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Eye movements during combined pursuit, optokinetic and vestibular stimulation in macaque monkey

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Abstract During natural behaviour in a visual environment, smooth pursuit eye movements (SP) usually override the vestibular-ocular reflex (VOR) and the optokinetic reflex (OKR), which stem from head-in-space and scene-relative-to-eye motion, respectively. We investigated the interaction of SP, VOR, and OKR, which is not fully understood to date. Eye movements were recorded in two macaque monkeys while applying various combinations of smooth eye pursuit, vestibular and optokinetic stimuli (sinusoidal horizontal rotations of visual target, chair and optokinetic pattern, respectively, at 0.025, 0.05, 0.1, 0.2, 0.4, and 0.8 Hz, corresponding to peak stimulus velocities of 1.25–40°/s for a standard stimulus of ±8°). Slow eye responses were analysed in terms of gain and phase. During SP at mid-frequencies, the eyes were almost perfectly on target (gain 0.98 at 0.1 Hz), independently of a concurrent vestibular or optokinetic stimulus. Pursuit gain at lower frequencies, although being almost ideal (0.98 at 0.025 Hz with pursuit-only stimulation), became modified by the optokinetic input (gain increase above unity when optokinetic stimulus had the same direction as target, decrease with opposite direction). At higher stimulus frequencies, pursuit gain decreased (down to 0.69 at 0.8 Hz), and the pursuit response became modified by vestibular input (gain increase during functionally synergistic combinations, decrease in antagonistic combinations).Thus, the pursuit system in monkey dominates during SP-OKR-VOR interaction, but it does so effectively only in the mid-frequency range. The results can be described in the form of a simple dynamic model in which it is assumed that the three systems interact by linear summation. In the model SP and OKR dominate VOR in the low- to mid-frequency/velocity range, because they represent closed loop systems with high internal gain values (>>1) at these frequencies/velocities, whereas the VOR represents an open loop system with about unity-gain (up to very high frequencies). SP dominance over OKR is obtained by allowing an ‘attentional/volitional’ mechanism to boost SP gain and a predictive mechanism to improve its dynamics.

Key words Pursuit eye movements · Vestibulo-ocular reflex · Optokinetic reflex · Visual-vestibular interaction · Macaque monkeys

Abbreviations *EH* Eye-in-head · *ES* eye-in-space (gaze) · *HS* head-in-space · *OKR* optokinetic reflex · *OPT* optokinetic stimulus (corresponding to PT, visual pattern-to-target, in the presence of a target, and to *PH* visual pattern-to-head, in the absence of target) · *PE* visual pattern-to-eye · *PH* visual pattern-to-head · *PS* visual pattern-in-space · *PT* visual pattern-to-target · *PURS* pursuit stimulus (corresponding to TH) · *TE* target-to-eye (retinal error) · *TH* target-to-head · *TS* target-in-space · *VEST* vestibular stimulus (=HS) · *VOR* vestibulo-ocular reflex

Introduction

During walking or driving a car, we normally track visual objects in the presence of visual flow of the surroundings relative to our eyes and of head movements in space. The visual flow and the head movements represent stimuli which, if presented alone, would yield an optokinetic reflex (OKR) and a vestibulo-ocular reflex (VOR), respectively. In the situation just described, however, OKR and VOR do not interfere to any considerable

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degree with the pursuit eye movement. It appears that the ineffectiveness of OKR and VOR in this situation is not achieved by a particular inactivation or suppression mechanism of OKR and VOR. Rather it is held by most researchers in the field (e.g. Merrill and Stark 1963; Robinson 1977) that smooth pursuit eye movements (SP), OKR and VOR interact mutually by way of linear summation. This, on first sight, surprising notion might be explained by the fact that SP and OKR dominate the VOR, because they represent closed loop systems with high internal gain values in the low- to mid-frequency/velocity range (Koerner and Schiller 1972; Dubois and Collewijn 1979), where their dynamics are not limited by the delay of visual processing, whereas the VOR represents an open loop system with about unity-gain and comes into play only at high frequencies/velocities (see Schweigart et al. 1995, 1997)[1]. On the other hand, SP dominates the OKR, because SP shows higher gain values and better dynamics than the OKR (see Barnes 1993). This is related, at least in part, to the fact that attentional/volitional mechanisms which enhance gain, together with predictive mechanisms which improve dynamics, are more effective in SP than in OKR (Barnes 1993). Thus it appears that the ineffectiveness of VOR or OKR in the above-described situation can be explained mainly by gain factors and dynamics in a network in which interaction basically operates by linear summation. Experimental evidence for this view is still incomplete with respect to SP-OKR interaction, whereas SP-VOR and OKR-VOR interaction have been widely investigated (see Barnes et al. 1978; Lau et al. 1978; Lisberger et al. 1981; Paige 1983).

SP and OKR in humans and non-human primates appear to have evolved during phylogenesis from the same source, so that it does not appear intuitive at first sight to consider them as two visuo-oculomotor systems that are independent of each other to some extent. OKR in these species displays two distinct components. Upon onset of optokinetic stimulation, eye velocity first shows a rapid rise; this component is considered to be phylogenetically ‘young’, because it developed only in mammals with frontal eyes (‘rapid’, ‘direct’ or ‘cortical’ component). There follows a slow further build-up of eye velocity; this component is considered to be phylogenetically older, being present already in vertebrates with lateral eyes (‘slow’, ‘indirect’ or ‘subcortical’ component; see Barnes 1993). Because of the latter component, eye velocity endures for some time when the visual stimulus is extinguished (optokinetic afternystagmus). The rapid component has often been associated with SP, but this is probably because it plays the largest role in SP, not because it is exclusive to SP (Barnes 1993).

Of fundamental importance for SP is the role played by attentional and volitional mechanisms, which apparently lead to an enhancement of the gain of the rapid direct pathway for a selected visual target, be this either one or the other of two independently moving superimposed optokinetic patterns (Niemann et al. 1994; dichoptic conditions: Enokkson 1961; Fox et al. 1975; Logothetis and Schall 1990) or of two presented light spots (Collewijn et al. 1982). The eyes then follow the attended stimulus with the properties of SP, yet slightly less effectively than with presentation of a single stimulus only.

Evidence for some independence, at least, of the two visuo-oculomotor subsystems also comes from studies using single neuron recordings. For instance, part of the cells in the nucleus of the optic tract (NOT) are active predominantly with OKR, others with SP, while still others fire similarly with both OKR and SP (e.g. Ilg and Hoffmann 1991). Evidence for some independence of SP and OKR also comes from studies on the cortical areas of MT (middle temporal area) and MST (medial superior temporal area). Some pursuit neurons in MST responded to the motion of a large pattern but showed little or no response to small spots and another group of pursuit neurons (foveal MT and many cells in the lateral-anterior MST) responded preferentially to small spot motion or equally well to small spot motion or large field motion (Komatsu and Wurtz 1988). Furthermore, the notion of two subsystems is in line with findings showing that there are clinical cases in which either SP or OKR is selectively impaired (Barratt et al. 1985). Also, bilateral lesions of a ‘pursuit area’ in the frontal lobe in monkey led to impairment of SP and spared OKR (Keating et al. 1996).

