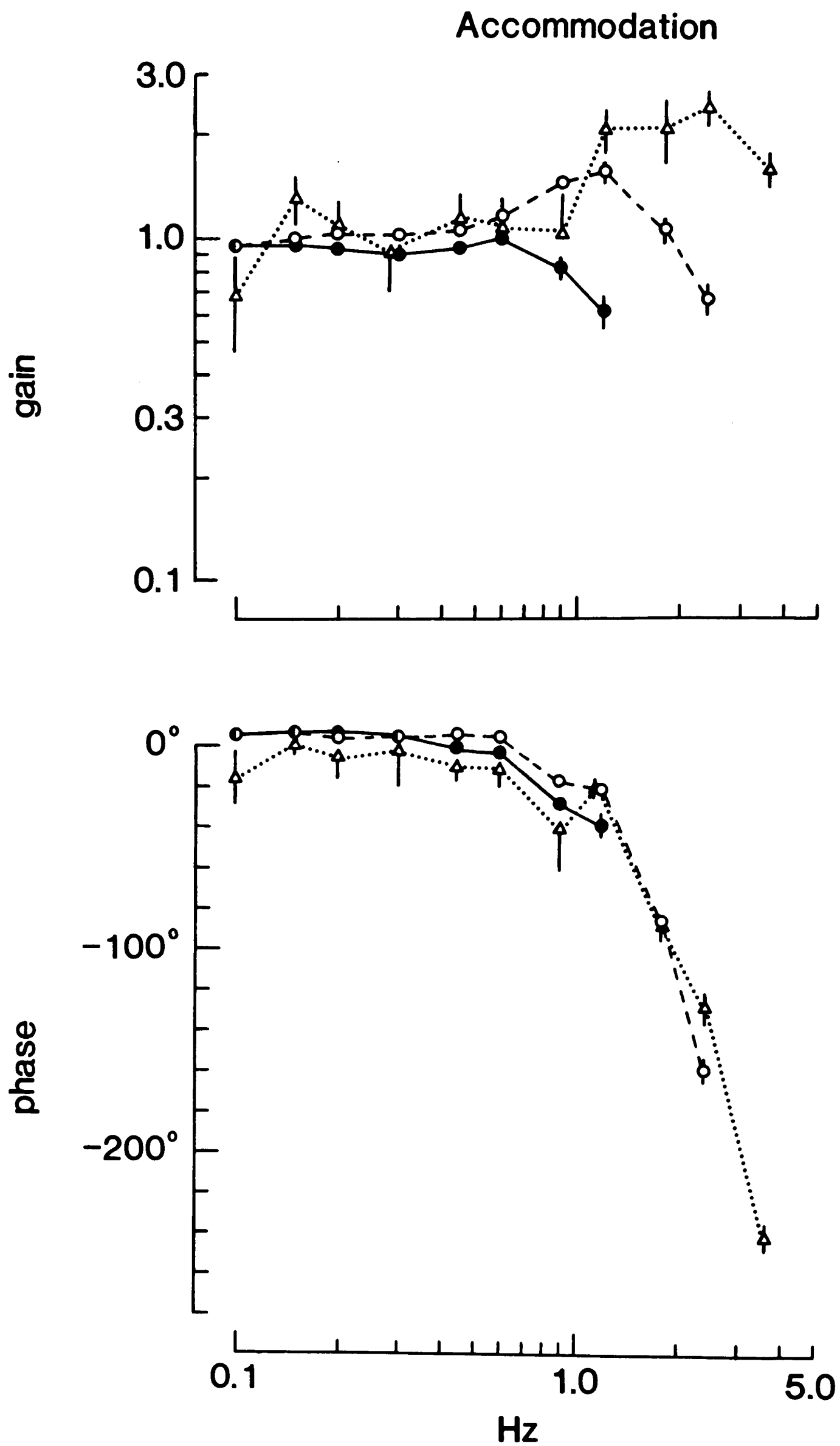
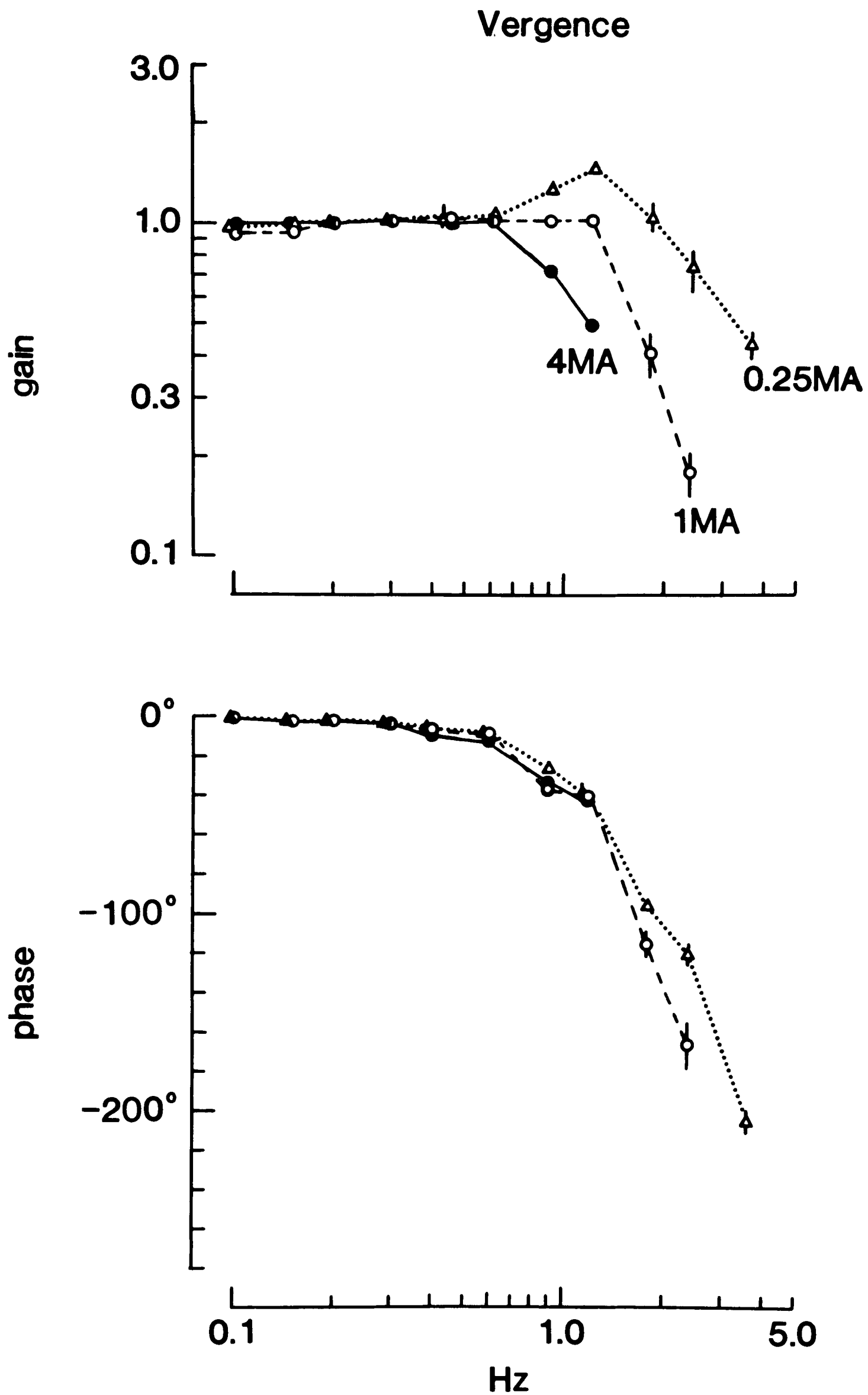


Figure 3.15 Bode plots of accommodation and vergence in binocular viewing for one monkey (M), obtained with stimuli of different amplitudes. Filled circles are 4 MA peak-to-peak stimuli, open circles are 1 MA peak-to-peak stimuli, and open triangles are 0.25 MA peak-to-peak stimuli.



Each point is based on at least 8 cycles of data (average 13 cycles). Standard errors are smaller than the data points unless explicitly shown. The error bar shown for the accommodation gain at 0.6 Hz shows the standard error for the estimate of the gain in response to the 0.25 MA peak-to-peak stimulus.

was presented. Although vergence stimuli with a peak-to-peak amplitude of 4 MA were presented at frequencies up to 3.6 Hz, Fig. 3 only shows results for which the gain of the vergence response was significantly different from zero (at the 5% level). The same non-linearity was clear in the responses of monkeys A and H, although the magnitude of the differences in gain were smaller in monkey H than in the other two monkeys. From comparison of Figs. 3.14 and 3.15 it is clear that the dynamic superiority of accommodation and vergence responses to a binocular stimulus (relative to a monocular stimulus) was more marked in response to small stimuli than in response to large stimuli.

The marked difference between the binocular responses to stimuli of different amplitudes clearly demonstrates an amplitude-dependent non-linearity in the vergence system. This non-linearity is not like any that have been described for the oculomotor plant (Robinson, 1981). The most likely source of this non-linearity is saturation at the input stage of the vergence system by large disparities. This interpretation is supported by the observation that in response to stimuli at frequencies of 2.4 and 3.6 Hz, the amplitude (as opposed to the gain) of the vergence responses was larger in response to smaller amplitudes of target motion, an effect which cannot be explained by non-linearities of the plant alone. Although some work has been published describing the dynamic properties of disparity detection in human subjects (Beverley and Regan, 1973; Regan and Beverley 1973; Beverley and Regan, 1975) the experiments involved small disparities (usually less than 20 minutes of arc) and so are not applicable to describing the detection of disparity during high frequency tracking of the vergence stimuli described here, since the amplitude of the disparity modulation is large during high

frequency dynamic tracking - in all three monkeys tracking a 4 MA peak-to-peak vergences stimulus at a frequency of 0.9 Hz produced a modulation in disparity of greater than ± 1 MA. Only the smallest stimulus used (0.25 MA peak-to-peak in monkey M) resulted in modulations in disparity smaller than ± 20 minutes of arc for stimulus frequencies of 0.9 Hz and above.

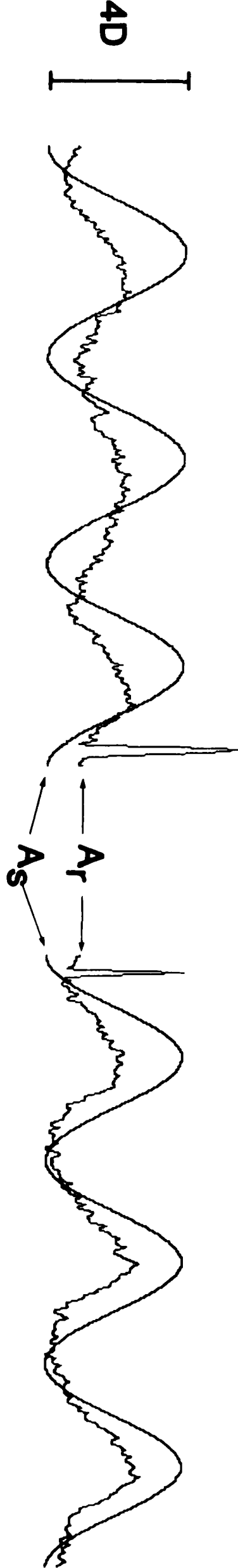
3.2.5 Monocular responses with cues other than blur

Although sections 3.2.2 and 3.2.3 showed that the results shown in Figs. 3.5, 3.6, and 3.7 were representative of the responses to blur stimuli, it is possible that the monocular performance when tracking target motion in depth is enhanced by the presence of monocular cues other than blur. In monkey M the performance of accommodation and of accommodative-vergence were measured during monocular viewing of target motion directly, without a Badal lens. Motion of the target in depth was then accompanied by changes in its angular subtense at the eye. Fig. 3.16 shows examples of the responses to a sinusoidal accommodation stimuli at a frequency of 0.6 Hz viewed with (Fig. 3.16A) or without (Fig. 3.16B) Badal lenses. In both cases the accommodation stimulus ranged from 3 D to 7 D. Note that although the changes in the accommodation stimulus are the same in Fig. 3.16A and Fig. 3.16B, the movement of the target was quite different (in Badal viewing the accommodation stimulus is linearly related to target displacement, while in direct viewing the accommodation stimulus is proportional to the reciprocal of the target distance). It can be seen that the responses during direct viewing have larger amplitudes and smaller phase lags than those during Badal viewing. In direct viewing, the response to the first

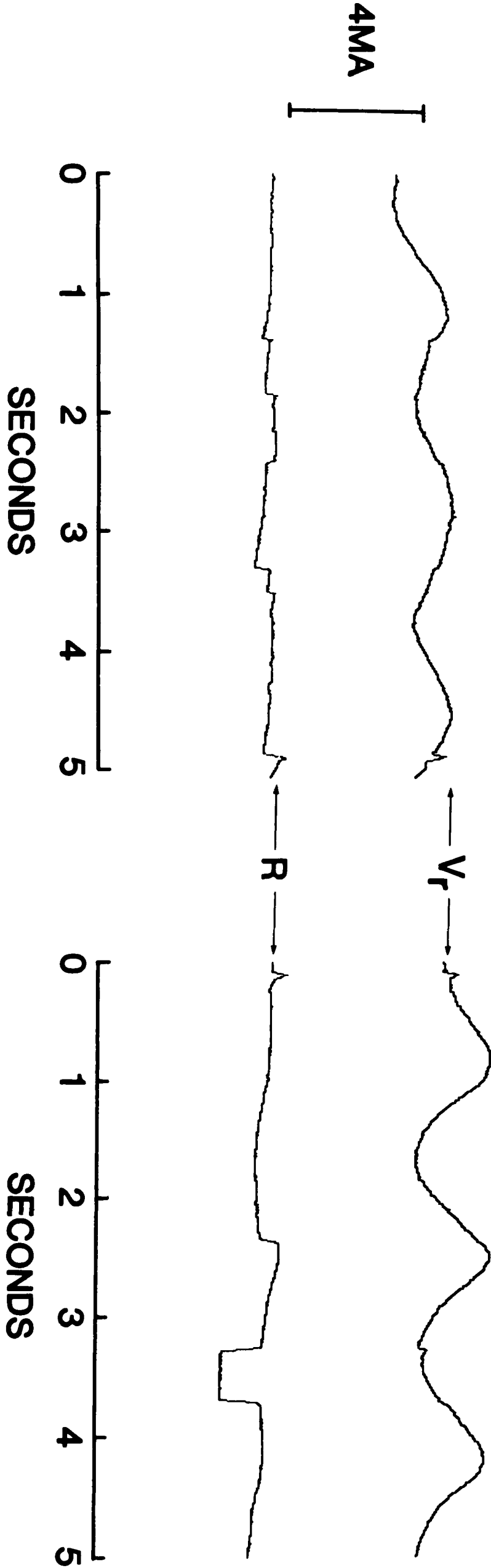
Figure 3.16

Accommodation stimulus (A_s) and response (A_r), accommodative-vergence response (V_r), and horizontal position of the right eye (R) during monocular viewing of an accommodation stimulus modulating with a sinusoidal time course between 3 D and 7 D. A) Shows the responses during viewing through a Badal lens (when changes in target distance were not accompanied by changes in the angular subtense of the target at the eye); B) Shows the responses when the target was viewed without the Badal lens. It can be seen that the phase lag between accommodation stimulus and accommodation response is much smaller in B) than in A).
Monkey M.

A) Badal viewing 0.6 Hz



B) Direct viewing 0.6 Hz



cycle of target motion was consistently different from that in subsequent cycles. Consequently, only data from cycles after the first were used in calculating the mean responses. Fig. 3.17 is a Bode plot comparing the responses to target motion viewed directly and the responses to target motion viewed through a Badal lens. There was a dramatic difference between the responses in the two conditions. For both accommodation and accommodative-vergence the gain of the responses were larger during direct viewing, and the phase lags were smaller. At low frequencies the accommodation response was phase advanced relative to the stimulus by up to 25 degrees.

On the first day when the responses to directly viewed target motion were measured, the amplitude of the monkey's accommodation responses were much greater than that appropriate for the stimulus - viewing an accommodation stimulus modulating between 3 D and 7 D with a frequency of 0.2 Hz the accommodation response had a gain of 1.4. On the next occasion when responses to directly viewed target motion were measured, the accommodation responses were more nearly appropriate for the stimulus (the data from this and two subsequent occasions were used for Fig. 3.17). These anomalous responses (on the first occasion the monkey experienced direct viewing of the target) may be related to the fact that the monkey had been presented with stimuli in which target motion in depth was not accompanied by changes in the angular subtense of the target at the eye for five weeks before the responses to directly viewed target motion were first observed. When changes in target angular subtense were first experienced in the haploscope, a powerful impression of target nearness

Figure 3.17

Bode plots for accommodation and accommodative-vergence for monkey M in response to a monocularly viewed stimulus with a peak-to-peak amplitude of 4 D. Open circles show the responses when target motion was viewed through a Badal lens, filled circles show the responses when the animal viewed target motion directly. The dynamic performance of accommodation and of accommodative-vergence was much improved by the availability of monocular cues other than defocus of the image of the target. Each data point is based on at least 8 cycles (average 13 cycles). Standard errors are smaller than the data points (typically ± 0.02 for gain, ± 2 degrees for phase) unless explicitly shown.

Accommodation

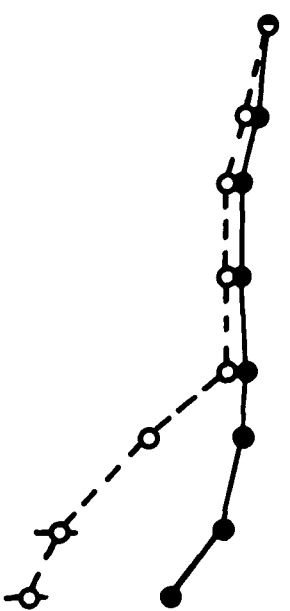
Monkey M

Accommodative-

vergence

gain

1.0
0.1

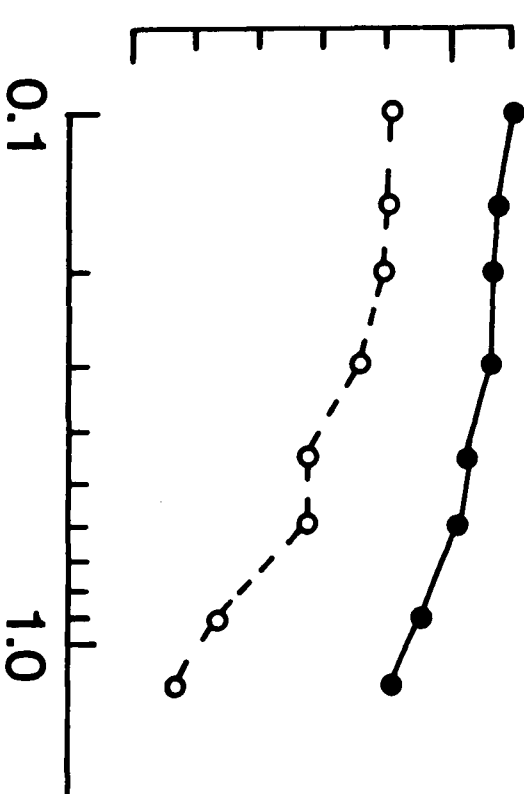
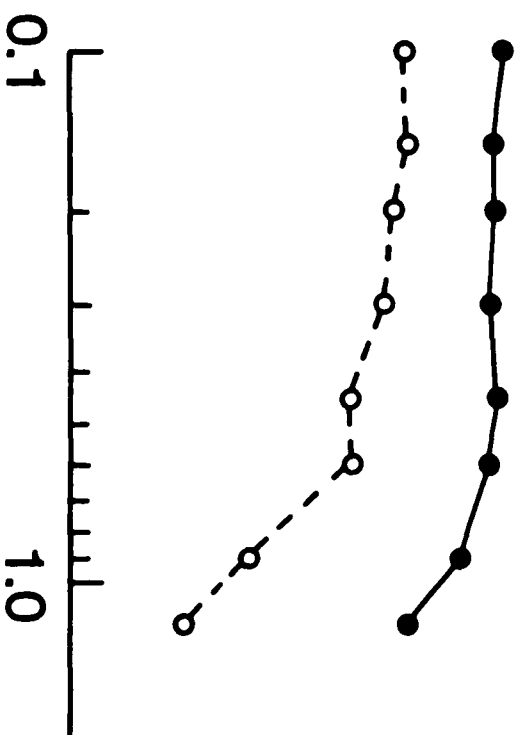


direct

Badal

phase

0°
-100°



Hz

Hz

may have been produced, resulting in large 'proximal' accommodation responses. This interpretation assumes that the relationship between changes in target angular subtense and 'proximal' accommodation is subject to adaptive regulation following periods of viewing when the relationship is unusual (as in Badal viewing). This possibility has never been investigated before, and the observation reported here, which suggests the existence of such adaptive regulation, has not yet been investigated further.

3.3 Discussion

The behaviour of accommodation and vergence was systematically studied in three trained rhesus monkeys. This is the first systematic study of the performance of accommodation and vergence in monkeys. There are several striking results common to all three monkeys. First, the latencies of accommodation and accommodative-vergence were shorter than those in humans, while the latency for vergence responses to disparity changes was very similar to that in humans.

The second striking result is that the dynamic performance of both accommodation and vergence were far better in binocular viewing than in monocular viewing. This was true both in sinusoidal tracking and in the responses to step changes, and was not explained by any difference in latency, nor was it merely the result of different non-linearities in the responses to monocular as opposed to binocular stimuli. Although vergence did accelerate during saccades in these monkeys, the superior dynamics of binocular vergence were evident before the first saccades occurred, and were also evident during sinusoidal tracking when saccades were infrequent. The dynamics of vergence-accommodation were shown to be

much better than those of blur-driven accommodation, and were sufficient to account for the dynamic performance of accommodation in normal binocular viewing.

The dynamic performance of accommodative-vergence was no better during monocular viewing with the left eye than during viewing with the right eye. This strongly suggests that the left eye was no more potent in driving accommodation than the right eye. In one monkey it was demonstrated that responses to a blur stimulus presented binocularly with no disparity stimulus were comparable to those in monocular viewing, and certainly had poorer dynamics than disparity-vergence and vergence-accommodation. It might be argued that the monocular responses were poor because the monkeys were not adequately trained to minimize blur. This seems unlikely because the monkeys received extensive training with both monocular and binocular stimuli before making any of the measurements presented above. Also, the monkeys' monocular performance was at least as good as published data for humans (Krishnan et al., 1973a; Stark et al., 1965). Fincham and Walton (1957) argued that static accommodation might be controlled mainly by disparity rather than blur cues - the results presented here show that disparity cues are certainly critical for the dynamic control of accommodation in monkeys.

Although it is clear that disparity cues are more effective than blur cues in controlling dynamic accommodation responses, it may be that monocular cues other than blur are also important in the control of accommodation. The majority of studies of accommodation dynamics in humans carefully eliminated cues derived from changes in the angular subtense and luminance of a target. When monocular stimuli including

these cues were presented to one monkey, there was a dramatic improvement in the dynamic responses of accommodation. The interaction between these 'extra' monocular cues and disparity cues was not examined, but is an interesting subject for future investigation.

CHAPTER FOUR

ATTEMPTS TO DESCRIBE THE RESPONSES OF ACCOMMODATION AND VERGENCE

MATHEMATICALLY

4.1 Introduction

In Chapter 3 it was demonstrated that vergence-accommodation is important for the dynamic control of accommodation, having a dynamic performance superior to that of blur-driven accommodation. Similarly, the dynamic performance of disparity-driven vergence was shown to be superior to that of accommodative-vergence. In this chapter an attempt has been made to describe disparity-driven and blur-driven responses with simple transfer functions in the hope of providing a mathematical description of the dynamic interactions of accommodation and vergence.

In human subjects attempts to describe disparity-driven vergence with simple transfer functions have not been very successful. Although the vergence system responds to step changes in disparity like a simple integrator, the responses to sinusoidally modulating disparities show much smaller phase lags than those of an integrator (Rashbass and Westheimer, 1961a; Zuber and Stark, 1968). As discussed in Chapter 1, the idea that this discrepancy results from an ability to predict repetitive stimulus waveforms has not been clearly established.

Attempts to describe the frequency response of blur-driven accommodation in human subjects with simple transfer functions have also been unsuccessful, again leading to the suggestions that prediction of repetitive stimulus waveforms is important (Stark et al., 1965). In

this chapter the responses of the monkey vergence system to maintained step changes in disparity are described, and the frequency response data presented in Chapter 3 are examined in an attempt to describe them with simple transfer functions. As it turns out not to be possible to describe the performance with simple transfer functions including the measured latency of the accommodation and vergence responses, the possible role of stimulus predictability is considered.

4.2 Results

4.2.1 Open-loop step responses of the vergence system

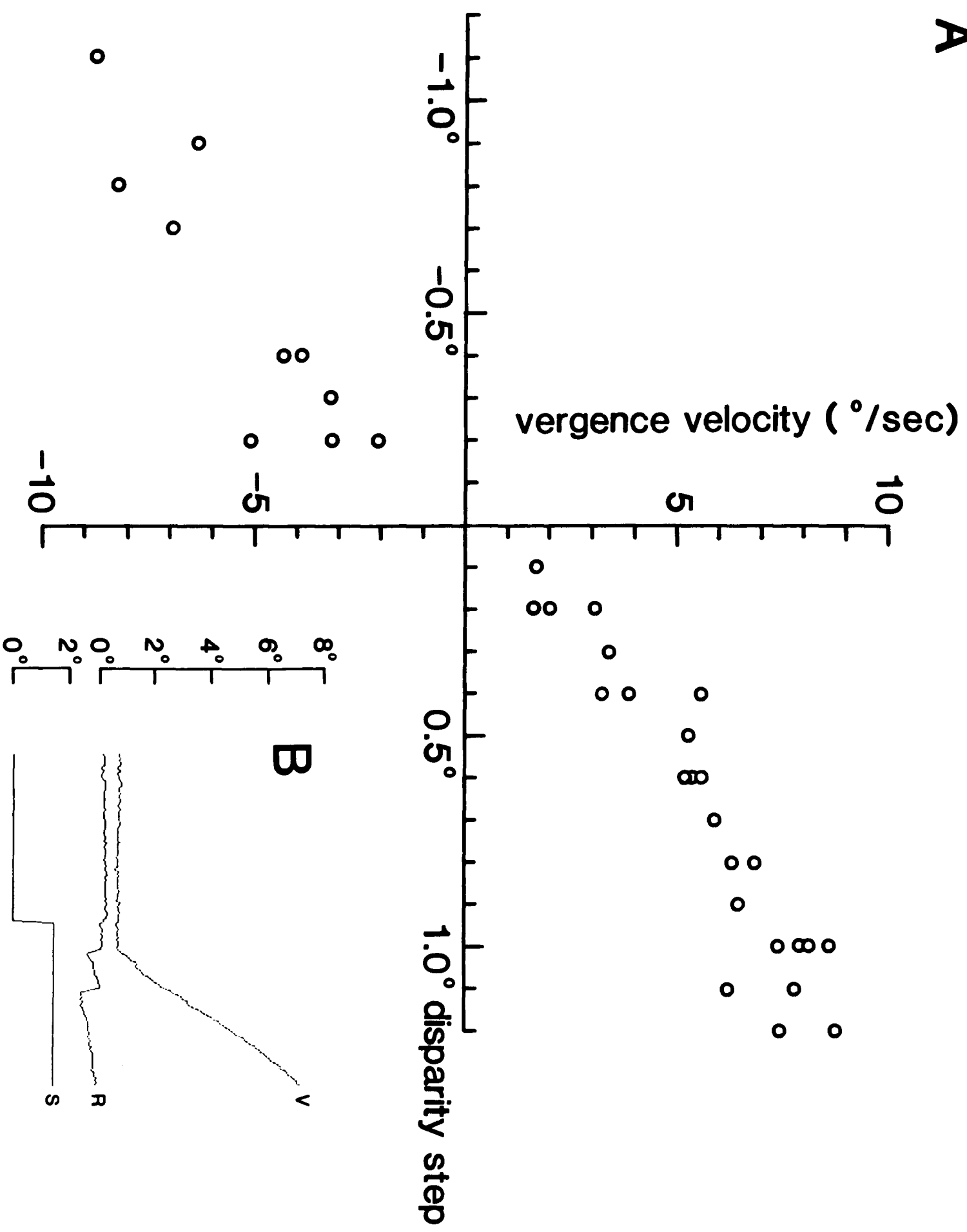
Rashbass and Westheimer (1961a) showed that the human vergence system responded to an open-loop step of disparity with a linear ramp, whose slope was proportional to the size of the disparity step. In monkeys A and H the same result was demonstrated, by using the measured vergence response to drive the mirrors of the haploscope. Fig. 4.1B shows an example of the open-loop step response in monkey A, and Fig. 4.1A shows the velocity of the vergence response as a function of step size. Thus the monkey vergence system, like that of the human, responded to step changes as though its open-loop transfer function were that of an integrator with delay.

Fig. 4.1A shows that the velocity of the vergence responses in monkey A increased less rapidly as a function of step size as the steps became larger than 0.5 degrees. The same saturation effect can be observed in Figs. 13 and 16 of Rashbass and Westheimer (1961a). These findings are in accordance with the suggestion from the closed-loop frequency data that large disparities saturate the input to the vergence

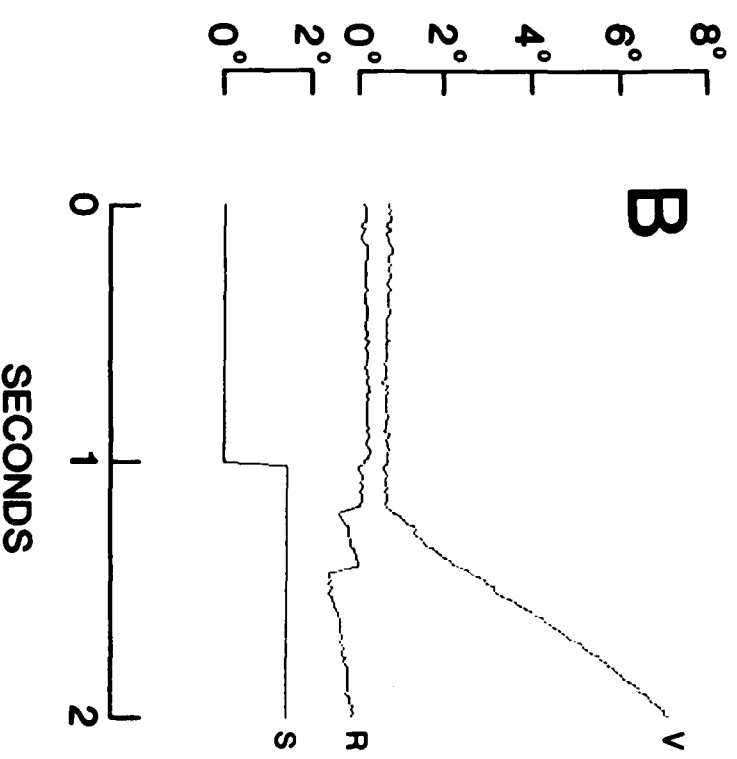
Figure 4.1

- A) Velocity of vergence as a function of size of disparity step.
- B) Vergence response (V) and right eye movement (R) of monkey A to a disparity-step stimulus (S) when vergence (but not accommodation) was open-loop.

A



B



system.

4.2.2 Calculated open-loop frequency response of vergence

In order to see whether the frequency data of Figs. 3.5, 3.6, and 3.15 were compatible with an open-loop transfer function of an integrator with delay, the closed-loop responses were used to calculate the open-loop response of the disparity vergence system, using the equation:

$$R_o = R_c / (1 - R_c), \quad (1)$$

where both R_c (the closed-loop response) and R_o (the open-loop response) are complex quantities, containing both gain and phase information. The variance associated with this estimate of the open-loop performance was estimated by a standard technique (Kendall and Stuart, 1973; p. 247) described in Appendix 5. Fig. 4.2 shows the calculated open-loop performance of disparity-vergence in monkey M, in response to the largest and smallest vergence stimulus amplitudes tested (4 MA peak-to-peak and 0.25 MA peak-to-peak respectively). The responses to the smaller stimulus in the frequency region 0.1 - 0.3 Hz are not shown since the variances associated with these estimates were very large (the standard deviations were larger than the means).

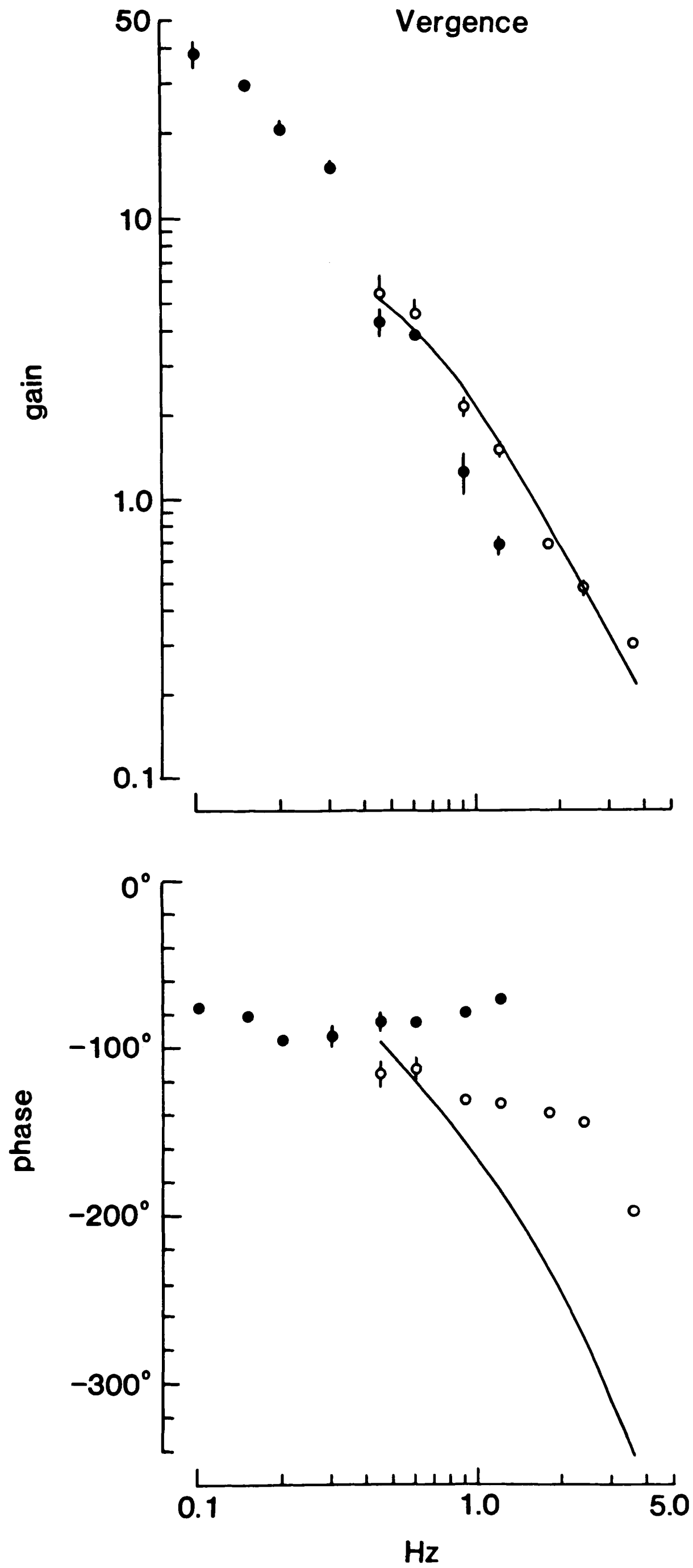
An attempt was made to describe the responses to the smallest stimulus amplitude in the hope that the disparity stimuli which resulted were small enough to avoid the complications introduced by the non-linearity demonstrated in Chapter 3 (Fig. 3.15). The gain of the responses decreased with increasing frequency much more rapidly than expected of an integrator. The gain roll-off had a slope of -12

Figure 4.2

Bode plot of the open-loop performance of disparity-driven vergence (calculated from the closed-loop data shown in Fig. 3.15) in monkey M. Filled symbols show the responses to vergence stimuli (not disparity stimuli) of 4 MA peak-to-peak amplitude; open circles show the responses to vergence stimuli of 0.25 MA peak-to-peak amplitude. The data from the latter condition in the frequency range 0.1 - 0.3 Hz are not shown since the S.D. of the gain was larger than the mean gain. The solid lines show the gain and phase of the transfer function

$$R(s) = 8.0 \exp(-0.14 s) / (3.77 s + 1)^2.$$

Although this transfer function provides a reasonable description of the gain of responses to the 0.25 MA peak-to-peak stimuli (open circles), the phase lags given by this function are much larger than those observed. Standard errors are smaller than data points unless explicitly shown.



dB/octave, requiring a second order transfer function to describe it. Since the variances associated with the estimates of open-loop gain were very large at low frequencies it was not possible to obtain a good estimate of the characteristic frequency of the transfer function, although it was possible to estimate an upper limit (0.6 Hz). The solid lines in Fig. 4.2 show the performance of gain and phase for the transfer function

$$R(s) = 8.0\exp(-0.14s)/(3.77s + 1)^2, \quad (2)$$

which was fitted by eye to the gain data in the frequency region 0.45 - 3.6 Hz (open circles in Fig. 4.2). Although this transfer function provides a reasonable description of the calculated open-loop gain performance, the observed open-loop phase lags are much smaller than those expected of this transfer function. The observed phase lags are also much shorter than those expected of an integrator with 140 msec delay (not shown in Fig. 4.2).

It is clear from Fig. 4.2 that the vergence responses to stimuli with a peak-to-peak amplitude of 4 MA would be even less well described by cascaded low-pass filters, since the gain rolls off more steeply with frequency, and the lowest reasonable characteristic frequency is lower than 0.6 Hz yet the open-loop phase lags are smaller than those observed in response to the smaller stimuli. The open-loop performance was also calculated for the vergence responses of monkeys A and H. In both animals the gain rolled off more steeply than shown by the solid line in Fig. 4.2, yet the phase lags were much smaller than those shown by the solid line in Fig. 4.2.

In conclusion, the responses of the monkey vergence system to sinusoidal vergence stimuli do not resemble those of a simple integrator with delay, nor do they resemble those of a combination of low-pass filters with delay. A similar conclusion has been reached for the human vergence system (Rashbass and Westheimer, 1961a; Zuber and Stark, 1968).

One striking feature of the vergence performance in these monkeys was the remarkable constancy of the closed-loop phase for responses to stimuli of different amplitudes at a given frequency, evident for monkey M in Fig. 3.15. The value of these phase lags were also very similar in the other two monkeys - in all three monkeys, at all amplitudes tested, the closed-loop phases of the vergence responses in normal binocular viewing at any one stimulus frequency were the same to within ± 8 degrees.

This constancy of the closed-loop phase, independent of variation in the closed-loop gain of the vergence response, cannot be accounted for by a reduction in the system's open-loop gain in response to larger inputs - the non-linearity observed in the open-loop step responses of monkey A (Fig. 4.1) and in the open-loop step responses of human subjects (Rashbass and Westheimer, 1961a). As can be seen from Fig. 4.2, the non-linearity must be described by changes both in the gain and the phase of the open-loop transfer function. One possible explanation of this effect is that the vergence system 'predicts' repetitive target motion. In order to examine this possibility the vergence responses to unpredictable target motion were examined.

4.2.3 Responses to unpredictable target motion

Pseudo-random target motion was produced by using filtered Gaussian noise to control the position of the target, as described in Chapter 2. The noise was low-pass filtered at 1.2 Hz and high-pass filtered at 0.1 Hz. The amplitude of the stimulus was tapered with a cosine smoothing function over the initial and final 0.5 seconds of each 6.7 second data collection period. This ensured that the stimulus had the same value at the beginning and end of each set of data, and since the stimulus approached its final value gradually, there was usually sufficient time to allow the animals responses to return to their initial values. Trials in which there was a clear difference between the initial and final values of the animals accommodation or vergence responses were discarded. Since the initial and final values of the stimulus and the responses were approximately the same, spectral analysis could be used to calculate the gain and phase of the responses. These were determined for the first eight harmonics (corresponding to the frequency range 0.15 - 1.2 Hz). The results from separate trials were averaged, harmonic by harmonic, by the method described in Appendix 5. The responses to pseudo-random target motion were measured in monkeys A and M. Fig. 4.3 shows an example of the pseudo-random stimulus and the responses in monkey A during normal binocular viewing. A Bode plot of the averaged responses for monkeys A and M is given in Fig. 4.4. The root mean square amplitude of the stimulus for each of the first eight harmonics was 0.33 MA. The most striking feature of these data is that the gains of the vergence responses were considerably smaller than unity, even for the responses to the fundamental component of the stimulus modulation. Furthermore, the gain hardly changed with frequency. Owing to the high

Figure 4.3

Accommodation stimulus (A_s) and response (A_r), vergence stimulus (V_s) and response (V_r), and horizontal position of the right eye (R), in response to pseudo-random target motion. Note that the initial and final values of the stimulus and response variables are closely similar. Monkey A.