Most previous studies on SP-OKR interaction considered steady-state smooth pursuit across a structured visual background, revealing a slightly reduced gain as compared to that across a homogeneous or dark background (humans: Merrill and Stark 1963; Yee et al. 1983; Collewijn and Tamminga 1984; Niemann et al. 1994; Masson et al. 1995; Worfolk et al. 1993; monkeys: Keller and Kahn 1986; Mohrmann and Thier 1995), with the effect being most prominent when pursuit target and optokinetic background are located in the same depth plane (humans: Howard and Marton 1992). Furthermore, motion of the background counter to the SP target motion decreases SP, while background motion in the same direction as the target enhances SP (humans: Yee et al. 1983; Niemann and Hoffmann 1997; also Merrill and Stark 1963; van den Berg and Collewijn 1986; Masson et al. 1995). SP decrease with counter motion of the back-

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[1] The reader who is not familiar with this ‘cybernetic view’ might imagine that in the SP or OKR closed loop system the deviation (the error) of the eye trajectory from the path set by the visual input signal tends to drag the eye continuously towards the path, and the more so the higher the internal gain of the system is. In contrast, the open loop vestibular signal sets an eye movement path according to the current head-in-space movement (with a negative sign, thus compensating for the head movement), without a feedback of the visual error signal to the head plant (neck muscles). This vestibular mechanism (the VOR) operates even in the absence of visual cues and, taking into account that the head represents the platform for the eyes, it allows for head movements without interfering with gaze (the eyes remain approximately stationary in space). There is experimental evidence that the VOR remains effective even in conditions in which the head participates in the tracking of a visual target (visual signal fed into head plant; Barnes 1979) and with rapid (saccadic) gaze shifts of small amplitude (<20°; Tomlinson and Bahra 1986).

ground becomes more pronounced with increasing SP target velocity and/or increased background velocity (Yee et al. 1983; Niemann et al. 1994; Masson et al. 1995). With only a rough symmetry of the ‘antagonistic’ and the ‘synergistic’ effect on steady state SP by counter and with background motion, respectively (e.g. Masson et al. 1995; Niemann and Hoffmann 1997), it is difficult to conclude that the underlying interaction between the two systems occurs by linear summation. In the study by Yee et al. (1983), who included patients with reduced SP in their study and observed in these a greater reduction on SP by background motion (also Hood 1975), the effects became more and more asymmetric with increasing target velocity. The latter authors concluded that an “algebraic summation of independently induced pursuit and OKR eye movements could not account for all the experimental observations”. Kowler et al. (1984), who made the physical characteristics of the moving target (1.2°/s) and the stationary background identical, observed only minor background effects on SP and attributed these to reduced effort and attention, rather than to a specific interaction mechanism.[2]

A detailed quantitative analysis of SP-OKR interaction which considers the differences in the dynamic characteristics of the two systems (i.e. differences of frequency characteristics) has not yet been reported. Furthermore, when considering the question of a linear interaction of SP and OKR in the context of closed loop systems with different gain values and dynamics (see first paragraph), it is clear that a simple hypothesis based on algebraic summation of effects of independently induced SP and OKR is not appropriate. In humans the study of SP-OKR interaction is hampered by the fact that SP (which mainly consists of a direct component only) is much stronger than OKR (which consists of both a direct and an indirect component; cf. “Discussion”), leaving little room to obtain clear effects [this led Yee et al. (1983) to study patients with reduced SP, see above, and Worfolk and Barnes (1992) to consider ways of degrading pursuit]. These considerations led us to study SP-OKR interaction in monkeys in which OKR is known to be relatively stronger than in man (e.g. an optokinetic afternystagmus is clearly present in monkeys, but hardly detectable in man). We applied a number of different stimulus combinations and, using sinusoidal stimuli, covered a rather broad range of stimulus frequencies. Choosing low stimulus intensities (velocities) we remained within the linear range of both SP and OKR in most of the trials. Furthermore, we addressed the question of linear interaction using a description of our findings in terms of a dynamic model that accounts for the closed loop nature of SP and OKR.

Our study represents a continuation of previous work we performed on OKR-VOR interaction in monkeys (Schweigart et al. 1995). In the present experiments we included, in addition to SP-OKR interaction, the interaction between SP and VOR, which is basically similar to that between OKR and VOR, as can be expected from previous work (Schweigart et al. 1995). For the sake of completeness we added trials in which all three systems, i.e. SP, OKR, and VOR, interacted. To our knowledge the present study is the first to characterise SP-OKR-VOR interaction over a broad range of stimulus frequencies and for a rather large number of different stimulus combinations and to interpret the findings in terms of a dynamic model.

Materials and methods

Two adult macaque monkeys were used for the experiments. They were seated on a rotation chair which allowed horizontal whole body rotations for vestibular stimulation. The chair was surrounded by a cylindrical screen (vertical axis; radius 0.9 m), onto which a black and white random patch pattern could be projected for optokinetic stimulation. The pattern covered horizontally about 80° of the visual field of either side, about 55° up, and full field down. It could be rotated in the horizontal plane. At the monkeys’ eye level the pattern was interrupted by a black horizontal strip of 4.5° width, onto which a visual target was projected (red light spot; diameter 0.5°). The target was projected via a mirror galvanometer and could also be moved in the horizontal plane. The black strip was introduced to prevent local interference effects of the background (pattern) on the pursuit target. The reason is that we had observed in psychophysical studies in man that there was a facilitating effect on vection (visually induced self-motion perception) when the target crossed the optokinetic pattern rather than when it passed the pattern at some distance. We suspected that the crossing might have an effect also on eye movements. By excluding it we wanted to reduce the importance of the pattern, in order to be on the safe side, because we found in the present experiments a considerable optokinetic response even in the presence of the fixation target (see “Results”).

The monkeys’ heads were attached to the chair by means of chronically implanted head holders such that the vertical axes of the rotation devices (chair, pattern projector and mirror galvanometer) passed through the intersection of the interaural and naso-occipital axes. Months before the experiments, monkeys had undergone surgery for head holder implantation with the animals under general anaesthesia (mixture of ketamine hydrochloride 25 mg/kg i.m., Ketavet, Parke-Davis, Berlin, Germany, and xylazine 2 mg/kg i.m., Rompun, Bayer, Leverkusen, Germany).

The monkeys’ eye position in the horizontal and vertical planes was recorded with an infrared technique (Bach et al. 1983). For eye position calibration, a pursuit task in the dark was used. Eye position gain was taken as unity when the monkey performed an essentially smooth pursuit eye movement for sinusoidal target rotations

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[2] Note that the initial part of the SP-OKR interaction will not be considered here, because it is complicated by the delay time of the visual signals. For instance, upon motion of SP target and optokinetic background counter to each other, eye acceleration in the earliest part of SP is enhanced, while in later parts it is diminished (see Niemann and Hoffmann 1997 for results, overview and interpretation). Furthermore, the initial part is complicated by the fact that there is a transition from fixation to SP; fixation is a behaviour that is distinct from pursuit, and thus not equal to pursuit with a velocity of 0°/s (see Robinson et al. 1986; Luebke and Robinson 1988). The distinction is of relevance with transitions between fixation and pursuit, but the effects observed are very discrete (Huebner et al. 1992). Therefore, also fixation is not considered separately in the present context, despite the fact that fixation in terms of viewing a head-stationary target during optokinetic stimulation was included in our experiments (see “Materials and methods” and “Results”). Thus, aspects of ‘non-retinal suppression of the VOR’, as described in both man (Gauthier and Robinson 1975; Barnes and Eason 1988) and monkey (Lisberger 1990; Cullen et al. 1991), remain outside the scope of the present study.

of ±8° at 0.2 Hz (peak stimulus velocity 10°/s). Such a unity-gain eye rotation is plotted as a ±8° response in the data presentations – this despite the fact that monkey's actual eye movements were approximately 0.4° (5%) larger than target rotation, because their eyes were located in front of the axes of the rotation devices.

The monkeys were trained by water reinforcement to fixate their eyes on the target, independently of whether their bodies (the chair), the target, and/or the pattern were rotated. Fixation periods for receiving reward were varied between 13 and 25 s, after which the target was switched off. In order not to suppress possible vestibular/optokinetic modifications of the pursuit response, a relatively large fixation-reward window was set (±4° about target). We were well aware of the danger that making the reward window rather broad could lead the monkeys to fixate/track the object sluggishly or not at all. Actually, we started the experimental series in both monkeys with a narrow window (±1°). However, it soon became evident that, when combining pursuit/fixation tasks with optokinetic and/or vestibular stimuli at certain frequencies, the monkeys often were not able to fulfil their task since the eyes were too often driven out of the window, with the consequence that the trial yielded no reward. This occurred despite the fact that the monkeys did an excellent job at other frequencies and with other stimulus combinations. To be on the safe side we continued to use the small window in some trials of the training sessions (which were interspersed between sessions for measurement). Thus, we convinced ourselves that the monkeys were doing their best. But we avoided using the small window too often, in order not to frustrate the animals. Fixation-reward windows even smaller than ±1° could not be used in most stimulus combinations/frequencies. In the intervals between target presentations, the monkeys usually looked attentively at the screen. These intervals were used to elicit pure vestibular or optokinetic eye responses (without augmenting the animals' vigilance by pharmacological means). The periods of reward, during which the monkeys licked the water, were not used for eye response evaluation. Also, evaluation of vestibular and optokinetic eye responses was restricted to recordings during which the eyes remained within the linear range of the oculometer.

Chair (head) rotation in space (HS) represented the vestibular stimulus (VEST). Target rotation relative to the head (TH) represented the pursuit eye movement stimulus (PURS). Rotation of the visual pattern relative to the target (PT) represented the optokinetic stimulus (OPT); assuming that the monkeys kept their eyes almost ideally on the target, OPT would be approximately determined by pattern movement relative to the eyes. In the absence of the target, OPT corresponds to visual pattern-to-head (PH). Figure 1A gives a schematic presentation of the stimulus conditions in order to illustrate the relationship between physical and physiological stimuli. Given a head-in-space (HS; VEST) stimulus of 8° towards the right side, for instance, an 8° in-phase target-to-head (TH; PURS) stimulus requires a rightward target-in-space (TS) rotation of 16°. Further addition of an 8° in-phase visual pattern-to-target (PT; OPT) stimulus would require a rightward visual pattern-in-space (PS) rotation of 24°. This figure may help the reader to consider the stimuli in a common coordinate system, i.e. space.

Rotations were sinusoidal with stimulus frequencies of 0.025, 0.05, 0.1, 0.2, 0.4, and 0.8 Hz. Stimulus amplitude was kept constant at ±8° for monomodal stimulation corresponding to peak stimulus velocities of 1.25, 2.5, 5, 10, 20, and 40°/s. Originally, we had also tried to use higher stimulus frequencies and amplitudes, up to a range where we previously observed that VOR-OKR interaction becomes non-linear (Schweigart and Mergner 1995; Schweigart et al. 1995, 1997) and where we observed an unexpected effect from the OKR (see "Results"). However, performance of our monkeys deteriorated dramatically with these stimuli, and monkeys tended to refuse to collaborate.

For combinations of stimuli the amplitude of one stimulus was kept constant (±8°; e.g. VEST) while that of a second stimulus was varied between 0°, ±8°, and ±16° (e.g., PURS or OPT). The two stimuli could have either the same direction (in-phase combination, Δφ=0°) or opposite directions (counter-phase, 180°). For simplicity, we shall denote in-phase stimuli by positive values (e.g., VEST=8°, OPT=8°) and a counter-phase stimulus by a negative sign (e.g., VEST=8°, OPT=–8°), irrespective of the absolute direction of the sinusoidal stimulus waveform used. Each stimulus combination and each frequency was tested in at least three different experimental sessions on three different days in each monkey.

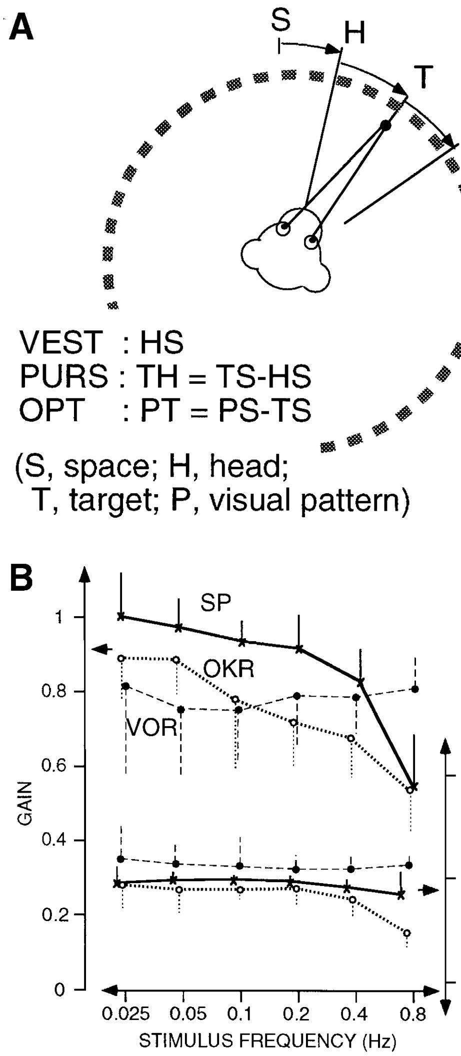

Fig. 1 **A** Schematic representation of the relation between physiological stimuli and physical stimuli (monkey from above, being rotated in space while viewing a visual target and optokinetic pattern). **B** Responses to monomodal stimuli. Gain and phase of VOR in the dark (*filled circles*), OKR (*open circles*), and smooth pursuit (SP; *crosses*) as a function of stimulus frequency (peak angular displacement 8°, peak stimulus velocity covaried with frequency, 1.25°/s at 0.025 Hz and 40°/s at 0.8 Hz). VOR phase is referred to an ideal counterrotation of the eyes compensating the head rotation (0°), while OKR phase and SP phase are referred to the rotation of the visual pattern and target relative to the head (0°). Here and in the following figures, mean values and standard deviations are given using the data of both monkeys

Readings of target, chair, and pattern position as well as of eye position were recorded with a sampling rate of 250 Hz and stored in a laboratory computer. Data analysis was off-line. Smooth (slow-phase) and saccadic (fast-phase) components of the eye response were separated using an interactive computer program (cf. Fig. 2A,B). The smooth eye response was characterised in terms of gain and phase of horizontal eye-in-head position using the fundamental waves of the fast Fourier transformation. Eye-in-space displacement (gaze) was obtained by vector summation of the eye-in-