Monkey A

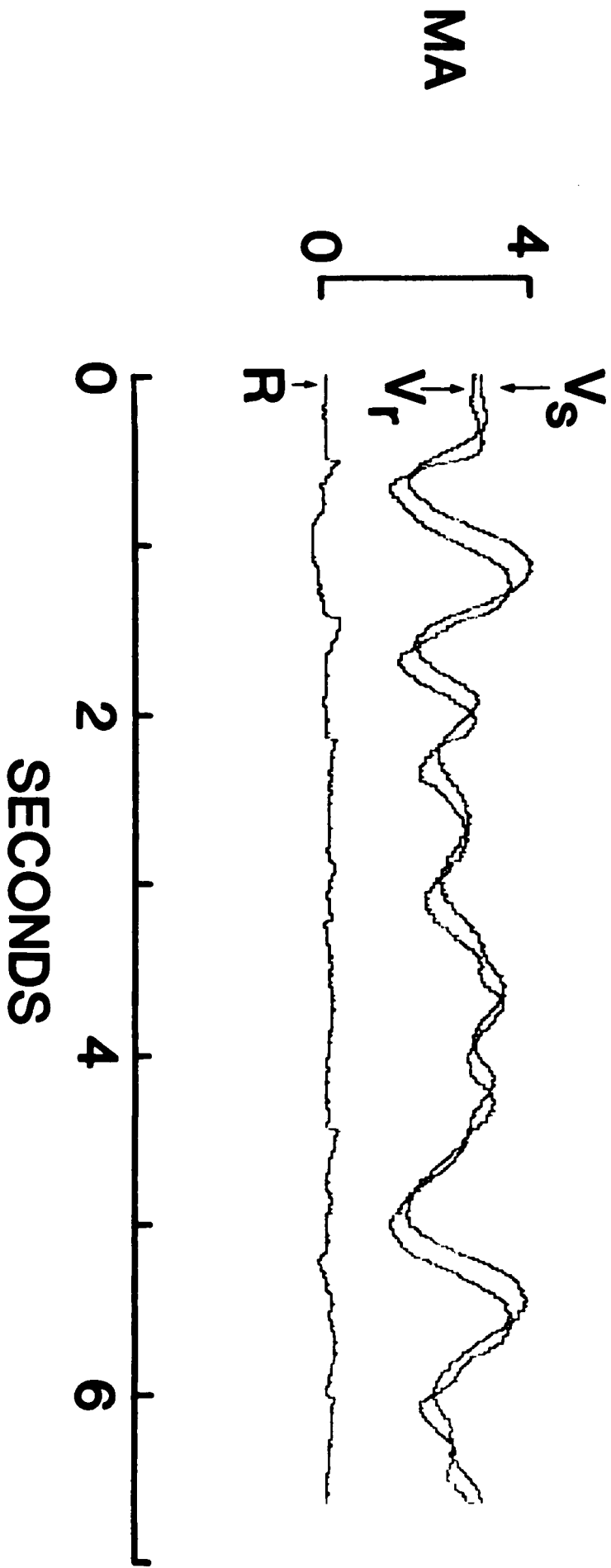
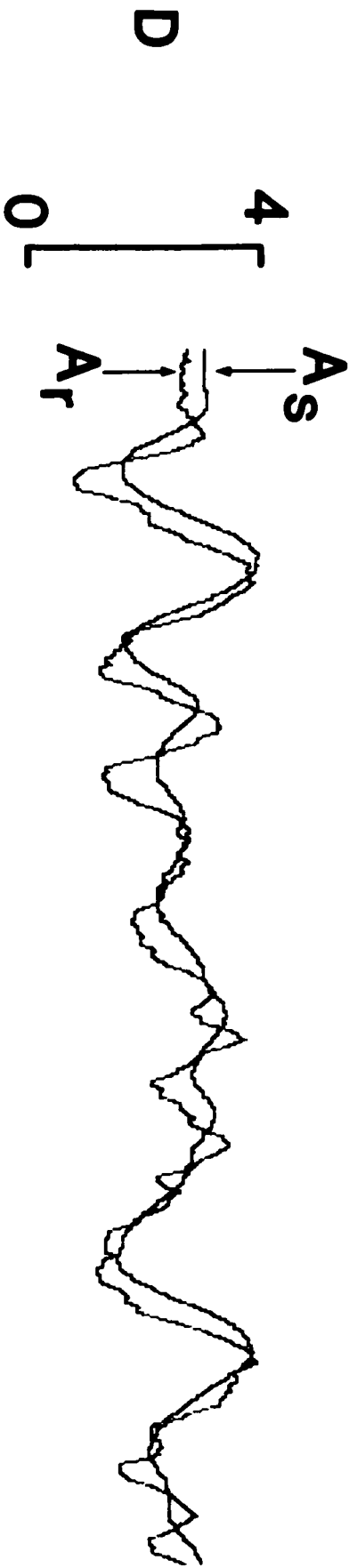


Figure 4.4

Bode plot of vergence responses to pseudo-random target motion (viewed binocularly). Open circles show the responses of monkey A, filled circles those of monkey M. The frequency on the abscissa is calculated as the product of the fundamental frequency (0.15 Hz) and the number of the harmonic for which the responses were calculated. For example, the points plotted at a frequency of 0.6 Hz show the gain and phase of responses for the fourth harmonic. Data collection period was 6.67 seconds. Standard errors are smaller than data points (typically ± 0.04 for gain, ± 3 degrees for phase) unless explicitly shown. The dotted lines show the closed-loop gain and phase of a system with the open-loop transfer function

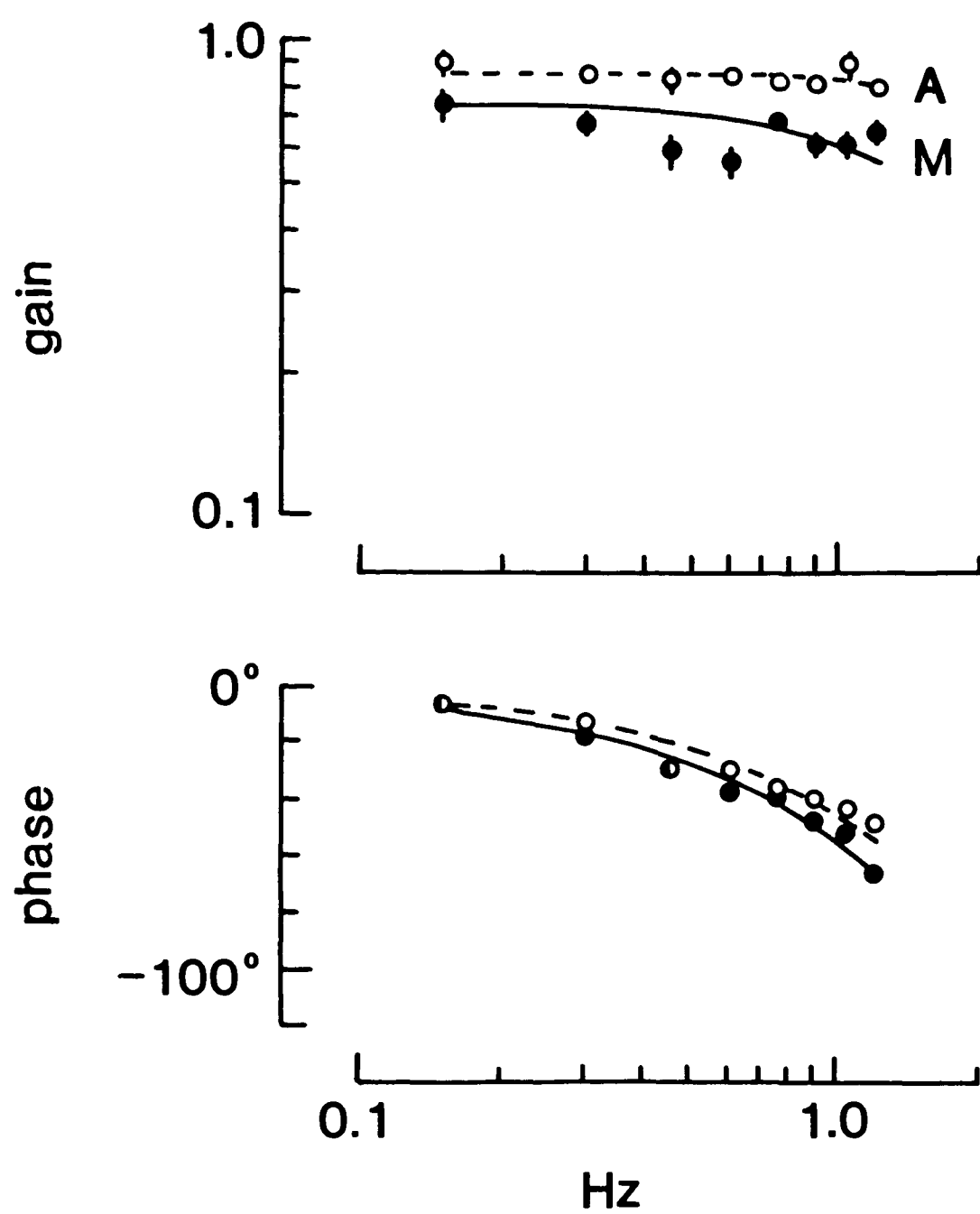
$$R(s) = 5.5\exp(-0.06s)/(0.76s + 1)$$

describing the behaviour of monkey A; the solid lines show the (closed-loop) performance of a system with the open-loop transfer function

$$R(s) = 2.8\exp(-0.05s)/(0.59s + 1)$$

describing the behaviour of monkey M. Note that the time delays used for these transfer functions (60 msec and 50 msec) were shorter than the measured latencies of vergence to step changes in disparity (160 msec for monkey A; 140 msec for monkey M).

Vergence



frequency components of the stimulus, large disparities frequently occurred during viewing of pseudo-random target motion. For monkey A disparities of 1.5 degrees frequently occurred while for monkey M disparities as large as 2.6 degrees were common. The difference between the responses shown in Fig. 4.4 and those seen in response to sinusoidal target motion (Fig. 3.15) may therefore be the result of the non-linearity evident in Fig. 3.15.

The phase lags of the responses are clearly larger than the phase lags observed in response to simple sinusoidal stimuli of any amplitude. Although this observation suggests that the small and consistent phase lags observed in response to sinusoidal stimuli are achieved by some form of prediction, this is not an inescapable conclusion. Since the gains of the responses are not generally comparable to the gains observed in response to sinusoidal stimuli, it is possible that both the responses shown in Fig. 4.4 and the responses observed with simple sinusoidal stimuli could be described by a complicated non-linearity which does not involve prediction. However, if the responses are compared at stimulus frequencies for which the response gains were similar (0.6 Hz in monkey A; 0.9 and 1.2 Hz in monkey M) it is still true that the phase lags were larger in response to unpredictable target motion than in response to predictable target motion. This strongly suggests that the vergence system is able to predict repetitive target motion.

When the data shown in Fig. 4.4 were used to estimate the open-loop performance of the vergence system, the change in open-loop gain with frequency was described approximately with a slope of -6 dB per octave,

as expected of an integrator. However, the open-loop phase lags were much smaller than those expected of an integrator with delay. The data could be described by simple low-pass filters only if delay terms smaller than the vergence latencies measured in Chapter 3 were used. The solid lines in Fig. 4.4 show the closed-loop gain and phase of a system with the open-loop transfer function

$$R(s) = 2.8\exp(-0.05s)/(0.59s + 1), \quad (3)$$

describing the performance of monkey M, while the dashed lines show the transfer function

$$R(s) = 5.5\exp(-0.06s)/(0.76s + 1), \quad (4)$$

describing the performance of monkey A.

It was shown above that the vergence responses to simple sinusoidal stimuli cannot be described by simple first order filters including the measured latency of the system. The same is true of vergence responses to pseudo-random stimuli. This failure to describe the system with simple transfer functions cannot therefore be the result only of prediction by the vergence system.

4.2.4 Can blur-driven accommodation be described by a simple transfer function?

Fig. 4.5 shows the calculated open-loop performance of blur-driven accommodation for monkey M. These data were calculated from the data shown in Fig. 3.14. The gain rolls off with increasing frequency with a slope of approximately -6 dB/octave, suggesting that the performance could be described by a first order low-pass filter. The solid line

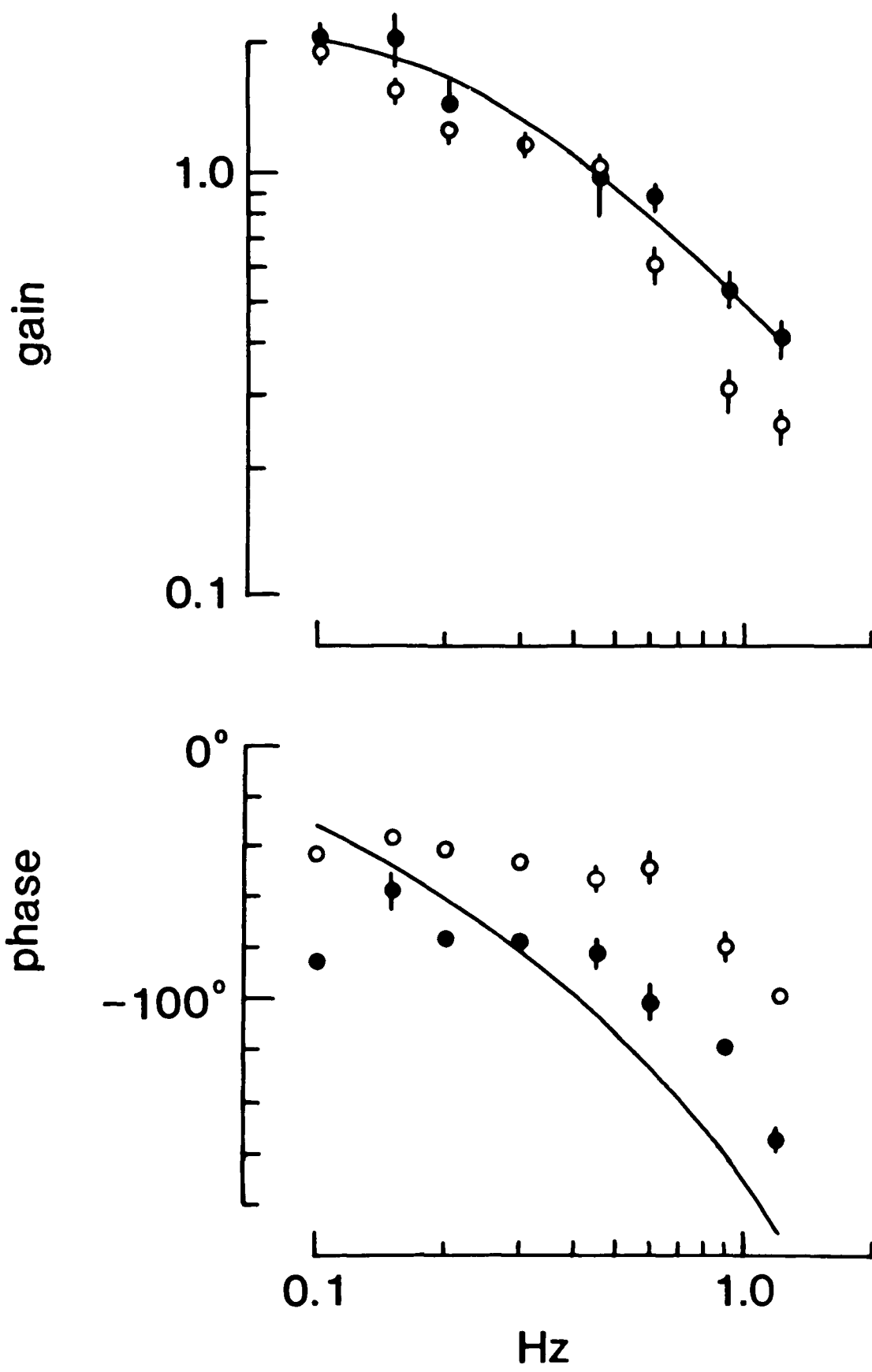
Figure 4.5

Bode plots of the open-loop gain and phase of blur-driven accommodation in response to monocularly viewed target motion. Data calculated from the closed-loop responses shown in Fig. 3.14. Open circles show the responses to accommodation stimuli with a peak-to-peak amplitude of 4 D, filled circles show the responses to stimuli with a peak-to-peak amplitude of 1 D. The solid lines show the gain and phase of the transfer function

$$R(s) = 2.2\exp(-0.26s)/(0.69s + 1)$$

which describes the open-loop gain reasonably, but over-estimates the changes in open-loop phase with frequency.

Monkey M
Accommodation



shown in Fig. 4.5 shows the performance of a first order low-pass filter with a characteristic frequency of 0.23 Hz, and a pure delay time of 260 msec (the measured latency of accommodation to blur stimuli). Although this transfer function describes the gain data well, the observed and expected phase lags are not in good agreement. In monkeys A and H second order transfer functions were necessary to describe the variation in the open-loop gain with stimulus frequency. These transfer functions greatly over-estimated the open-loop phase lags of the system.

In monkey M, the responses to pseudo-random target motion, viewed monocularly, were measured to examine the possibility that these small phase lags were the result of the accommodation system predicting repetitive target motion. The root mean square stimulus amplitude was 0.39 D for each harmonic. Fig. 4.6 shows the results: both the gain and phase of the responses usually lie within the region covered by the responses to simple sinusoidal stimuli of different amplitudes (see Fig. 3.14). Therefore, the predictability of target motion had little effect upon the performance of blur-driven accommodation. As with the responses to simple sinusoidal stimuli, these responses could not be described by simple low-pass filters with a pure delay of 260 msec. The accommodation responses to pseudo-random target motion could however be described by a first order low-pass filter with a delay term of only 120 msec: the solid lines in Fig. 4.6 show the closed-loop performance of a system with the open-loop transfer function

$$R(s) = 1.2\exp(-0.12 s)/(0.53 s + 1). \quad (5)$$

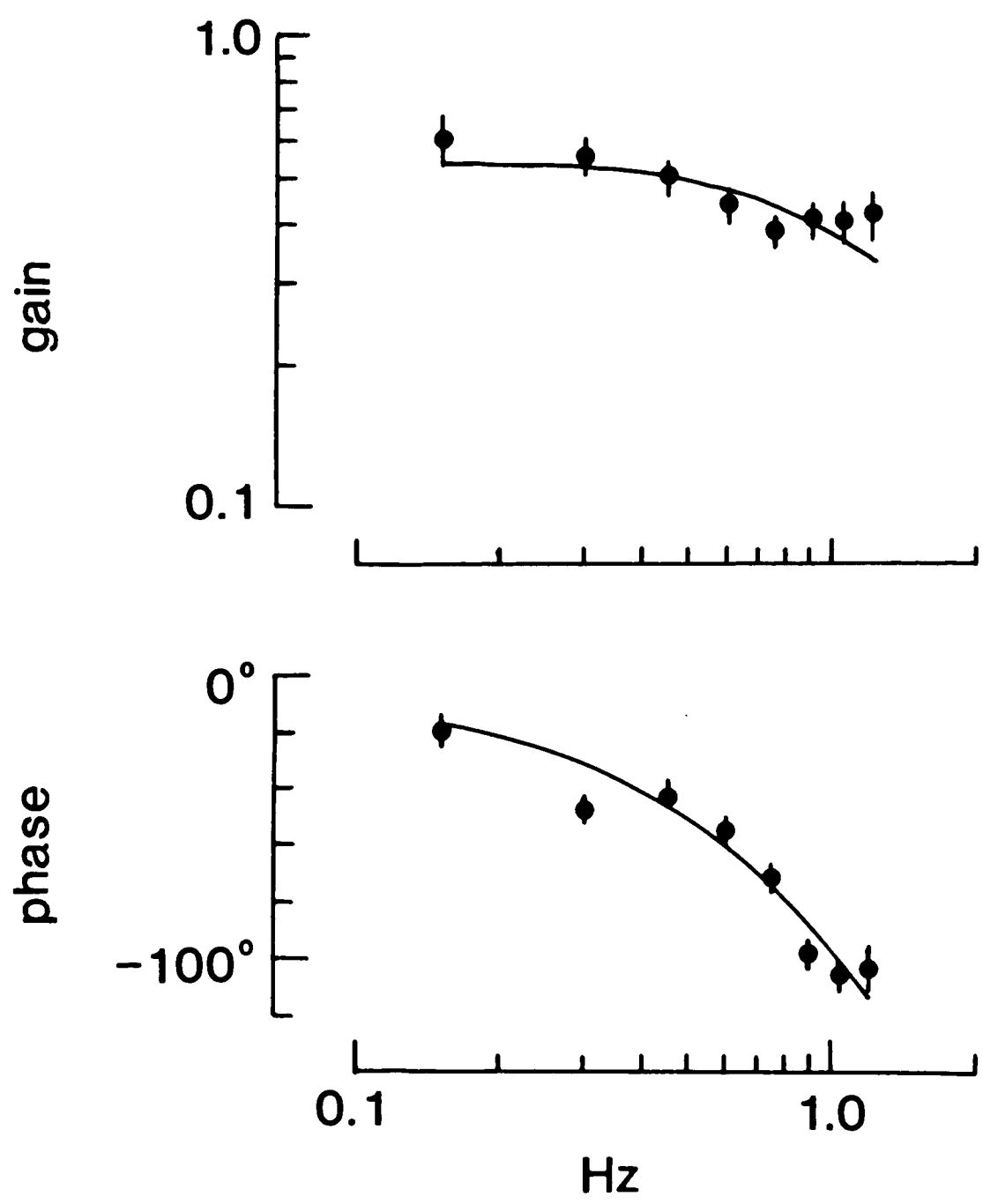
Figure 4.6

Bode plot of accommodation responses to pseudo-random target motion (viewed monocularly) for monkey M. The frequency on the abscissa is calculated as the product of the fundamental frequency (0.15 Hz) and the number of the harmonic for which the responses were analysed. Standard errors are smaller than data points (typically ± 0.05 for gain, ± 6 degrees for phase) unless explicitly shown. The solid lines show the closed-loop gain and phase of a system with the open-loop transfer function

$$R(s) = 1.2\exp(-0.12 s)/(0.53 s + 1)$$

Note that the time delay used for this transfer function (120 msec) is shorter than the measured latency of accommodation to step changes in blur (260 msec).

Monkey M
Accommodation



4.2.5 Interaction of blur-driven and disparity-driven responses.

Although it was not possible to describe the responses of disparity-driven vergence or of blur-driven accommodation with simple linear transfer functions, it was still possible to examine the hypothesis that the interaction of blur-driven and disparity-driven responses was linear at a given frequency.

The monkeys' responses were measured when the accommodation and vergence stimuli were combined in ways which did not correspond to the stimuli produced by any real object in 3-dimensional space. Stimuli were presented in which the amplitude of the accommodation stimulus modulation was one third, one half, or double that of the vergence stimulus. Fig. 4.7 shows an example of the responses in each of these three conditions. Fig. 4.8 compares the observed responses with those calculated (by the method described in Appendix 7) on the assumption of linear interaction between blur- and disparity-driven responses. In all cases the vergence response was close to the vergence stimulus, while the accommodation response was approximately 30% smaller or greater than it would have been in normal binocular tracking with the same vergence stimulus. The expected and observed vergence performances were in close agreement, as were the expected and observed values of the accommodation response gains. In monkey M, and monkey A in the condition with double amplitude accommodation, the expected and observed phases of the accommodation response differed by between 7 and 15 degrees, while the expected and observed accommodation phases were in good agreement in the remaining cases.

Figure 4.7

Accommodation stimulus (A_s) and response (A_r), vergence stimulus (V_s) and response (V_r), and the horizontal position of the right eye (R) during a variety of tasks in which the accommodation and vergence stimuli presented did not correspond to stimuli generated by any target in three-dimensional space. In A) the amplitude of the accommodation stimulus modulation was twice that of the vergence stimulus, (monkey A); in B) the amplitude of the accommodation stimulus modulation was one half that of the vergence stimulus, (monkey M); C) The amplitude of the accommodation stimulus modulation was one third that of the vergence stimulus, (monkey H).

A) Monkey A B) Monkey M C) Monkey H

X2 X0.5 X0.33

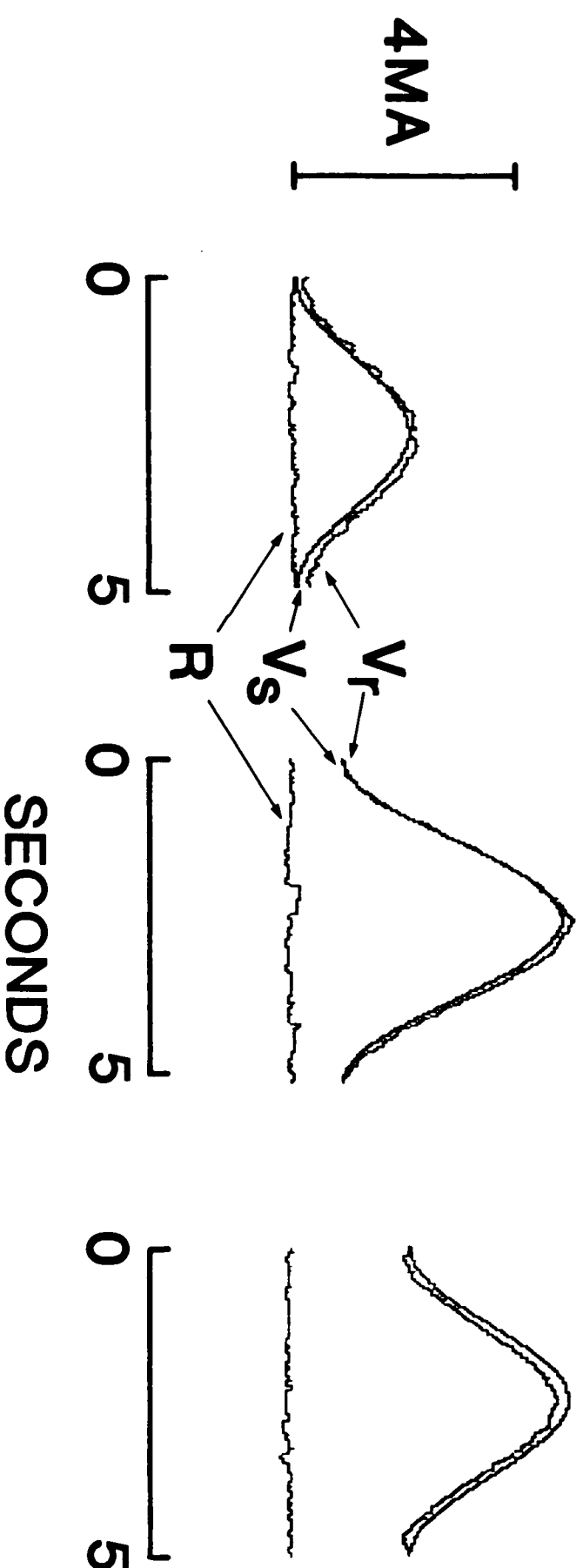
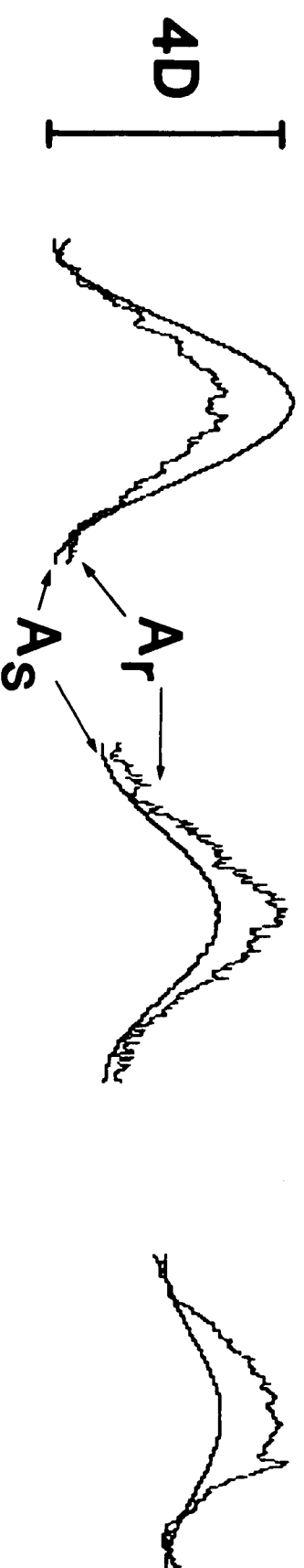
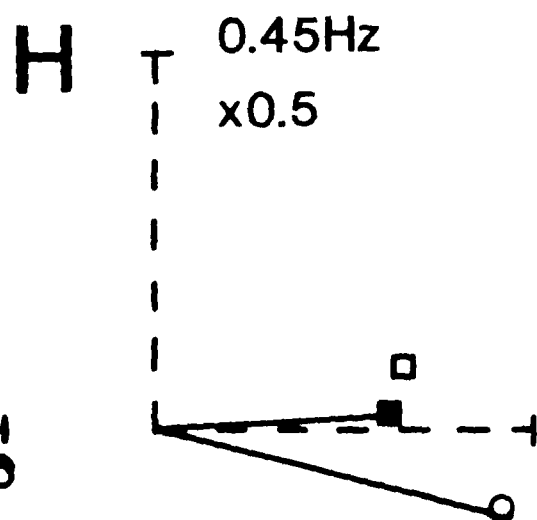
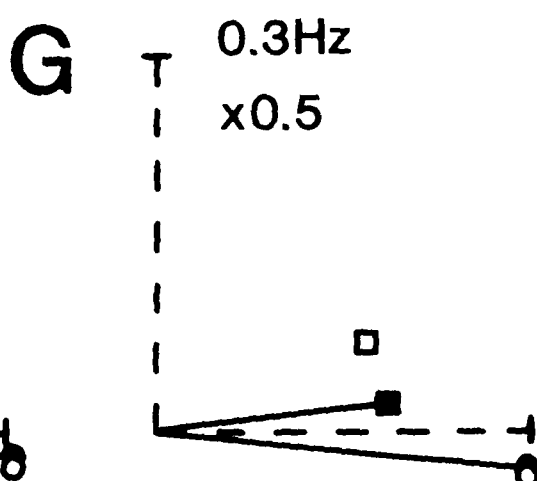
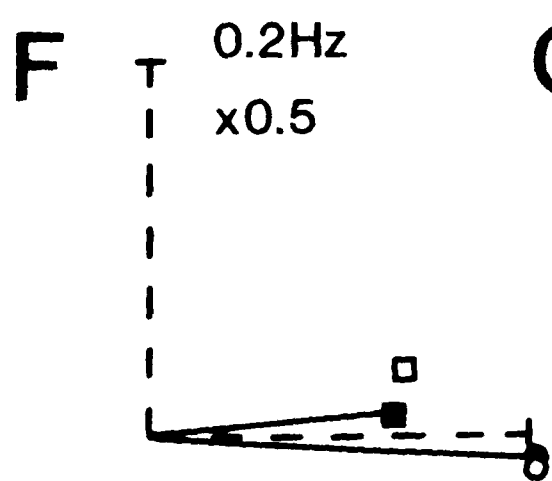
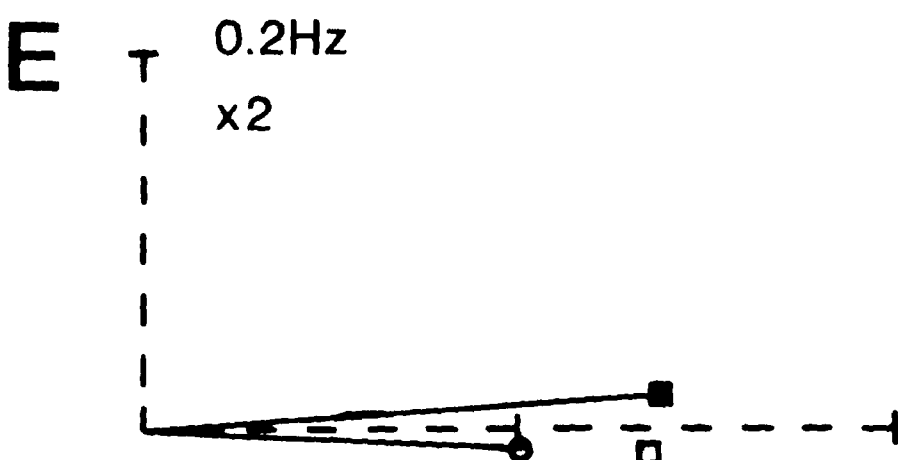
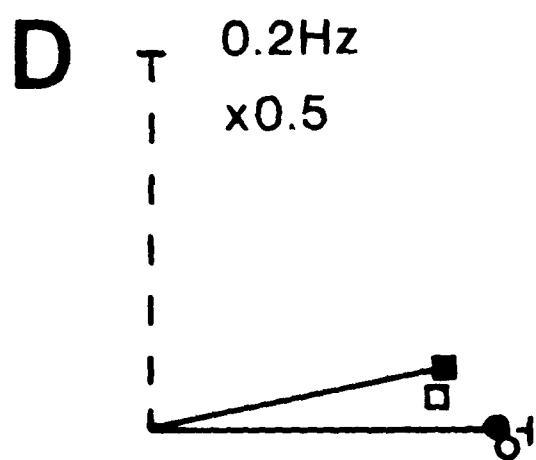
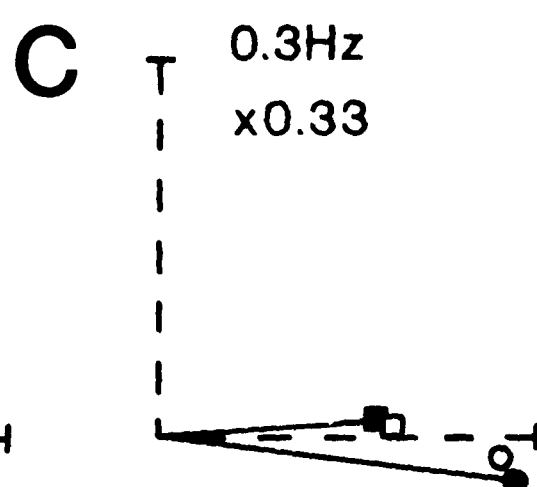
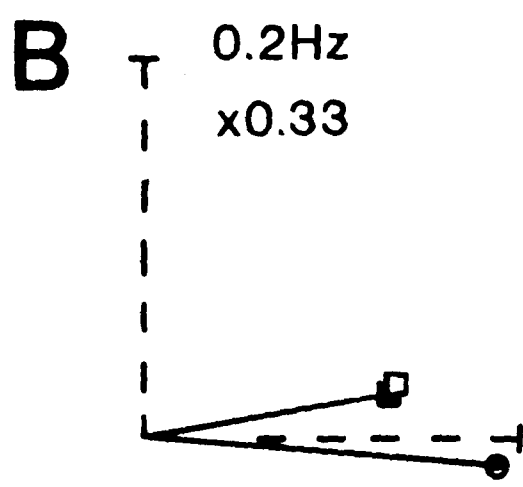
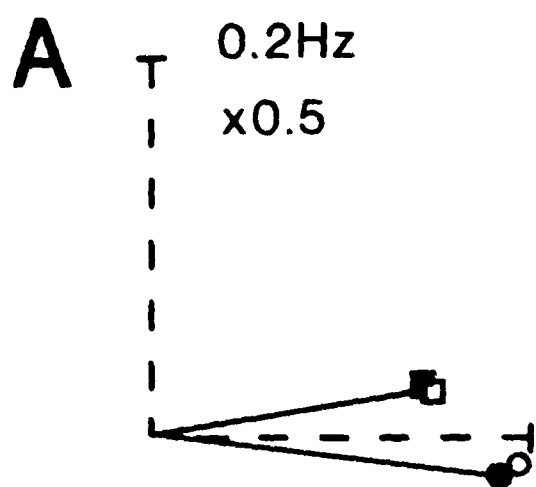


Figure 4.8

Vector plots of measured (filled symbols) and predicted (open symbols) accommodation (squares) and vergence (circles) in conflict tasks, where the accommodation stimulus amplitude was half (A), D), F), G), H)), one-third (B), C)) or double (E) the vergence stimulus amplitude. A), B) and C) monkey H; D) and E) monkey A; F), G) and H) monkey M. Dashed axes indicate unit vectors in phase and in quadrature with the stimulus. Each point is based on at least 6 cycles of data (average 23 cycles). Standard errors of measured responses are smaller than data points (typically ± 0.01 for gain, ± 1 degree for phase).



4.3 Discussion

As in humans (Rashbass and Westheimer, 1961a; Zuber and Stark, 1968) the responses of the monkey vergence system to sinusoidal stimulation over a range of frequencies did not resemble those of an integrator with delay, although the open-loop step responses were those of an integrator. The responses to pseudo-random stimuli could not be described with this simple transfer function either, so the discrepancy cannot be explained as the result of prediction by the vergence system. Attempts to describe the monkey vergence performance with combinations of first order filters including a delay term equal to the measured latency also failed. The transfer functions which described the behaviour of the open-loop gain greatly over-estimated the open-loop phase lags. One possible explanation of the small phase lags observed is that the system is sensitive to finite rates of change in disparity. Such sensitivity would have to be non-linear to account for the lack of any derivative responses in the open-loop step responses (see Fig. 4.1). No experiments were performed which demonstrated an influence of the rate of change of disparity on the monkey's vergence response, and the calculated open-loop frequency response data showed no clear sign of a falling gain at low frequencies (as one would expect in the presence of a derivative element). Consequently, no attempt has been made to describe the frequency response data with a model incorporating an element sensitive to the rate of change of disparity.

It should be noted that the procedure of describing the gain behaviour alone by a transfer function, and then looking at the expected phase lags, is only one way of demonstrating the failure to account for

the responses with simple transfer functions. One could equally well fit a transfer function to the phase performance and predict the behaviour of the gain.

A striking feature of the vergence responses to sinusoidal stimuli in normal binocular viewing was the very close similarity of the closed-loop phase of the responses in all three monkeys. The closed-loop phase performance was also unaffected by changes in the amplitude of the stimuli. This might be described as a non-linearity producing changes in gain and phase (open-loop) with changes in the amplitude of the input, which happened to be the same in all three monkeys. Alternatively, it may be that observed phase lags are the result of attempts to predict the motion of the target. The vergence responses of two monkeys to pseudo-random target motion were quite different (showing larger phase lags) from their responses to simple sinusoidal target motion, suggesting that prediction is important in the monkey vergence system. However, since large disparity stimuli frequently occurred during viewing of pseudo-random target motion it is difficult to exclude the possibility that a non-linear relationship between the vergence response and the amplitude of the disparity inputs (demonstrated in Chapter 3 for simple sinusoidal stimuli) accounts for much of the difference between responses to predictable and unpredictable stimuli.

It is possible that the latency of responses to changes in the rate of change of disparity are shorter than the latency of responses to step changes in disparity. If this were true, the latencies measured in response to step changes in target position (Chapter 3) would not be appropriate to the description of responses to sinusoidal target motion.

However, even if a latency of zero is assumed in equation (2), the predicted open-loop phase lags are slightly larger than those observed in response to simple sinusoidal stimuli. The responses to unpredictable target motion can be described by first order low-pass filters, if latencies are assumed (50 or 60 msec) which are shorter than those observed during step changes in target position. This suggests that a combination of prediction and a short response latency (for gradual changes in disparity) may produce a model accounting for the frequency response of the monkey vergence system.

The responses of accommodation in monocular viewing could not be described by a simple transfer function (also noted in human subjects by Stark et al., 1965) which included the measured latency of the system. The responses to unpredictable target motion were not very different from those to predictable target motion, excluding an explanation based upon the predictability of the sinusoidal stimuli (such as proposed by Stark et al.). As discussed for the vergence system, if the latency of accommodation to change in the rate of change of blur were shorter than the latency of responses to change in the magnitude of blur stimuli, it would be possible to account for the frequency response of the system with a simple transfer function.

The monkeys' responses to conflicting accommodation and vergence stimuli are interesting for three reasons. First, the close agreement between the predicted and observed responses is good evidence that the interaction of blur and disparity-driven responses is linear, at least at low frequencies. Second, since the extent to which the accommodation and vergence responses could be dissociated was rather modest, it is

interesting to consider how the responses could be dissociated statically. The obvious possibility seems to be that dissociation is possible only because of rapid prism adaptation altering tonic vergence (as discussed in Chapter 1). If this is true, then the familiar clinical tests of the zone of clear vision are principally testing the efficiency of rapid prism adaptation, and the results obtained would be expected to depend upon how rapidly the tests were carried out. Finally, the dissociation of the normal tight coupling between accommodation and vergence provided a useful technique for exploring whether the activity of cells recorded in the monkey midbrain were related to vergence or to accommodation, as described in the next chapter.

CHAPTER FIVE

EXTRACELLULAR RECORDINGS FROM NEAR-RESPONSE CELLS IN THE MIDBRAIN

5.1 Introduction

In this study extracellular recordings were made from isolated single units in the midbrain of two awake monkeys (monkeys A and H used for the behavioural experiments), trained to track target motion in depth. The methods and apparatus were described in detail in Chapter 2. Briefly, glass insulated tungsten microelectrodes were lowered to a region dorsal and dorso-lateral to the oculomotor nucleus (OMN). A computer controlled the accommodation and vergence stimuli presented by a haploscope, and recorded the horizontal position of both eyes, the accommodative state of the right eye, and the unit discharge rate. The accommodation and vergence stimuli modulated with a sinusoidal time course, so spectral analysis could be used to calculate the fundamental component of the modulation in unit discharge rate, the accommodation response, and the vergence response.

Recent studies have demonstrated the existence of cells in the paraoculomotor area related to vergence or accommodation (Mays, 1981 and 1984; Bando et al., 1981b and 1984a). This study was intended to clarify the nature of such cells. The activity of cells was recorded while the animal tracked a target which appeared to move directly towards the right eye, and also while the animal tracked a target moving directly towards the left eye. If the modulation in unit discharge rate was approximately the same in both tasks the cell was classified as a near response cell (NR cell). In both tasks stimuli of the same frequency and amplitude were used (frequency 0.1 or 0.2 Hz, peak-to-peak amplitude 2 D

or 4 D). An attempt was made to perform all tests using a stimulus range where the unit discharge rate did not show signs of saturation, and did not fall to zero. However, for 20% of identified NR cells there was no firing during part of the cycle. A method for estimating the amplitude of the fundamental component of the modulation in firing rate for such 'cut off' cells is presented in Appendix 5.

Once identified as an NR cell, the firing rate was recorded during tracking of targets whose accommodation and vergence components were of conflicting amplitudes. As shown in Chapter 4, the ratio of the amplitude of the accommodation response to the amplitude of the vergence response is different during such conflict tasks from the ratio in normal binocular viewing. Examining whether the activity of the cell had a constant relationship to the vergence response or to the accommodation response allowed cells to be classified as accommodation-related, vergence-related, or related to both accommodation and vergence.

In order to determine whether or not NR cells were related to the motor output of the near triad, or whether they were related to one of the stimuli which activate the triad (i.e. blur or disparity), the activity of NR cells was recorded both during monocular tracking of a target moving in depth (blur stimulus alone) and during binocular tracking with no blur stimuli (accommodation-open-loop (AOL) viewing achieved by the method described in Chapters 2 and 3). If the activity of the cell in each of these tasks was similar to that in normal viewing, the cells were presumed to play a motor rather than sensorimotor role. Referring to Fig. 1.1 of Chapter 1, the tests

described above determined whether the signals carried by the NR cells were those expected of cells at sites corresponding to points Y_a , Y_v , X_a or X_v .

The dynamic properties of the relationship between NR cell activity and the near response were also examined. The activity of a sample of cells was recorded during step changes in the accommodation and vergence stimuli, and also during tracking of sinusoidal motion in depth over a range of frequencies.

5.2 Results

119 Penetrations were made¹ in two monkeys (85 in monkey H, 34 in monkey A) covering every 1 mm in a grid covering the oculomotor nucleus (OMN) and vicinity. 1198 single cells were isolated in the region extending approximately 5 mm dorsal to the OMN, and all were tested for a relationship to the near response. Tracks were terminated when the electrode tip entered the OMN (identified by the characteristic 'singing' of the background activity, and by the burst tonic relationship of isolated cells to one component of eye movements). Tracks were also terminated if the electrode tip entered the magnocellular red nucleus (mRN, identified by the large action potentials of the neurones and by their relationship to movements of the contralateral limbs - Gibson et al., 1985).