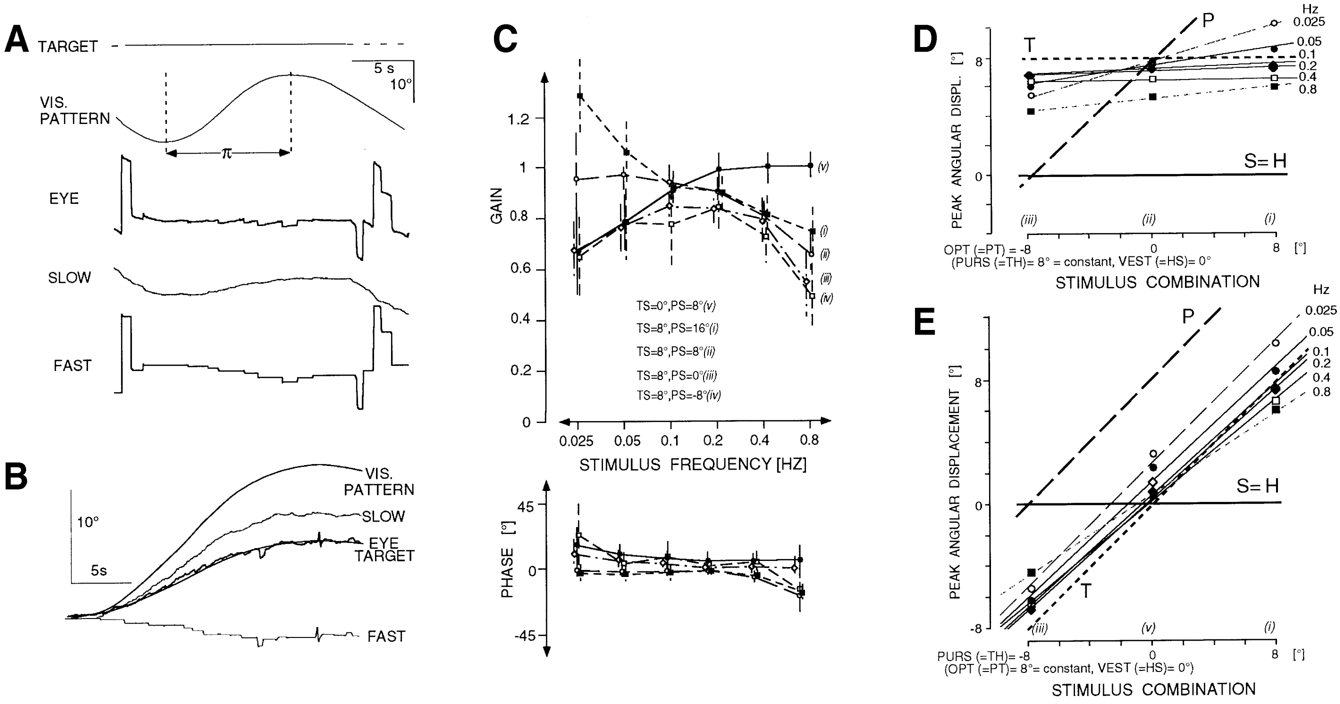

Fig. 2A–E Pursuit (*SP*)–optokinetic (*OKR*) interaction. **A** Example of original eye response during sinusoidal rotation of the visual pattern at 0.05 Hz (peak velocity 2.5°/s) with target stationary. Illumination of target indicated by *full line*. The two lowest traces give slow and fast eye responses after separation with the help of a computer program, respectively. The period indicated by π was used for analysis. **B** Example at 0.025 Hz, in which visual pattern was rotated in the same direction as target, but with twice the amplitude (target 1.25°/s; pattern 2.5°/s). **C** Bode plot for the five different stimulus combinations tested. Mean gain and phase values plotted as a function of stimulus frequency. **D, E** Eye-in-space displacement curves as a function of stimulus combination for the two sets of optokinetic (*OPT*) and pursuit (*PURS*) stimulus combinations used (**A** combination set OPT=varied, PURS=constant; **B** set PURS=varied, OPT=constant; VEST always 0°). Regression lines are given separately for each stimulus frequency. The *horizontal full line at 0° displacement* represents space (*S*). Target (*T*) and pattern (*P*) displacements are indicated by the *dotted* and *dashed lines*, respectively. *Abscissas, from left to right* **D** OPT=–8°/0°/8° (*minus sign* indicating counterphase and *plus sign* in-phase combination); **E** PURS=–8°/0°/8°

head response with the head-in-space (chair) signal (peak displacement, vector length; phase, vector direction). The data of each animal were averaged separately (*n*=4–30 values per stimulus condition). A comparison across the two monkeys' data showed that they were very similar. We therefore lumped the data of the two animals together, presenting them as mean values (±SD). All experiments were carried out in accordance with the German Law for the Protection of Animals and with the principles of laboratory animal care (NIH publication No. 86–23, revised 1985).

Results

Monomodal stimulation

Figure 1B gives the responses to monomodal stimulation (vestibular, optokinetic, smooth pursuit). These data have already been reported in a previous study on VOR-OKR interaction (Schweigart et al. 1995). They are repeated here, since they serve as a basis for comparison for the results obtained with the SP-OKR, SP-VOR and SP-OKR-VOR stimulus combinations in the same monkeys presented here. Although they essentially reproduce the known characteristics of SP (in the dark), VOR (in the dark) and OKR in monkeys, they will be briefly described. The figure shows the mean gain and phase values (and standard deviations) as a function of stimulus frequency (0.025–0.8 Hz; with the constant peak displacement of ±8° used, peak angular velocity amounted to 1.25–40°/s). SP gain after removal of quick phases (thick lines) was approximately unity at 0.025 Hz (1.25°/s) and showed only a modest decrease when increasing frequency up to 0.2 Hz (10°/s), and a more pronounced decrease at 0.4 Hz (20°/s; gain=0.83) and 0.8 Hz (40°/s; gain=0.54). SP phase ranged between 0° and –6.5° (negative values indicating phase lag with respect to visual target displacement). Similarly, OKR gain (dotted lines) was highest at low frequencies [almost 0.9 at 0.025 Hz and 0.05 Hz (2.5°/s)] and decreased with increasing frequency (0.53 at 0.8 Hz). OKR phase exhibited a slight lag at 0.025–0.4 Hz (–4° at 0.025 Hz; with respect to pattern displacement in space) and developed a more considerable lag at 0.8 Hz (–27°). In contrast, VOR gain (dashed lines), which ranged between 0.75 and 0.85, remained approximately constant across frequency/velocity. VOR phase showed a slight and almost constant lead (here plotted with respect to –HS, i.e. it is assumed to be compensatory).

Pursuit-optokinetic stimulus combinations

Two examples of the eye response during combined pursuit and optokinetic stimulation are shown in Fig. 2A,B. One example gives the eye response during sinusoidal rotation of the visual pattern at 0.05 Hz (peak stimulus velocity 2.5°/s) with the target remaining stationary (Fig. 2A). When the target was illuminated (for 17 s), the monkey tried to fixate it, but its eyes became slightly shifted in the direction of pattern motion and were reset by small saccades. This can well be appreciated from the lower two traces of the figure, which show the slow and fast eye responses after separation with the help of a computer program. After extinction of the target, the eyes resume following of the pattern, in a similar way to before target appearance. The period indicated by π was used for analysis in this example. Figure 2B gives the other example, in which the target was rotated at 0.025 Hz by 8° to the right (1.25°/s) whilst the visual pattern rotated in the same direction by 16° (2.5°/s). Note that the slow component of the eye movement was clearly larger than the target movement, due to the effect of the optokinetic stimulus.

Five different pursuit-optokinetic stimulus combinations were tested (head and body always stationary). They are shown in Fig. 2C: (i) target and pattern rotated in the same direction, but pattern with twice the amplitude/velocity (TS=8°, PS=16°); (ii) target and pattern rotated together (TS=8°, PS=8°); (iii) target rotated, pattern stationary (TS=8°, PS=0°); (iv) pattern rotated by same amount/velocity as target, but in the opposite direction (TS=8°, PS= –8°); (v) target stationary, pattern rotated (TS=0°, PS=8°). In combinations (i)–(iv) gain was calculated by the ratio of eye-in-space to target-in-space displacement (ES/TS) and phase was referred to TS, whereas in combination (v) gain was taken from the ratio of eye-relative-to-pattern displacement to target-relative-to-pattern displacement (EP/TP) and phase was referred to TP. Noticeably, by way of this presentation an ideal stabilisation of the eyes on target would be represented in all combinations in Fig. 2C by a gain of unity and a phase of 0° across frequency. The given results were obtained by using the data of both monkeys.

The phase curves in Fig. 2C are almost ideal (close to zero) over the frequency range tested (exceptions 0.8 Hz). Thus, eye and target movements were fairly well synchronised independently of the stimulus combination. In contrast, the gain clearly depended on the stimulus combination, more clearly at low than at high frequency/velocity. In particular, target rotation together with pattern (ii; TS=8°, PS=8°) yielded a response similar to pursuit alone (see Fig. 1B), with a gain close to unity at low frequency and some gain attenuation at high frequency. A clear gain attenuation at low frequencies was obtained with target rotation against the stationary pattern (iii; TS=8°, PS=0°). A similar gain attenuation at low frequency was found with pattern rotation by the same amount, but in the opposite direction to the target (iv; TS=8°, PS=–8°) and with pattern rotation relative to the stationary target (v; TS=0°, PS=8°). On the other hand, when rotating the pattern in the same direction as the target, but with twice the amplitude/velocity (i; TS=8°, PS=16°), gain was increased above unity at low frequency.