Quantitative data were collected on 110 cells identified as NR

¹ 10 of the penetrations made in monkey H were made by Dr. S.J. Judge in my absence. 109 cells were isolated in those penetrations, of which 14 were NR cells.

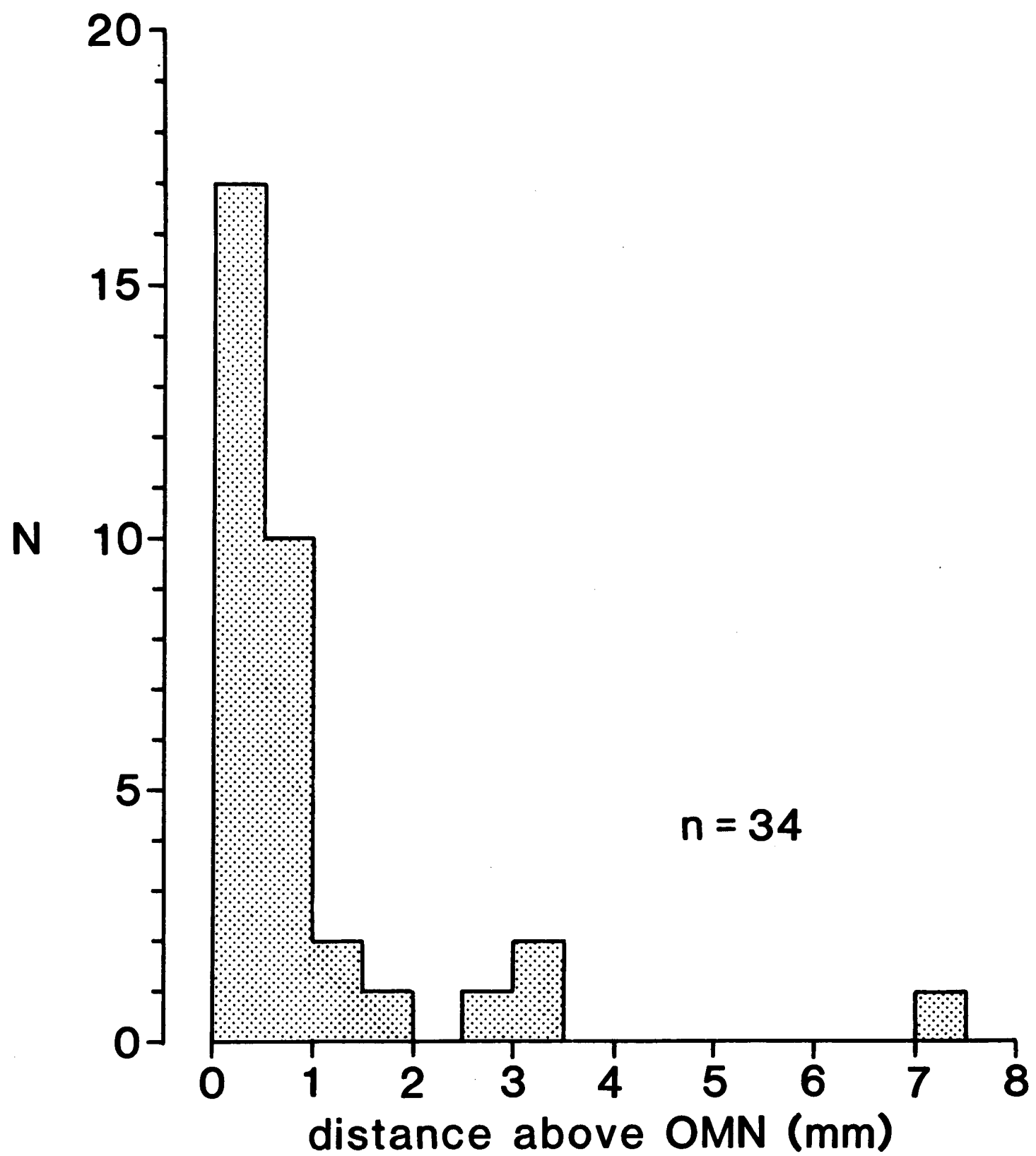
cells (84 in monkey H, 26 in monkey A), of which 55 were recorded on penetrations where cells were also recorded in the OMN or mRN. The position of NR cells relative to these cells in the OMN and mRN was estimated from recording how far the micro-drive was moved between recording of the different cell types. Fig. 5.1 shows histograms of the number of NR cells recorded at different distances above the first OMN cells or mRN cells. On penetrations where OMN cells were recorded, 27 out of 34 NR cells were recorded at distances less than 1 mm away from the OMN. In two cases oculomotor motoneurons were recorded simultaneously with NR cells (A048 and H188). In penetrations where cells were recorded in the mRN, 14 out of 21 NR cells were in a region between 1.0 and 2.5 mm away from the mRN. During the last few days of recording in monkey H, three sets of lesions were made at the sites of identified NR cells (by passing a current of 20 microamps through the electrode for 20 seconds, electrode positive), two of which were clearly visible in histological sections. Both were just dorsal to the OMN.

Although it was not possible to reconstruct the exact location of most of the tracks in the histological material, it was clear (from the estimates of the position of cells made on the basis of the recorded position of the micro-drive) that eleven NR cells were somewhat dorsal to the main concentration. All eleven of these cells modulated their firing much less strongly during the near response than the average for all NR cells. Eight of these cells were in a region 4-5 mm dorsal to the estimated dorsal limit of the OMN, and 1-3 mm away from the midline. Examination of the histological material suggested that these cells were probably in the Superior Colliculus. Of these eight cells, four decreased their firing when the monkey converged.

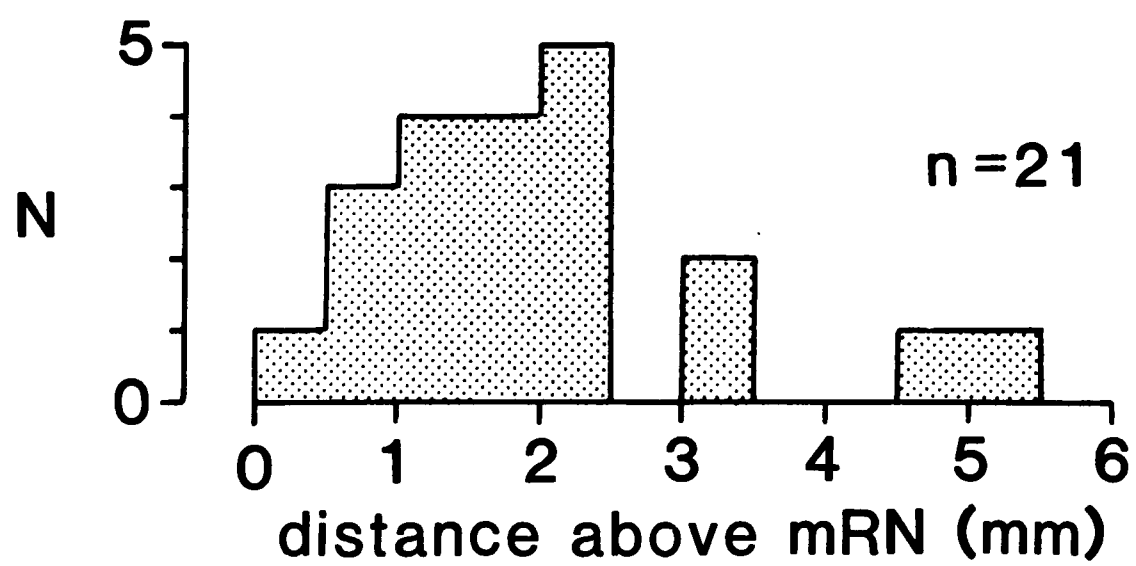
Figure 5.1

A) Histogram of number of near response cells (N) isolated at different distances above the first oculomotor motoneurons recorded on the same penetration. B) Histogram of the number of near response cells (N) recorded at different distances above the first magnocellular red nucleus cells i.e. cells which had large action potentials and discharged during movement of the monkey's contralateral forelimb.

A)



B)



5.2.1 NR Cells

The majority of NR cells recorded in this study (81) had firing rates which increased as the animal converged (henceforth called positively modulated NR cells), while a smaller number (27 cells) showed an increase in firing rate during divergence (negatively modulated NR cells). It would be begging the question to call these cells "convergence cells" and "divergence cells" respectively, since they may be related to any aspect of the near response (accommodation, vergence, or pupil constriction). Two cells modulated their firing rate approximately 90 degrees out of phase with vergence and accommodation. Fig. 5.2 shows the firing pattern of a positively modulated cell (A027) which is typical in the sense that its vergence gain (33.9 ± 1.2 (S.E.) spikes. $\text{sec}^{-1}\text{MA}^{-1}$, $n = 8$) and its phase lead over the vergence response (31.4 ± 2.1 (S.E.) degrees) were close to the vector average for all positively modulated NR cells tested at 0.2 Hz (27.0 spikes. $\text{sec}^{-1}\text{MA}^{-1}$ and 30 degrees). The term 'vergence gain' refers to the amplitude of the fundamental component of the modulation in unit discharge rate divided by the amplitude of the fundamental component of the vergence response. Fig. 5.2 shows the activity of the cell during vergence with the right eye alone (A) and the left eye alone (B) adducting. Notice that the change in the direction of conjugate gaze modulates in opposite senses in Fig. 5.2A and Fig. 5.2B, while the unit firing is similar in both cases. During conjugate eye movements, the cell's activity is not modulated (Fig. 5.2C shows smooth pursuit, Fig. 5.2D shows saccades). Fig. 5.3 shows the vergence gain of 94 cells in two test conditions - left eye only adducting (abscissa) and right eye only adducting (ordinate). For all cells the firing rate is similar in both conditions

Figure 5.2

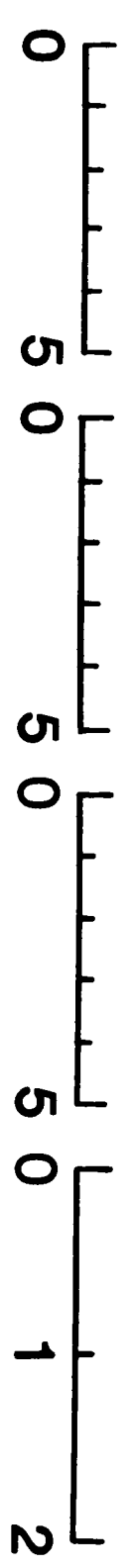
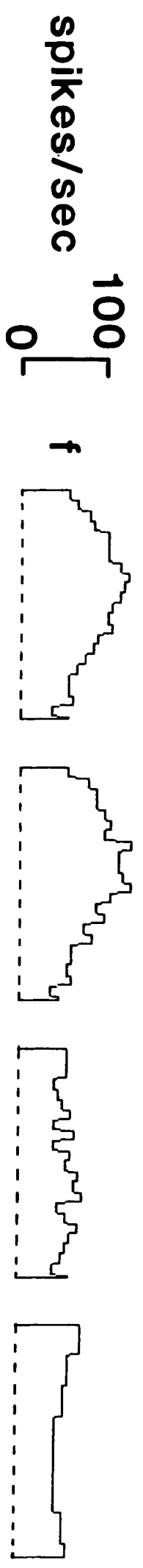
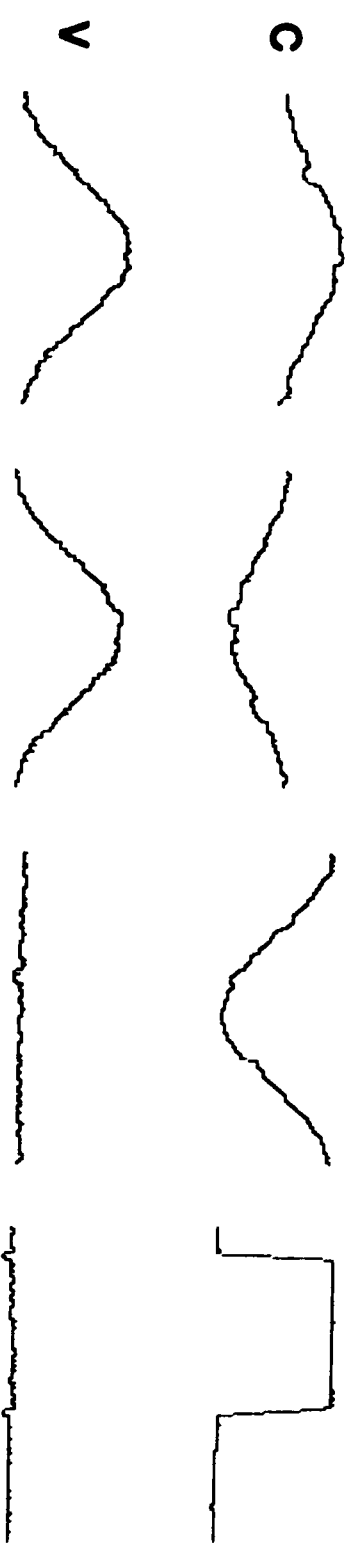
Discharge of one cell (A027) recorded while the monkey tracked a target moving A) in depth towards and away from the left eye, B) in depth towards and away from the right eye, and in the fronto-parallel plane (C and D). Successive rows of the figure are left eye position, l ; right eye position, r ; conjugate direction of gaze, $c = (r + l)/2$; vergence, v and neurone firing rate, f . In A) and B) the movement was sinusoidal with frequency 0.2 Hz and peak-to-peak amplitude 4 MA. The cell's firing was strongly modulated during tracking in depth but not during motion in the fronto-parallel plane (whether smooth pursuit (C) or saccadic (D)). Eye movements are expressed in metre-angles (MA) so as to be commensurate with accommodation (in dioptries). See text for further details.

A

B

C

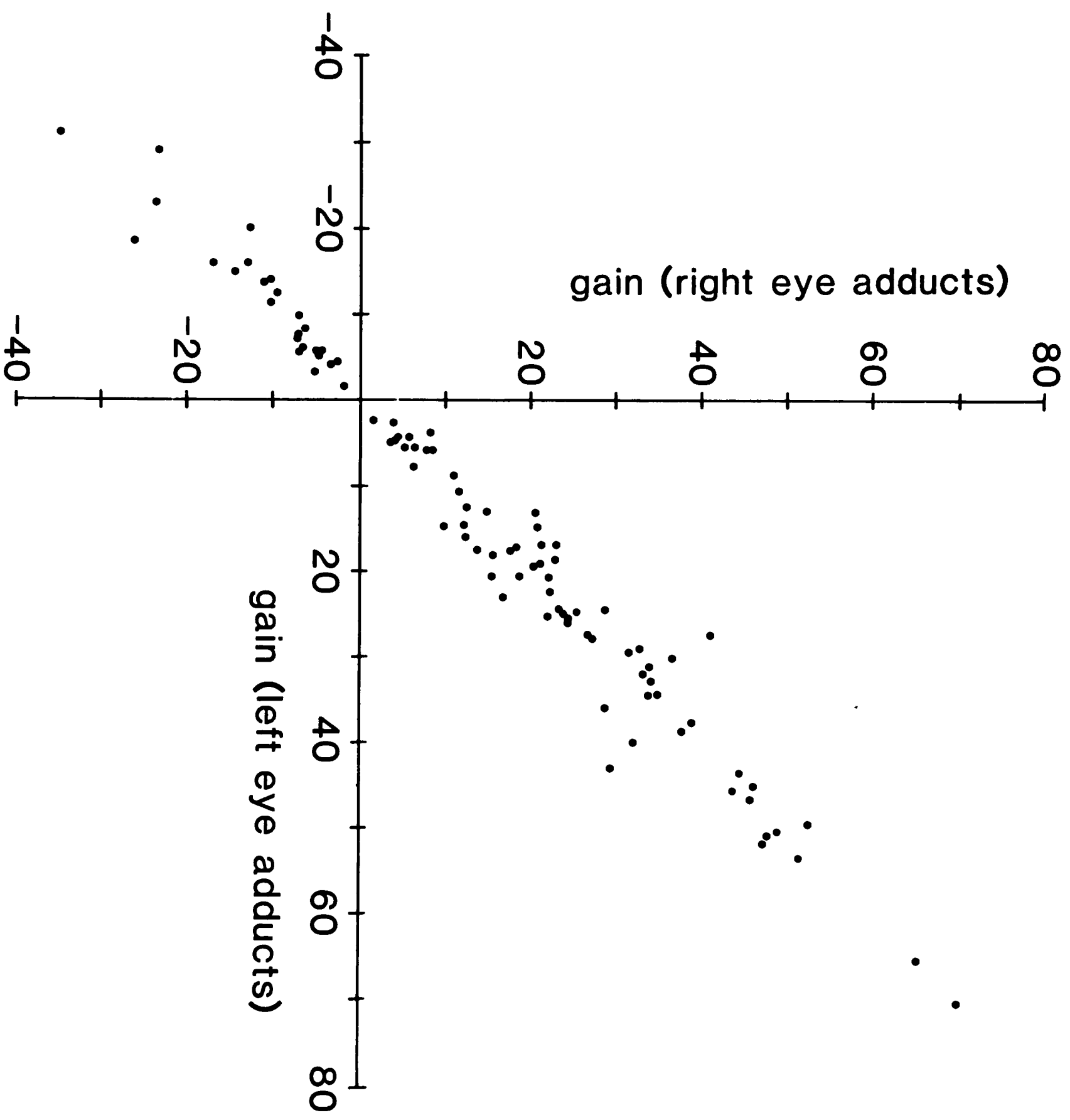
D



SECONDS

Figure 5.3

Vergence gain ($\text{spikes} \cdot \text{sec}^{-1} \cdot \text{MA}^{-1}$) of 94 near response cells compared during target movement towards the right eye (abscissa) and towards the left eye (ordinate). Target vergence change was sinusoidal, with frequency 0.1 or 0.2 Hz and peak-to-peak amplitude usually 4 metre-angles. For most cells, vergence gain was similar whether the vergence was achieved by adduction of the right eye or of the left eye.



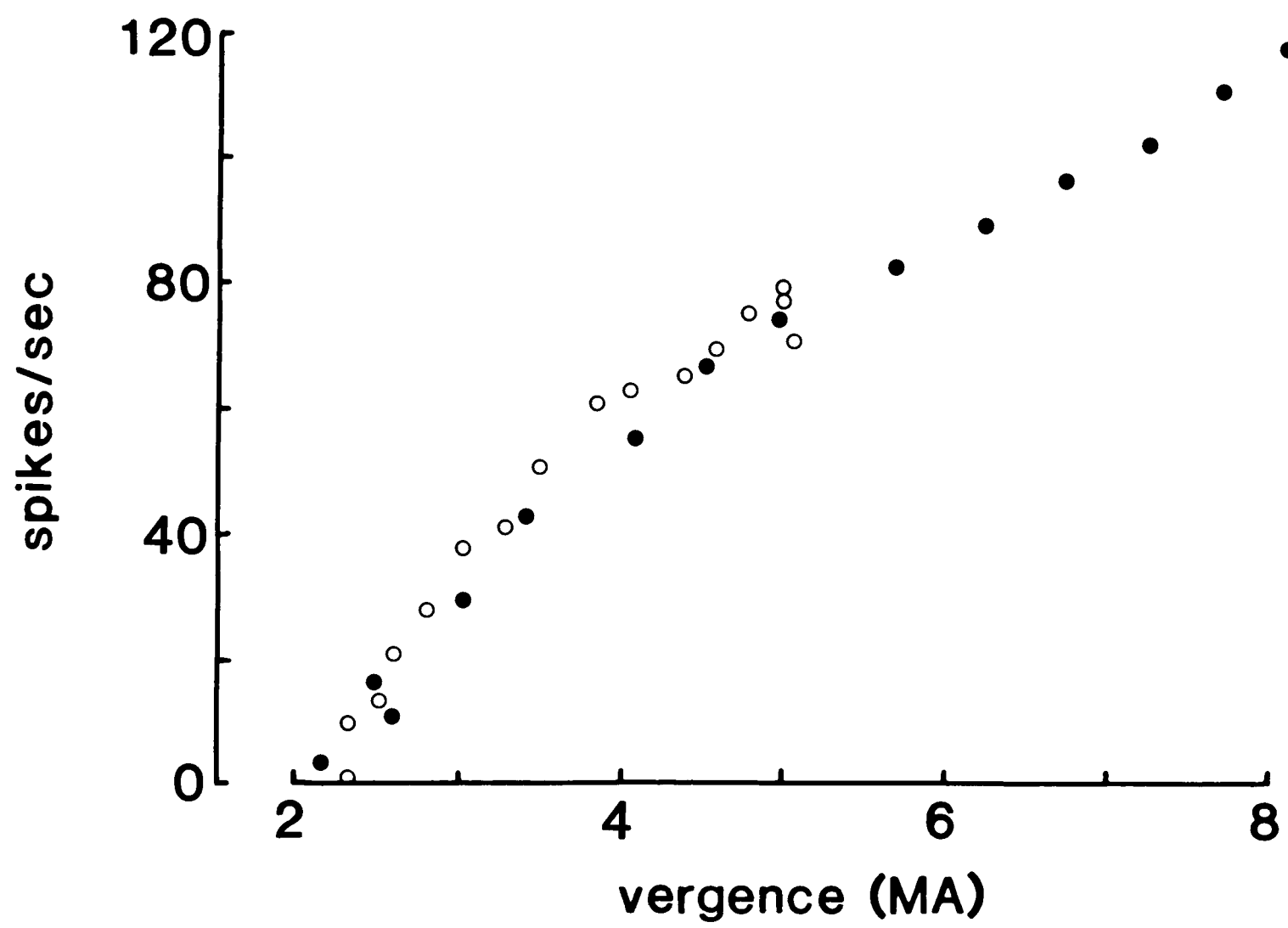
- in no case was the difference in vergence gain between the two conditions significant at the 0.01 level (t-test). The performance was determined with considerable precision: the mean S.E. of the gain estimates was $1.3 \text{ spikes} \cdot \text{sec}^{-1} \text{MA}^{-1}$, and the mean S.E. of the phase measurements was 5.0 degrees. (For 30 cells statistical comparisons could not be made because only one sample was obtained under one condition or other.)

5.2.2 Linearity of responses

Two methods were used to assess whether or not the relationship between neurone firing rate and the near response (vergence or accommodation) was linear. The first method consisted simply of displaying the unit firing rate as a function of vergence angle on an X-Y display, made with the calculated phase difference between the firing rate and vergence removed to simplify the judgement of linearity. Of the 81 positively modulated cells, 45 (56%) were judged to be linear, 22 (27%) were non-linear in the sense that the slope of the firing rate was higher at low values of convergence and accommodation than elsewhere (where it was linear), 11 (14%) were non-linear in that their firing rate showed a soft saturation' characteristic, and 3 (4%) had firing rates too irregular to allow a judgement of linearity. Fig. 5.4 shows an example of one cell which showed a non-linear relationship between unit firing and the vergence response. The slope of the relationship is steeper for vergence responses between 2 and 4 MA than it is in the region between 4 and 8 MA. This non-linearity is distinct from 'soft saturation' in that the relationship is linear for vergence responses between 4 and 8 MA.

Figure 5.4

Firing rate (abscissa) plotted against vergence angle (in MA, ordinate) for an identified vergence cell (H093) which had a non-linear relationship between vergence angle and unit firing rate. The unit firing rate is plotted against the vergence response recorded 300 msec after the firing rate, in order that the phase lead of the unit firing over the vergence response (21 degrees) does not complicate the judgement of linearity. Open circles show the responses while viewing a stimulus with a peak-to-peak amplitude of 3 MA, filled circles show the responses to a stimulus with a peak-to-peak amplitude of 6 MA. (Stimulus frequency was 0.2 Hz in both cases.) In both cases the responses are averaged from three separate cycles. The relationship between unit firing and vergence is steeper for vergence angles smaller than 4 MA than it is for vergence angles greater than 4 MA. See text for discussion.



In order to give a quantitative estimate of deviations from linear behaviour, the total harmonic distortion of the cells firing rate was calculated (see Appendix 5). Since the vergence response varied with a sinusoidal time course, the unit firing should also have modulated sinusoidally if the relationship was linear. The distortion coefficients calculated were small (0.097 ± 0.049 S.D.; $n=50$) for positively modulated cells whose vergence gains were greater than 10 spikes.sec.deg⁻¹. Cells with lower gains had larger distortion coefficients, presumably because small random fluctuations in firing rate contributed more to the distortion coefficient. For cells which were silent for part of each cycle the distortion coefficient was not meaningful, since the responses of the cell were inevitably not sinusoidal.

5.2.3 Gains and thresholds of NR cells

Fig. 5.5 shows a histogram of the vergence gain for all positively modulated NR cells ($n = 81$), and Fig. 5.6 shows the threshold at which these cells began to fire, estimated from the mean firing rate and the gain of the fundamental component of the neurone response by the equation

$$t = \bar{v} - \bar{f}/g ,$$

where t represents the threshold, $\bar{f}$ the mean firing rate, g the vergence gain of the unit, and $\bar{v}$ the mean vergence response. In both figures the stippling shows the data of Mays (1984) for comparison. In both cases the NR cells reported here have less tightly clustered properties than those of Mays, but since the measurements were made by quite different

Figure 5.5

Histogram of the number of near response cells (N) with different vergence sensitivities (solid line). Dotted line and stippled histogram shows the data of Mays (1984) for comparison. Sensitivities are in $\text{spikes} \cdot \text{sec}^{-1} \cdot \text{degree}^{-1}$. See text for details.

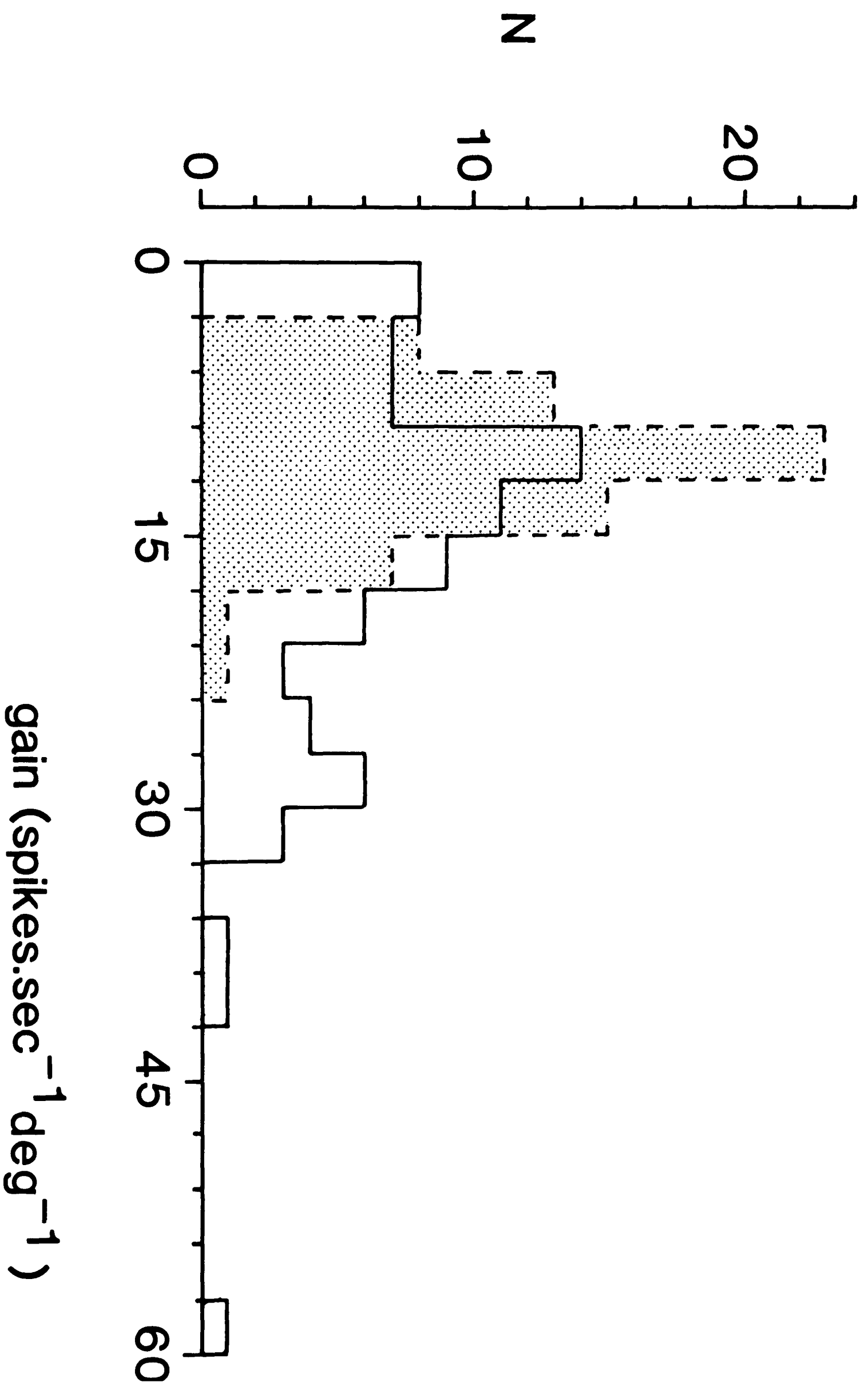
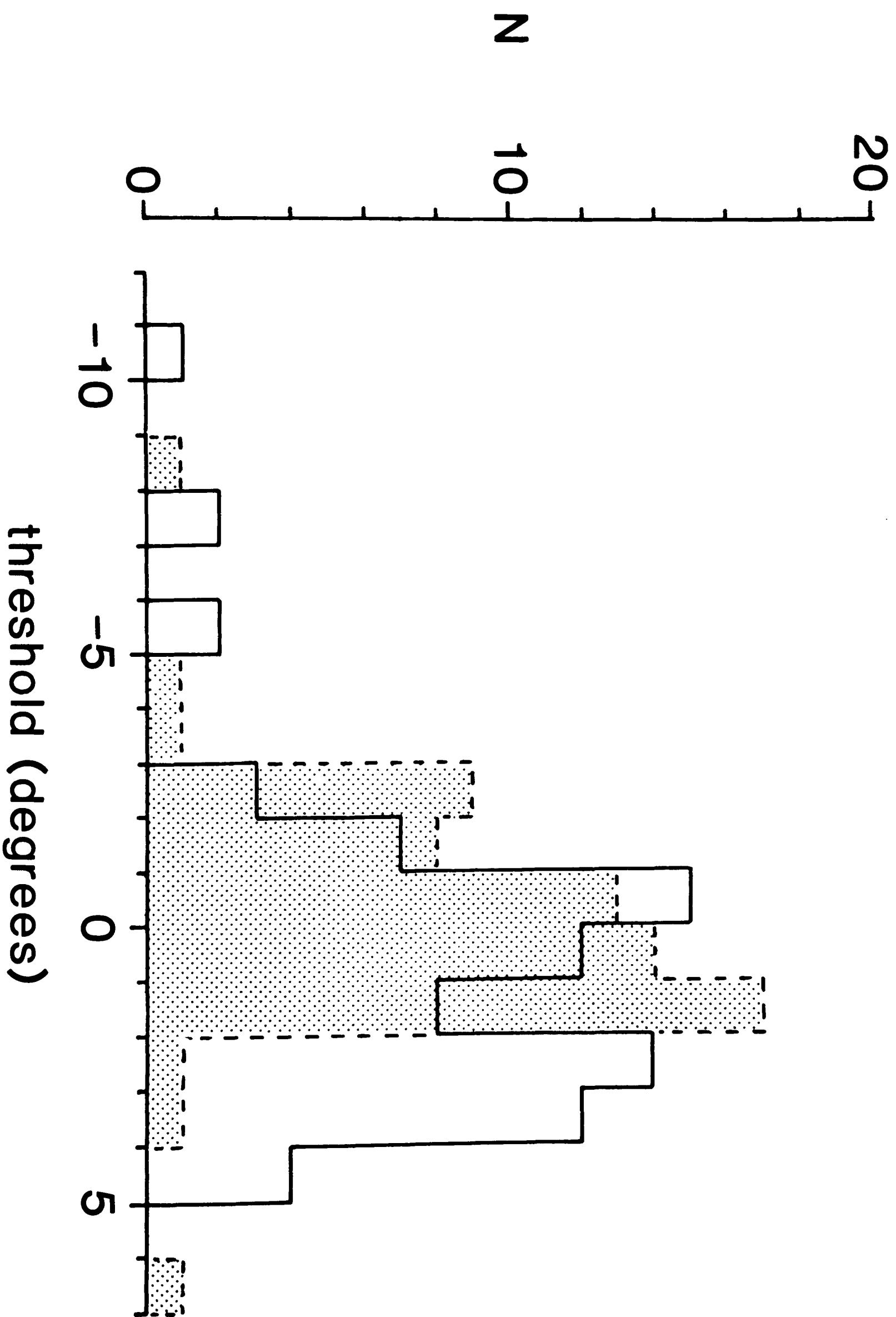


Figure 5.6

Histogram of the number of near response cells (N) with different thresholds (solid line). A positive threshold indicates that the monkey needed to converge for the neurone to begin to fire. Dotted line and stippled histogram shows the data of Mays (1984) for comparison. Thresholds were estimated from dynamic performance (0.1 or 0.2 Hz) in the present experiments, whereas Mays (1984) estimated thresholds from static performance.



methods (Mays's data came from static measurements, rather than low frequency dynamic measurements), this difference is probably not important. The mean threshold for monkey A was -0.62 degrees, which is close to the mean reported by Mays (-0.5 degrees). For monkey H the mean threshold was $+0.85$ degrees.

5.2.4 Distinguishing accommodation cells from vergence cells

In order to distinguish whether the firing of a cell was related to vergence movements or to accommodation changes, the cell firing in normal binocular viewing was compared with its firing during binocular viewing when the accommodative and vergence stimuli were in conflict. As shown in Chapter 4, the tight coupling between vergence and accommodation is partially dissociated in this condition. Fig. 5.7 compares the relationship between accommodation and vergence in normal binocular viewing with that in which the ratio of the accommodation stimulus amplitude to the vergence stimulus amplitude was 0.5 ('X0.5' viewing). The accommodation response in X0.5 viewing was approximately 72% of that in normal binocular viewing ('X1'), whereas the vergence response was nearly unchanged (94% of that in normal binocular viewing). Fig. 5.8 shows the neural response of a cell recorded during the behaviour shown in Fig. 5.7, plotted with vergence on the abscissa in Fig. 5.8A, and against accommodation in Fig. 5.8B. The relationship between accommodation and unit firing was consistent, while the relationship to vergence changed, hence this was classified as an accommodation cell.

The quantitative method used to make this classification consisted of describing the fundamental component of each neural response (f) by

Figure 5.7

Accommodation response (ordinate) in dioptres against vergence response (abscissa) in metre-angles during tracking of a target moving sinusoidally in depth at 0.2 Hz with a 4 dioptre peak-to-peak amplitude and the normal relationship between stimulus vergence and accommodation (X1), and during the conflict task in which the accommodation stimulus amplitude was 2 dioptres peak-to-peak while the vergence stimulus amplitude was 4 metre-angles (X0.5). In both cases accommodation lead vergence (i.e. the loops were traversed in a clockwise sense). Average of data from six cycles in each condition. The accommodation response in the X0.5 condition was 72% of that in the X1 condition.

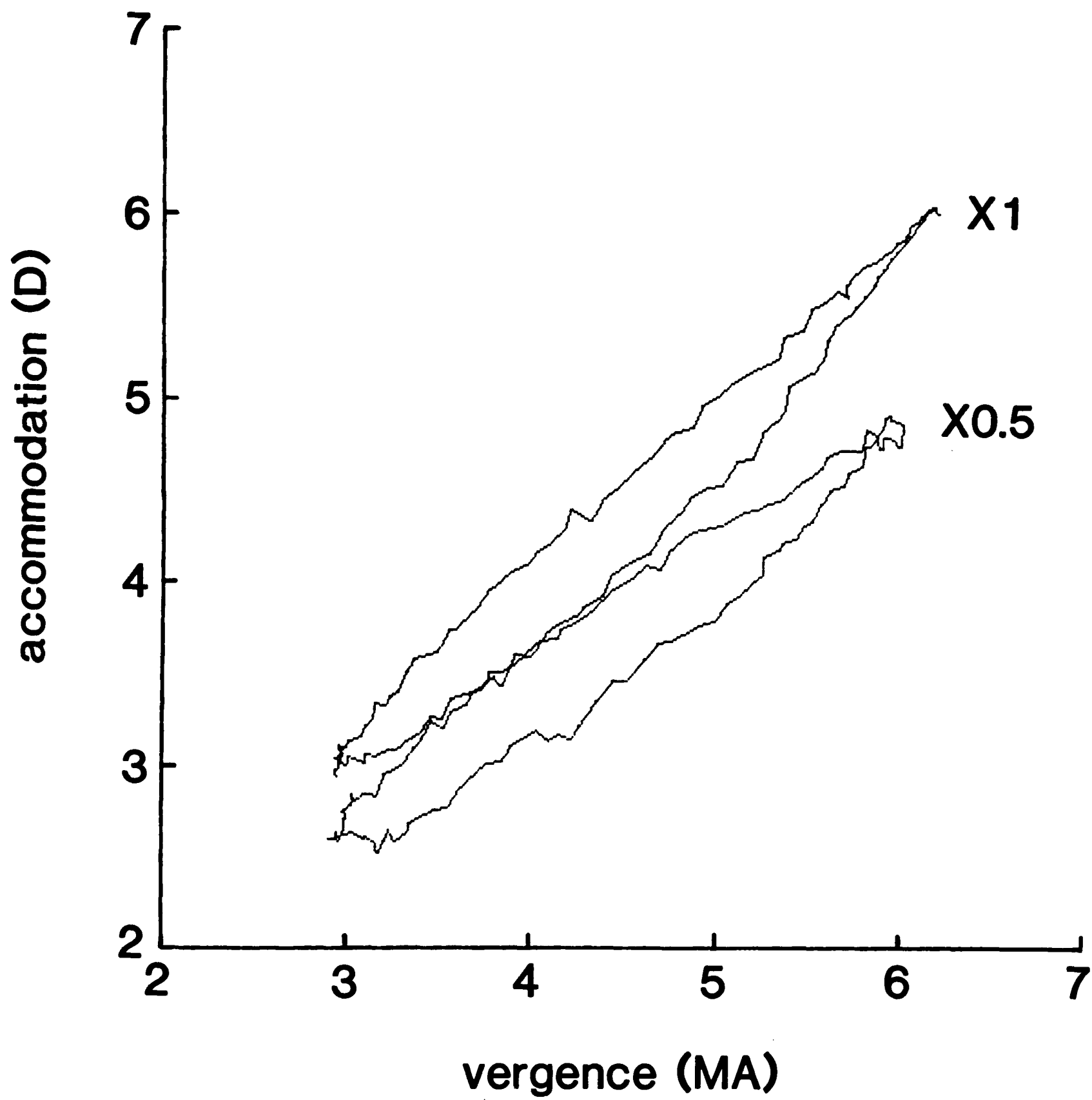
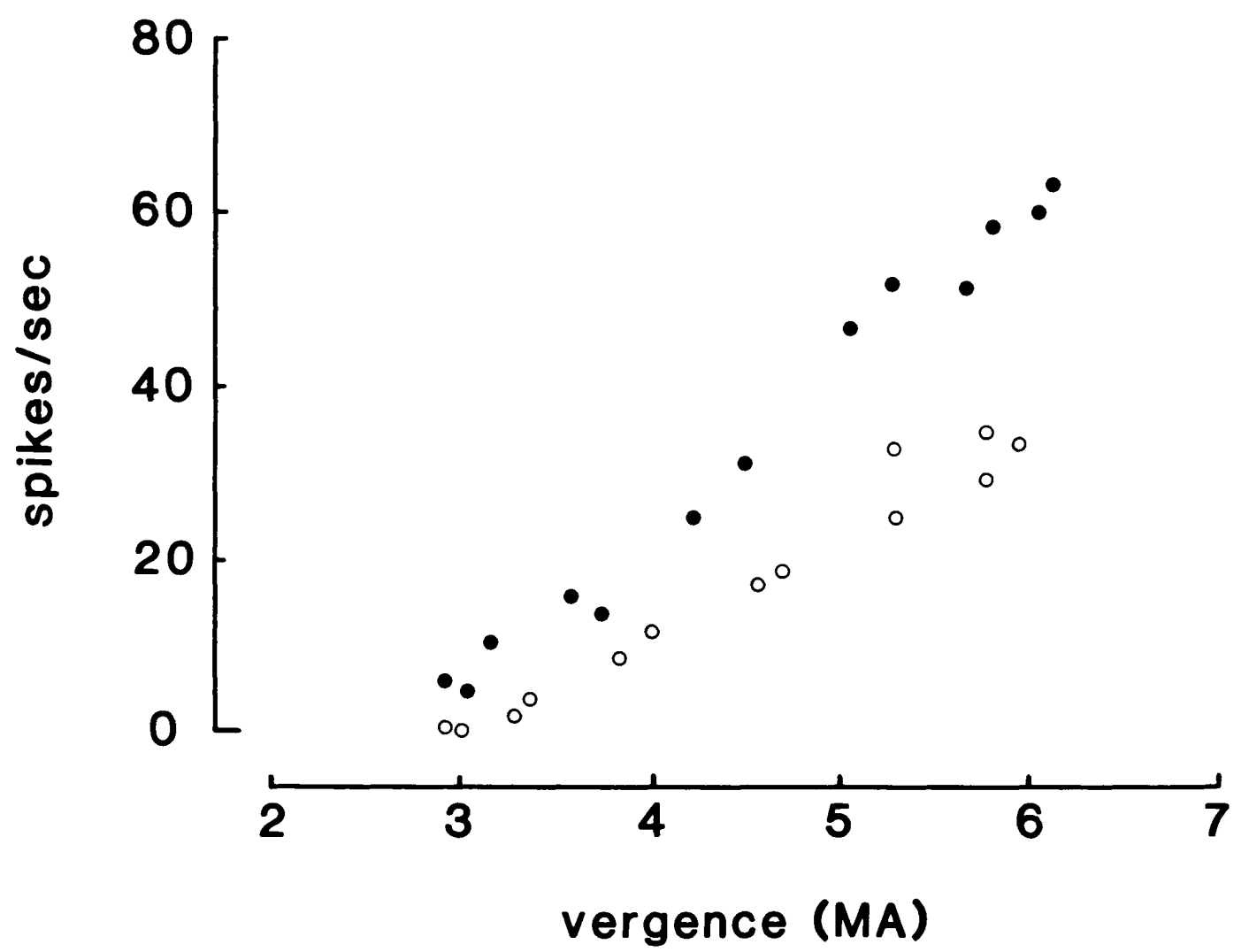


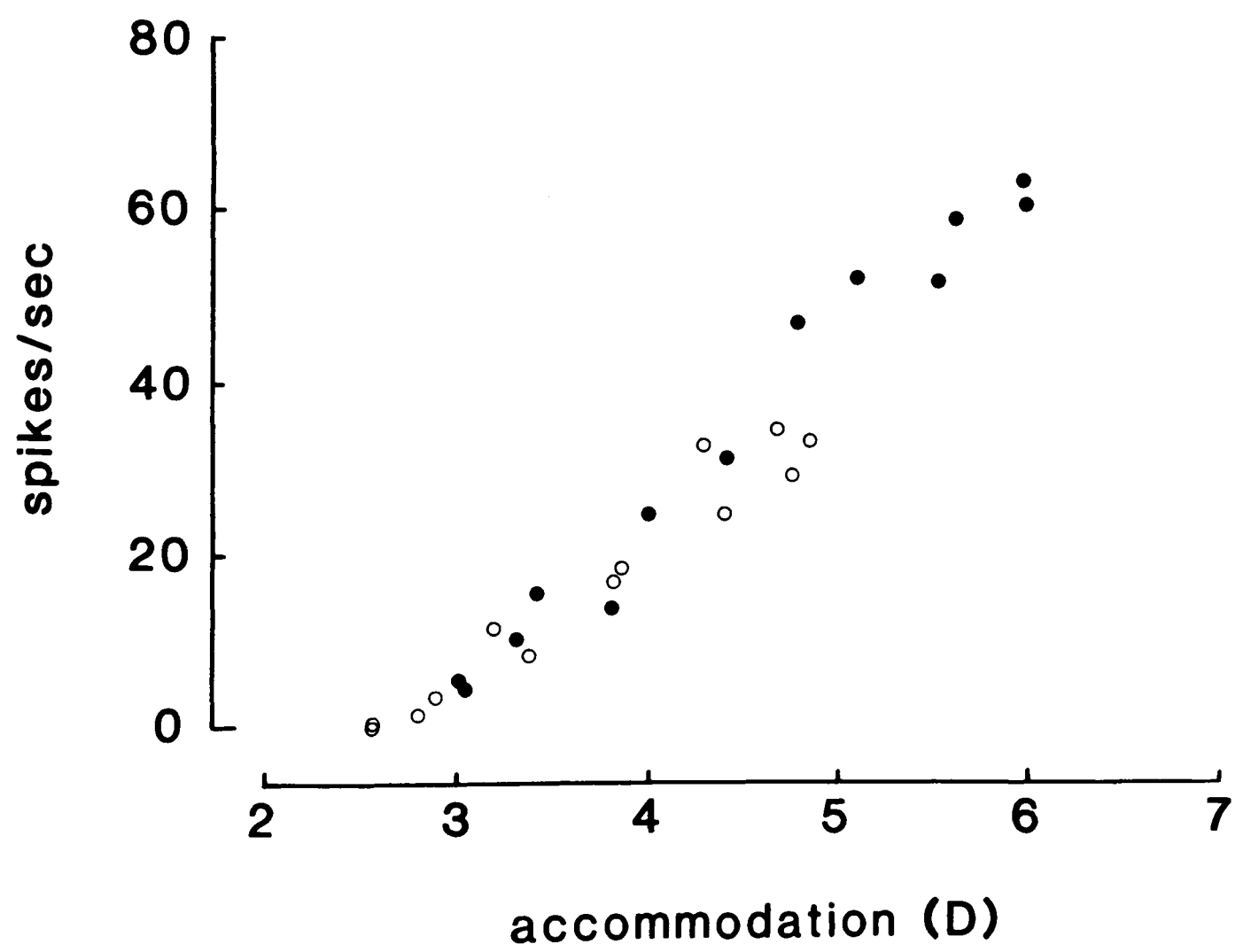
Figure 5.8

A) Firing of a single cell (H127) as a function of vergence (in metre-angles) in normal binocular viewing (filled circles) and in conflict viewing (open circles). B) The same data as a function of accommodation response (in dioptries). The slope of the relationship between accommodation response and cell firing is consistent between the X1 and X0.5 conditions, whereas the slope of the relationship between cell firing and vergence alters between the two conditions. The cell was an identified accommodation cell. These data are taken from the same cycles as in Fig. 5.7. The cell's activity was averaged over six cycles in bins of width 375 msec.

A)



B)



the linear sum of a vergence and an accommodation component:

$$f = k_a A + k_v V,$$

where A and V are the fundamental components of the accommodation and vergence responses. All the quantities in the above equation are complex variables, containing both gain and phase information. The method used for estimating the value of k_a and k_v , and for determining whether either coefficient was significantly different from zero, is described in Appendix 8. Cells with k_v , but not k_a , significantly greater than zero (at the 5% level) were classified as vergence cells, while cells with k_a but not k_v significantly different from zero were classified as accommodation cells.

Table 5.1 shows the characteristics of k_a and k_v estimated for the 36 cells where at least one coefficient was significantly different from zero. Nineteen cells (53%) were vergence cells, 8 cells (22%) were accommodation cells, while 9 cells (25%) had both coefficients significantly different from zero. Although four of these 9 cells had vergence coefficients more than twice as great as their accommodation coefficients, and might be called 'predominantly vergence' cells, no such simple description applies to the remaining 5 cells. One explanation of how cells may have had both k_a and k_v greater than zero is that they might have discharged in relation only to blur-driven or in relation only to disparity-driven responses. For example, a cell related only to disparity-driven responses would have shown an increased vergence gain in X0.5 viewing (compared with normal binocular viewing), since blur-driven components contributed less to the responses. Such a cell would have been described with a positive k_v and a negative k_a , as is the case for cells A051, A053, and H139.

TABLE 5.1

Vergence and accommodation coefficients of all near response cells where at least one coefficient was significantly greater ($p < 0.05$, $\chi^2 > 6.0$) than zero. Cells h049, h059, h072 and h077 were tested at 0.1 Hz; all other cells were tested at 0.2 Hz. Three cells (A055, H082 and H151) had extremely small k_a s associated with large variances. In these cases the method (described in Appendix 8) for providing unbiased estimates of the gain and phase yielded gains less than zero and meaningless phases. This is denoted in the table by a gain of 0.0, and n.s. in the phase column.

CELL TYPE	CELL	K_v			K_a		
		gain	phase	χ^2	gain	phase	χ^2
VERGENCE	a027	24	48.0	6.4	7.5	-15.6	2.0
	a028	39.9	28	25.7	7.6	-179	2.3
	a036	33.8	37	6.1	8.7	178	1.1
	a040	52.9	49	7.0	10	-96.8	1.2
	a044	15.6	-147	8.9	4.9	26	2.1
	a048	33.6	43	25.0	12	1.2	2.8
	a049	43.1	36	50.9	6.6	-8	3.4
	a055	29.4	27	20.3	0.0	n.s.	0.0
	h049	6.2	16	38.9	0.0	120	0.9
	h082	9.03	36	9.3	0.0	n.s.	0.3
	h093	13.7	34	16.5	6	-0.8	1.9
	h097	45.3	44	28.0	7.9	-30	2.8
	h118	15.1	-87	9.6	4.0	140	1.6
	h124	115	26	16.4	1.8	24	1.2
	h128	36.9	52	11.2	22.9	-33	3.5
	h148	4.8	70	8.5	1.3	-150	1.8
	h151	5.9	40	23.2	0.0	n.s.	0.4
	h158	16.5	46	9.8	5.3	4	1.1
	h189	37.0	51	7.1	14.4	-71	3.2
ACCOMMODATION	a024	12.9	-98	5.2	16.2	65	8.0
	a033	3.41	-35	1.5	13.3	37	28.1
	a038	9.7	91	0.8	38.3	2	10.8
	h043	6.0	106	3.9	12.3	-24	7.5
	h072	21.9	106	4.0	120.5	-30	205.3
	h077	4.6	109	2.8	14.3	-159	232.2
	h080	28.9	-69	2.3	43.8	65	14.4
	h127	4.1	-165	0.8	21.4	7	7.5
BOTH	a026	10.7	66	15.4	7.2	-98	7.6
	a029	16.7	87	6.9	28.0	-15	34.6
	a051	62.7	17	78.2	16.3	167	9.5
	a053	88.5	14	35.2	34.5	175	16.3
	a054	22.7	73	9.6	21.6	-22	15.1
	a056	73.3	26	49.0	35.9	-153	33.2
	h059	17.5	-174	46.8	31.2	2	104.6
	h139	43.7	33	77.4	17.7	-155	12.1
	h159	16.0	44	20.3	14.6	14	30.2

In order to examine whether all cells participated equally in blur-driven and in disparity-driven responses, the firing rate of cells was examined in monocular viewing, when only blur-driven responses were present, and in binocular AOL viewing, when only disparity-driven responses were present.

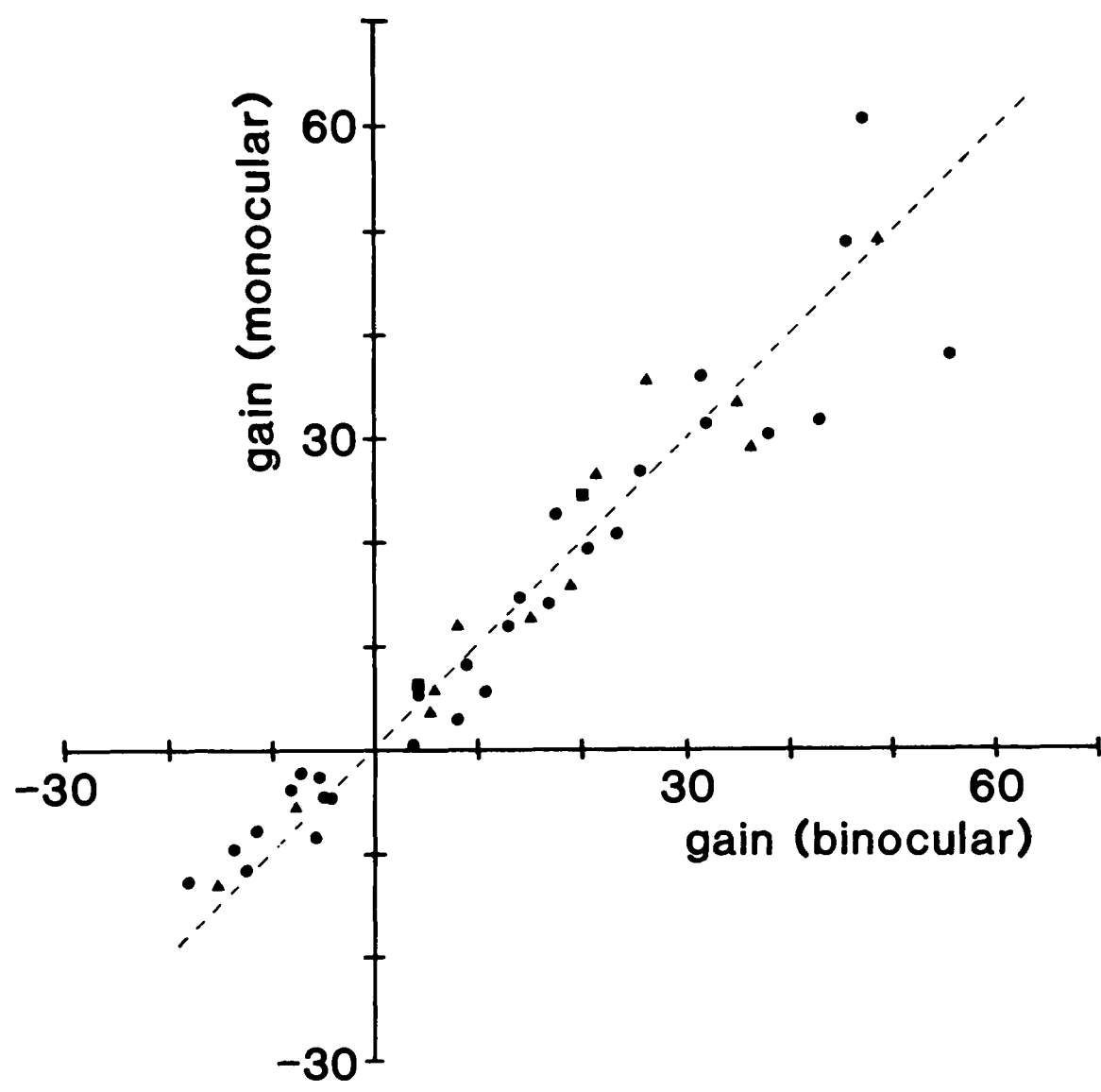
5.2.5 Responses of NR cells in normal binocular viewing, monocular viewing, and binocular viewing with accommodation open-loop.

The responses of 43 cells were compared in normal binocular viewing and monocular viewing, of a target moving towards the right eye with the same amplitude and at the same frequency in each condition. Fig. 5.9A plots the gain in normal binocular viewing against the gain in monocular viewing with the right eye. The squares show the unit firing gain relative to accommodation for identified accommodation cells, triangles show the vergence gain of identified vergence cells, and circles show the vergence gain of cells not falling into either category. Two highly non-linear negatively modulated units are excluded from the figure. Although it can be seen that the gains are usually similar in binocular and monocular viewing, they were not always identical. One identified accommodation cell (H127) had a gain relative to accommodation which was significantly different at the 0.05 level between the two conditions. Excluding accommodation cells, three neurones had vergence gains which differed significantly (at the 0.01 level) in the two tests. Of these cells one was an identified vergence cell (H082) and two (A051 and A054) had both k_a and k_v significantly different from zero. Six other neurones had vergence gains which were significantly different at the 0.05 level, of which two were vergence cells, and one had both k_v and k_a

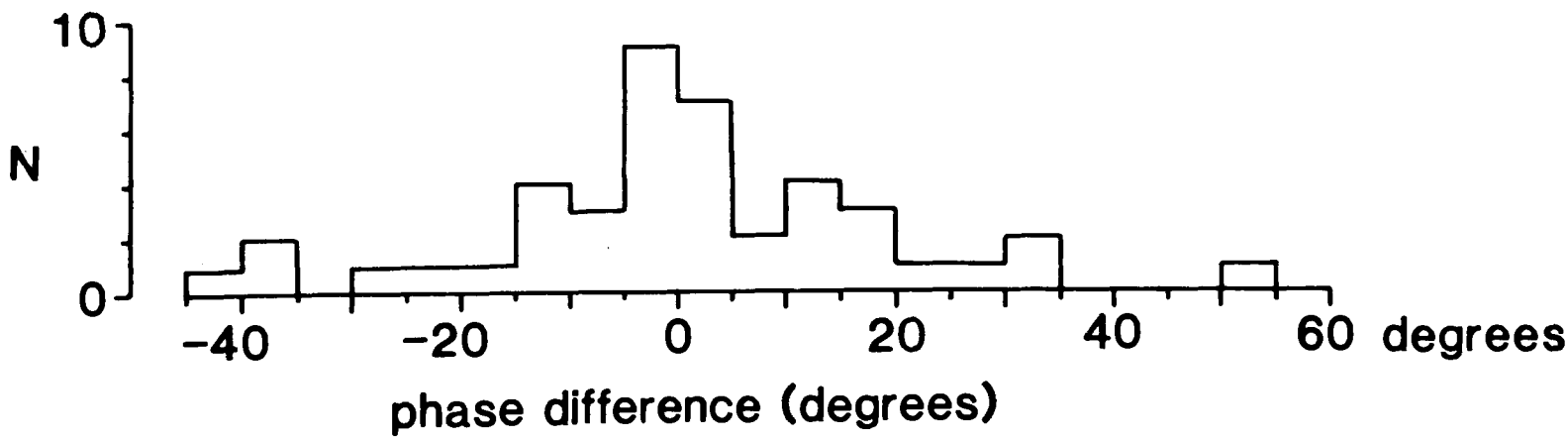
Figure 5.9

A) Sensitivity of 43 near response cells compared in normal binocular viewing (abscissa) and monocular viewing (ordinate). Triangles indicate the vergence gain of identified vergence cells, squares the accommodation gain of identified accommodation cells. Circles show the vergence gain of all other near response cells. Units are commensurate ($\text{spikes} \cdot \text{sec}^{-1} \cdot \text{MA}^{-1}$ for vergence gain; $\text{spikes} \cdot \text{sec}^{-1} \cdot \text{D}^{-1}$ for accommodation gain). B) Histogram of the number of near response cells (N) with various differences in phase between normal and monocular viewing.

A



B



significantly non-zero. Fig. 5.9B shows a histogram of the phase difference between the responses in binocular and in monocular viewing. The mean phase difference was small: -2.3 ± 18.7 degrees S.D.

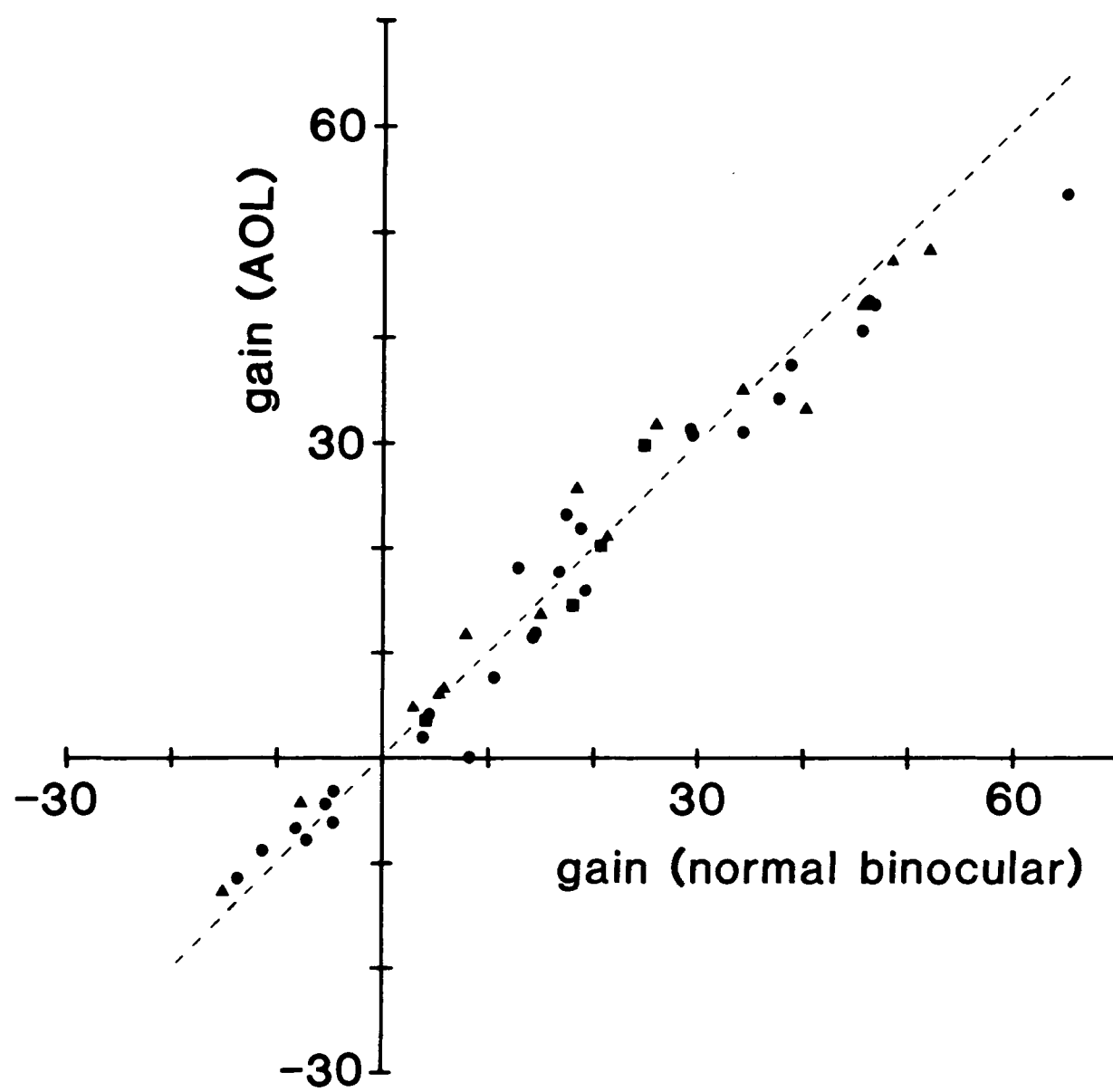
The responses of 46 cells were compared in normal binocular viewing and in binocular AOL viewing. The gain and phase of the response are compared in Fig. 5.10, following the same conventions as Fig. 5.9. No identified accommodation cells had gains relative to accommodation significantly different (at the 0.05 level) in the two conditions. Only three other cells had vergence gains which were significantly different (at the 0.05 level) in the two conditions, two of which (A044 and H148) were identified vergence cells. (For seven cells statistical comparisons were not possible because in one condition or other only one sample was available.) The mean phase difference between the response in normal binocular viewing and in binocular AOL viewing was small: 1.6 ± 12.0 (S.D.) degrees.

Figs. 5.9 and 5.10 show that most NR cells tested fired with similar patterns in normal binocular viewing, monocular viewing, and binocular AOL viewing. It therefore cannot be true that these cells fired only in relation to the disparity-driven (or blur-driven) components of the near response. However, the signals related to the different components of the responses do not always seem to have been equally matched on single NR cells, so that a small number of cells showed significant differences between their firing rate when disparity (or blur) cues alone were present, compared with the responses when both cues were present. Such cells would not have been expected to maintain a constant relationship either to the vergence response or to the

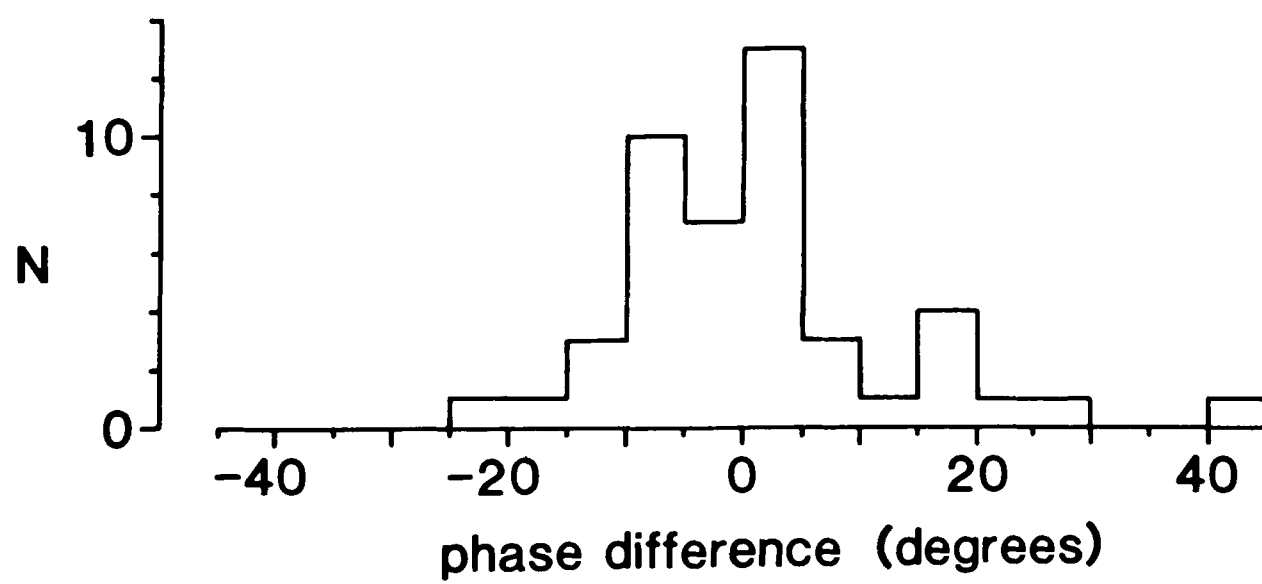
Figure 5.10

A) Vergence gain (in $\text{spikes} \cdot \text{sec}^{-1} \cdot \text{MA}^{-1}$) of 46 near response cells compared in normal binocular viewing (abscissa) and in accommodation-open-loop (AOL) viewing (ordinate). Triangles show identified vergence cells; squares show identified accommodation cells; circles show other near response cells. B) Histogram of the number of near response cells (N) with various differences in phase between normal and AOL binocular viewing.

A



B



accommodation response in normal and in conflict viewing, and therefore would have been described with both k_v and k_a significantly different from zero.

Cells which were more sensitive to to disparity-driven responses than to blur-driven responses (having a larger vergence gain in AOL viewing than in monocular viewing) would be expected to show an increased vergence gain when the accommodation stimulus amplitude was reduced in conflict viewing. This is because in conflict viewing with a small accommodation stimulus amplitude blur-driven components are smaller than in normal binocular viewing, and the disparity-driven components are correspondingly larger. Conversely, if a cell's vergence gain decreased when the accommodation stimulus was reduced, it would suggest that the cell was more sensitive to the blur-driven components of the response than to the disparity-driven components. One would therefore expect that the vergence gain of such cells would be smaller in AOL viewing than in monocular viewing. Data were available from all four test conditions for 5 of the 9 cells which had both k_a and k_v significantly different from zero. Two of these cells (A051 and H139) behaved in conflict viewing as if they were more sensitive to disparity-driven responses than to blur-driven responses. Cell H139 had a vergence gain in monocular viewing significantly smaller (at the 0.05 level) than the vergence gain in binocular AOL viewing, as expected, but for cell A051 the opposite was true. Three cells (A029, A059, and H059) behaved in conflict viewing as if they were more sensitive to blur-driven responses than to disparity-driven responses. All three of these cells had vergence gains in monocular viewing significantly greater (at the 0.05 level) than in binocular AOL viewing, as expected. One of these

cells (H059; shown in Fig. 5.11) behaved as if it was sensitive exclusively to blur-driven responses - comparing Fig. 5.11A with Fig. 5.11B, it can be seen that in X0.5 viewing the magnitude of the vergence response and of the accommodation response are greater than in normal binocular viewing (with a smaller stimulus amplitude), yet the cell is active only in the latter case. In Fig. 5.11B the blur stimulus is in the opposite direction to that in Fig. 5.11A - this cell was active only when a positive blur stimulus was present. This interpretation is also supported by the observation that the cell was silent during binocular AOL viewing of target motion, but did modulate its firing rate during monocular viewing.

5.2.6 Dynamic properties of NR cells

According to Robinson (1981) the relationship between oculomotor motoneurone firing and eye position is approximately that of a first order low-pass filter with a time constant of 0.24 seconds. Such a relationship implies that during tracking of a target moving sinusoidally at a frequency of 0.2 Hz, motoneurone firing should lead eye position by 16.8 degrees. For the 17 positively modulated vergence cells tested at 0.2 Hz, the mean phase lead of their activity (relative to vergence) was 35.0 (± 11.8 S.D.) degrees when the data were averaged without regard to the differences in vergence gain between cells. This phase lead is highly significantly greater than that expected of motoneurones (16.8 degrees). For all 56 positively modulated NR cells tested at 0.2 Hz, the mean phase lead relative to vergence was 31.2 (± 12.2 S.D.) degrees, which is not significantly different from that for identified vergence cells alone.

Figure 5.11

Activity of one cell (H059) in normal binocular viewing (A) and in binocular viewing in which the amplitude of the accommodation stimulus was half that of the vergence stimulus (X0.5 viewing - (B)). The traces shown are: Accommodation stimulus (A_s) and response (A_r); vergence stimulus (V_s) and response (V_r); and the horizontal position of the right eye (R). This cell was exceptional in that its activity seemed to be related only to the blur-driven components of the near response. In B) both the accommodation and vergence responses are larger than in A), but the unit is silent in B). This is presumed to result from the difference in the blur stimuli between A) and B): In B) the blur is in the opposite sense to that in A). The same cell was silent during binocular viewing with accommodation-open-loop, but modulated its firing rate during monocular viewing of target motion in depth.

A) x1

B) x0.5

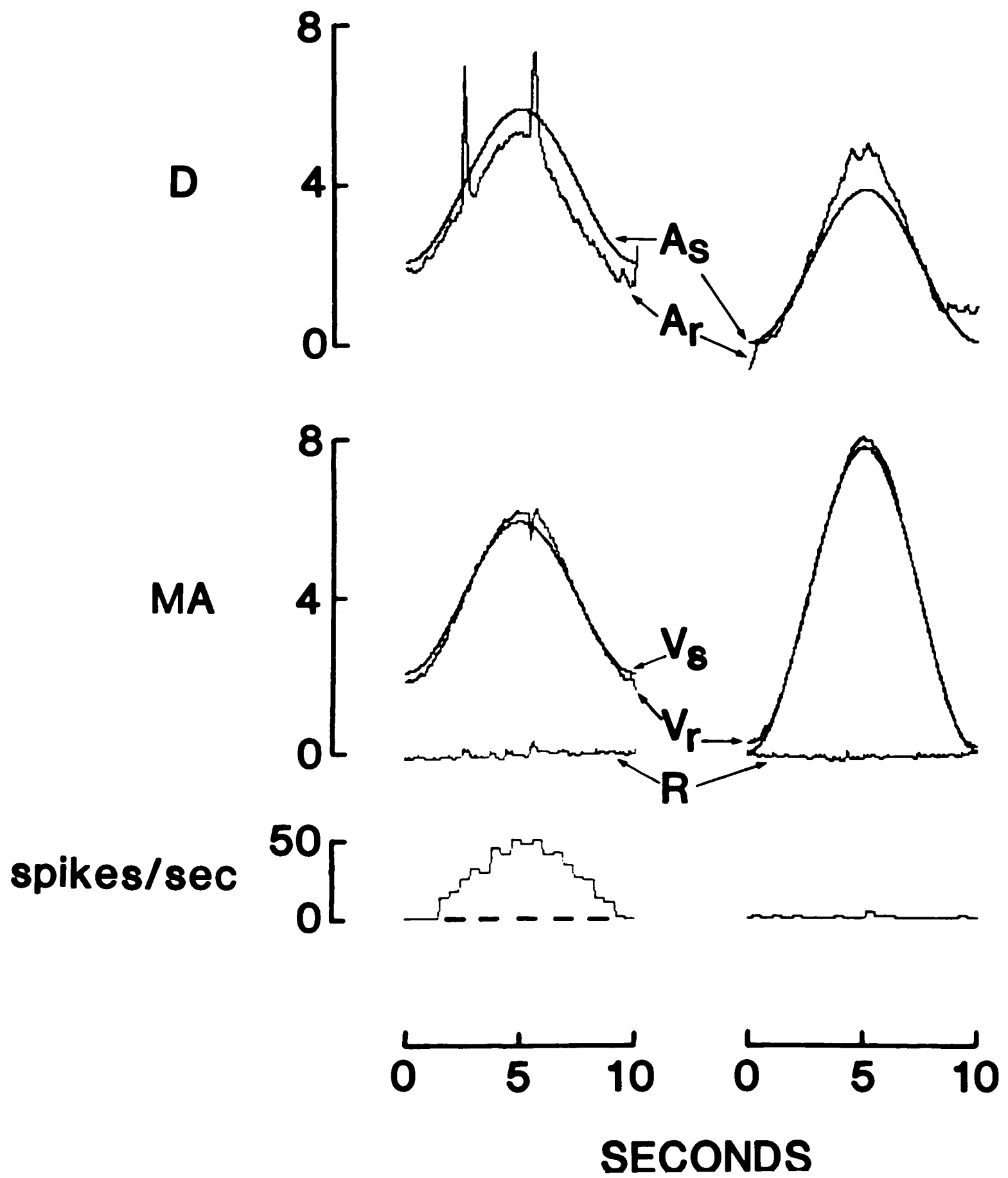


Fig. 5.12 is a Bode plot of the gain and phase (relative to vergence) of five identified vergence cells, four from monkey A and one from monkey H. The dashed line shows the behaviour of Robinson's (1981) archetypal motoneurone. Over the range of frequencies employed, the phase leads of the vergence cells were all much greater than those of the archetypal motoneurone. Only one cell (H082, indicated by open circles in Fig. 5.12) had a relationship to vergence which could accurately be described by a first order function, and the time constant required was 0.55 seconds, much longer than that of the archetypal motoneurone. This time constant lies outside the range of time constants estimated for 10 motoneurons by Skavenski and Robinson (1973), who used sinusoidal head rotation to elicit eye movements. For the activity of the other four neurones to be even crudely approximated by first order transfer functions, much longer time constants than 0.24 seconds were required. It is also interesting that the gains of vergence cells were much greater than those of the archetypal motoneurone.

In step responses the relationship between neurone firing and vergence was not always like that of a first order low-pass filter, either. Although the vergence response was approximately exponential, cell firing frequently showed an overshoot. Fig. 5.13 shows the firing of four typical cells following step changes in target distance, two of which (A and C) show overshoot and two of which (B and D) do not.

Although the sampling rate used in this study for recording neurone firing did not allow accurate determination of the delay between changes in neurone firing and the onset of vergence movements, it was possible

Figure 5.12

Gain and phase (relative to the vergence response) of five positively modulated identified vergence cells as a function of frequency of target motion in depth. The dashed lines show the mean motoneurone data of Robinson (1981). The phase lead of the vergence cells was always greater than that of the archetypal motoneurone and the gain was always higher.

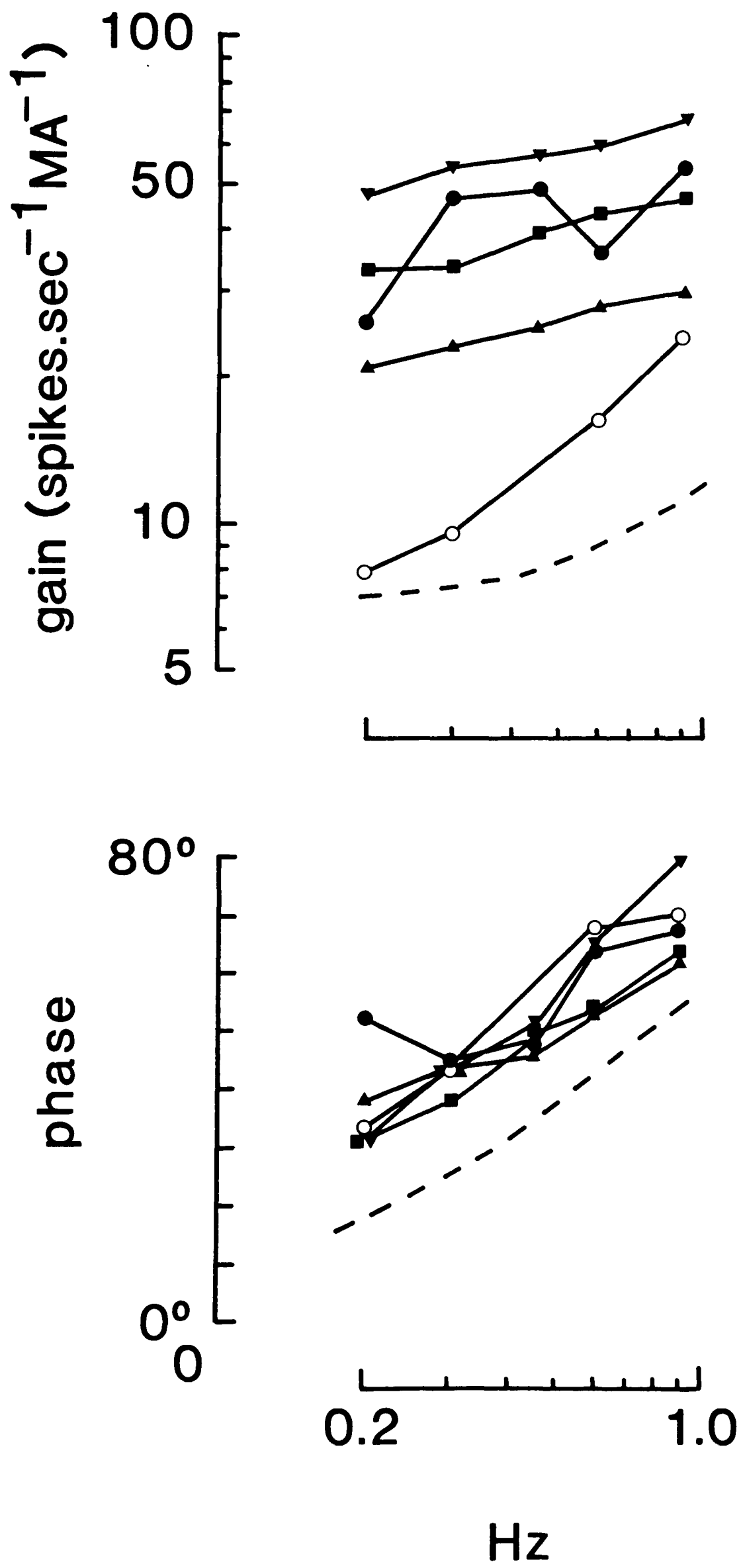
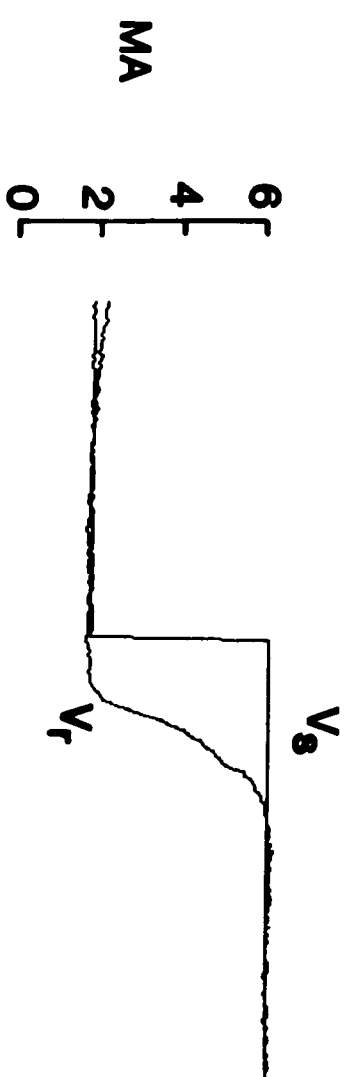


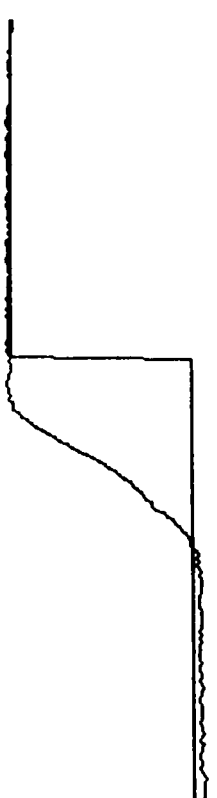
Figure 5.13

Unit firing rate during tracking of a target stepping towards the monkey for four cells (H124 in A); H093 in B); A028 in C) and A051 in D)). Each quadrant of the figure shows the vergence stimulus, V_s , the vergence response, V_r and the unit firing rate, each taken from a single trial. A) - C) show identified vergence cells and D) shows a cell for which both k_a and k_v were significant, but k_v was three times as large as k_a (a 'predominantly vergence' cell). In A) and C) the responses of the units are underdamped while in B) and D) the unit firing rate gradually approaches the value appropriate for the change in vergence response, without overshooting that value.

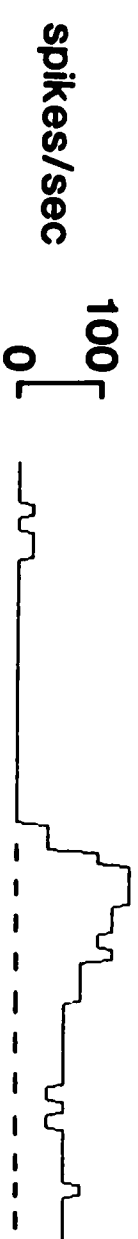
A)



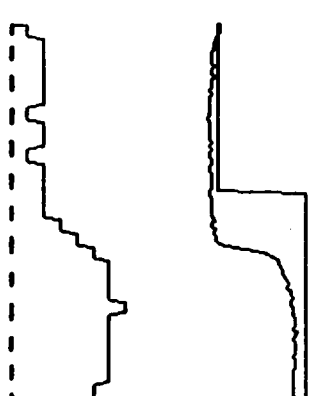
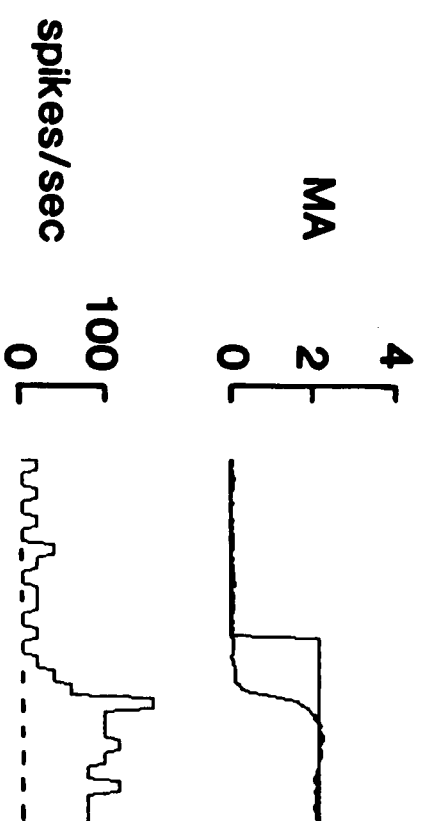
B)



C)



D)



to estimate this delay for a few cells. For one identified accommodation cell the delay between the onset of the cell's change in firing rate and the accommodation onset was 70 ± 11 (S.E.) msec (n=7). For one identified vergence cell the lead time over vergence was 60 ± 11 (S.E.) msec (n=5). For a further six NR cells the mean lead time over vergence was 35 ± 26 (S.D.) msec.