In order to better understand the dependence of the response on stimulus combination, the data of combinations (i)–(iii) and (i), (iii), (v) are replotted in Fig. 2D,E separately for each stimulus frequency, in terms of peak eye displacement relative to space. In Fig. 2D the optokinetic stimulus was varied but the pursuit stimulus always had the same magnitude [combinations (i), (ii), and (iii); PURS=TH: 8°=constant, i.e. the target was rotated relative to the stationary head/space; OPT=PT was varied: –8°, 0°, and 8°; VEST=HS: always zero].[3] To also illustrate the physical motion of the stimulus, the plots show the displacements of target and of visual pattern (T and P lines, respectively) relative to space and to the head that was stationary in this set of combinations (S=H=0°).

Four observations can be made from Fig. 2D: (1) eye displacement values for a given frequency are well described by a regression line, indicating that optokinetic and pursuit effects sum linearly over the stimulus range plotted [cf., however, Fig. 2C: a further increase of the optokinetic stimulus in combination (iv) appears to have no considerable additional effect as compared to combination (iii), so that one could assume, on first sight, that linearity holds only for this limited range; see “Discussion”]. (2) The regression lines in the 0.1–0.4 Hz frequency range (peak stimulus velocities 5–20°/s for the pursuit stimulus) are essentially parallel to the T line, indicating that eye following is almost independent of the varied optokinetic stimulus in the combination at these frequencies, with the amount of eye displacement slightly decreasing with increasing frequency. (3) At 0.05 Hz (2.5°/s) and even more at 0.025 Hz (1.25°/s), the regression lines develop a positive slope, indicative of a growing response to visual pattern motion. (4) Note also that the regression line for 0.8 Hz (40°/s) develops a slight positive slope, suggestive of some following response to the pattern also at high frequency.

In combinations (iii), (v), and (i), which are shown in Fig. 2E, the pursuit stimulus was varied (PURS=TH: –8°, 0°, and 8°) and the optokinetic stimulus was always of the same magnitude (OPT=PT: 8°=constant; the head was stationary, VEST=HS: 0°). In terms of physical motion of target and pattern: (i) target rotated and pattern stationary, (v) target stationary and pattern rotated, and (iii) target rotated and pattern rotated in same direction, but with double amplitude (velocity). The eye displacement values again could be described well by regression lines for each frequency, which fell close to the T line. At low frequency, the regression lines are parallel, but shifted toward the P line, confirming that the eyes followed the visual pattern to some extent. At high frequency, the slope of the regression lines decreases, indicating an attenuation of pursuit gain.

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[3] Note that OPT is defined here as relative motion between pattern and target. Consider the case that pattern and target are moved together and pursuit of target is close to ideal; then the optokinetic stimulus has essentially no effect on the eye response. We express this by denoting the stimulus combination as PURS=8°, OPT=0°. In terms of the physical motion of the pattern, the combinations PURS=8°, OPT=–8°/0°/8° mean the pattern was stationary in space/rotated together with the target/rotated in the same direction as the target, but with double amplitude (velocity). Only in conditions in which there was no target do we define OPT in the conventional way as pattern-to-head rotation (which is identical to pattern-in-space rotation when the monkey is stationary).

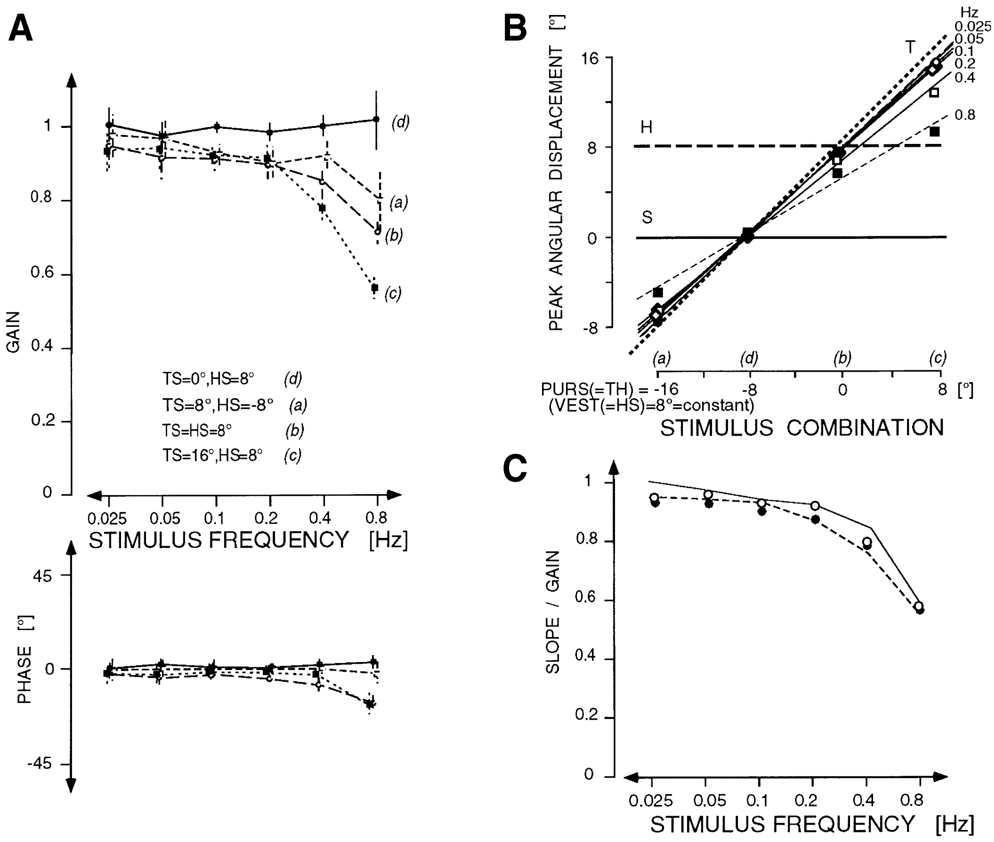

Fig. 3A–C Pursuit (*SP*)–vestibular (*VOR*) interaction. **A** Gain and phase curves of different SP-VOR combinations [gain: unity defined as ES (eye in space)=TS (target in space); phase re TS, in combination *d* re TH (target to head)]. For details see text. **B** Peak angular displacement of eye in space as a function of stimulus combination, replotted from results in **A** [combination set PURS=varied, VEST=constant]. Regression lines obtained for each stimulus frequency are given (presentation as in Fig. 2D,E). *Abscissa, from left to right:* PURS=–16°/–8°/0°/8°. **C** Slope of regression lines plotted as a function of stimulus frequency. *Black circles* give the slope values derived from Fig. 3B (*dashed curve* gives the results of a computer simulation of this combination set), while *open circles* were obtained from a combination set in which VEST=varied (–8°, 0°, and 8°) and PURS=constant (8°). *Solid curve* represents gain values of the pursuit response alone in darkness (taken from Fig. 1B)

Pursuit-vestibular stimulus combinations

Four different pursuit-vestibular stimulus combinations were tested (with the optokinetic pattern extinguished and only target visible in darkness). These combinations are shown in Fig. 3A: (a) target rotated by the same amount as the head, but in the opposite direction (TS=8°, HS=–8°); (b) target kept in fixed alignment with the head that was rotated (TS=8°, HS=8°); (c) target and head rotated in the same direction, but the target with twice the amplitude (TS=16°, HS=8°); and (d) target stationary, head rotated (TS=0°, HS=8°). In combinations (a)–(c) gain was calculated by the ratio of eye-in-space to target-in-space displacement (ES/TS) and phase was referred to TS, whereas in combination (d) gain was taken from the ratio of eye-in-head to target-to-head displacement (EH/TH) and phase was referred to TH. By way of this presentation, an ideal stabilisation of the eyes on the target would be represented by a gain of unity and a phase of 0° in all combinations. In Fig. 3A gain and phase of the responses are plotted as a function of stimulus frequency. Note that the phase curves are almost ideal (close to zero) over the frequency range tested [exceptions: combinations (b) and (c) at 0.8 Hz]. Thus, eye and target movements were rather well synchronised, independently of the stimulus combination. In contrast, the gain clearly depended on the stimulus combination, more clearly at high than at low frequency, exhibiting, to different degrees, a monotonic decrease above 0.2 Hz (peak velocities, 10°/s for VEST and 0–20°/s for PURS). An exception was the combination d (TS=0°, HS=8°; target stationary, head rotated), where the gain remained close to unity across frequency (note that unity gain in this case means that the eyes are almost stationary in space).