5.2.7 Cells recorded other than NR cells

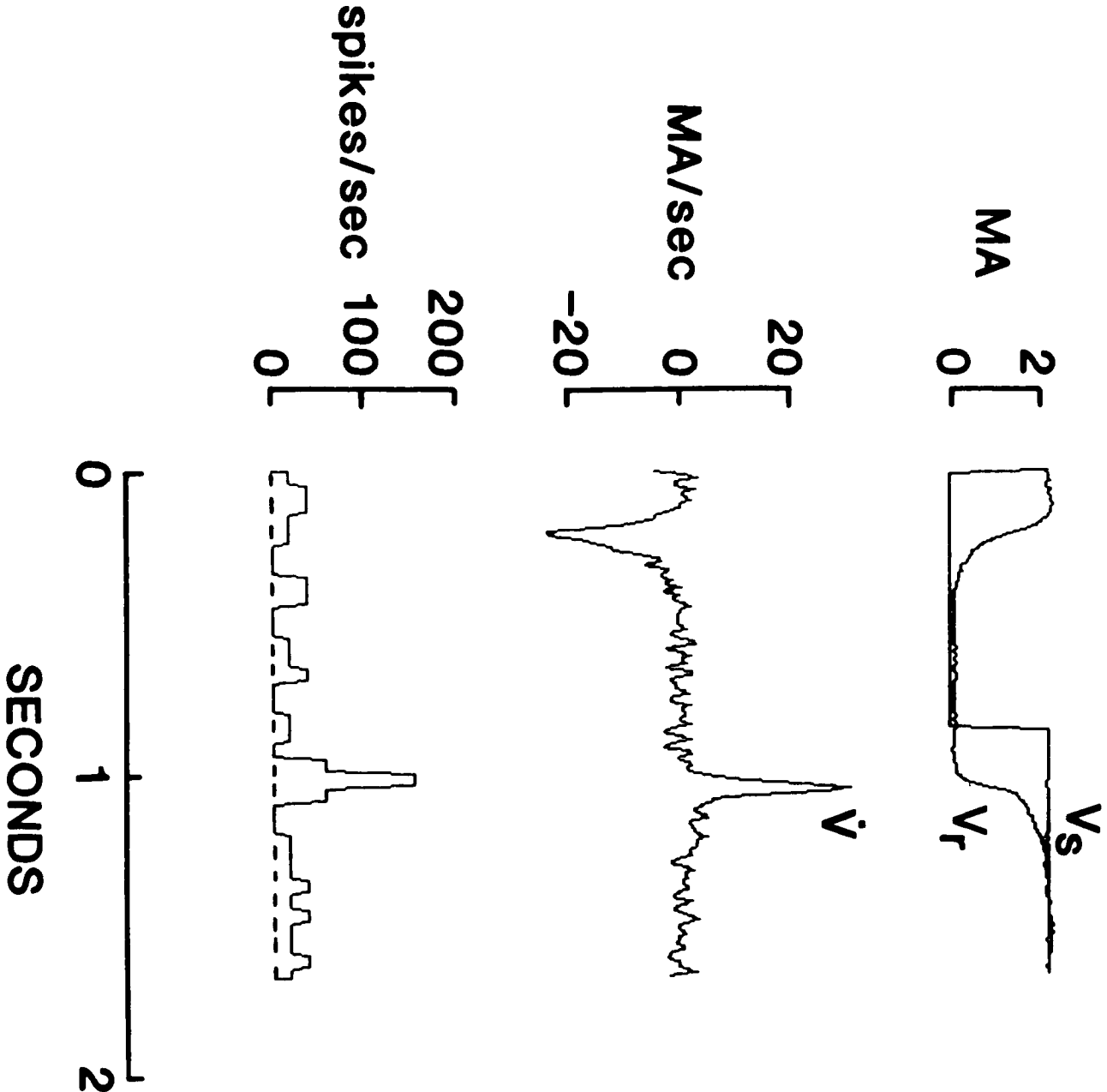
In addition to the NR cells described above, recordings were made from seven cells which discharged for only a small part of a cycle of tracking in depth. The pattern of firing was similar when vergence was achieved by adduction of the left eye to that when the right eye adducted. Of these seven cells, five were active only as the target moved away from the monkey, and two were active only as the target approached the monkey. For 5 of these 7 cells a transient discharge following step changes in the vergence stimulus was observed, but no sustained response related to the change in vergence angle. Two examples of such responses are shown in Fig. 5.14. The time course of the unit firing is similar to that of the vergence velocity, suggesting that these cells may be involved in the dynamic control of the near response. A similar finding has been briefly reported by Mays (1983).

Recordings were also made from 13 oculomotor motoneurones, six of which had a burst-tonic relationship to the upward component of eye movements. Recordings from four of these cells showed that there was a small but consistent decrease in their firing rate during convergence, in the absence of any vertical eye movement. Fig. 5.15A shows the relationship between discharge rate of one motoneurone and vertical eye

Figure 5.14

Examples of two cells which discharged transiently during changes in the vergence response (V_r) following step changes in the vergence stimulus (V_s). The peak firing rate for the cells precedes the peak vergence velocity ($\dot{V}$). A) Shows a cell (A031) active only during increasing convergence; B) Shows a cell (A021) active only during decreasing convergence.

A)



B)

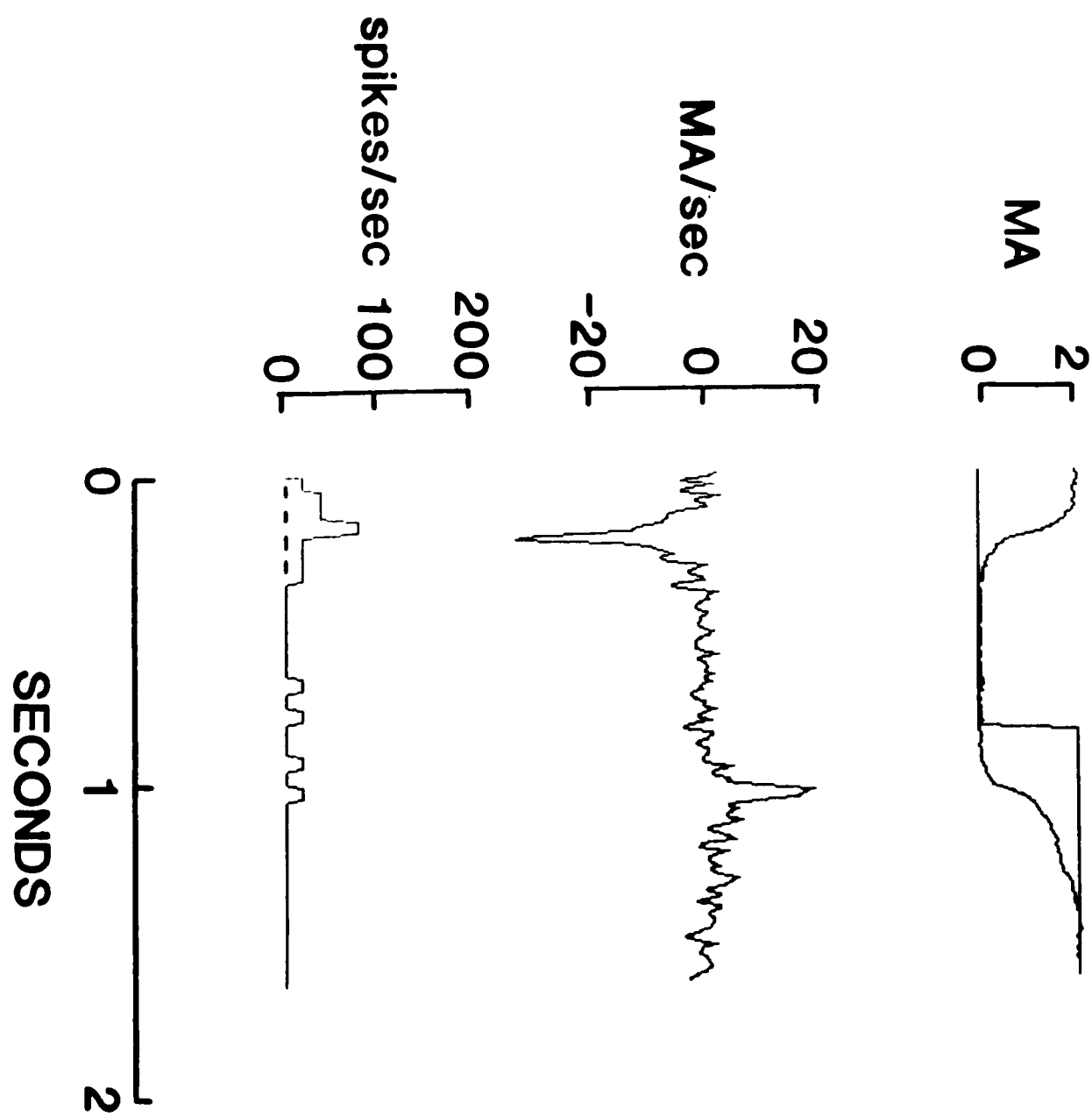
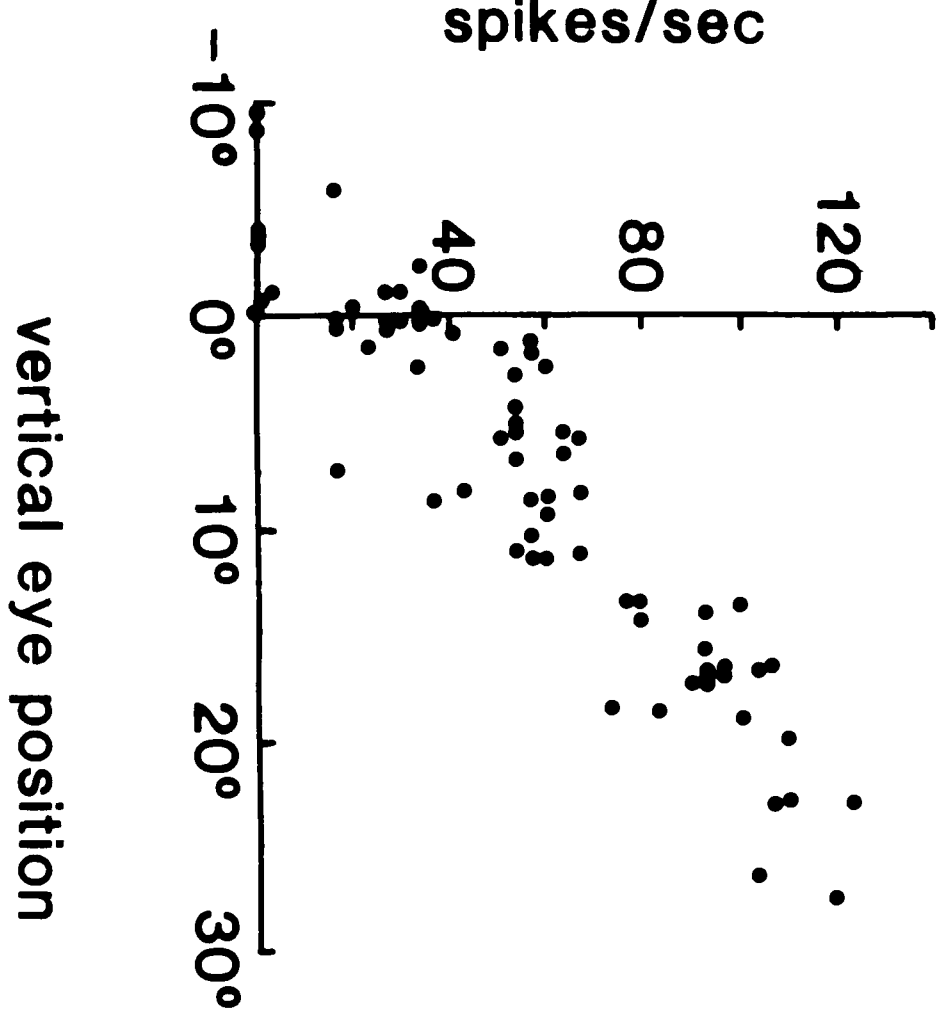


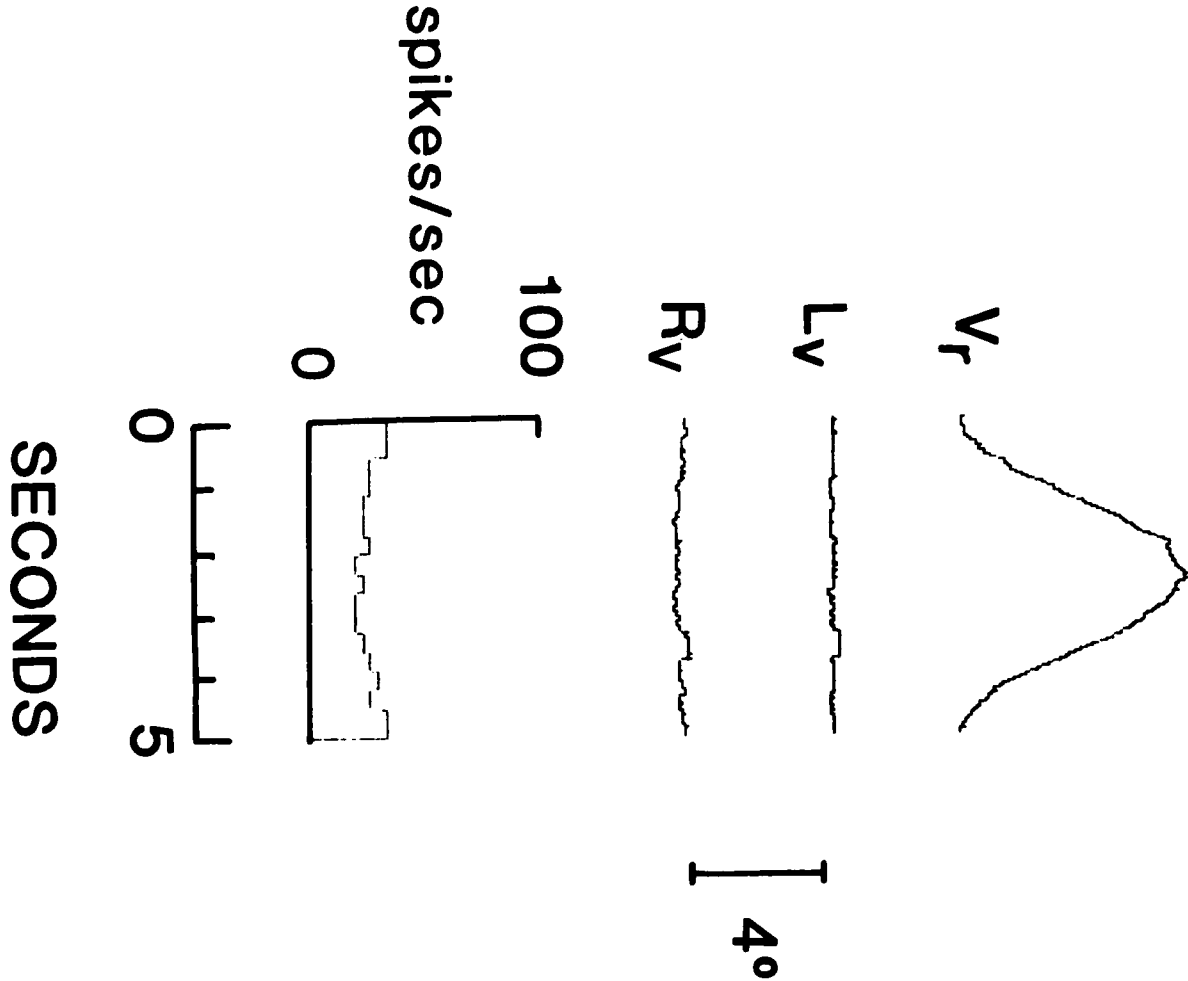
Figure 5.15

A) A plot of unit firing rate (abscissa) against the vertical position of the right eye (ordinate) during spontaneous eye movements for one presumed superior rectus motoneurone (A037). B) The activity of the same cell during changes in the vergence response (V_r), which were not associated with changes in the vertical position of the right eye (R_v) or of the left eye (L_v). The firing rate of the unit shows a small but clear modulation (peak-to-peak amplitude 10.8 spikes/second), while the vertical eye movement is very small (peak-to-peak amplitude less than 0.25 degrees for each eye). Upward eye movements are shown as positive in A) and upwards in B).

A)



B)



position, during spontaneous eye movements. The relationship has a slope of approximately $3.7 \text{ spikes} \cdot \text{sec}^{-1} \cdot \text{degrees}^{-1}$. Fig. 5.15B shows the modulation of the discharge rate of the same cell during convergence. The amplitude of the modulation in cell firing rate ($10.8 \text{ spikes} \cdot \text{sec}^{-1}$ peak-to-peak) is an order of magnitude larger than can be explained by the observed vertical eye movements (less than 0.25 degrees peak-to-peak). This observation could be explained (assuming that the cell is a superior rectus motoneurone) by proposing that the inferior oblique muscle contracts during convergence. Since one action of inferior oblique is to move the direction of gaze upwards, relaxation of the superior rectus would be necessary to maintain the vertical direction of gaze. Contraction of inferior oblique (or relaxation of superior oblique) during convergence has been proposed previously to account for the torsional movements of the eyes during convergence (Allen and Carter, 1967; Enright, 1980) - during asymmetrical convergence extorsion was usually observed in the eye which did not alter its direction of gaze. Extorsion is the primary action of the inferior oblique muscle.

Recordings were also made from 28 cells in the mRN (27 of which were related to arm movements), 36 cells which modulated their firing when the monkey took a fluid reward, and 27 cells with responses to visual stimuli but which were not NR cells. The reward-related cells were not systematically investigated, but it seems likely that they were related to movements of the tongue, lips, or jaw. In some cases it was possible to demonstrate that passive manipulation of the jaw was sufficient to cause the change in firing rate observed when rewards were given. This suggests that these cells were perhaps jaw muscle spindle efferents, in the mesencephalic nucleus for the fifth nerve (Goodwin and

Luschei, 1975).

5.3 Discussion

The findings presented here are in agreement with the recent results of Mays (1984) in describing a concentration of near-response related cells, dorsal and dorso-lateral to the oculomotor nucleus in the monkey. The quantitative properties of the neurones described here (vergence gain and threshold) are similar to those described by Mays. Although Mays did not discuss in detail the dynamic properties of the cells during changes in vergence, none of the figures shown in his report show overshoot of cell firing following step changes in vergence stimulus like that which can be seen in Fig. 5.13. The reason for this difference is unclear.

5.3.1 Are NR cells related to pupil constriction?

None of the tests excluded the possibility that some NR cells were actually related to pupil constriction. Although no NR cells were found to modulate their firing rates during changes in background illumination, not all cells were tested in this way. In any case, this test would not have identified any neurones related only to pupil constriction produced by the near response and not to pupil constriction to light. However, it seems unlikely that a large number of these NR cells were related to pupil size changes. Warwick (1954) showed that 97% of ciliary ganglion cells project to the ciliary muscle, and that only 3% project to the iris musculature, so it seems likely that the great majority of cells in the Edinger-Westphal nucleus are related to accommodation rather than the pupil. Interestingly, in the rabbit, which

lacks accommodation, there are approximately 40 neurones in the Edinger-Westphal nucleus (Johnson and Purves, 1981), whereas in the monkey there are approximately four hundred (Burde and Loewy, 1980).

5.3.2 The relationship of NR cells to accommodation or vergence

Since the components of the near response were tightly coupled in normal viewing and in viewing with blur or disparity cues alone, it was necessary to present conflicting accommodation and vergence stimuli in order to dissociate the responses. Using this technique it was possible to demonstrate that some of the neurones were related to the vergence response, and some were related to the accommodation response, but not all cells could be classified so easily. These more complicated cells may have received inputs related both to blur-driven and disparity-driven components of the responses, if the strength of the two inputs was not well matched.

Almost all of the NR cells described here fired in a similar fashion during normal binocular viewing, monocular viewing, and binocular AOL viewing, showing that they were not related to blur or disparity stimuli alone, but to some part of the motor output of the near response. Quantitative analysis of the responses in normal binocular viewing compared with those in monocular viewing and in binocular AOL viewing revealed significant differences in the relationship between the activity of some cells and the vergence response. These differences support the view that some cells were more sensitive to responses produced by blur (disparity) stimuli than to responses produced by disparity (blur) stimuli. Referring to Fig. 1.1 of Chapter 1, the NR cells recorded carried signals corresponding to

those expected of points Y_a or Y_v in the diagram, but the signals at the summing points to the left of Y_a and Y_v were not always equally matched on a single cell. (One cell, an extreme example, responded as if it was related only to the blur-driven component of the responses, not firing at all in relation to responses produced by disparity stimuli - corresponding to point X_a in Fig. 1.1.) If this interpretation is correct, it suggests that the signals related to the blur-driven components of the near response and the disparity-driven components may be combined for the first time at the level of these NR cells. This suggests that there may not be a cortical area where the components of the near response are co-ordinated, contrary to widely held beliefs (e.g. Duke-Elder and Wybar, 1961). The areas of the brain from which the midbrain NR cells may receive inputs are discussed in Chapter 7.

5.3.3 Do vergence cells selectively activate motoneurones with tonic properties?

The vergence cells recorded had phase leads much larger than those previously reported for motoneurones. This is certainly consistent with the idea that these neurones (directly or indirectly) activate the fibres in the orbital layer of the medial rectus muscle which are presumed to be tonic (Buettner-Ennever and Akert, 1981). Buettner-Ennever (1981) and Buettner-Ennever and Akert (1981) have shown that these orbital muscle fibres are innervated by small motoneurones (the 'C' subgroup) lying on the dorso-medial border of the OMN - outside the classical medial rectus subdivision (Warwick, 1953). Buettner-Ennever suggests that neurones in subgroup 'C' could play an important role in convergence. (The existence of the 'C' subgroup of medial rectus

motoneurones has been confirmed by other workers - Porter et al. 1983; Spencer and Porter, 1981). Mays and Porter (1984) have recently shown that the vergence and version sensitivities of medial^{rectus} and abducens neurones are usually not well-matched, calling into question the view that all motoneurones participate in the same way in generating conjugate and vergence movements (Robinson, 1981). A functional subdivision of medial rectus motoneurones (those with longer time constants subserving slow eye movements such as vergence) is consistent with all of these findings.

The two NR cells which were recorded simultaneously with motoneurones activated during upward eye movements could have been in Buettner-Ennever's 'C' subgroup of medial rectus motoneurones. However, there is no direct physiological evidence that cells in this subdivision are exclusively related to vergence eye movements. Furthermore all motoneurones tested by Keller and Robinson (1972) and Keller (1973), and nearly all motoneurones tested by Mays and Porter (1984), were found to discharge in relation both to vergence and versional movements. In any case, it is unlikely that the majority of NR cells were such motoneurones, because there were many tracks on which we either failed to encounter the OMN at all, or on which we recorded NR neurones at least 0.5 mm above the first classic motoneurones.

CHAPTER SIX

EFFECTS OF MICROSTIMULATION IN THE MIDBRAIN AND IN THE OCCIPITO-TEMPORAL
CORTEX

6.1 Introduction

Two investigations were performed using microstimulation in monkey H. Regions in the midbrain where near response cells had been recorded were stimulated to examine whether or not it was possible to evoke accommodation and/or vergence responses, as one would expect if the near response (NR) cells recorded there were truly motor in nature. The second experiment involved stimulation over an area of the occipital and temporal cortex on each side of the superior temporal sulcus (STS) in an attempt to confirm in an awake monkey the result of Jampel (1960). Jampel claimed that stimulation in areas 19 and 22 of lightly anaesthetized monkeys produced all three components of the near response, both separately and in conjunction. However, the effects he observed were variable and often not repeatable. Since eye movements were not recorded, and stimulation frequently produced changes in the direction of gaze, it is difficult to be sure that his observations of changes in vergence were accurate. Jampel did not report how deep into the cortex his electrodes were placed nor what currents were used for stimulation. Consequently, the sites activated by stimulation may have been some distance away from the points on the cortical surface where the electrodes were inserted. That he reported effective sites on both sides of the Superior Temporal Sulcus (cortical areas with quite different functions) suggests that his localization of effective

stimulation sites was indeed inaccurate. Finally, it is known that anaesthetics have many effects upon eye movements, abolishing smooth pursuit movements (Rashbass, 1961), and reducing the speed of vergence movements (Westheimer and Rashbass, 1961). In the monkey Robinson and Fuchs (1969) showed that electrical stimulation in the frontal eye fields produced only saccades in awake animals, but following the administration of sodium pentobarbital stimulation produced a number of slow eye movements, including apparent vergence movements. In view of these difficulties with Jampel's study, it seemed worth re-examining the effects of stimulation in the occipital-temporal cortex on accommodation and vergence in the awake monkey.

The apparatus and methods were described in detail in Chapter 2. Briefly, tungsten microelectrodes were used to stimulate cells by passing trains of current pulses. The current pulses used were bipolar - each pulse consisted of a cathodal pulse of 0.5 msec duration followed by a small anodal current (one tenth of the cathodal current for 5 msec) so that there was no net flow of charge from the electrode. The 0.5 msec pulse duration was selected since Gustaffson and Jankowska (1976) showed that such pulses could excite cell bodies with currents (0.15 microamps) as low as those reported by others (Jankowska and Roberts, 1972; Jankowska and Smith, 1973; Stoney et al., 1969) for activation of myelinated fibres. The pulses were repeated at frequencies of 300 or 400 Hz. Since repetitive stimulation enhances transsynaptic activation of cells at a distance from a stimulating electrode (Asanuma et al., 1976; Jankowska et al., 1975) this maximized the chances of evoking responses by stimulation.

In both experiments reported below, the monkey fixated monocularly during stimulation, eliminating disparity feedback, which could have masked effects of stimulation on vergence movements. In order to minimize the effects of blur feedback on accommodation responses, the surround of the fixation target was not illuminated during stimulation. Sites where vergence responses were evoked were also stimulated while the animal sat in darkness.

6.2 Results

6.2.1 Microstimulation in the midbrain

Microstimulation was performed on six penetrations which passed into the area of the midbrain dorsal and dorso-lateral to the oculomotor nucleus, where the NR cells discussed in Chapter 5 were recorded. Starting from a position approximately 3 mm dorsal to the OMN, sites were stimulated at intervals of 0.25 mm. Initially the cathodal current pulses had a magnitude of 35 or 50 microamps. When responses were evoked by stimulation, smaller currents were used in order to identify the current threshold for the response. This threshold was determined separately for vergence, accommodation, and pupil responses (the latter were measured by using the optometer as a pupillometer, as described in Appendix 4).

Accommodation and pupil responses were evoked on four of the six penetrations, and although suprathreshold stimulation usually produced both accommodation and pupil constriction, the threshold currents for pupil constriction were often smaller than those for accommodation. Accommodation responses were evoked using currents as small as 3

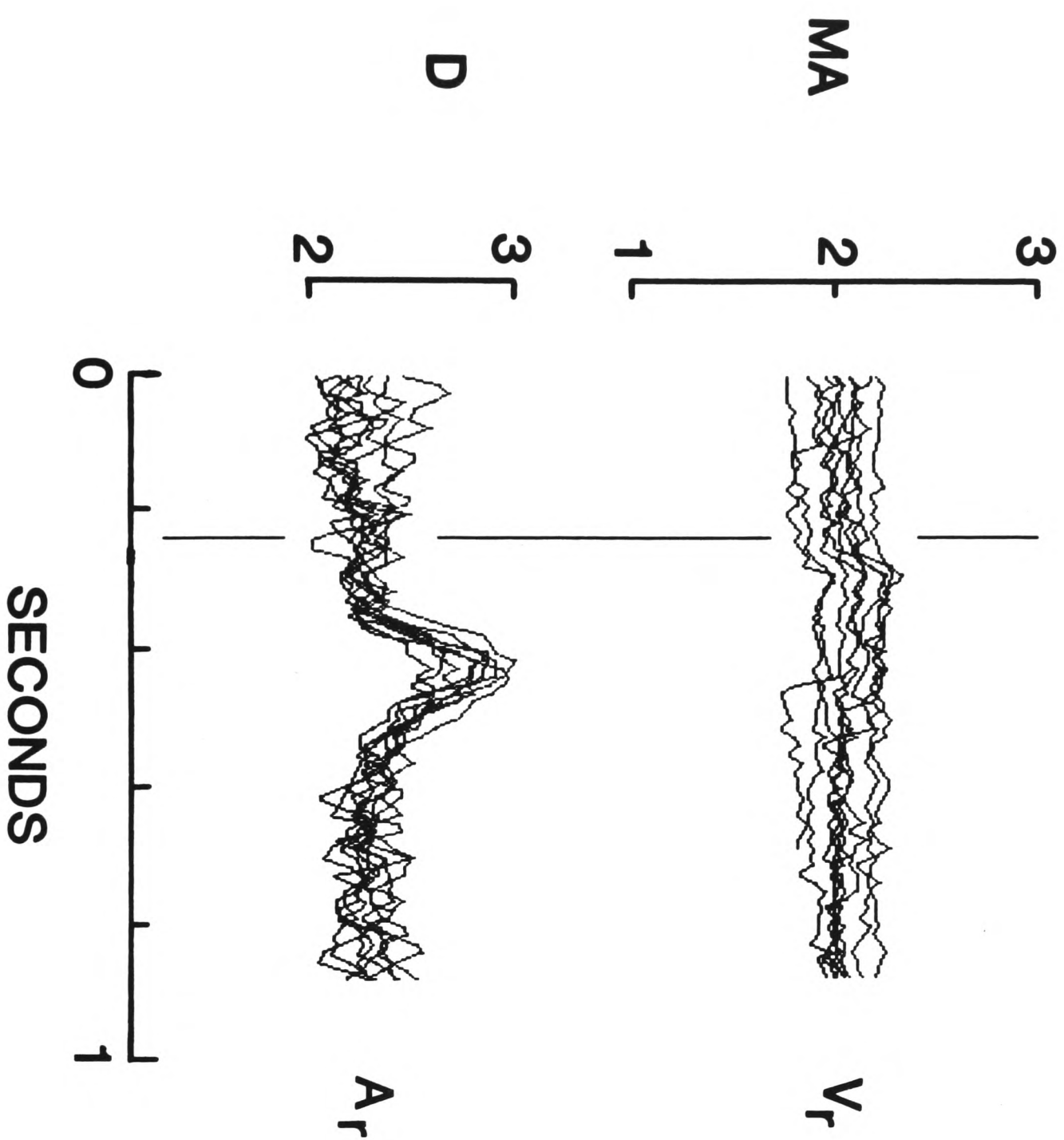
microamps, while the lowest current effective in producing pupil constriction was 2 microamps. The effects were consistent and reproducible, as can be seen from Fig. 6.1A (lower part), which shows eight responses of accommodation to stimulation (with 20 microamp current pulses) at one site. Fig. 6.1B shows the average of these 8 responses, from which it can be seen that there was a considerable delay between the stimulus and the onset of the accommodation response. For all effective sites stimulated the mean latency of the accommodation response was 119 ± 18 (S.D) msec; the shortest latency ever observed was 75 msec. Fig. 6.1A shows that a small vergence response was sometimes evoked by stimulation at this site. From the average response in Fig. 6.1B it is clear that this had a much shorter latency than the accommodation response.

Stringent criteria were adopted for accepting an evoked response as 'convergence' - both eyes had to move medially at short latency (50 msec or less). Clear convergence responses were evoked on only three penetrations. Fig. 6.2 (A and B) illustrates one such response (stimulus current 20 microamps), which is compared with a response elicited on a separate track which was not classified as a true convergence response (Fig. 6.2C; stimulus current 25 microamps). Note that in Fig. 6.2C the left eye did not begin to move until 200 msec after stimulation, suggesting that this was a visual tracking response. The movement could have been the result of stimulation to the cells of the medial rectus subdivision of the right OMN. This would have produced medial movement of the right eye at short latency, so that a tracking movement was necessary to maintain fixation. Kawano and Miles (1983) have shown that ocular following responses in the monkey occur with latencies as short

Figure 6.1

Effects of microstimulation in the midbrain dorsal to the oculomotor nucleus. The stimulus consisted of a train (frequency 400 Hz, duration 40 msec) of 0.5 msec, 20 microamp current pulses (electrode negative). The narrow vertical lines indicate the time at which stimulation began. A) The effects of 8 separate trials at the same site on accommodation (A_r) and vergence (V_r). B) The average of the 8 responses shown in A). The long latency of the accommodation responses (120 msec) to electrical stimulation can clearly be seen.

A)



B)

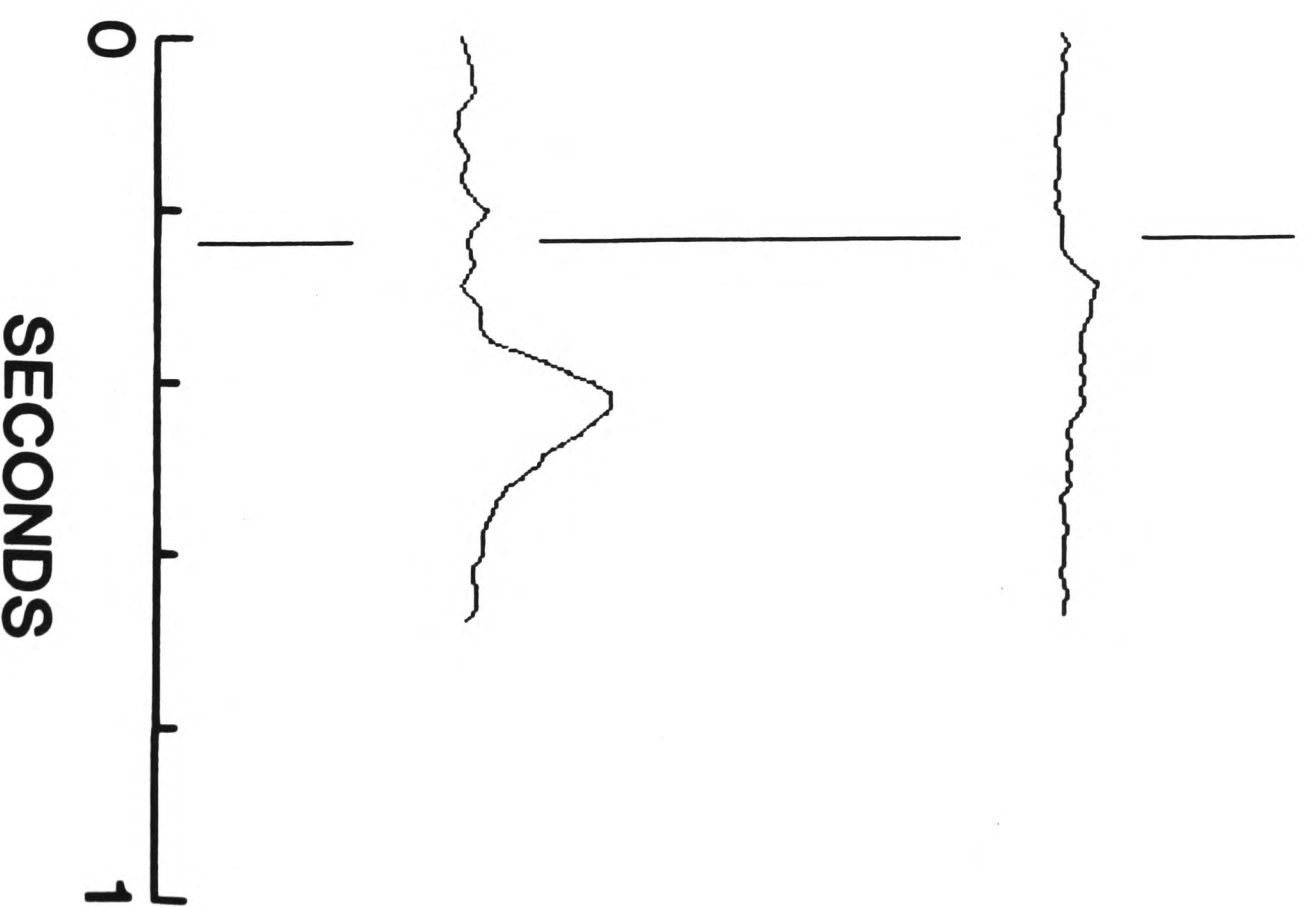
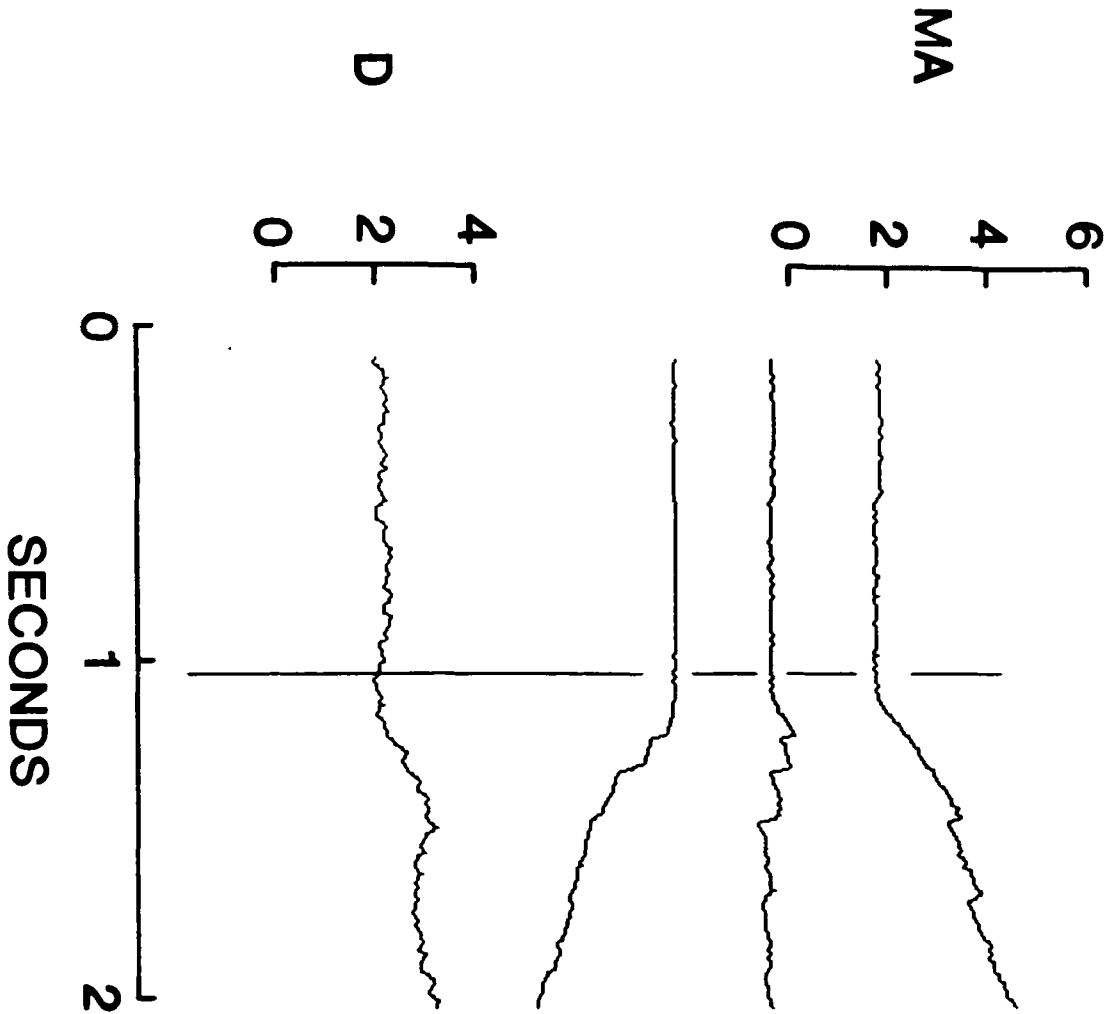


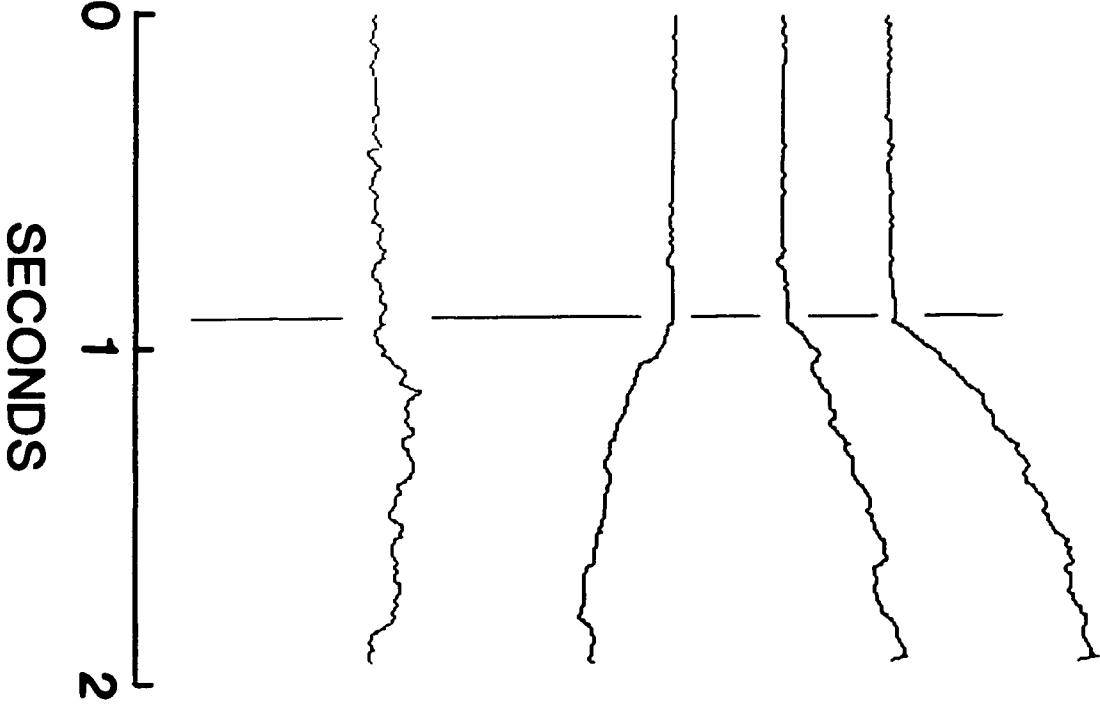
Figure 6.2

Effects of electrical stimulation dorsal to the oculomotor nucleus upon vergence (V_r), the horizontal positions of the right (R) and left (L) eyes, and accommodation (A_r). Rightward eye movements are shown as downward. The narrow vertical lines indicate the times at which the stimulation began. A) Shows a true convergence response in which both the right and left eyes move medially with a short latency. B) Shows that stimulation at the same site as in A) while the animal sat in darkness produced a symmetrical vergence movement. In A) and B) the stimulus consisted of trains (frequency 400 Hz, duration 1 second) of 20 microamps current pulses each lasting 0.5 msec (electrode negative). C) Shows a response to stimulation at a different site, not classified as true convergence. The stimulus consisted of a train (frequency 400 Hz, duration 0.5 seconds) of 25 microamp, 0.5 msec current pulses (electrode negative). Note that the left eye did not move until approximately 200 msec after the stimulus started. For discussion see text.

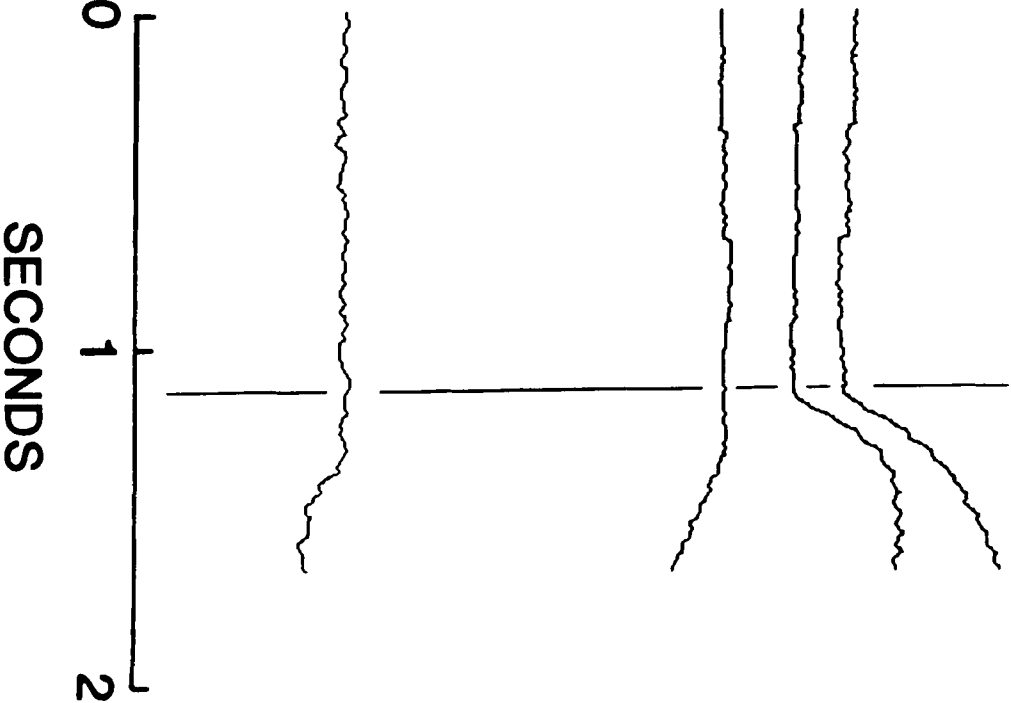
A) Right eye viewing



B) Darkness



C) Right eye viewing



as 50 msec. In the case of the true convergence response shown in Fig. 6.2A, both eyes moved medially with a latency shorter than 50 msec. Fig. 6.2B shows that at this site stimulation while the animal sat in darkness produced a symmetrical vergence movement.

The current necessary to evoke vergence responses was typically 20-35 microamps, although currents as low as 7.5 microamps were sometimes effective. The mean latency of the vergence responses was 30 ± 14 (S.D.) msec with a minimum latency of 13 msec.

On three of the penetrations where microstimulation was performed, extracellular unit recordings were also made. On two penetrations NR cells were isolated, and stimulation at one of these sites produced accommodation and pupil responses, but not vergence responses. On the third penetration, recording at a site where accommodation and pupil responses had been produced revealed that the electrode was in the OMN. It is possible that stimulation here excited fibres from the Edinger-Westphal nucleus passing around the OMN (see Burde and Loewy (1980) for a description of the course taken by the fibres from the Edinger-Westphal nucleus). Neither divergence nor negative accommodation were ever observed following stimulation, although as the monkey was fixating a target at a distance of 50 cm, such responses would certainly have been possible.

6.2.2 Stimulation in the occipito-temporal cortex

Since the stimulation of the cerebral cortex was performed without removing the dura, it was difficult to assess during the experiment in which part of the cortex these penetrations were made. In order to

estimate their position, five penetrations were made through the posterior part of the area covered by the chronically implanted chamber. Extracellular unit recordings were made on these penetrations, while the animal fixated a small L.E.D. and simple visual stimuli (moving or stationary white bars, with various orientations) were presented. The responses recorded fell into two categories. On two penetrations, cells had small receptive fields (less than 1 degree in diameter) centred within 1 degree of the fovea and within 0.5 degrees of the vertical meridian. These cells were presumed to be in visual area V1 close to the ventral limit of the lunate sulcus. On three penetrations, cells were found with much larger receptive fields (greater than 4 degrees in diameter) centred from 4 - 7 degrees from the fovea, within 2.5 degrees of the vertical meridian. These cells were presumed to be in area V2, in the posterior bank of the lunate sulcus. From the positions of these tracks it was possible to estimate the location of the lunate sulcus, and from the position of Jampel's (1960) area relative to the lunate sulcus in his drawings, an estimate was made of the position of this area relative to the the chamber. Fifty-one penetrations were made covering every 1.5 mm in a grid 7.5 mm square, centred on the estimated centre of Jampel's area.

A number of the penetrations used for this experiment appeared clearly in histological sections of monkey H's brain. These sections had been cut in a plane tilted 26 degrees back from the coronal plane (parallel to the penetrations in the midbrain region). The position of penetrations were measured relative to the position of the STS (on the same section) and these measurements were used to determine the sites on the cortical surface where each penetration began. These sites lay in an

area between 2.5 mm posterior to, and 1.5 mm anterior to the STS, and between 2 mm medial to, and 4 mm lateral to, the posterior limit of the lateral sulcus. It is clear that this area included a large part of the area where Jampel (1960) claimed that electrical stimulation evoked vergence, accommodation, and pupil constriction.

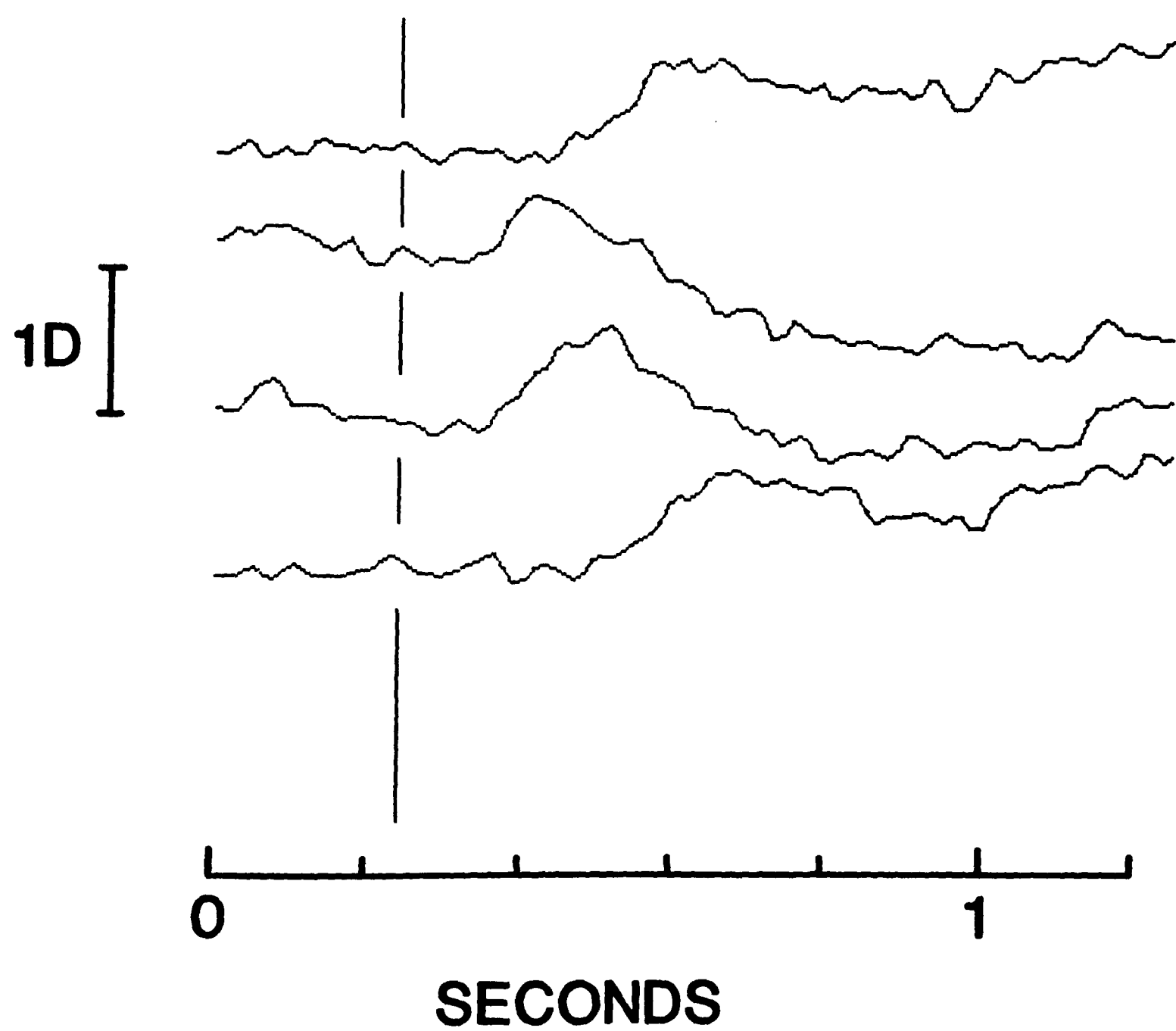
During the first 13 penetrations, 35 microamp current pulses of 0.5 msec duration were used, repeated at 300 Hz. Stimuli were delivered every 0.25 mm from the surface of the cortex to a depth of 6 - 7 mm. As no accommodation or vergence responses were evoked using these parameters, on the subsequent 38 penetrations 330 microamp stimuli were applied every 0.5 mm. Accommodation and vergence (but not pupil area) were routinely recorded during stimulation.

On only one penetration were any components of the near response evoked by microstimulation. However, upon withdrawing the electrode it was found that it was severely damaged, with a 30 degree bend in the shaft several millimetres back from the tip, and the glass coating cracked so that the insulation near the tip was poor. It is therefore not possible to be sure what part of the brain was stimulated on this penetration.

Stimulation on this one occasion produced accommodation responses and pupil constriction, but no eye movements. The responses were rather variable as can be seen in in Fig. 6.3, which shows 4 accommodation responses evoked by stimulation at the same site. As these were the only positive effects observed in all 51 penetrations, it does not constitute a clear demonstration of a cortical near response centre. In all, eight penetrations were made at sites within 1.5 mm of this site where

Figure 6.3

Accommodation responses (A_r) to stimulation at one site in the occipito-temporal cortical region. Each of the 4 traces shows the response to stimulation (330 microamps, 0.5 msec pulses at 300 Hz for 0.5 sec, electrode negative) at the same site. The narrow vertical line indicates the time at which stimulation began. The responses are presented in the order in which they were evoked (i.e. the top trace was the first evoked response, the bottom trace was the fourth). The accommodation responses were variable, both in latency and in form. No effects on eye movement were observed.



accommodation was evoked and accommodation was only observed on the one occasion when the electrode was found to be damaged. The accommodation and pupil responses may have resulted from some non-specific effects such as intense autonomic stimulation, which may have occurred if the animal was shocked or felt pain from current passing through the damaged electrode into the subdural space.

6.3 Discussion

The results of microstimulation in the midbrain support the conclusion, based upon the extracellular unit recordings described in Chapter 5, that there is a group of cells dorsal and dorso-lateral to the OMN involved in the control of vergence eye movements and accommodation, stimulation there producing convergence and accommodation at short latencies. Convergence responses could be evoked by small current pulses so it is unlikely that the responses resulted from simultaneous excitation to the medial rectus subdivisions of both oculomotor nuclei. The criteria adopted for classifying a response as convergence excluded the possibility that the effects were the result of exciting only one medial rectus subdivision.

The long latency of accommodation responses to stimulation (compared with the latency for vergence) is in accordance with the suggestion made from behavioural observations (Chapter 3) that delays in activating the accommodation plant are longer than those for the vergence plant. The difference between the accommodation and vergence latencies to electrical stimulation (89 msec) is very similar to the difference in the latencies of the two responses to changes in target distance (74 msec in binocular viewing, 93 msec in monocular viewing,

see Table 3.1 in Chapter 3).

The long latency for accommodation responses reported here is quite similar to that reported by Thompson (1975) for responses to electrical stimulation of the ciliary nerve in anaesthetized monkeys (80 msec), but considerably shorter than that reported by Bando et al. (1984a) for responses to electrical stimulation of the midbrain in cats (270 msec).

Stimulation of the occipital and temporal cortex in the vicinity of the STS in an awake monkey did not produce good evidence for the existence of a centre for co-ordinating the near response in this area, but this negative result must be interpreted with caution. One obvious possibility is that the area stimulated by Jampel (1960) was different from that stimulated here. It is however clear that many sites stimulated in this study were in the region where Jampel claimed to elicit responses. It may be that the cells actually activated in Jampel's study lay rather lateral to the area he described - Jampel only sketched the position of effective stimulation sites, so it is difficult to assess what errors might be involved in his description of the position of these sites.

One possible difficulty with the study reported here comes from the observation (Jankowska and Roberts, 1972; Roberts and Smith, 1973) that large cathodal current pulses can block the excitation of nearby fibres. This inhibition probably affects cells within a radius which is approximately one quarter of the distance over which cells are excited (Ranck, 1975). Since 330 microamps should excite cells up to approximately 0.75 mm away from the electrode tip (see Fig. 1 of Ranck, 1975), the area over which cells were inactivated may have had a radius

of 0.2 mm. Unless the near response centre was extremely small, the activation of cells between 0.2 and 0.75 mm from the electrode tip should have evoked some responses. Furthermore, cells several millimetres away from the electrode tip should have been excited transsynaptically by the stimuli used here (Asanuma et al., 1976; Jankowska et al., 1975). It is therefore unlikely that there was even a small group of cells within the area covered by this stimulation study which were not activated. Since Jampel reported effective stimulation sites over a wide area, it seems unlikely that inhibition of cells near the the electrode can account for the failure to evoke accommodation of vergence responses in this experiment. Since the size of the pupil was not routinely monitored during stimulation, this experiment does not exclude the possibility that some part of the occipital or temporal cortex is involved in the control of pupil constriction.

These negative findings call into question Jampel's (1960) claim that areas 19 and 22 of the macaque cortex are involved in co-ordinating the near response. It is possible that there is an area of the occipital or temporal cortex which is important to the near response, but it must be lateral to the area shown in Jampel's sketches. There are several difficulties in interpreting Jampel's results, discussed above, so it is clear that further experiments on awake animals will be necessary before a role in the co-ordination of the near response can be ascribed to the occipital or temporal cortex close to STS.

CHAPTER SEVEN

DISCUSSION

7.1 The importance of vergence-accommodation

Previous studies in human subjects have shown that the dynamic responses of disparity-driven vergence are faster than accommodative-vergence (Krishnan et al., 1973a; Semmlow and Wetzell, 1980). Furthermore, Semmlow and Wetzell (1980) showed that the dynamics of disparity-driven vergence were not much affected by the presence or absence of a blur cue. They concluded that disparity stimuli were more important than blur stimuli in the dynamic control of vergence eye movements. The results presented in Chapter 3 demonstrated that this was also true in the monkey. Chapter 3 also showed that the dynamic performance of vergence-accommodation was similar to that of disparity-driven vergence, and that vergence-accommodation accounted for the improvement in accommodation dynamics in binocular viewing (compared with monocular viewing). During binocular viewing, disparity cues are therefore more important in the dynamic control of both accommodation and vergence than blur cues. It seems likely that vergence-accommodation is equally important in humans - Krishnan et al., (1977) reported that in response to step changes in target position accommodation changes were accomplished more rapidly during binocular viewing than during monocular viewing. Yoshida and Watanabe (1969) measured the vergence-accommodation responses to vergence stimuli which modulated with a sinusoidal time course, and compared them to the responses of accommodation during monocular viewing. Although they found

that the amplitude of the vergence-accommodation responses were larger than those of blur-driven accommodation (for frequencies up to 0.8 Hz), they reported large phase lags of the vergence-accommodation response (relative to the vergence stimulus), even at low frequencies (their Fig. 19b shows a phase lag of 30 degrees at 0.2 Hz). However, their experiment involved placing a pinhole in front of one eye only while the other eye viewed a target at fixed distance. Vergence-accommodation would therefore have produced some blurring of the image in this eye, and the resulting blur-driven response would have opposed vergence-accommodation. Furthermore, Yoshida and Watanabe (1969) only studied one subject, who was 40 years old. Since Fincham and Walton (1957) showed that the gain of vergence-accommodation (in the steady state) decreases in proportion to the age of a subject, it is not clear what significance the results of Yoshida and Watanabe have for young subjects. Further investigation of accommodation performance during binocular viewing is clearly necessary to clarify the importance of vergence-accommodation in the dynamic control of accommodation in human subjects.

7.2 What is the purpose of accommodative-vergence?

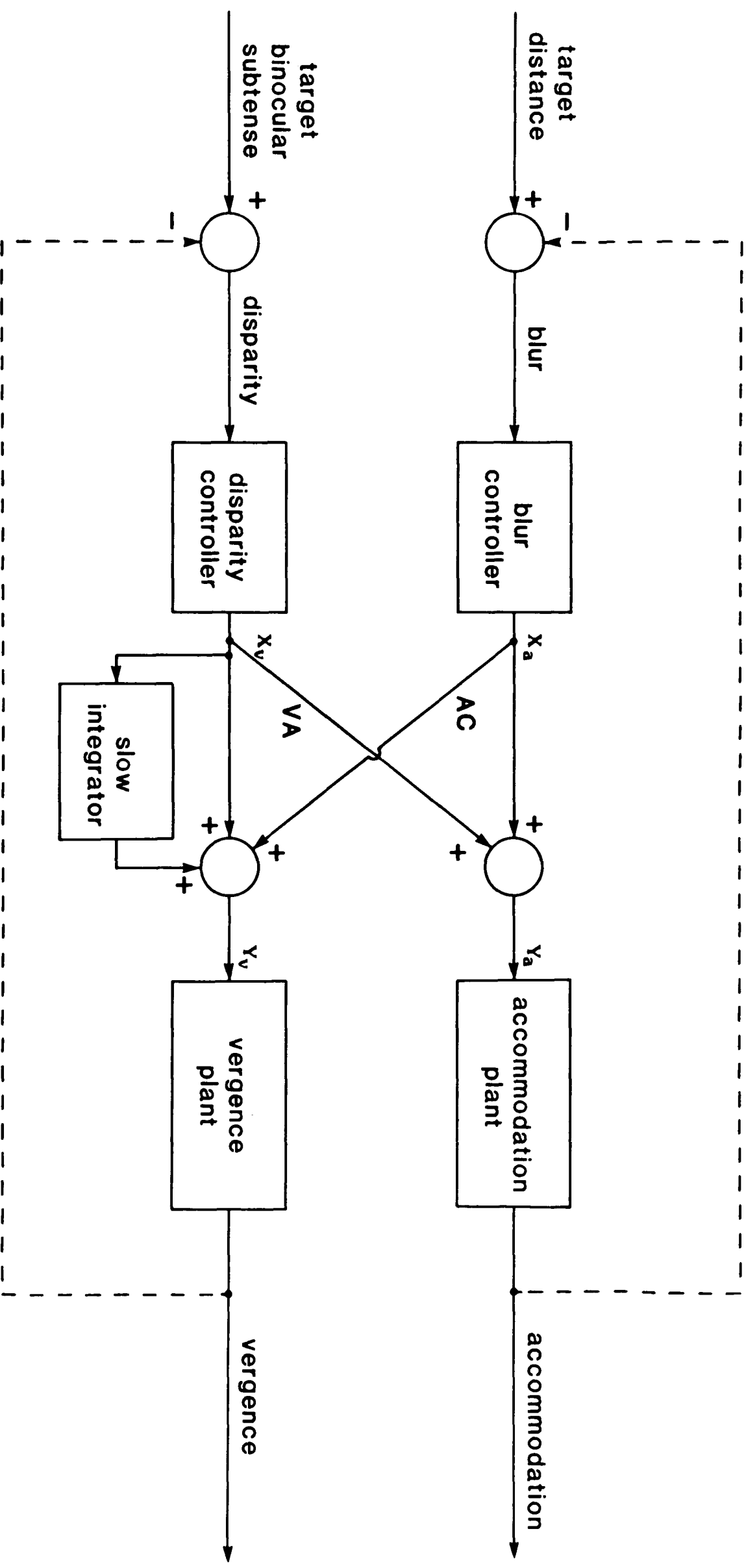
During binocular fixation, fusional vergence is controlled much more precisely than monocular accommodation - Chapter 1 discussed (for human subjects) the large errors (up to 0.5 D) tolerated by accommodation during monocular viewing, and also described the very small errors (a few minutes of arc) tolerated by the fusional vergence system. From Chapter 3 a similar difference can^{be} inferred for the monkey, since the gains of monocular accommodation responses were smaller than

those of binocular accommodation responses, even at the lowest frequencies tested (0.1 Hz). Blur-driven accommodation may be useful in correcting for the effects of a slightly inappropriate vergence-accommodation response, but it is hard to believe that accommodative-vergence contributes much to the fine control of vergence. This raises the question: what is the functional importance of accommodative-vergence? Miles (1984) has argued that accommodative-vergence is of very little significance, and suggested that it arose early in evolution before the appearance of disparity detectors. It is also possible that accommodative-vergence plays a similar role during ontogeny, helping to maintain roughly appropriate alignment of the eyes before the accurately controlled feedback mechanism for controlling vergence is functional. Duke-Elder and Wybar (1973, p. 240) stated that congenital myopia is a cause of strabismus, an observation consistent with the view that accommodative-vergence is important for the development of disparity-driven vergence.

Careful consideration of the diagram shown in Fig. 7.1 (which is the same as Fig. 1.1) suggests another possible role of accommodative-vergence during binocular viewing in normal adults. During fixation of a target at a given depth the existence of a fixation disparity causes the slow vergence integrator to charge. As this happens the vergence-accommodation drive is reduced, so that blur-driven accommodation becomes important for maintaining the accommodation response. This must also be associated with an increase in the accommodative-vergence drive. During the steady state, the output from the fast vergence integrator must be small (since the slow integrator is not charging) and hence there must be little vergence-accommodation drive. Consequently,

Figure 7.1

Block diagram of accommodation and vergence control. Two separate feedback controllers are shown - the dotted lines indicate the feedback by the outputs of the system (accommodation or vergence) reducing the inputs to the controllers (blur and disparity respectively). The two feedback loops are cross coupled by accommodative-vergence (AC) and vergence-accommodation (VA). The slow integrator produces prism adaptation (see text).



accommodation must be supported mainly by blur-feedback, and accommodative-vergence will contribute a large part of the vergence response. Thus the presence of an accommodative-vergence response minimizes the extent of prism adaptation during normal binocular viewing.

7.3 The addition of vergence-accommodation to blur-driven accommodation, and of accommodative vergence to disparity-driven vergence.

The above discussion has assumed that the control of accommodation and vergence can be described accurately by the linear interaction of the elements shown in Fig. 7.1. Several observations in human subjects suggest that this is a reasonable assumption. Ogle et al. (1967) demonstrated the influence of accommodative-vergence during binocular viewing by measuring changes in fixation disparity produced by wearing (inappropriate) spectacle lenses. They calculated the stimulus AC/A ratio during binocular viewing from consideration of which lenses produced the same fixation disparities as a range of wedge prisms. If blur-driven and disparity-driven responses interact linearly, this measurement should yield the same result as the stimulus AC/A ratio determined during monocular viewing (see Judge (1985) for a theoretical discussion). Ogle et al. (1967) measured the AC/A ratio in 256 subjects using the fixation disparity method, and reported a mean value similar to those reported by large clinical surveys which used monocular testing. However, both Ogle et al., and Hebbard (1960) found that the two measurements of the AC/A ratio in individual subjects sometimes gave different results.

Hung and Semmlow (1980) showed that during binocular fixation with

accommodation-open-loop, fixation disparities were smaller than during viewing with an accommodation stimulus fixed at 0 D. This observation was explained by invoking the effects of both vergence-accommodation and accommodative-vergence during binocular viewing. Semmlow and Hung (1981) used a computer simulation of a model like that in Fig. 7.1 to describe measured fixation disparities and errors of accommodation over a range of stimulus conditions. Although their model assumed non-linearities in the responses to blur and in the responses to disparity, the interaction of these two components was assumed to be linear. These observations all support the view that the interactions of blur-driven and disparity-driven components in the steady state can be described as a linear addition of vergence-accommodation to blur-driven accommodation and of accommodative-vergence to disparity-driven vergence.

The dynamic interaction of accommodative-vergence and disparity vergence can also be described as a linear summation according to Semmlow and Wetzell (1980). They showed that the small changes in the dynamic performance of vergence, produced by the presence of an accommodation stimulus, were of the magnitude expected from the measured responses of accommodative-vergence. However, since the differences they measured were rather small, the test was not a very sensitive one. The same objection can be made to the observation made in this study (Chapter 3) that a linear combination of the measured blur-driven and disparity-driven responses described the performance of accommodation and vergence during normal binocular viewing at frequencies below 0.9 Hz - the differences between the vergence-accommodation responses and the accommodation responses in normal binocular viewing were small. Chapter 4 described the dynamic responses to vergence and accommodation stimuli

which were combined in ways which were not equivalent to the stimuli generated by any target moving in three-dimensional space. The amplitude of the accommodation responses were quite different from those observed in response to normal binocular viewing of a target producing the same vergence stimuli. Comparing the responses in this conflict task with those expected from a linear summation of disparity-driven and blur-driven components therefore provided a clearer test of the linear interaction model than either of the other experiments described above. The measured responses of both accommodation and vergence were in reasonable agreement with those predicted by a the model.

In conclusion, the diagram shown in Fig. 7.1 provides a good working model for the description of accommodation and vergence behaviour in the monkey (and in humans). This diagram shows two separate feedback loops connected by two cross-links. An attempt was made in Chapter 4 to provide a mathematical description of the elements shown in Fig. 7.1, using simple transfer functions. It was not possible to describe the performance of disparity-driven vergence or of blur-driven accommodation with cascaded low-pass filters since the open-loop phase lags were usually larger than those expected of a transfer function which described the open-loop gain properties. A significant complication arose from the demonstration of amplitude-dependent nonlinearities, both in disparity-driven vergence and in blur-driven accommodation. Since the data were collected using a constant amplitude of target motion, the amplitude of the disparity (or blur) stimuli varied with frequency. It may be that if the systems were studied with disparity (or blur) stimuli with a constant amplitude of modulation at different frequencies, harmonic analysis would be more fruitful.

Experiments of this kind could certainly be useful in describing accurately the nature of the non-linearity observed in the closed-loop frequency response. A comparison of vergence responses to pseudo-random target motion with those to simple sinusoidal target motion suggested that the vergence system was able to predict repetitive target motion. However, a precise description of the effects of this prediction must await the characterization of the non-linearities in the relationship between disparity input and vergence response.

A system such as that shown in Fig. 7.1 could be implemented neurophysiologically without any need for a single 'centre' for the co-ordination of the responses, although it is common to assume such a centre exists (Duke-Elder and Wybar, 1961; Semmlow, 1981; Robinson, 1981). In order to investigate the neurophysiological organization of accommodation and vergence, the activity of cells in the monkey midbrain were recorded during a variety of tasks requiring changes in accommodation and vergence responses.

7.4 The neurophysiological organization of the near response.

The Edinger-Westphal nucleus (which contains cells projecting to the ciliary ganglion, innervating the intra-ocular muscles) lies immediately dorsal to the oculomotor nucleus (OMN). This area of the midbrain is therefore one in which signals related both to accommodation and to vergence must exist in close anatomical proximity, so it seemed possible that some of the interactions of vergence and accommodation might have been organized in this area. As described in Chapter 5, single cells were recorded dorsal and dorso-lateral to the OMN, which modulated their firing rate in relation to vergence and accommodation.

For most cells the amplitude of this modulation was similar whether the monkey tracked monocularly (blur cue alone), binocularly with accommodation-open-loop (disparity cue alone), or in normal binocular viewing. It was concluded that the activity of these cells was related to the motor output of accommodation or vergence. Referring to Fig. 7.1 again, the cells recorded behaved as if they were at points Y_a or Y_v , rather than at any sites further to the left on the diagram. By comparing the modulation in normal binocular viewing with that when the blur and disparity cues were in conflict it was possible to show for some cells whether they were related to the accommodation response or to the vergence response.

That the signals recorded in the midbrain were related to the final motor output of accommodation and vergence prompts the question: what areas of the brain are involved in synthesizing these signals? In addition to the paraoculomotor area, there is physiological evidence suggesting that at least three other areas of the brain may be involved in some part of the control of the near response - the prestriate cortex, the posterior parietal cortex, and the cerebellum. The evidence for the involvement of the prestriate cortex in primates rests mainly on the claim of Jampel (1960) that stimulation in areas 19 and 22 of lightly anaesthetized monkeys produced accommodation, vergence, and pupil constriction. It was not possible here to replicate this result in one awake monkey (Chapter 6). In the anaesthetized cat, however, cells in part (PMLS) of the Clare-Bishop area discharge in relation to spontaneous fluctuations of accommodation and electrical stimulation in this area produces accommodation (Bando et al., 1984b). Although there is no widely accepted homology between the PMLS area in the cat and any

part of the monkey cortex, Bando et al. noted that Heath and Jones (1971) 'suggested that the pattern of corticocortical fiber connections of the lateral suprasylvian (LS) area resembled those in the parietotemporal region of the monkey'. Zeki (1974) noted that the visual responses of cells in the posterior bank of STS in the macaque monkey were very similar to those of cells in the Clare-Bishop area of cats.

A possible involvement of the posterior parietal cortex in the control of accommodation or vergence is suggested by recent extracellular recording studies in awake monkeys. Sakata et al. (1980) reported neurones in the posterior parietal cortex whose activity was modulated by the distance at which the monkey fixated, and Sakata et al. (1984) reported neurones whose activities modulated during tracking of targets moving in depth, but which did not discharge in relation to the distance at which fixation was maintained.

Miles et al. (1980) reported that a large number of Purkinje cells in the flocculus of the cerebellum altered their firing rates when monkeys transferred fixation between near and far targets lying along the same cyclopean axis. Electrical stimulation of the interpositus nucleus produces both accommodation and pupil constriction in the cat (Hosoba et al., 1978). Hultborn et al. (1973) showed that stimulation of the interpositus nucleus of the cat produced EPSPs in the short ciliary nerve with a latency of 5.7 msec. They therefore postulated a monosynaptic projection from the interpositus nucleus to the Edinger-Westphal nucleus.

In addition to the areas discussed above, both the superior

colliculus and the prefrontal cortex may also be involved in the control of vergence or accommodation. These possibilities are suggested by the demonstration of anatomical projections from these areas to the paraoculomotor areas where NR cells were recorded in this study. Hartmann von Monakow et al. (1979) described a projection from the precentral and premotor frontal cortex to the Edinger-Westphal nucleus, and Leichnetz et al. (1982, 1984) have demonstrated a projection from the prearcuate frontal cortex (in some cases from the frontal eye fields alone) to the paraoculomotor area. Kuenzle and Akert (1977) found no evidence for a projection from the frontal eye fields to the paraoculomotor area, but Leichnetz et al., (1984) suggested that their own anterograde HRP technique was superior to the autoradiographic method used by Kuenzle and Akert (1977).

A projection from the Superior Colliculus to an area dorsal to the OMN has been described both in the cat (Edwards and Henkel, 1978) and in the monkey (Harting et al., 1980). As mentioned in Chapter 5, some of the cells which discharged during tracking of targets moving in depth were probably in the Superior Colliculus. Lawler (1981) and Cowey (1985) have shown that monkeys with lesions in the superior colliculus (combined either with frontal eye field lesions or inferotemporal cortex lesions) had impairments of global stereopsis. Moreover, these monkeys behaved as if they were diplopic. However, the lesions in these animals also caused some damage in the pretectum, which may have been the critical factor in causing the diplopia, as the authors suggested. Monkeys with lesions to the tectum or pretectum often give the impression of staring fixedly as if they had defective vergence or accommodation (Cowey, et al., 1984; Cowey, 1985).

Excluding the paraoculomotor area, there is evidence suggesting that at least five areas of the monkey brain may be involved in the control of the near response. None of these areas has yet been investigated in a study where both vergence and accommodation responses were recorded. Experiments like those described in Chapter 5, coupled with single unit recordings in these five parts of the brain, may allow the role of each in the control of accommodation, vergence, or their interactions, to be specified more precisely.

APPENDIX ONE

THE PROCEDURE FOR CALIBRATING THE HAPLOSCOPE

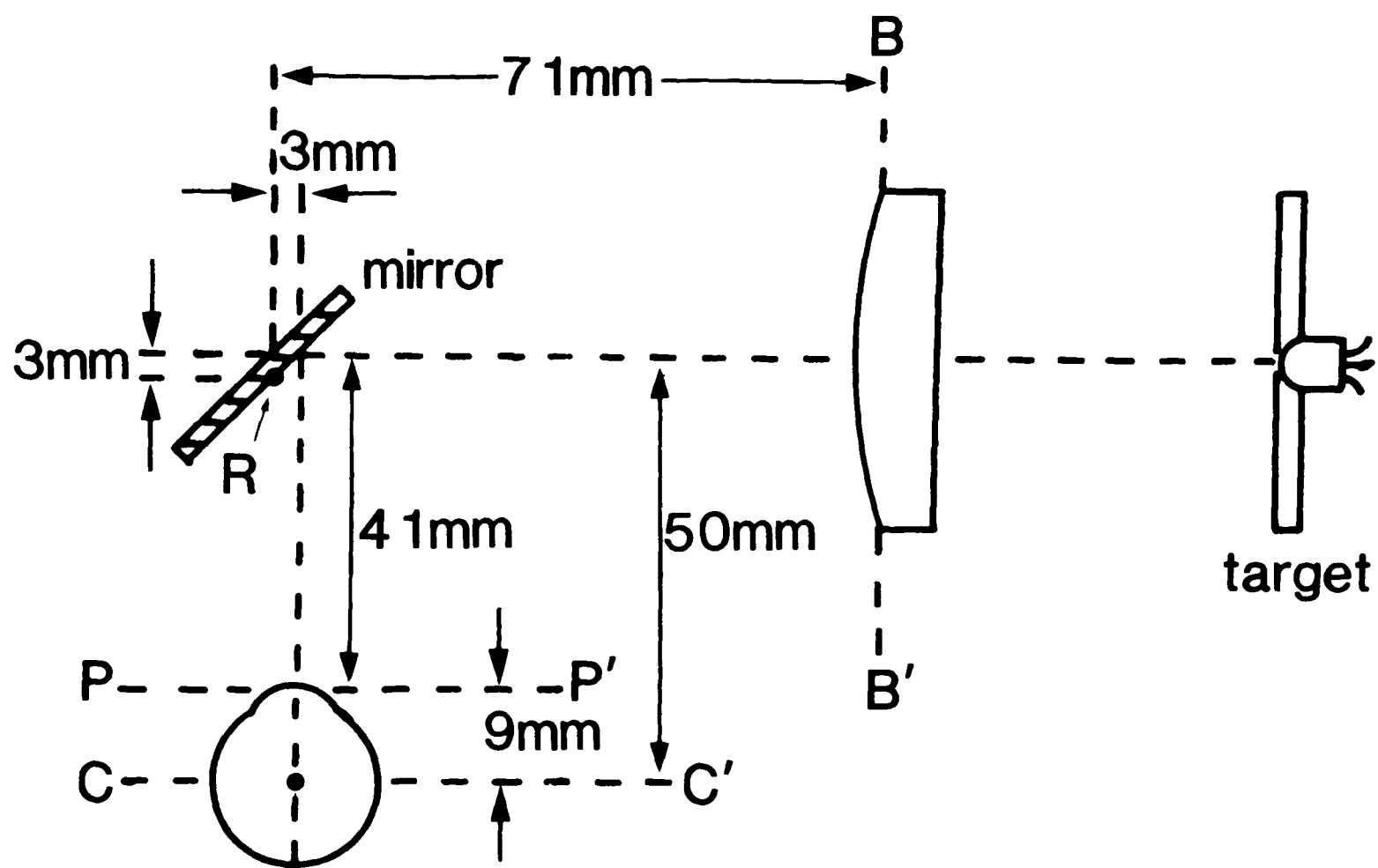
The animals were placed with the centres of rotation of the eyes (Plane CC' in Fig. A1.1) 50 mm behind the axes of the Badal viewing system, which meant that the estimated position of the principal plane of each eye was 41 mm behind this axis (plane PP' in Fig. A1.1). The following procedure was used to set up the apparatus.

First, the axes of the two mirrors were set a distance apart 6 mm shorter than the inter-ocular separation (IOS) of the animal. Thus, since the axis of the Badal viewing system was 3 mm behind the mirror axes, the two targets appeared separated by a distance equal to the IOS (if the vergence stimulus was zero degrees). The Badal lenses were placed with their principal planes 71 mm lateral to the mirror axes, so the distance from this point to the plane PP' was 109 mm, the focal length of the lenses. The tracks along which the targets moved were checked by direct measurement to ensure that they were in line with one another, and that the target motion did not have any vertical component.

The apparatus was then calibrated by using the data collection program to set up stimuli equivalent to known real target positions, and ensuring that the haploscope images had no motion parallax relative to an object at that distance. The offset of the accommodation stimulus servo systems was adjusted first, using an accommodative stimulus of 0.21 D and marks on a wall 4.76 metres from plane PP'. The gain of the servo controller was then adjusted to give no parallax between between a stimulus of 7 D and an object 0.143 m from plane PP'. The offset was re-checked at 0.21 D, and if any adjustment was required, the procedure

Figure A1.1

Diagram showing the position of one eye relative to parts of the haploscope. BB' represents the principal plane of the Badal lens (focal length 109 mm), PP' the principal plane of the eye, CC' a plane parallel to PP' passing through the centre of rotation of the eye, and R represents the axis about which the mirror rotated. The eye is shown looking 'straight ahead'.



was repeated, until no parallax was observed at 0.21 or 7 D . The method of checking motion parallax was precise enough to detect 0.1 D mismatches between the optical positions of the targets being compared.

The gain and offset of the General Scanning controllers for the mirrors was then adjusted using marks on the distant wall and an accommodative stimulus fixed at 0.21 D. The marks on the wall were at 2 degree intervals for 10 degrees either side of straight ahead. When both the mirror galvanometer and the accommodation stimulus servo systems had been calibrated in this way, it was possible to check that the motion in depth stimuli produced by the apparatus were accurate. First, setting different accommodative stimuli while maintaining a zero vergence stimulus, it was shown that the movement of the two images was parallel, along axes separated by a distance equal to the IOS, and that the motion was purely horizontal. Second, by setting a combination of vergence and accommodative stimuli which corresponded to the same real point in depth, it was possible to check that the two target images did superimpose on an object placed at that depth. This second procedure also acted as a check that the signals applied to the mirrors to compensate for the movement of the accommodation stimulus servos (see Appendix 2) were appropriate.

When this procedure was complete, all that remained was to ensure that the apparatus was correctly positioned with respect to the animal before doing an experiment. The animal was placed so that the centre of rotation of each eye was 50 mm in front of the axis of the Badal viewing system. With the left eye covered, the vertical position of the animals head was adjusted so that there was no detectable vertical eye movement

as the animal tracked a target moving towards the right eye. The lateral position of the animal was then adjusted so that there was no horizontal movement of the right eye in the same task. Finally, the right eye was covered and the left eye uncovered in order to check that during monocular tracking of a target moving directly towards the left eye there was no horizontal or vertical eye movement. If this was true the position of the animal was carefully measured and noted, so that it could readily be placed in the correct position at the beginning of each day's experimentation.

This procedure for aligning the apparatus assumed that the centres of rotation of the eyes did not move as the animal converged, an assumption widely held to be true (see Westheimer, 1981). However, Enright (1984b) claimed that in human subjects the globe moved to the temporal side of the orbit during accommodative-convergence, by about 0.13 mm for a 7 diopter stimulus. Such displacement would have very little effect on the stimuli delivered in this apparatus - 0.13 mm at 7 diopters only requires a rotation of 0.05 degrees to maintain fixation. Enright (1984b) also claimed that the centre of rotation of the eye moved forward within the globe during accommodative-convergence, by about 1 mm for a 7 diopter stimulus. The result of such a displacement would be that for near targets, larger rotations of the eye would be needed to fixate the target than if the centre of rotation had not moved. Since for a target at 7 diopters the size of the rotations required is increased by less than 1%, this effect would not seriously compromise the results presented in this study. Furthermore, before the effect of these displacements on a vergence stimulus can be assessed, it is necessary to measure the displacements in both eyes (Enright only

recorded the position of one eye in an asymmetrical vergence task).

The dynamic properties of the apparatus (over the frequency range used for these experiments) were measured by using the program for data collection, which routinely recorded the position of the accommodation stimulus servos, and recording the position of the mirror galvanometers on the channels usually used to record eye position signals. These records were then analysed by spectral analysis using the same program as that used to analyse the responses of the animal (see Appendix 5). The properties of the accommodation and vergence stimuli were measured over the frequency range 0.1 - 3.6 Hz. For both the accommodation stimulus servos and the mirror servos the gain was within 0.5% of unity over this frequency range, and the phase lags increased as an approximately linear function of frequency. For the accommodation stimulus servos this relationship had a slope of 4.1 degrees per Hz, while for the mirror movement the slope was 1.6 degrees per Hz. Thus at 1.2 Hz, there was a phase lag of three degrees between the motion of the mirrors and that of the target itself. For both the accommodative and vergence stimuli, these properties were independent of stimulus amplitude. The step response of the accommodation stimulus servo system showed a small delay (8 msec) followed by a slightly underdamped response (see Fig. 3.1 in Chapter 3). Since the response was slew rate limited, the completion time for a step change depended upon the step size. A 2 D step was completed 44 msec after the stimulus change was applied. The step response of the mirror rotation was extremely rapid, 4 degree steps being completed within 8 msec.

APPENDIX TWO

COMPENSATION FOR THE EFFECTS OF THE DISTANCE BETWEEN THE CENTRES OF
ROTATION OF THE HAPLOSCOPE MIRRORS AND THE CENTRES OF ROTATION OF
THE EYES

Because the mirrors of the haploscope did not rotate about the centres of rotation of the eyes, movements of the accommodation stimulus servo produced a change in both the vergence stimulus and the accommodation stimulus (except in the case where the vergence stimulus was zero). Compensatory mirror rotation allowed target motion in depth to take place without changes in the vergence stimulus. The same compensatory signals also ensured that vergence stimulus changes were of the desired magnitude.