In order to understand the dependence of the response on stimulus combination, these data are replotted in Fig. 3B, separately for each stimulus frequency, in terms of peak eye displacement relative to space as a function of stimulus combination. One stimulus was kept constant (VEST=HS: 8°=constant) and the other was varied (PURS=TH varied: –16°, –8°, 0°, and 8°).[4] In other words, the monkeys were always rotated with a peak displacement of 8° and the direction and displacement of target rotation was varied (see H and T lines, respectively, which give the displacements of target and head relative to space).

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[4] Note that, again, we had to extend some of the commonly used stimulus definitions in the context of the present experiments. For instance, a pursuit stimulus, with the monkey remaining stationary, often is defined in terms of target motion in space. This is a simplification which no longer is feasible when the monkey is rotated in space. This point becomes immediately clear if one considers a target rotation in space, with the monkey being rotated in the same direction and by the same amount as the target. In this condition the pursuit stimulus is zero (no relative motion between target and head or eyes, given the eyes are not moving in the orbits). Any additional assumption of a VOR that is to be compensated for by the pursuit system in the mid- to high frequency range would make the considerations in the present context much more complicated. Therefore, we defined the pursuit stimulus (PURS) as relative motion between target and head.

Three observations can be made from Fig. 3B: (1) eye displacement values for a given frequency are well described by regression lines, indicating that vestibular and pursuit effects sum linearly. (2) The regression lines at low stimulus frequencies/velocities (0.025–0.2 Hz/ 1.25–10°/s for VEST, 1.25–20°/s for TS and PURS) almost coincide with the T line, indicating that the eyes are rather effectively locked on target at these frequencies, independent of the stimulus combination. With increasing frequency (0.4, 0.8 Hz – 20, 40°/s for VEST; 20, 40, 80°/s for TS and PURS), in contrast, the slopes become smaller and the regression lines progressively rotate towards the horizontal S (space) line, indicating that the eyes become increasingly stabilised in space. (iii) The intersection point of the regression lines essentially coincides with the intersection of the T and S lines, which corresponds to combination d (TS=0°, HS=8°; head rotated, target stationary). Remarkably, gaze stabilisation on target with this combination is essentially independent of stimulus frequency; yet it represents only a special case in a continuum across the different combinations.

In order to compare the pursuit response to the different PURS-VEST stimulus combinations with that to the monomodal PURS stimulation, the slopes of the regression lines are plotted in Fig. 3C as a function of frequency. In this graph, a slope of 1 would indicate that the regression line is parallel to the target line, i.e. that the eye displacement varies in perfect concert with target displacement, whereas a slope of 0 would indicate that the eyes do not follow the target. The black circles give the slope values derived from Fig. 3B; they are close to unity at 0.025 Hz, but decrease with increasing frequency. Similar slope values were obtained from additional regression calculations for stimulus combinations in which VEST (HS) was varied and PURS (TH) was held constant (open circles in Fig. 3C). Also, for comparison, the gain curve of the monomodal pursuit response is superimposed on the slope plot (solid curve, taken from Fig. 1B). Noticeably, slope values and pursuit gain almost coincide, indicating that pursuit performance is always close to 100% in the combination responses. Thus, in these combinations pursuit is never suppressed or changed to any considerable degree.

Combined stimulation of all three modalities

As shown in the previous two sections, the interactions between pursuit and VOR eye movements and between pursuit and OKR eye movements are linear over the indicated frequency and amplitude ranges, and we have shown previously that OKR-VOR interaction is linear (Schweigart et al. 1995). Therefore, we would predict that the interactions of all three inputs also are linear. To verify this hypothesis, we applied several stimulus combinations in which both target and visual pattern were presented and, in addition, the monkeys were rotated. The results confirmed the linear interaction hypothesis. We give two examples for the three-modal interaction in terms of eye-in-space displacement plots as a function of stimulus combination. In the first example (Fig. 4A), the head was displaced in space with the target kept in fixed alignment relative to head (TS=HS=8°=constant), while visual pattern-in-space displacement was varied (PS: 0°, 8°, and 16°). This generated, in terms of physiological stimuli, a vestibular stimulus of constant peak displacement, a zero pursuit stimulus, and optokinetic stimuli of different peak displacements or direction, respectively (VEST=8°, PURS=0°, and OPT: –8°, 0°, and 8°). Note that, compared to the combinations shown in Fig. 2D, head and target were rotated together, instead of rotating only the target and keeping the head stationary. The results closely resembled those in Fig. 2D, however, indicating that pursuit was essentially independent of whether the head followed the target (here by passive head rotation) or the eyes did it (exception: regression line at 0.8 Hz is affected somewhat less).

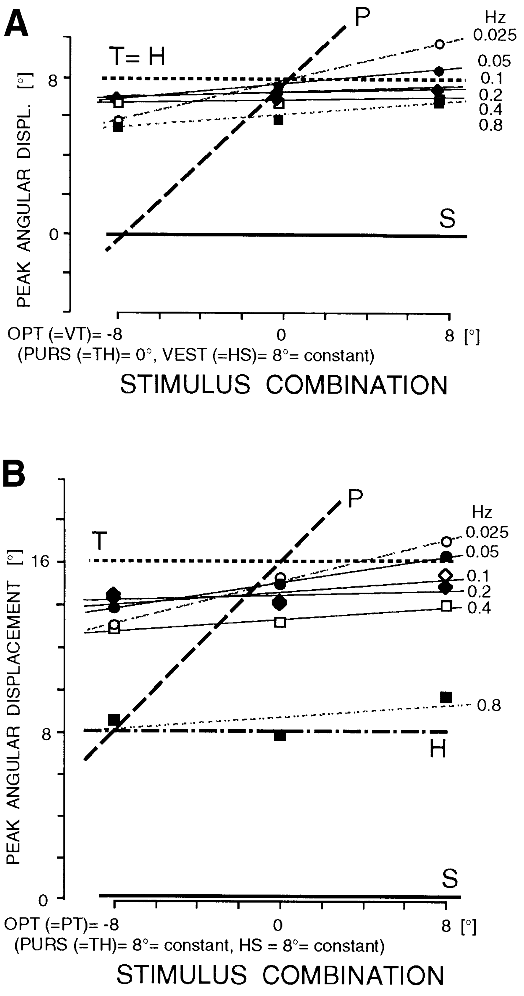

Fig. 4A, B Interaction of VOR, OKR and SP. **A** Eye-in-space displacement curves for SP-OPT-VEST combination set in which OPT was varied (–8°, 0°, and 8°), VEST remained constant (8°) and target was head-stationary [PURS(=TH)=0°]. **B** Eye-in-space displacement curves for a combination set in which OPT was varied (–8°, 0°, and 8°) and both VEST and PURS remained constant (8°). **A, B** *Abscissa* OPT=–8°/0°/8° (presentation as in Fig. 2D,E)

In the second example (Fig. 4B), head and target were displaced in space as before, but the target with twice the amplitude of the head (HS=8°=constant; TS=16°=constant), while visual pattern-in-space displacement again was varied (PS: 8°, 16°, and 24°; compare T, P, H and S lines in Fig. 4B). In physiological terms this generated a vestibular stimulus of constant peak displacement, a pursuit stimulus in the same direction and by the same amount as the head, and optokinetic stimuli of different peak displacements and direction (VEST=8°, PURS=8°, and OPT: –8°, 0°, and 8°). Eye displacement values again were well described by regression lines. The results once more were similar to those in Fig. 2D in that the regression lines for 0.1–0.2 Hz (5–10°/s for both PURS and VEST) are essentially parallel to the T line, whereas those at 0.025 and 0.05 Hz (1.25, 2.5°/s) as well as at 0.8 Hz (40°/s) developed a positive slope (growing influence from the optokinetic pattern). However, with frequency rising to 0.4 Hz (20°/s) and, very pronounced, 0.8 Hz (40°/s), eye displacement becomes shifted towards space (S line), reflecting the growing influence of the VOR at frequencies/velocities where the pursuit deteriorates.

Discussion

Optokinetic responses during fixation and pursuit

A point of departure for the present study was that OKR in monkey is stronger than in man and that this fact may possibly allow us to investigate the interaction of OKR with pursuit eye movements, which in man are so clearly dominating oculomotor behaviour (cf. “Introduction” and next section). Our findings show that this, indeed, is the case. The eye response during the OKR-PURS combination was clearly modulated by the OKR stimulus. This modulation reached considerable values in terms of eye displacement (and forced us to use a rather large reward window for the monkeys; see “Methods”), but is rather small in terms of eye velocity at the low stimulus frequencies where the effect became most prominent. We hold that previous work on this issue has not looked at this phenomenon using low-velocity optokinetic stimulation, as we did, but used instead considerably higher velocities. Still, there remains the question of whether the response modulation could simply be due to the fact that our monkeys did not fixate the fixation point with enough effort.

We can clearly state that this was not the case. Our arguments are the following: (1) As shown in Fig. 2C, the monkeys did accurately fixate the fixation point in the mid-frequency range. It was only at the lower frequencies that a response to the optokinetic stimulus was observed. (2) The modulation of the eye response evoked by the optokinetic stimulus was systematic, in the sense that it monotonically increased when lowering frequency, for instance. If the animals had not complied with the fixation task, the response very likely would not show such a systematic change. (3) The modulation of the eye response evoked by the optokinetic stimulus was a consistent finding. It did not vary from one trial to the next to a major degree. In particular, we never observed that the monkeys were switching between a ‘fixation strategy’ and an ‘OKR strategy’. (4) The modulation of the eye response evoked by the optokinetic stimulus without fixation point (without the fixation task), i.e. the ‘pure OKR’, was manifold larger than that obtained with fixation point (and the task). (5) We repeatedly made control sessions with a smaller reward window, in which we checked whether the monkeys complied to the fixation task (see “Methods”).

Linearity of pursuit-optokinetic-vestibular interactions

The two major conclusions that may be derived from our experiments are that (a) there is a continuous interaction between the pursuit, optokinetic and vestibulo-ocular mechanisms in the monkey and (b) that this interaction itself appears to be linear over the range tested here, despite the fact that, individually, each of these subsystems exhibits considerable non-linearity with respect to frequency and velocity. The linearity has been demonstrated by comparing the magnitude of the smooth component of eye movement over a range of combinations of the vestibular, pursuit and optokinetic stimuli (Figs. 2D,E, 3B, 4A,B). It should be noted that all velocities used here were in a range in which these responses are normally accepted to be linear (Robinson 1965; Schalen 1980) and it is likely that the apparent linearity might not extend to a higher velocity of pursuit/optokinetic stimuli.

The basic interaction process appears to be similar to that demonstrated previously in humans (Worfolk and Barnes 1992; Worfolk et al. 1993), but, as we will show in the following discussion, there are interesting differences brought about by the different dynamic characteristics of the subsystems in the two species. In humans, a number of experiments have shown that the decrement in gain of smooth pursuit caused by the background is generally only around 10% and extends up to frequencies as high as 1.6 Hz (Collewijn and Tamminga 1984; Barnes and Crombie 1985; Worfolk and Barnes 1992; Worfolk et al. 1993). In the monkey there are two major differences that reveal the interaction to a much greater extent; the pursuit system is weaker than in humans and the indirect component of the optokinetic system is much stronger. The weak pursuit is revealed in our experiments by a considerable reduction in smooth pursuit gain in the presence of the optokinetic pattern at all frequencies. To demonstrate this effect in humans it is necessary to degrade pursuit in order to reveal the fact that the pattern still has a potent effect on smooth eye movement (Worfolk and Barnes 1992; Worfolk et al. 1993). In monkeys, the strength of the optokinetic system is revealed by the interaction that takes place at low frequencies (≤0.05 Hz). Such effects have not been demonstrated for humans. The relative contributions of these components can be demonstrated through the development of a model combining the effects of visual-vestibular interaction

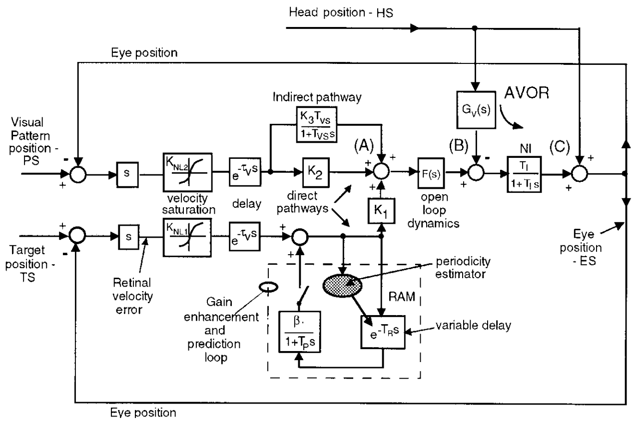

Fig. 5 Model of interaction between pursuit, optokinetic and vestibular systems in control of smooth eye movement in monkey. $F(s)=1/(1+0.08s)$ [*AVOR* angular vestibulo-ocular reflex, $G_V(s)=10s^2/(1+10s)$, *RAM* reafferent memory simulated by variable delay network ($T_R=0$, $\beta=0.9$ for initial transient, t less than $T/2$; $T_R=T/2-\tau v$, $\beta=-0.9$ for steady-state periodic, $t>T/2$, where t=time, T=stimulus period, τv=visual feedback delay=0.06s), *KNL* non-linear velocity saturation characteristic given by $-K_{NL}=(1+\varepsilon/2)^{-0.5}$, ε retinal velocity error, *NI* neural integrator, $T_I=20$ s, $K_1=1$, $K_2=1$, $K_3=0.5$, $T_{VS}=10$]

(Schweigart et al. 1995) and the role of active enhancement in the direct pathway for pursuit (Barnes and Hill 1984).

Model description

The model consists of a visual and a vestibular part (Fig. 5). The visual part itself constitutes two components: one related to pursuit of the small target, the other to optokinetic stimulation from the pattern. For the optokinetic part we have simply referred to what is known about the OKR in primates; as mentioned in the "Introduction", it contains two components, a 'direct' component characterised by a rapid rise in eye velocity after stimulus onset, and an 'indirect' component that builds up slowly and endures for some time when the visual stimulus is extinguished (optokinetic afternystagmus). The pursuit part also contains a direct pathway, but no indirect pathway, in accord with established characteristics of the pursuit response in monkeys (Lisberger et al. 1981). It is assumed that the basic feedback mechanism associated with the two direct pathways is essentially the same, although there may be different specific sensitivities to retinal velocity error depending on features such as the size and spatial frequency of the target and pattern stimuli (see Barnes 1993). When the monkey pursues the target against the pattern, both direct pathways become active. Therefore, if the target and pattern have similar feedback, how does pursuit dominate the response? The answer appears to lie in the role of volitional control, which leads to the enhancement of the gain of the fast direct pathway for the selected pursuit target. Evidence for active gain enhancement comes from numerous experiments on humans in which it has been shown that the oculomotor response to a moving stimulus can be greatly increased if the subject actively attends to the target rather than allowing it to be passively driven (Dubois and Collewijn 1979; Cheng and Outerbridge 1975; Barnes and Hill 1984; Pola and Wyatt 1985). Increasing the gain of the selected target allows the potentially stronger effect from the direct and indirect pattern pathways to be effectively overridden.