Fig. A2.1 shows the experimental arrangement, with the eye viewing along an axis at an angle, V , to 'straight ahead'. The target (T) is seen through a mirror whose centre of rotation (R) is a distance m medial to the eye's centre of rotation (C), and the same distance in front of the axis along which the target moved. The target is shown at a distance r lateral to, and a distance s in front of, the eye's centre of rotation. When the mirror makes an angle U with the 'straight ahead' axis, the line of sight intersects the mirror at a distance x medial to, and a distance y in front of, the eye's centre of rotation. From Fig. A2.1 it can be seen that:

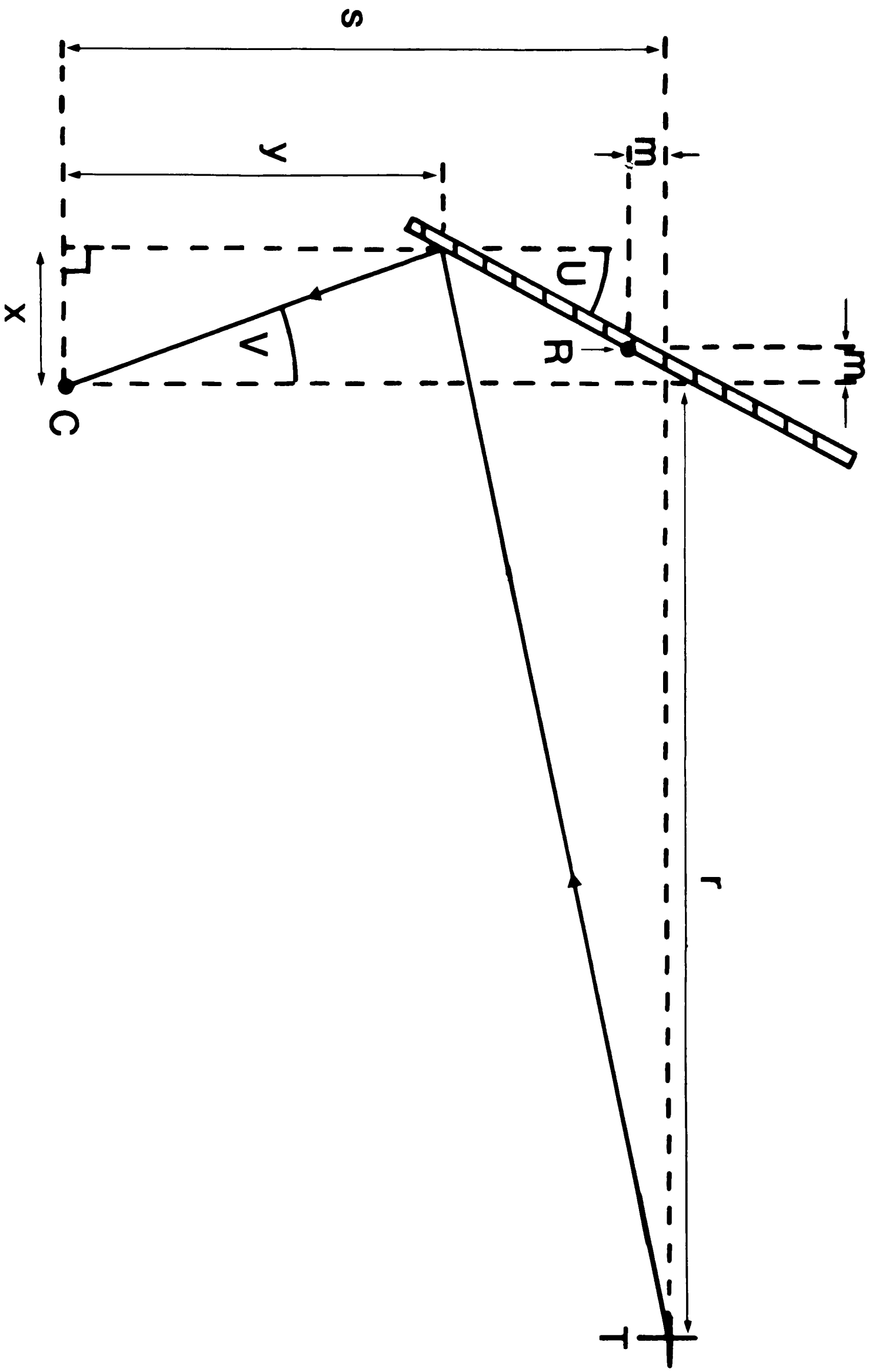
$$x = y \cdot \tan(V), \quad (1)$$

$$\text{and } x - m = (s - y - m) \tan(U). \quad (2)$$

Subtracting (2) from (1), and rearranging, we get:

Figure A2.1

Diagram showing the relationships between the position of the target (T), the centres of rotation of the eye (C) and of the haploscope mirror (R), the angle (U) between the plane of the mirror and 'straight ahead', and the angle (V) between the line of sight (necessary to foveate the target) and 'straight ahead'. Distance $s = 50$ mm, $m = 3$ mm. Distance r depends upon the accommodation stimulus, while distances x and y also depend upon angle V . The exact relationships between these variables are described in the text.



$$y = [m + (s - m)\tan(U)]/[\tan(U) + \tan(V)]. \quad (3)$$

It also follows from Fig. A2.1 that

$$(r + x)/(s - y) = \tan(2U + V). \quad (4)$$

Substituting (1) into (4) and rearranging we get:

$$r = (s - y)\tan(2U + V) - y.\tan(V). \quad (5)$$

where y is defined by equation (3).

Although equations (5) and (3) describe implicitly the relationship between angle V and angle U in terms of r , s , and m , it is not easy to solve for this relationship analytically. A program (written in the 'C' programming language) solved the equation iteratively - adjusting angle U until the value of r calculated from equation (5) was close to the nominal value of r . The iteration stopped when the nominal accommodative stimuli calculated from the two values of r differed by less than 10^{-7} dioptres. The nominal accommodative stimulus is given by:

$$A_s = 1/(r + s - p), \quad (6)$$

where p is the distance from the principal plane of the eye to its centre of rotation. For a fixed value of A_s , the relationship between angle V and angle U was accurately linear, the slope of the relationship varying as a function of A_s . In order to allow rapid, on-line calculation of the mirror angle, U , required to produce a vergence stimulus, V , the relationship between A_s and the ratio U/V was approximated by a quadratic equation:

$$U/V = (1 + 0.0425 A_s + 0.0031 A_s^2)/2 \quad (7)$$

For combinations of stimuli in the range 0 - 8 dioptres and 0 - 8 MA, the estimate for angle U was accurate to within 2 minutes of arc, so the vergences stimulus delivered was accurate to within 4 minutes of arc.

From inspection of Fig. A2.1 it is also clear that the true accommodation stimulus is not exactly equal to the nominal value given by equation (6). The true accommodative stimulus is determined by the distance from the principal plane of the eye to the mirror (d_1) and the distance from the mirror to the target (d_2), where d_1 and d_2 are given (from Fig. A2.1) by:

$$d_1 = y/\cos(V), \quad (8)$$

$$\text{and } d_2 = (s - y)/\cos(2U + V). \quad (9)$$

For stimuli in the range 0 - 8 D and 0 - 8 MA, the true accommodation stimulus never differed from the nominal value by more than 0.05 dioptres, which was considered negligible.

APPENDIX THREE

DETAILS OF HAPLOSCOPIC STIMULUS PRESENTATION

A3.1 Accuracy of simulation of real target motion

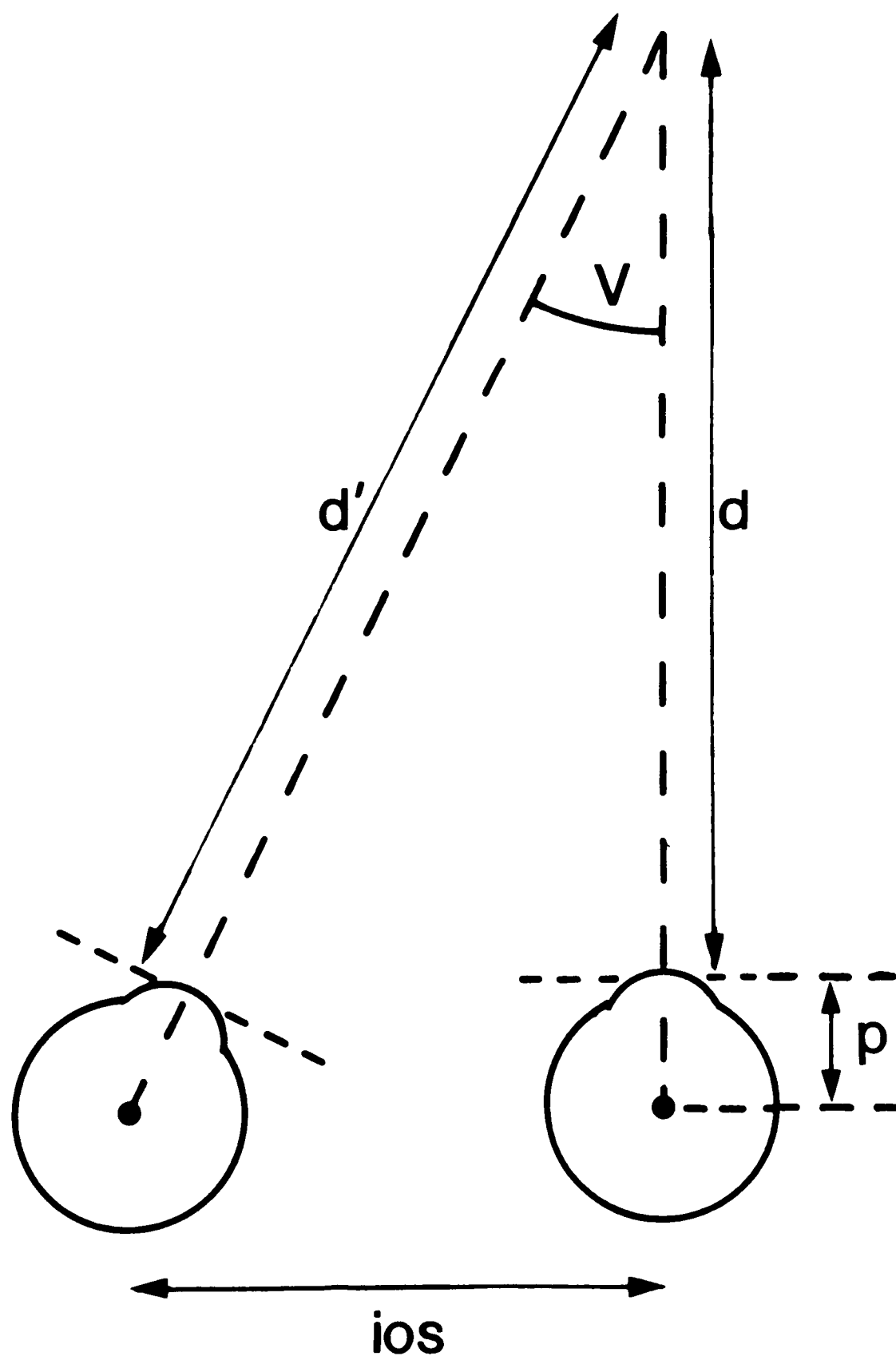
The apparatus described in Chapter 2 presented accommodation and vergence stimuli which were approximately (but not exactly) equivalent to those produced by real targets moving in depth. The largest discrepancies arose from the approximation that the vergence and accommodation stimuli produced by a target at different depths are linearly related. This approximation was used because it simplified the control of the haploscope, and also because if the exact (non-linear) relationship between accommodation and vergence had been maintained, the analysis of responses to binocularly viewed stimuli would have been much more complicated. Since the stimuli usually used in the haploscope simulated a target moving directly towards one eye or the other, this situation is depicted for a real target in Fig. A3.1. It is immediately apparent that the accommodation stimulus is not the same for each eye. For a target producing a vergence stimulus, V , the distance, d , from target to the principal plane of the eye looking 'straight ahead' is given by

$$d = ios/\tan(V) - p, \quad (1)$$

where ios is the monkeys' inter-ocular separation, and p is the distance from the principal plane of the eye to its centre of rotation. The distance of the target from the principal plane of the other eye (d') is given by

Figure A3.1

Diagram illustrating the relationship between the vergence stimulus (V) and the accommodation stimuli ($1/d$, $1/d'$) associated with a real target positioned 'straight ahead' of the right eye of a subject with an inter-ocular separation of ios , and a distance p between the centres of rotation and the principal planes of each eye.



$$d' = i \cos(v) / \sin(v) - p \quad (2)$$

Fig. A3.2 shows these relationships between the vergence and the accommodation stimuli for each eye ((a) shows the accommodation stimulus for the eye looking 'straight ahead' (c) shows that for the adducted eye), compared with the stimuli presented by the haploscope (b), for an animal with an inter-ocular separation of 30 mm. For a given vergence stimulus, the accommodation stimulus delivered to both eyes by the haploscope was close to the average of the stimuli produced in each eye by a real target.

A3.2 Dynamic limitations of stimulus presentation

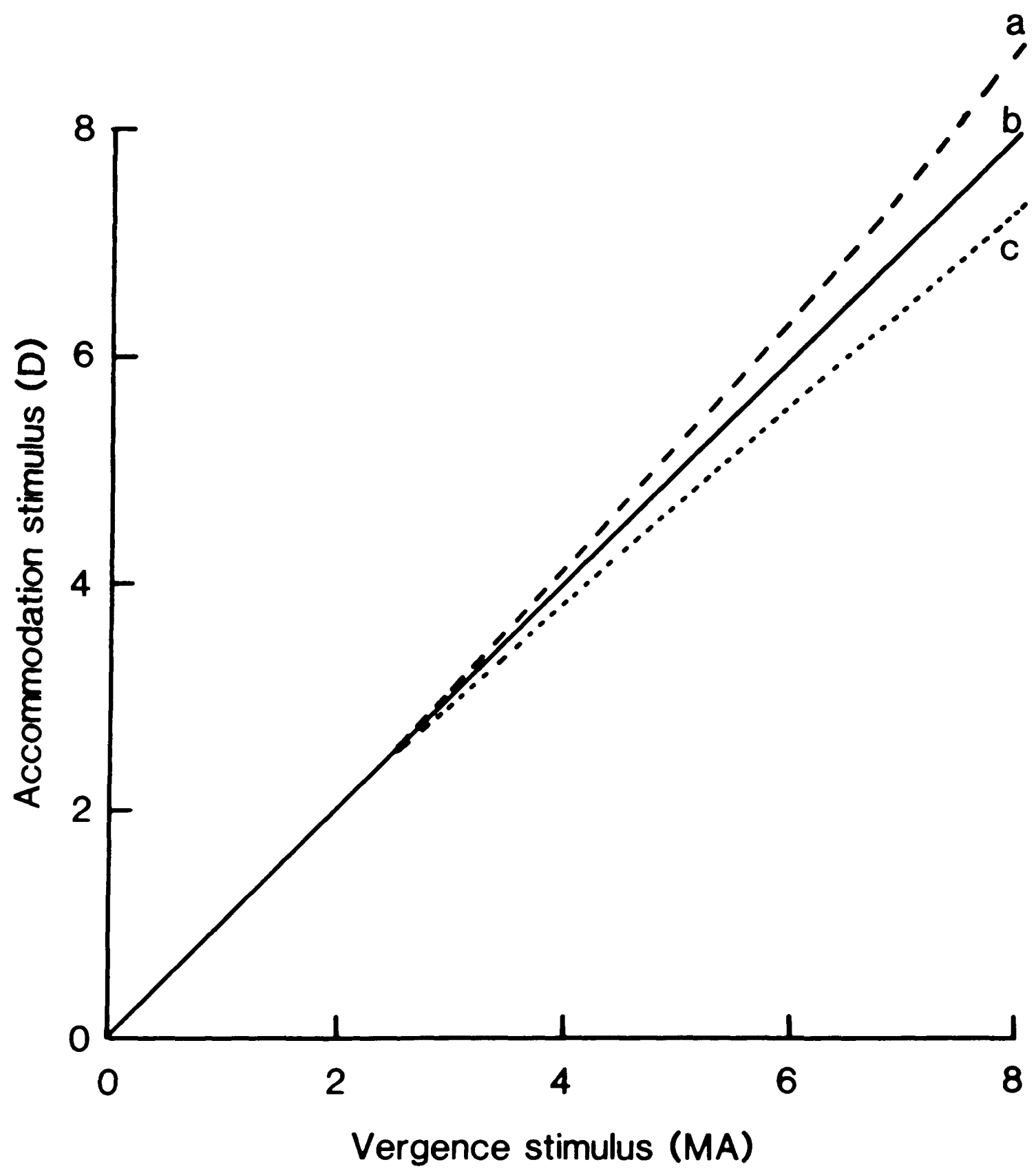
A minor limitation of the stimulus presentation by the haploscope arose from the dynamic performance of the servo system which controlled the accommodation stimulus. At a stimulus frequency of 1.2 Hz, the movement of the accommodation stimulus servo lagged the rotation of the mirrors by three degrees. The effect of this lag was small compared with the errors introduced by assuming a linear relationship between the accommodation and vergence stimuli discussed above.

A3.2.1 Limitations of accommodation-open-loop viewing, imposed by the dynamic performance of the optometer and the accommodation stimulus servo

During binocular viewing with accommodation-open-loop, the phase lags introduced by the optometer and the accommodation stimulus servo system were both interposed between an accommodation response and the attempted cancellation of blur by feedback of the response. At a

Figure A3.2

Plot of accommodation stimulus (abscissa) against the vergence stimulus (ordinate) for subjects with an inter-ocular separation of 30 mm. The relationships are shown between the vergence stimulus and the accommodation stimuli in three situations - the accommodation stimulus (a) for the eye looking straight ahead in asymmetrical vergence (the right eye in Fig. A3.1); the accommodation stimulus (c) to the adducted eye in asymmetrical vergence; and the accommodation stimuli (b) for both eyes presented by the haploscope.



frequency of 1.2 Hz (the highest frequency where binocular AOL viewing was attempted) the combined phase lag introduced by the optometer and the accommodation stimulus servo was 20 degrees. The amplitude of the blur introduced by this delay depended upon the amplitude of the vergence-accommodation response.

The effect of this residual blur on measurements of vergence-accommodation can be estimated from the monocular performance of accommodation, assuming that the accommodation response (A_r) is a linear combination of the accommodation stimulus (A_s) and the vergence stimulus (V_s). (This method is described in more detail in Appendix 7.)

$$A_r = c_{aa} A_s + c_{va} V_s \quad (3)$$

where all variables and coefficients are complex quantities, containing both gain and phase information. Monocular viewing is simulated by setting $V_s = V_r$. Normalizing to $A_s = 1$ gives:

$$A_m = c_{aa} + c_{va} V_m \quad (4)$$

Hence:

$$c_{aa} = A_m - c_{va} V_m \quad (5)$$

where A_m and V_m are complex variables describing the performance of accommodation and accommodative-vergence respectively. Similarly, we can describe the performance of vergence-accommodation, A_v , by setting $A_s = A_r \exp(-ip)$, where p is the phase lag introduced by the optometer and accommodation servo dynamics, and normalizing to $V_s = 1$:

$$A_v = c_{aa} A_v \exp(-ip) + c_{va} \quad (6)$$

Hence:

$$c_{va} = A_v(1 - c_{aa} \exp(-ip)) \quad (7)$$

From Equations (5) and (7) we have:

$$c_{aa} = (A_m - A_v V_m) / (1 - A_v V_m \exp(-ip)) \quad (8)$$

If the apparatus introduced no phase lag ($p = 0$ in Equation (6)) the vergence-accommodation, A_t , would be:

$$A_t = c_{aa} A_t + c_{va} \quad (9)$$

Hence:

$$A_t = c_{va} / (1 - c_{aa}) \quad (10)$$

From equations (7) and (10) we have:

$$A_t = A_v(1 - c_{aa} \exp(-ip)) / (1 - c_{aa}) \quad (11)$$

The ratio of the measured vergence-accommodation to that expected if the accommodation system is truly open-loop is then given by:

$$A_v / A_t = (1 - c_{aa}) / (1 - c_{aa} \exp(-ip)) \quad (12)$$

where c_{aa} is defined by Equation (8). These calculations were performed to estimate the errors in the measurements of vergence-accommodation in all three monkey's, for all frequencies tested. These calculations showed that in all cases the measured vergence-accommodation under-estimated the gain of the true response, but the two estimates agreed to within 10% in all but three cases: for monkey H at 0.9 Hz the gain was under-estimated by 16%, and by 12% at 1.2 Hz, while for monkey A the

gain was under-estimated by 11% at 0.9 Hz. The errors in the estimates of the phases were smaller than 5 degrees except in two cases: in monkey H at 0.45 Hz and at 0.6 Hz the phase lag was over-estimated by 6 degrees.

APPENDIX FOUR

THE OPTOMETER

A4.1 General principle of operation

The dynamic infra-red optometer used in this study operated on the Scheiner principle, like that used by Campbell, Robson, and Westheimer (1959). Fig. A4.1 illustrates the Scheiner principle. An eye views a distant point source through a small aperture. If the eye is emmetropic then moving the aperture from A to B will not produce any displacement of the image on the retina. If the eye is not emmetropic, the image will move across the retina as the aperture is moved (Fig. A4.1b and A4.1c). By examining the magnitude and direction of the image movement it is possible to measure the accommodative state of the eye.

A4.2 Layout of optometer

In the instrument described here the movement of the aperture was achieved by an optical system in which two infra-red-emitting diodes, imaged in the pupil, were illuminated alternately (at a frequency of 400 Hz). Infra-red 'light' reflected from the retina fell onto a detector which provided a measure of the magnitude of the movement of the images on the retina, as described below.

The optical layout of the instrument is shown in Fig. A4.2. The lenses $L_1 - L_4$ were all achromats (supplied by H.W. English and Co.). Two infra-red sources, S (Plessey GAL 10) in the focal plane of lens L_1 (focal length approximately 0.08 m) illuminated an aperture, ST1. A

Figure A4.1

Diagram illustrating the Scheiner principle. A point target at infinity is imaged through a small aperture that alternates between two positions, A and B. The position of the image on the retina will be stationary if the eye is emmetropic (a). The image will move with the aperture if the eye is focussed beyond infinity (b), or opposite to the aperture if the eye is focussed closer than infinity (c).

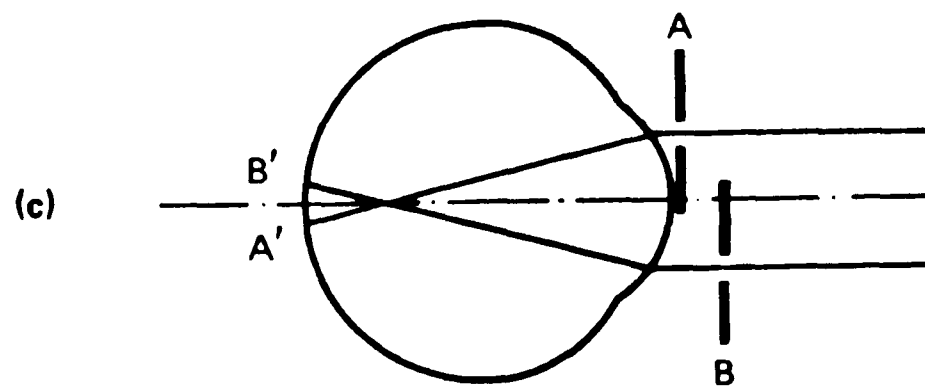
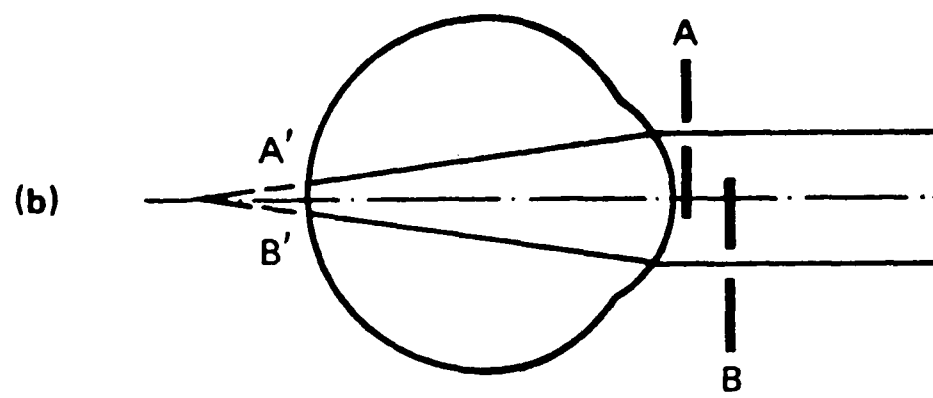
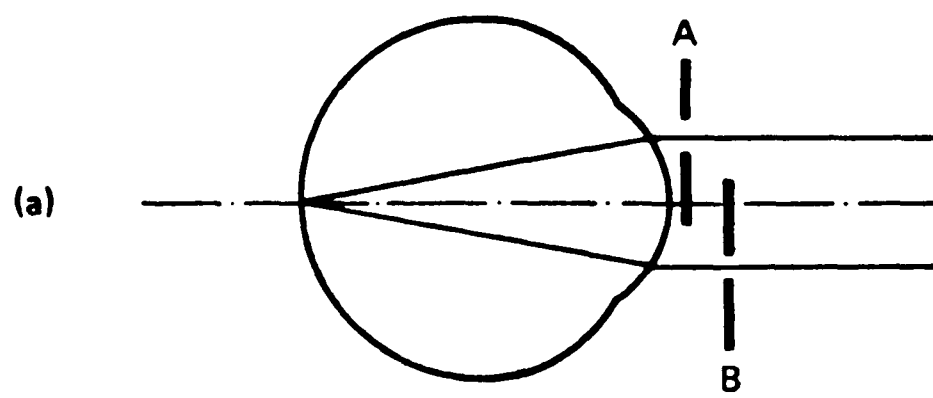
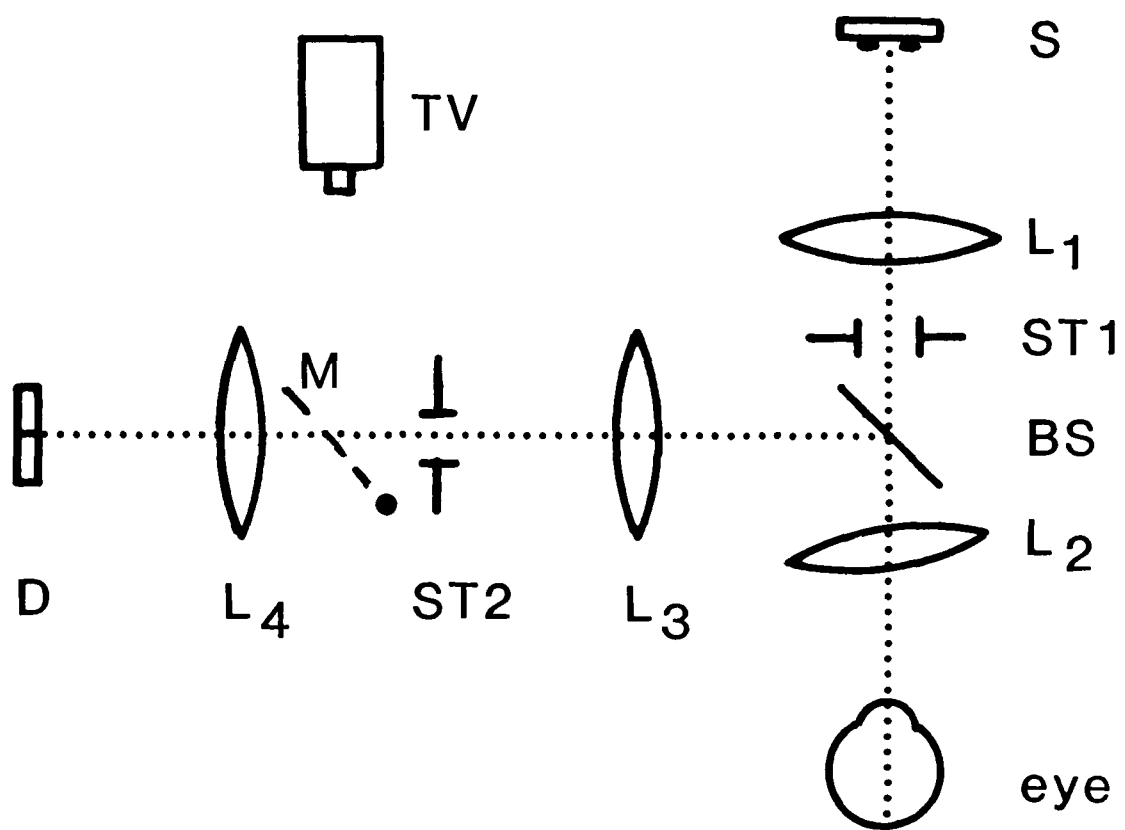


Figure A4.2

Diagram showing the optical layout of the optometer (not to scale). Two infra-red emitting diodes (S) lie in the focal plane of lens L_1 and alternately illuminate the stop (ST1). The sources are imaged in the pupil by lens L_2 . Infra-red radiation returning from the retina is reflected via a pellicle beam-splitter (BS) into the detection limb of the instrument. The near focal plane of lens L_3 is coincident with the far focal plane of lens L_2 . An iris diaphragm forms a second aperture (ST2) in the far focal plane of lens L_3 (which is also the near focal plane of lens L_4 and optically coincident to the pupil of the eye). A mirror (M) allows an image of the pupil to be formed in an infra-red sensitive TV camera (TV). When the optometer is in use the mirror pivots out of the beam to allow infra-red light to pass onto the four quadrant planar silicon diode detector (D).



second lens, L_2 (focal length approximately 0.11 m), was placed with its far focal point in the plane of the pupil, so that images of the sources were formed (at a slight magnification) in the pupil, and an image of the aperture ST1 was formed on the retina. This image was in focus regardless of the refractive state of the eye, since the infra-red light from ST1 was focussed in the plane of the pupil. Infra-red light returning from the retina was reflected by a pellicle beam splitter (Melles Griot 03BPL001/02), BS, into the detection limb of the instrument. The reflected light was relayed via a pair of lenses L_3 and L_4 , onto a four-quadrant planar silicon diode detector, D (SDC SD-380-23-21-051). Since the detector was optically coincident with ST1, when the eye was accommodated at a distance equivalent to the plane of ST1 (2 dioptres) the two images of the aperture were superimposed on the detector. If the eye was accommodated at any other distance, the images were not superimposed on the retina or on the detector.

There were two advantages to using the relay formed by lenses L_3 and L_4 . Firstly, it produced a plane between the two lenses optically conjugate to the pupil, so that by placing an artificial pupil (ST2, an iris diaphragm) in this plane, it was possible to ensure that changes in the size of the actual pupil did not alter the quantity of light returning from the retina to the detector (provided that the real pupil was always larger than the artificial pupil). Secondly, the relay provided space for a mirror, M, to be moved into the path of the reflected light, so that an image of the pupil could be obtained on a TV Camera (Hitachi HV-620K) fitted with an infra-red sensitive silicon - diode-array tube. The TV camera was used to align the optometer each day, ensuring that no light was reflected from the cornea into the

instrument, and that the source images were not vignetted by the iris. To ensure that the pupil did not constrict to a size where the iris vignetted the incoming infra-red light, the pupil was dilated each day with 2 or 3 drops of 10% phenylephrine. This was sufficient to ensure that the pupil did not interfere with the optometer for 3 hours or more in monkeys A and H. In monkey M, pupil constriction 2.5 hours after administering phenylephrine interfered with the optometer. The difference between monkey M and the other monkeys was probably the result of the spectacle correction worn by monkey M (see Appendix 6), since this minified the image of the pupil at ST2. An additional advantage of dilating the pupil was that small eye movements did not then cause the iris to obstruct the passage of infra-red light into the eye. In control experiments where accommodation was recorded during movement of the right eye, the optometer was unaffected by horizontal movements of the right eye in the region between 2.3 degrees medial and 3.5 degrees lateral of the primary position.

A4.3 Theory of optometer operation

As described above, images of ST1 formed on the retina were reflected onto a detector in the optometer. This detector measured the displacement of these images from the optical axis of the instrument. It is possible to calculate the magnitude of the image displacement, and thus the performance of the optometer in the following way. If the eye was accommodated D dioptres, then the image of the retina formed by the reflected infra-red light is at a distance $1/D$ from the principal plane of the eye. Since L_2 is positioned so that its near focal plane coincides with the principal plane of the eye, applying the Newtonian

lens formula to lens L_2 gives the distance, y , of the image formed by lens L_2 from its far focal plane as

$$y = Df_2^2. \quad (1)$$

The displacement of this image from the optical axis can be calculated with the help of the construction shown in Fig. A4.3. A light ray is shown leaving one infra-red source (A) and traversing the path BCEFGH to the retina. Note that the ray passes through the centre of the aperture ST1 (C). Because the source is in the focal plane of L_1 , all light rays leaving L_1 must be parallel. Hence angle α between BCEF and the optical axis is the same as the angle between ray AI and the axis, i.e.

$$\tan(\alpha) = x/f_1 \quad (2)$$

Applying the principle of reversibility, one light ray leaving the eye must traverse the path HGECEB, and since the eye is focussed at plane EJ, all light rays leaving the eye must pass through E. Hence to calculate the displacement, d , of the image from the optical axis, we need only to note that in triangle CEJ

$$\tan(\alpha) = d/[(D - D_0)f_2^2] \quad (3)$$

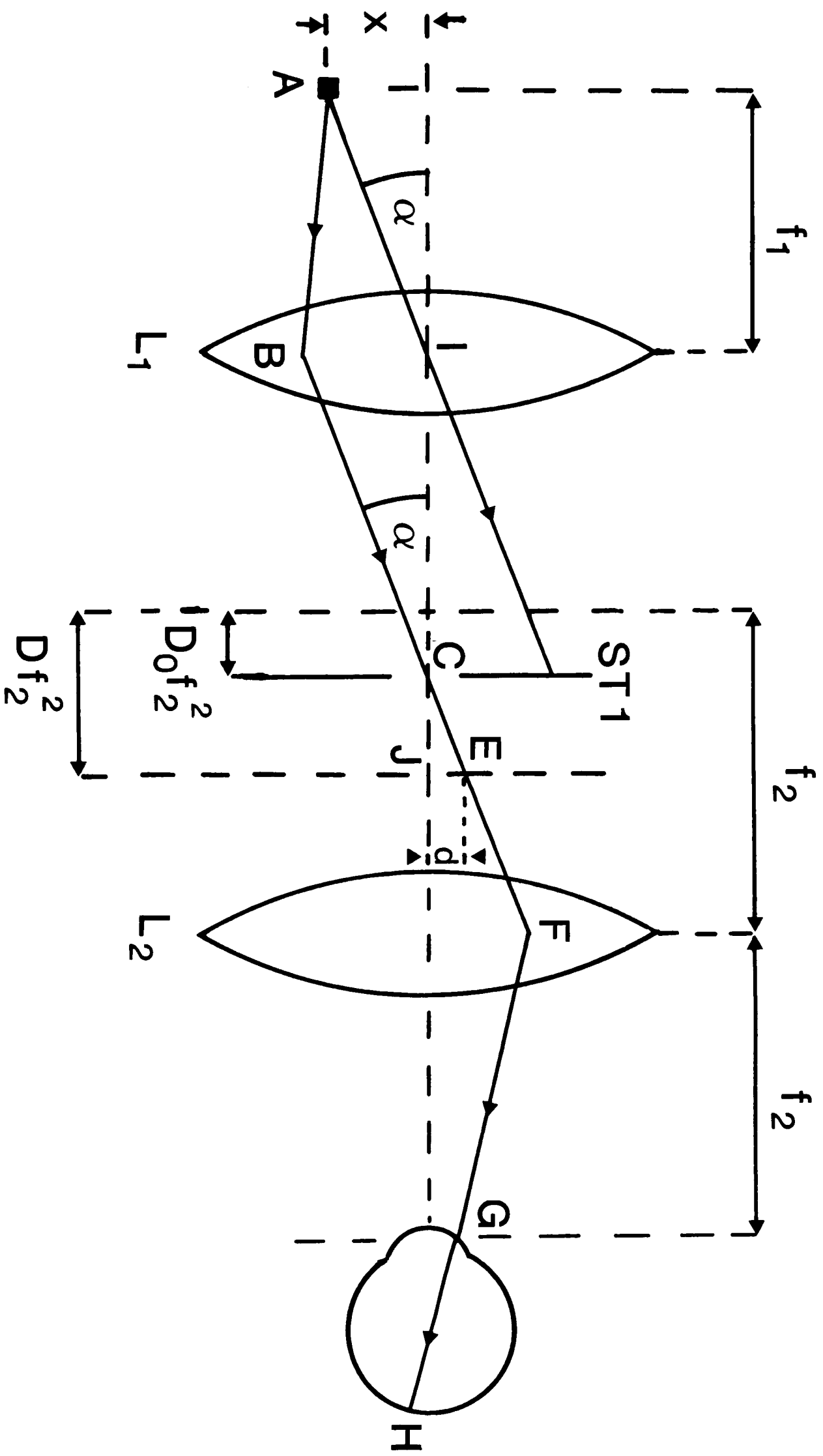
Substituting from Equation (2),

$$d = (D - D_0)f_2^2 x/f_1 \quad (4)$$

i.e. the displacement, d , is a linear function of D , the refractive power of the eye.

Figure A4.3

Construction for calculation of relationship between refractive power of the eye and the optometer output signal. See test for details.



Since the detector is conjugate to ST1, not to the plane (EJ) of the image, it is necessary to calculate the displacement of the (blurred) image in the plane of ST1. This is in fact practically identical to d , because the beam passing out of the eye and through L_2 runs essentially parallel to the axis. This can be seen from consideration^{of} the ray of light defining the centre of the beam - that which passes through the nodal point of the eye. Since the focal plane of L_2 is coincident to the principal plane of the eye, which is very close to the nodal point, this ray must emerge from L_2 nearly parallel to the axis. In this instrument $F_1 = 0.078$ m, $F_2 = 0.115$ m and $x = 0.0007$ m, so each image moved 0.12 mm for each diopetre of accommodation.

The optometer output signal consisted of that component of the difference in the signal from the right and left halves of the detector which alternated with the alternation of the sources. This signal was smoothed to produce a voltage proportional to the displacement of the images from the centre of the detector, and therefore proportional to the dioptric power of the eye. This was true only if the total light flux from the infra-red sources which fell on the detector was independent of the refractive state of the eye. Apart from the effects of changing pupil size, discussed above, there are two ways in which the infra-red light flux falling on the detector might have been reduced. Firstly, a large accommodative response could have displaced the image of the aperture so far from the centre of the detector that a significant part of the image fell off the surface of the detector. As described above, the images were displaced 0.12 mm from the centre of the detector for each diopetre of accommodation. Since the detector was

10 mm wide, and the aperture was 5.5 mm wide, accommodation responses up to 8 D would not cause the images of ST1 to be displaced off the detector. Secondly, if the image of the aperture was blurred over an area larger than the detector, the quantity of infra-red light falling on the detector would have been reduced. It can be shown that the width of the area on the detector covered by the blurred image of a point source is

$$d = D \times f \times P \quad (5)$$

where D is the defocus, P is the diameter of the artificial pupil (4 mm), and f was the focal length of lens L_4 (0.11 metres). For an accommodative response 6 dioptres away from the plane of the ST1, this caused the width of the image on the detector to be increased by 2.64 mm. The same response caused each image to be displaced 0.71 mm from the centre of the detector. Since the detector had a diameter of 10 mm, and the aperture was 5.5 mm wide (extending vertically beyond the limits of the detector), neither of these factors much affected the infra-red light flux reaching the detector. In order to verify that this was the case, a simple modification to the optometer electronics allowed the measurement of the total light falling on to the detector with one infra-red source on to be compared with the total light falling on the detector with no infra-red source on. By recording this 'pupillometer' signal while the animals tracked targets moving in depth over the full range allowed by the haploscope, it was possible to show that with the artificial pupil in place, the total infra-red light flux falling on the detector did not vary with accommodation, with either of the two sources used to illuminate the aperture. The instrument could be switched

between the pupillometer and optometer modes in a matter of a few seconds.

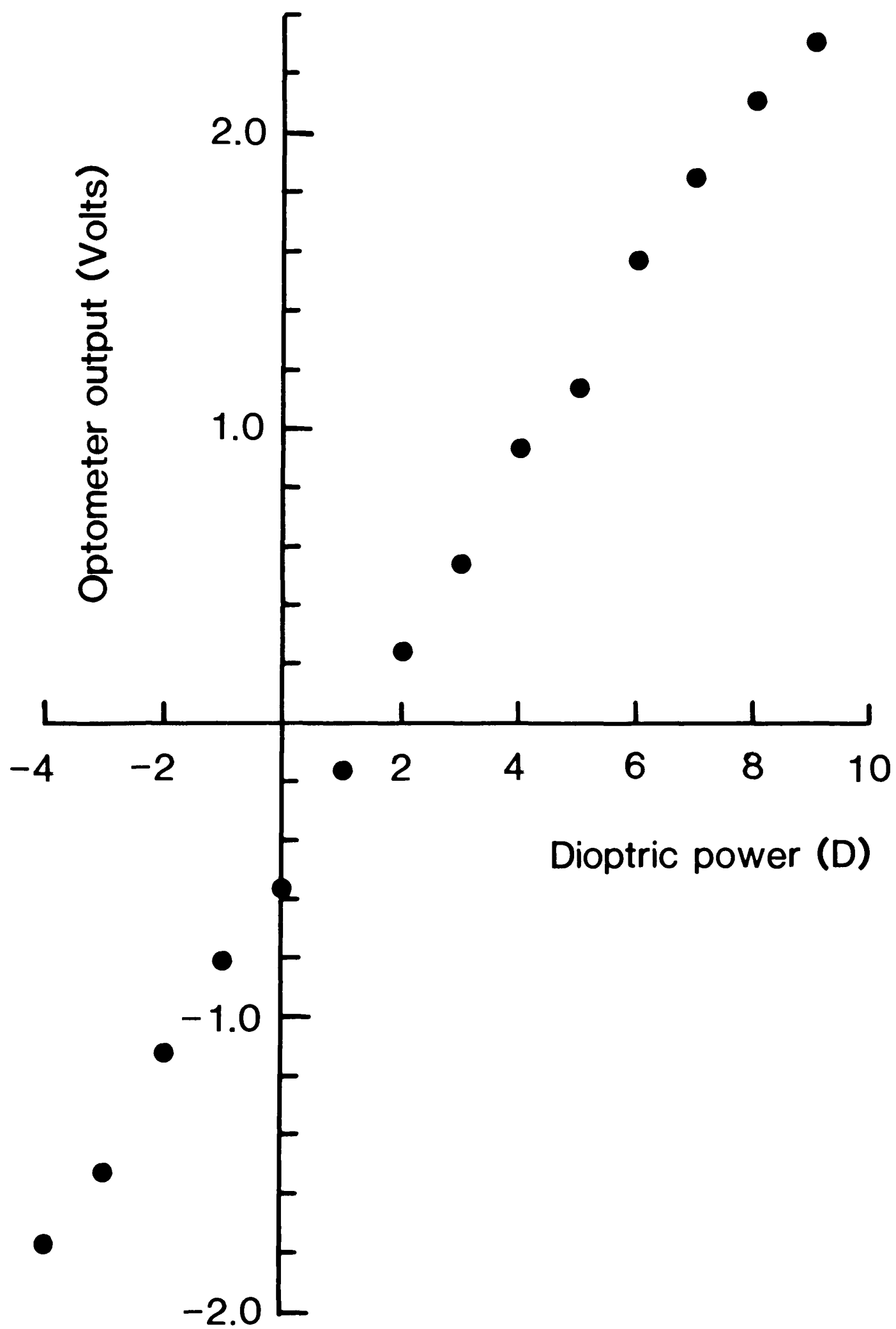
A4.4 Calibration

Since the infra-red light flux reaching the detector was constant, the output of the optometer was linearly related to the displacement of the images of ST1 on the detector, which was in turn linearly related to the accommodation response. Furthermore, the slope of the relationship between accommodation and output voltage was determined only by the flux reaching the detector and the optical layout of the instrument. Thus the ratio of the pupillometer signal to the gain of the optometer signal was a constant, characteristic of the instrument, which I shall call the P/O ratio.

In order to provide an absolute calibration of the optometer gain, the P/O ratio was measured using an artificial eye. The artificial eye consisted of a 40 dioptre lens with a diameter of 10 mm and a piece of black card mounted behind the lens so that it was conjugate to a plane 0.5 m in front of the lens's principle plane (viewed in white light). The power of the eye was varied by placing trial lenses in a holder directly behind the 40 dioptre lens. The optical power of combinations of different trial lenses with the 40 dioptre lens were determined by illuminating a fine cross-hairs with visible light and forming an image of this on the 'retina' of the artificial eye. The optometer and pupillometer signals were then measured for combinations of lenses giving optical powers from -5 to +12 dioptries. Although the relationship between power of the eye and optometer output was not linear over the whole of this range, it can be seen from Fig. A4.4 that the output was

Figure A4.4

Calibration of the optometer with an artificial eye focussed at distances from -4 D to $+9$ D. The optometer output is approximately linearly related to the refractive state of the artificial eye over the range -4 to $+8$ D.



very close to linear in the range from 0 to 8 dioptres (the region of interest for this study). Six separate sets of measurements were made, and a linear regression fitted to each set of data in the range from 0 to 8 D. Next the mean of all the pupillometer signals for each run was calculated. Before calculating the P/O ratio it was necessary to make an adjustment to the pupillometer signal to account for the fact that some infra-red light was reflected internally within the instrument, and this stray light biased the pupillometer signals. The magnitude of the bias was determined by measuring the pupillometer signal with no eye in front of the optometer and with a dark cloth hung one metre away from the instrument. The mean pupillometer signal was adjusted to account for this bias, and the adjusted value was divided by the coefficient determined from linear regression to give the P/O ratio. The mean value for P/O was 8.24 D with a standard error of 0.33 D.

In monkeys A and H the optometer was set up each day so that in binocular viewing at 0.2 Hz the gain of the optometer signal was 1.0 and there was no offset. The electronic gain settings used from day to day were quite consistent (for monkey A the S.D. was 5% of the mean, for monkey H this figure was 9%). When the pupillometer signals were measured after setting the optometer up in this way, they were within 10% of the value predicted from the measurement of the P/O ratio. A different procedure was used for monkey M: the electronic gain was adjusted until the measured pupillometer signals indicated that the optometer gain was correct. After setting up in this way, the mean value of the optometer gain in 0.2 Hz binocular tracking was 0.90 with a S.D. of 0.07. The electronic gain settings used with this monkey had an S.D. which was 5% of the mean.

The absolute calibration of the offset of the optometer was less simple. Although the aperture was at a distance equivalent to 2 D, it is not true that the output of the optometer should have been 0 volts when the eye was accommodated at 2 D. Firstly, when the eye was accommodated for a target at 2 D in visible light, it was probably only accommodated at approximately 1 D in infra-red light (Cornsweet and Crane, 1970). Secondly, since neither source image passed through the pupil along the optical axis of the eye, any spherical aberration or off-axis astigmatism of the eye would have affected the positions of the images of ST1 on the retina. Any off-axis astigmatism would also mean that when the eye was accommodated at any given distance for the fovea, the periphery was not well focussed at this distance, and the optometer actually measured the accommodation of the eye on an axis at an angle of approximately 32 degrees to the visual axis. In spite of these difficulties, the offsets used were quite consistent with each monkey. In order to measure what the optometer signal was when the images of ST1 were superimposed on the retina, the output was recorded with the mirror M positioned so as to prevent any light reaching the detector (in both cases there is no difference between the output of the two halves of the detector). For monkey H the mean value of this offset was 1.93 D, with a S.D. of 0.88 D ($n = 25$), for monkey A the mean was 2.11 D with a S.D. of 0.36 D ($n = 43$), and for monkey M the mean was 6.01 D with a S.D. of 0.53 D ($n = 15$). The large difference between the measures for monkey M and the other monkeys probably resulted from aberrations of the spectacle lenses worn by monkey M (see Appendix 6), since the infra-red light passed near the edge of the lenses, at an angle of 32 degrees to the optical axis.

The dynamic performance of the optometer was limited by the filtering of the signal from the detector, which consisted of three second order Butterworth filters (each with a characteristic frequency of 23 Hz) and a first order low-pass filter with a characteristic frequency of 34 Hz. For frequencies much smaller than 23 Hz, therefore, the gain should have been close to unity, and the phase lag should have increased nearly linearly with frequency (with a slope of 12.2 degrees per Hz). The actual dynamic performance of the optometer was determined using an artificial eye in which the retina was mounted on a General Scanning GS 300 PD servo motor, and changes in the power of the eye were achieved by oscillating this 'retina' with a sinusoidal time course. The position of the servomotor and the optometer output were measured for frequencies up to 3.0 Hz. Each signal was analysed by spectral analysis, and the ratio of the two determined to give the optometer gain. The gain was close to unity over this frequency range, and the phase lag increased linearly with frequency (slope 12.6 degrees per Hz), in close agreement with the expected performance. The measured phase lags of the monkey accommodation performance were adjusted to take account of the phase lags introduced by the optometer.

APPENDIX FIVE

SPECTRAL ANALYSIS OF DATA AND AVERAGING OF RESULTS

A5.1 Spectral analysis

Responses to sinusoidal stimuli were analysed by spectral analysis. The components of the responses at the fundamental frequency were described by a function of the form

$$R(t) = \bar{r} + y.\cos(\omega t) + x.\sin(\omega t). \quad (1)$$

The coefficients $\bar{r}$, x and y were estimated by the equations (given by Chatfield (1982), p. 130)

$$\bar{r} = \sum r_i / N, \quad (2)$$

$$x = 2 \sum r_i . \cos(2 \omega i / N) / N, \quad (3)$$

$$y = 2 \sum r_i . \sin(2 \omega i / N) / N. \quad (4)$$

where r_i represents the measured response variable in the i^{th} sample from a series of N samples.

Equation (1) may also be written in the form

$$R(t) = \bar{r} + A.\sin(\omega t + B), \quad (5)$$

where

$$A = (x^2 + y^2)^{\frac{1}{2}}, \quad (6)$$

$$B = \arctan(y/x). \quad (7)$$

The total harmonic distortion (the difference between the power in the fundamental component of the response and the total power in the

response) was also calculated. The total harmonic distortion expressed as a fraction of the power in the fundamental component of the response was called the distortion coefficient.

The responses to pseudo-random target movement were analysed using the same algorithm to calculate the responses at several harmonics of the fundamental frequency (simply by substituting $n\omega$ for ω in Equations (3) and (4), to calculate the responses at the n^{th} harmonic). In the analysis of responses to both pseudo-random and pure sinusoidal stimuli, the gain and phase of the response variables were expressed relative to the gain and phase of the stimulus.

A5.2 Averaging of responses to sinusoidal stimuli

The components of the the fundamental responses (x_i and y_i) were calculated for each cycle of target motion and the means ($\hat{x}$ and $\hat{y}$) and variances of the two components were calculated separately. It was assumed that x_i and y_i had zero covariance. If, as is usually argued (Bendat and Piersol, 1971), x and y are independent random (Gaussian) variables, $\hat{x}$ and $\hat{y}$ are unbiased estimates of the true response components (x and y), but simple trigonometrical conversion of $\hat{x}$ and $\hat{y}$ to describe the response in terms of gain (A) and phase (B) does not yield unbiased estimates of A and B . The bias in the estimates for A and B and the variances associated with these estimates can be estimated by considering the first three terms in Taylor's expansions for A (and B) in terms of x and y (as described by Kendall and Stuart, 1971; p. 247). This method gives

$$E[(\hat{x}^2 + \hat{y}^2)^{\frac{1}{2}}] = (x^2 + y^2)^{\frac{1}{2}} + \frac{1}{2}[\hat{y}^2 \text{var}(\hat{x}) + \hat{x}^2 \text{var}(\hat{y})]/(\hat{x}^2 + \hat{y}^2)^{3/2}, \quad (8)$$

$$E[\arctan(\hat{y}/\hat{x})] = \arctan(y/x) + 2\hat{x}\hat{y}[\text{var}(\hat{x}) - \text{var}(\hat{y})]/(\hat{x}^2 + \hat{y}^2)^2, \quad (9)$$

where $E[f(x,y)]$ is the expected value of a function $f(x,y)$.

Unbiased estimates for the gain and phase of the response are therefore given by:

$$A = (\hat{x}^2 + \hat{y}^2)^{\frac{1}{2}} - \frac{1}{2}[\hat{y}^2\text{var}(\hat{x}) + \hat{x}^2\text{var}(\hat{y})]/(\hat{x}^2 + \hat{y}^2)^{3/2} \quad (10)$$

$$B = \arctan(\hat{y}/\hat{x}) - 2\hat{x}\hat{y}[\text{var}(\hat{x}) - \text{var}(\hat{y})]/(\hat{x}^2 + \hat{y}^2)^2. \quad (11)$$

This estimate for B is very close to $\arctan(\hat{y}/\hat{x})$ when $\text{var}(\hat{x})$ is similar to $\text{var}(\hat{y})$. The estimates for the variance of A and B are given by:

$$\text{var}(A) = [\hat{x}^2\text{var}(x) + \hat{y}^2\text{var}(y)]/(\hat{x}^2 + \hat{y}^2), \quad (12)$$

$$\text{var}(B) = [\hat{x}^2\text{var}(y) + \hat{y}^2\text{var}(x)]/(\hat{x}^2 + \hat{y}^2)^2. \quad (13)$$

A5.3 Averaging of responses to psuedo-random stimuli.

In the presentation of pseudo-random stimuli the power present in the stimulus for any given harmonic varied between trials. The variance of the accommodation (or vergence) gains was found to be larger amongst trials with small stimulus amplitudes. The magnitude of the variance in gain was approximately proportional to the reciprocal of the square of the stimulus amplitude. The weighted mean gain and phase of the responses (represented by the complex variable $\hat{g}$) was therefore calculated as:

$$\hat{g} = \sum (s_i^2 g_i) / \sum s_i^2, \quad (14)$$

where s_i represents the stimulus amplitude, and g_i represents the calculated gain and phase of the accommodation or vergence response.

The variances of the responses were calculated by the equation:

$$\text{var}(g) = \sum (\hat{g}s_i - g_i s_i)^2 / \sum s_i^2. \quad (15)$$

The means and variances of the x and y components of the responses were calculated separately, and these were converted into means and variances of gain and phase by the method described above.

A5.4 Calculation of open-loop responses from closed-loop responses

The mean and variance of a response calculated by the method in sections A3.2 and A3.3 above can be used to estimate the open-loop performance of the system (for the vergence system the open-loop performance describes the relationship between the disparity input and the vergence response). The relationship between the closed-loop response of a feedback controller, r_c , and its open-loop response, r_o , is given by the relationship:

$$r_o = r_c / (1 - r_c). \quad (16)$$

Unbiased estimates for the values of r_o and the variances associated with them were obtained from consideration of the first three terms in Taylor's expansion of Equation (16). Let x and y represent the x and y components of the closed-loop response, and r_{ox} and r_{oy} the x and y components of the open-loop response. It is convenient also to define a term p, where:

$$p = (1 - x)^2 + y^2. \quad (17)$$

If it is assumed that x and y are independent random (Gaussian) variables, and that Equation (16) is differentiable (i.e. r_c is not equal to the unit vector) it can be shown that:

$$r_{ox} = [x(1-x) - y^2]/p - (1-x)[(1-x)^2 - 3y^2]/p^3 \cdot [\text{var}(\hat{x}) - \text{var}(\hat{y})] \quad (18)$$

$$\text{and } r_{oy} = y/p - 2y[3(1-x)^2 - y^2]/p^3 \cdot [\text{var}(\hat{x}) - \text{var}(\hat{y})], \quad (19)$$

and the variances are given by:

$$\text{var}(r_{ox}) = \text{var}(x)[(1-x)^2 - y^2]^2/p^4 + \text{var}(y)[2y(x-1)]^2/p^4, \quad (20)$$

$$\text{and } \text{var}(r_{oy}) = \text{var}(x)[2y(1-x)]^2/p^4 + \text{var}(y)[(1-x)^2 - y^2]^2/p^4. \quad (21)$$

A5.5 Analysis of cell firing which was 'cut off'

Some neurones stopped firing during part of each cycle of target motion. Since the form of the modulation in firing rate in such cases was clearly not sinusoidal, the algorithm presented above was inappropriate for estimating the magnitude of the modulation. However, it was possible to use the figures calculated to describe the cells' activity with an equation of the form

$$f(t) = \begin{cases} A[\cos(\omega t) - \cos(\omega t_0)] & 0 < t < t_0, \frac{2\pi}{\omega} - t_0 < t < \frac{2\pi}{\omega} \\ 0 & t_0 < t < \frac{2\pi}{\omega} - t_0, \end{cases} \quad (22)$$

where $f(t)$ represents the firing rate of the unit at time t , and t_0 the time at which the cell becomes silent. Equations (3) - (6) above would estimate the amplitude of the fundamental component of firing-rate modulation to be A' , where

$$A' = 2A/\pi \int_0^{t_0} \cos(\omega t) \cdot [\cos(\omega t) - \cos(\omega t_0)] dt, \quad (23)$$

which gives:

$$A' = A/\pi[t_0\omega - \frac{1}{2}\sin(2\omega t_0)]. \quad (24)$$

We can define the proportion of the cycle during which the cell was not firing, c , by

$$c = (\pi - \omega t_0)/\pi. \quad (25)$$

Equation (24) is then equivalent to

$$A' = A.(1 - c + \sin(2\pi c)/2\pi). \quad (26)$$

The mean value of the firing rate, $\bar{f}$, calculated by Equation (2) would be:

$$\bar{f} = A.[(1-c)\cos(\pi c) + \sin(\pi c)/\pi]. \quad (27)$$

The ratio $\bar{f}/A'$ is monotonically related to c , such that when $\bar{f}/A'$ is less than unity c is greater than zero, which is to say that the cell was silent for part of the cycle. In this case, the procedure for estimating A (the amplitude of the firing rate modulation) consisted of using the ratio $\bar{f}/A'$ to calculate the value of c , which could then be used to calculate A from A' (Equation 26). For cells where the ratio $\bar{f}/A'$ was equal to or greater than one, no adjustment was made.

All of these calculations were performed by subroutines written in the 'C' programming language. The program which performed the spectral analysis also displayed the data used for the calculation on a video display. The calculations were done one cycle at a time, and the calculated parameters describing the responses were stored on disk for further analysis.

APPENDIX SIX

OCULOMOTOR ABNORMALITIES OF MONKEY M

Several abnormalities were observed in the oculomotor behaviour of monkey M. These observations were all made after the surgical operation described in Chapter 2 but it seems likely that only one of these (a nystagmus) could have been caused by the operation. The abnormalities were: a leftward beating nystagmus, a severe myopia, esotropia when viewing distant targets, and a curious asymmetry of vergence eye movements. These abnormalities are discussed individually below.

A6.1 Nystagmus

When monkey M sat in darkness a nystagmus was observed, both eyes drifting to the right during the slow phase. When the nystagmus was first measured, one week after the operation, the velocity of drift during the slow phase was approximately 10 degrees per second. There was also a small upwards component with a velocity of approximately one degree per second. Seven weeks after the operation the slow phase velocity observed was much smaller (2-3 degrees per second rightwards, with almost no discernible vertical component). This reduction in the velocity of the slow phase suggests that the nystagmus may have resulted from damage to the semicircular canals during surgery. This damage might have been caused by pressure applied to the external auditory meatus by the stereotoxic head holding equipment used during surgery. The nystagmus was not evident during fixation of targets within the monkey's far point in the light.

A6.2 Myopia with esotropia.

Fig. A6.1 shows the relationship between the accommodative stimulus and the accommodative-vergence response for monkey M. The measurements were made during monocular fixation of stationary targets at different distances. Fig. A6.1A shows the responses during monocular fixation with the right eye, and Fig. A6.1B shows the responses during monocular fixation with the right eye. It is quite clear that stimuli in the region 0 - 4 D produced no change in accommodative-vergence, while stimuli in the region 5 - 8 D were associated with changes in accommodative-vergence and over this latter range the stimulus AC/A ratio was close to unity. This suggested that the monkey was at least 4 D myopic - stimuli between 0 and 4 D did not produce any change in accommodation so that no accommodative-vergence was observed.

In order to examine the monkey's myopia more directly he was tranquilized with ketamine, and 2 drops of 1% cyclopentolate were placed in each eye. Cyclopentolate paralyzes accommodation and dilates the pupil¹. The refractive state of both eyes was then measured by retinoscopy. The right eye was found to be 6.5 D myopic, while the left eye was 6.75 D myopic.

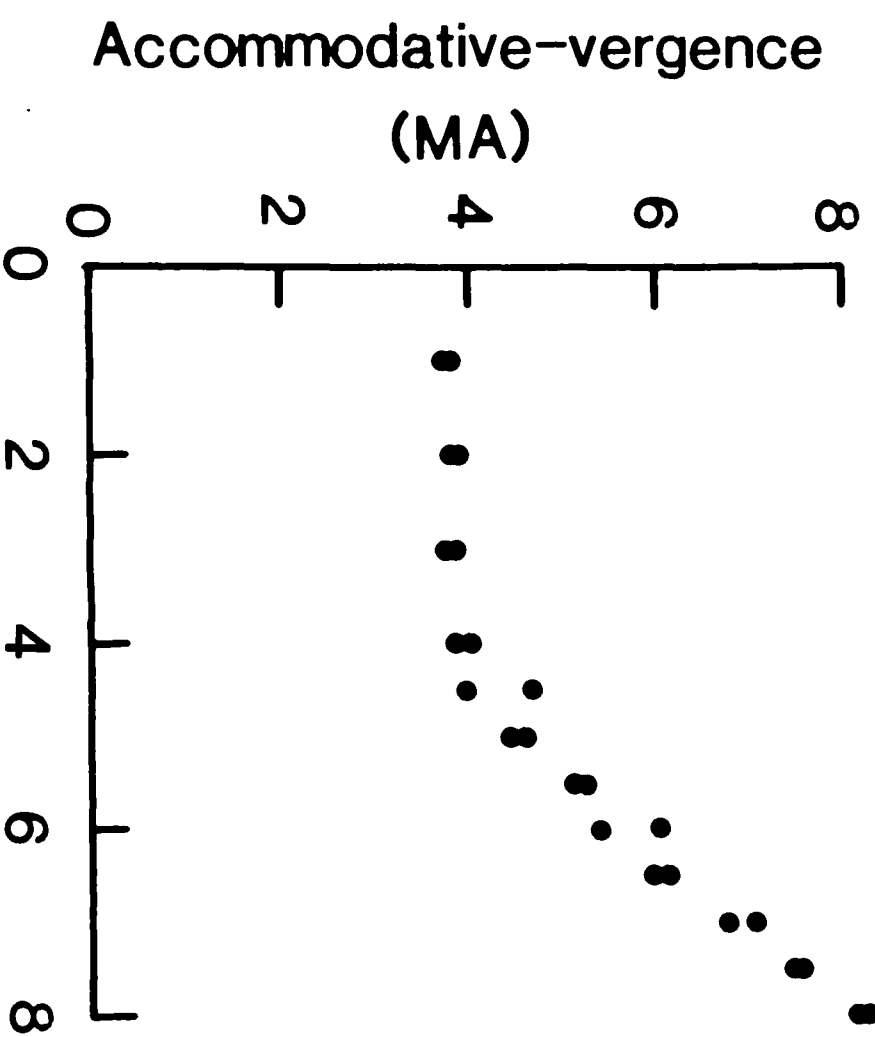
In the right eye a third estimate for the extent of the myopia was obtained, using the optometer to measure accommodation. As a target moved towards the animal, no change in the optometer signal occurred until the target reached a position of 6.7 D, after which the optometer

¹ Cyclopentolate is a competitive antagonist for acetylcholine at muscarinic receptors. It therefore prevents cholinergic activation of the pupil sphincter muscle and of the ciliary muscle.

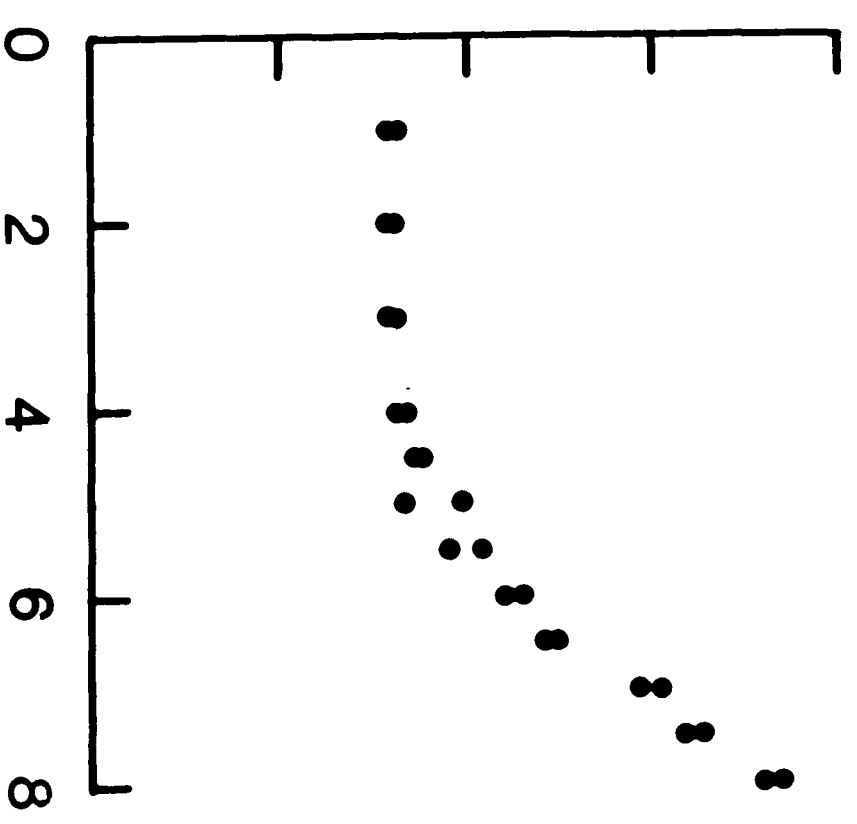
Figure A6.1

The relationship between the accommodation stimulus (ordinate) and accommodative-vergence in monkey M (abscissa) during viewing of stationary targets. The stimuli were presented before monkey M was fitted with lenses to correct for his refractive errors. The target was viewed by the right eye monocularly in A) and by the left eye monocularly in B). Note the lack of any change in accommodative-vergence associated with stimuli in the region 0 - 4.0 D.

A) Right eye viewing



B) Left eye viewing



output increased as the target approached. This suggested a myopia of 6.7 D in the right eye, in good agreement with the value determined by retinoscopy (6.5 D).

It can also be seen from Fig. A6.1 that this monkey was approximately 3.9 MA (9 degrees) esophoric when viewing distant targets with the right eye (3.2 MA when viewing with the left eye). Recording the position of both eyes during binocular fixation, both of stimuli presented in the haploscope and of a single L.E.D. placed at different distances in front of the animal, it was clear that the animal was unable to fixate with both eyes targets which required less than 2 degrees of convergence. The animal had a large range of movement in both eyes, so it is unlikely that this esotropia was the result of damage to the extra-ocular muscles during the surgical operation to implant eye coils. The association of myopia with esotropia has been observed in human patients, but it is a rare condition - Duke-Elder and Wybar (1973, p. 592) state that only 4% of esotropic squinters are myopic.

During the experiments described in Chapter 3, the monkey's myopia was corrected with lenses (-6.5 D for the left eye, -6.0 D for the right eye) placed 14.5 mm in front of the cornea of each eye. Since these lenses were not in the principal planes of the monkey's eyes, they under-corrected the animals' myopia (the equation given by Davson (1972) on p. 566 shows that these lenses were equivalent to a correction of 5.9 D at the principal plane of the monkey's eyes). Stimuli in the haploscope were therefore always presented with an accommodation stimulus of at least 1 D.

An important consequence of these spectacle lenses was that they

changed the effective vergence stimulus produced by mirror rotation. With a -6.5 D lens, 25 mm in front of the centre of rotation of the eye (14.5 mm from the lens to the cornea, 10.3 mm from the cornea to the centre of rotation), calculation suggested that the actual vergence stimulus was 16% smaller than the nominal stimulus. Recording eye position during rotation of the mirrors (viewed monocularly) also suggested that the effective stimulus was approximately 16% smaller than that normally associated with a given mirror position. An adjustment was made for this effect by increasing the mirror rotation to a value 16% greater than that required for the same stimulus with an uncorrected animal. This effect of the spectacle lenses on the vergence stimulus made experiments involving the use of feedback to cancel disparities (opening the vergence feedback loop) difficult, so the experiments described in Chapters 3 and 4 which involved this technique were not performed on monkey M.

During binocular viewing (through the refractive correction) of a target at 1 D, an (effective) vergence stimulus of 7.8 degrees was necessary to permit the animal to fuse readily. As a result of this the range of stimuli which could be presented in the haploscope was significantly reduced. In binocular viewing of a target apparently moving towards one eye, targets closer than 5 D were not visible to the other eye. This is because the rotation of the mirror was large enough that the image of the target fell off the medial edge of the mirror.

Viewing through the spectacles this monkey could accommodate accurately a target with an accommodative stimulus of 1 D (as determined by measurements with the optometer). However, during monocular tracking

the dynamic performance of accommodation was poor as targets approached 1 D, so that responses to a sinusoidal variation in the accommodation stimulus from 1 - 5 D were non-linear. Consequently the monocular performance of this animal was measured with stimuli in the range 3 - 7 D, where the responses were linear. Unfortunately it was not possible to measure the responses to the same stimuli viewed binocularly, as binocular viewing of targets closer than 5 D was not possible (as explained above). The performance of accommodation and vergence during binocular viewing were therefore measured in response to stimuli in the range 1 - 5 D.

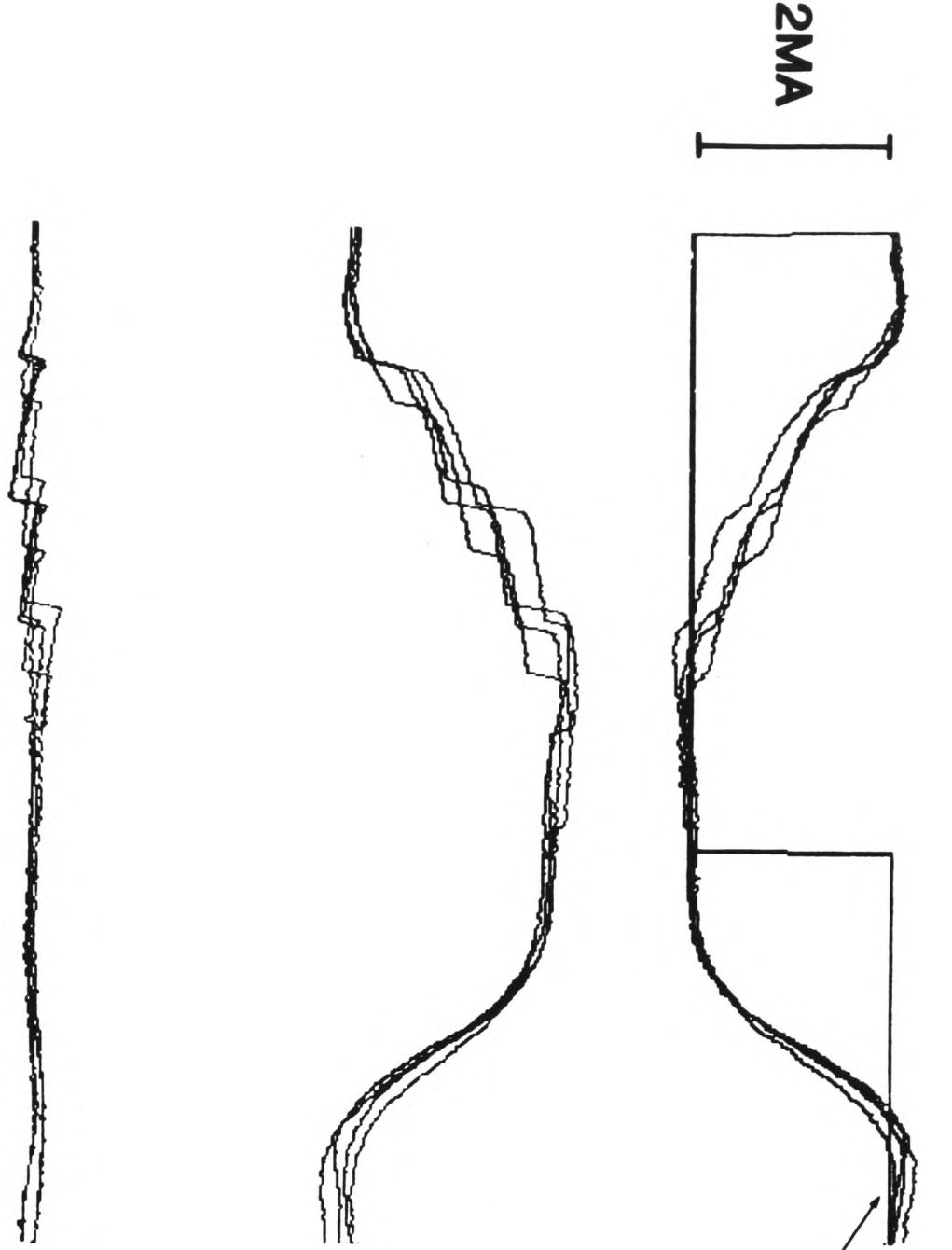
A6.3 Abnormalities of vergence eye movements.

During step changes in the vergence stimulus an unusual asymmetry in the vergence responses of monkey M was observed. This is illustrated in Fig. A6.2. When the target moved directly towards the right eye (Fig. A6.2A, right hand side) no saccades occurred during convergence. In monkeys A and H (illustrated in Fig. 3.1 in Chapter 3) and in human subjects (Alpern and Ellen, 1956; Rashbass and Westheimer 1961b, Westheimer and Mitchell, 1956) saccades are usually observed in this task. During divergence monkey M made several small saccades in the usual way (Fig. A6.2A, left hand side). When the target moved directly towards the left eye (Fig. A6.2B, right hand side) convergence was achieved almost entirely by movement of the left eye, which was followed by saccades to bring the target on to the foveae of both eyes. During divergence a combination of symmetrical vergence movements and saccades were observed, in the normal way (Fig. 6.2B, left hand side). During smooth pursuit of a target not moving in depth, medial movements of the

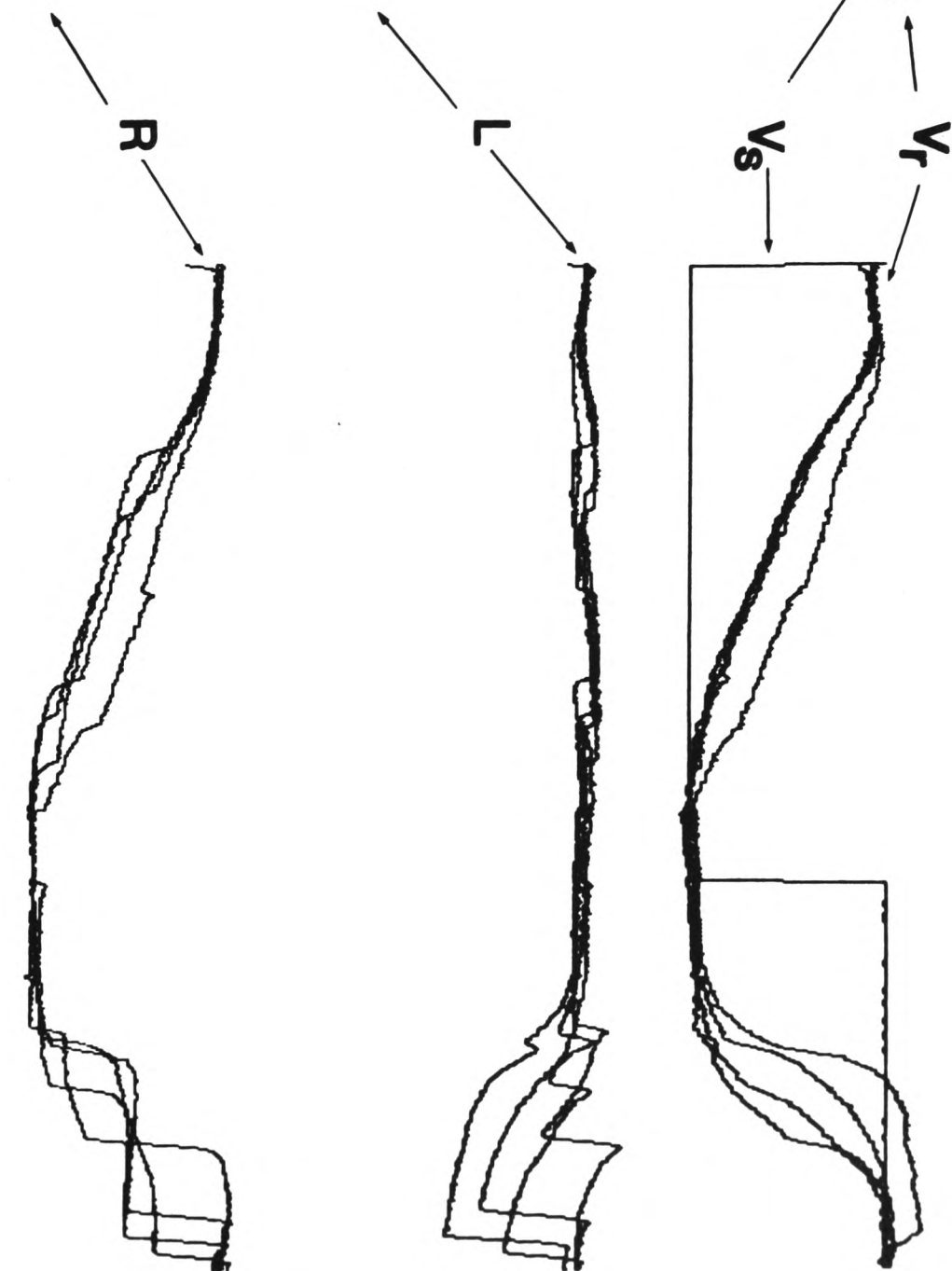
Figure A6.2

Asymmetrical vergence movements in monkey M. The horizontal positions of the right eye (R) and the left eye (L) are shown, rightward movements being shown as downward. The vergence stimulus (V_s) and response (V_r) are also shown. In A) the target appeared to move directly away from and towards the right eye. Note the absence of any saccades during convergence. In B) the target appeared to move directly towards the left eye, yet convergence was achieved almost entirely by rightward movement of the left eye (so that neither eye foveated the target) followed by saccades to foveate the target in both eyes. Note the absence of any significant smooth movements of the right eye. Each half of the figure shows the results of four typical trials superimposed.

A)



B)



0 1 2
SECONDS

0 1 2
SECONDS

right eye appeared normal.

During monocular viewing of target motion towards the left eye it was observed that accommodative-vergence was also achieved predominantly by medial movement of the left eye. The asymmetrical vergence movements were therefore not simply the result of a powerful dominance by the right eye.

One possibility considered was that blurring of the image (following a sudden change in target position) prevented suppression of the animal's incipient nystagmus by the visual stabilization mechanism. The absence of any evident slow medial movement of the right eye would then be attributed to the suppression of the vergence movement to the left by the nystagmus slow phase to the right. Sustained blurring of the image was produced by sudden movements of the target from 1 D to -5 D, in monocular viewing. No movement of either eye was observed until approximately 0.5 seconds after the target moved, and then only a very slow (approximately 0.5 degrees/second) drift of eye position to the right was observed. This movement was too slow, and had too long a latency, to account for the lack of any smooth movements of the right eye in Fig. A6.2B.

It is difficult to account for all these observations together other than by proposing that this animal achieved convergence only by innervation to the left eye, although divergence movements were normal. Since the majority of the experiments described in Chapters 3 and 4 involved targets moving directly towards the right eye, it is possible that this disorder did not much affect the vergence performance described there. The similarity between the data for monkey M and those

for monkeys A and H suggested that this was true, so the data from all three monkeys is presented together in Chapters 3 and 4.

APPENDIX SEVEN

PREDICTION OF ACCOMMODATION AND VERGENCE PERFORMANCE IN CONFLICT TASKS
AND IN NORMAL BINOCULAR VIEWING

A7.1 Prediction of performance in conflict viewing

Assuming that accommodation and vergence responses, A_r and V_r respectively, are linear combinations of the accommodation stimulus and the vergence stimulus, A_s and V_s , we can write:

$$A_r = c_{aa} A_s + c_{va} V_s, \quad (1)$$

and
$$V_r = c_{av} A_s + c_{vv} V_s, \quad (2)$$

where the stimulus and response variables and the coefficients are complex quantities. Note that A_s and V_s are not the blur and disparity inputs to the feedback controllers but the accommodative and vergence components of the stimulus. In normal binocular viewing, $A_s = V_s$. Normalizing to $A_s = V_s = 1$ we have:

$$A_b = c_{aa} + c_{va}, \quad (3)$$

$$V_b = c_{av} + c_{vv}, \quad (4)$$

where A_b and V_b refer to the accommodation and vergence responses (respectively) in normal binocular viewing. We can simulate monocular viewing (absence of a binocular stimulus) by setting $V_r = V_s$. Normalizing to $A_s = 1$ gives:

$$A_m = c_{aa} + c_{va} V_m, \quad (5)$$

$$V_m = c_{av} + c_{vv} V_m, \quad (6)$$

where A_m and V_m are the accommodation and vergence responses

(respectively) in monocular viewing. In a conflict situation where the accommodation stimulus is a factor, k , times the vergence stimulus:

$$A_k = c_{aa}k + c_{va}, \quad (7)$$

$$V_k = c_{av}k + c_{vv}, \quad (8)$$

where A_k and V_k are the accommodation and vergence responses (respectively) in the conflict task. From Equations (3) and (5) we have:

$$c_{aa} = (A_m - A_b V_m)/(1 - V_m), \quad (9)$$

$$c_{va} = (A_b - A_m)/(1 - V_m). \quad (10)$$

Hence upon substituting (9) and (10) into (7) and rearranging:

$$A_k = (A_b(1 - kV_m) + A_m(k-1))/(1 - V_m). \quad (11)$$

Similarly, from Equations (4), (6) and (8):

$$V_k = (V_b(1 - kV_m) + V_m(k-1))/(1 - V_m). \quad (12)$$

A7.2 Prediction of performance in normal binocular viewing

Using a similar method it is possible to use the responses measured in monocular viewing combined with those measured in binocular viewing with accommodation-open-loop to calculate the expected performance of accommodation and vergence in normal binocular viewing. Accommodation-open-loop viewing is simulated by setting $A_s = A_r \exp(-ip)$ where p is the phase lag introduced by the optometer and the accommodation stimulus servo dynamics and i is $(-1)^{\frac{1}{2}}$:

$$A_v = c_{aa} A_v \exp(-ip) + c_{va}, \quad (13)$$

$$\text{and } V_v = c_{av} A_v \exp(-ip) + c_{vv}. \quad (14)$$

Adding Equation (5) $\times (1 - A_v)$ to Equation (13) $\times (1 - V_v)$ and rearranging:

$$c_{aa} + c_{va} = \frac{[A_m(1 - A_v \exp(-ip)) + A_v(1 - V_m)]}{a - V_m A_v \exp(-ip)}, \quad (15)$$

which is the accommodation response in normal binocular viewing (from Equation (3)). Similarly, it can be shown from Equations (6), (14), and (4) that:

$$V_b = [V_v(1 - V_m) + V_m(1 - A_v \exp(-ip))]/(1 - V_m A_v \exp(-ip)). \quad (16)$$

APPENDIX EIGHT

CALCULATION OF VERGENCE AND ACCOMMODATION SENSITIVITIES DESCRIBING
NEURON FIRING

The firing of each neurone was fitted with a linear equation:

$$f = k_v V + k_a A \quad (1)$$

where f is the modulation of the neurone firing, V is the vergence response, A is the accommodation response, and k_v and k_a are vergence and accommodation coefficients respectively. All the terms in this equation are complex quantities with x and y components, and the calculations were performed assuming that the two components were independent random variables. In normal viewing we can write:

$$f_n = k_v V_n + k_a A_n \quad (2)$$

hence:

$$k_a = f_n / A_n - k_v V_n / A_n \quad (3)$$

In viewing with conflicting cues we write:

$$f_c = k_v V_c + k_a A_c \quad (4)$$

hence:

$$k_a = f_c / A_c - k_v V_c / A_c \quad (5)$$

from Equations (3) and (5) we get:

$$k_v = (f_c / A_c - f_n / A_n) / (V_c / A_c - V_n / A_n) \quad (6)$$

and by symmetry:

$$k_a = (f_c / V_c - f_n / V_n) / (A_c / V_c - A_n / V_n) \quad (7)$$

The variance of the denominator in Equations (6) and (7) was small

compared to the variance of the numerator. The variance of the denominator was therefore neglected in the calculation of the variances of the x and y components of the expressions. The variances of f_c/A_c and f_n/A_n were calculated separately and then used to calculate standard errors for the x and y components of k_v , using a standard technique (Armitage, 1977; p. 120) which pooled the variances of f_c/A_c and f_n/A_n . First the variance of the x component of the numerator in Equation (6) ($\text{var}(X)$) was calculated:

$$\text{var}(X) = [(n - 1)\text{var}(f_c/A_c)_x + (m - 1)\text{var}(f_n/A_n)_x]/(n + m - 2), \quad (8)$$

where n is the number of samples obtained from the conflict task, and m is the number of samples obtained during normal binocular viewing. A similar expression was used to calculate the variance of the y component ($\text{var}(Y)$) of the numerator in Equation (6). The variance of the x and y components of k_v were then obtained by dividing the complex variable ($\text{var}(X), \text{var}(Y)$) by the square of the denominator of Equation (6). Since these variances were obtained assuming that $\text{var}(f_c/A_c)$ and $\text{var}(f_n/A_n)$ were equal, the standard errors for the x component of k_v is given by:

$$\text{S.E.}(x) = [(1/n + 1/m)\text{var}(x)]^{1/2} \quad (9)$$

and the equivalent expression gives the standard error for the y component of k_v . It was assumed for both the x and y components of k_v that the mean divided by the standard error was normally distributed. In this case $[x/\text{S.E.}(x)]^2 + [y/\text{S.E.}(y)]^2$ has a Chi-squared distribution with two degrees of freedom. This expression was calculated to estimate confidence limits for k_v . A similar procedure was used to estimate confidence limits for k_a .

The x and y components, along with their variances, were used to describe k_v and k_a in terms of gain and phase, by the method described in Appendix 5.

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