Both direct and indirect pathways contain a finite delay of 0.06 s and a soft saturation element that progressively reduces feedback gain for retinal slip greater than a few degrees/s (see Barnes 1993 for evidence of this). The indirect pathway contains an additional low-pass filter with a large time constant (T_{VS}=approx. 10 s) that effectively integrates the retinal velocity error signal and yields the slow-onset response associated with 'velocity storage' (Raphan et al. 1977). With respect to the stimuli we used, the 0.025-Hz stimulus activates both the direct and the indirect component of the OKR pathway and the direct one of the pursuit pathway, and the 0.8-Hz stimulus is most effective via the direct pathways of the two systems. All three pathways merge at summing junction (A) before passing through a first-order filter with a time constant of 0.08 s which, empirically, is necessary to describe the dynamics of the visuomotor mechanisms (Barnes 1994). Output from this filter merges with the input from the vestibular apparatus at junction (B), before passing through the final common neural integrator (NI). It is assumed that the dynamics of the oculomotor plant are centrally compensated for and therefore do not appear in the model.

When the target is selected for pursuit, its feedback gain is increased by a large factor (approx. 10), allowing it to dominate the response. We have represented the mechanism for increasing gain by a positive feedback pathway, similar to that postulated by Barnes and Hill (1984). This pathway incorporates a gain (β) that is slightly less than unity (0.9 in the simulations that follow), a first-order filter with a time constant (T_p) of approximately 0.06 s and a variable delay (T_R), the function of which will be explained later. With T_R at zero, this pathway effectively allows the gain to be increased without incurring instability. [The reason for this is that the dynamics of the loop may be represented by a transfer function of the form: $K_0=(1+T_ps)/(1+T_0s)$, where $K_0=1/(1-\beta)$ and $T_0=K_0T_p$. As β increases, both K_0 and T_0 also increase, and this automatically maintains the stability of the closed-loop response. Note that a finite delay of 0.06 s, as used by other authors (Lisberger et al. 1990), would have a similar effect to the filter.] The open-loop gains of the basic direct pathway components for the target (K_1) and optokinetic pattern (K_2) have been set at 1 and 0.5, respectively, to ensure stability of the passive response.

The variable delay element in the positive feedback loop enables the effects of prediction to be simulated. It consists of a delay equivalent to the half-period of the predictable sinusoidal waveform. The delay is assumed to be determined by a periodicity estimator that derives timing information from the motion stimulus itself, although in the following simulations it has been preset as appropriate for the stimulus. In the initial, transient part of the response, the delay is set to zero and $\beta=+0.9$, so that the model operates in a similar way to other positive feedback models of pursuit (Robinson et al. 1986). After one half-cycle, when periodicity can be established by a simple zero-crossover detector, the delay is set to one half-period and $\beta=-0.9$. This pathway then essentially feeds an anticipatory drive to the direct pathway that is a copy of the drive during the previous half-cycle of the response. It has been shown that such a simple device realistically simulates the anticipatory eye movements observed to occur prior to the onset of target movement and allows the phase error for sinusoidal stimuli to be minimised whilst maintaining stability (Barnes and Wells 1998).

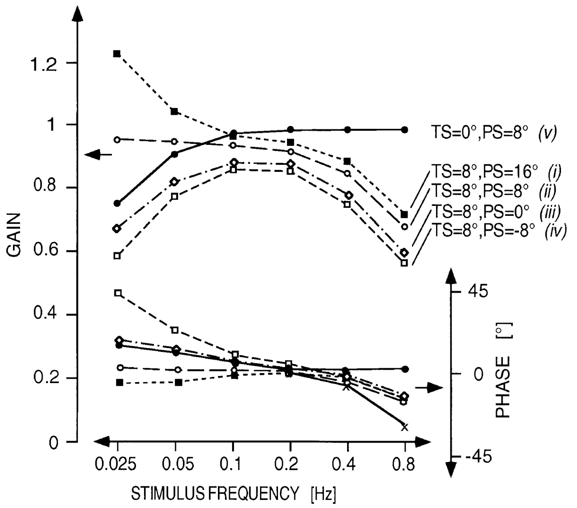

Fig. 6 Simulated gain and phase characteristics for pursuit/optokinetic interactions [*TS* target position in space, *PS* background (pattern) position in space]. *Numbers in legend* define peak displacement of sinusoidal stimulus. All simulations include prediction except phase values defined by *crosses*

Model simulations

The frequency response characteristics of this model are shown in Fig. 6 for each of the target and pattern stimulus conditions tested experimentally. When the target and background move together (TS=8; PS=8), gain is near unity at low frequency but is slightly reduced at the highest frequency. When the background is stationary (TS=8; PS=0), gain is attenuated at all frequencies, but particularly so at low frequencies. Motion of the pattern in the opposite direction to the target (TS=8; PS=–8) causes a further small reduction in gain, whereas motion of the pattern at twice the speed in the same direction (TS=8; PS=16) raises the gain to above unity at the lowest frequency. It can easily be shown that these effects of the pattern at the lowest frequency are directly attributable to the activity of the indirect pathway. The fact that this effect is not observed in humans (unpublished observations from experiments in our laboratory) is probably attributable to the relative weakness of this pathway compared with that in the monkey. Conversely, the indirect pathway has a negligible effect on the response at higher frequencies, where the changes in gain associated with different target/pattern combinations are attributable to the inhibitory effect of the direct pathway for the pattern. These simulations have been obtained by setting the variable delay T_R as appropriate for prediction. The effect of this prediction component is to specifically reduce the phase error at frequencies above 0.1 Hz. If prediction is not invoked (i.e. T_R is set at zero and $\beta=+0.9$ as in a simple positive feedback model), unrealistically large phase errors are generated as shown in Fig. 6. The effect of the predictive element on the gain, however, is negligible at all frequencies (not shown because it is so similar).

The vestibular part of the model consists of the VOR, which is fed forward in order to compensate for head movements in space and tends to shift the eyes away from the target or pattern. The transfer function [G_V (s)] of the vestibular system is assumed to be a high pass with a time constant of 16 s (behavioural time constant). The gain is adjusted to the data in Fig. 1B. Note that we made no attempt to include into the topology of the model the earlier evidence that certain parts of the network are shared by the VOR and the OKR (e.g., Robinson 1977; Raphan et al. 1977), because this would mask the simple and straightforward view on the basic features of the mechanisms.

Conclusions

The results showed that the interaction of SP in the dark and of VOR is basically linear (Fig. 3B). It essentially resembled that of OKR-VOR interaction (Schweigart et al. 1995) and, therefore, it need not be described in detail in this paper. In short, due to the feedback character of the visual systems it is the pursuit (or the OKR in absence of a target) which is the primary system for the maintenance of clear vision. However, the VOR contributes to eye stabilisation on the target if the target is stationary; during this combination the eyes keep close to the target even with high frequency head rotation. Our results indicate that there is a continuum of SP-VOR interaction across synergistic and antagonistic combinations. This supports the notion that it is not necessary to assume that the VOR is suppressed or switched off during SP-VOR interaction but rather its unity-gain open loop system is dominated at low to mid-frequencies by the visual pursuit system with its high open loop gain. This is unlike during large and fast head saccades during which the VOR is suppressed (Tomlinson and Bahra 1986). A different view on the VOR-SP interaction, in terms of space coordinates, would be the following one:

The VOR makes it possible for us to rotate the head, which represents the ‘platform’ for the eyes, in space without interfering with an ongoing target tracking in space by the pursuit system. This applies to the extent to which VOR gain is unity, so that the eye-in-head rotation is exactly counter to the head-in-space movement (cancellation of AVOR and HS in Fig. 5).

In conclusion, we were able to extract from our experimental data a mathematical description of pursuit-optokinetic-vestibular interaction in the form of a model which suggests that the interaction of these three signals is linear.

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