The Horizontal Optokinetic Response of the Goldfish

Abstract

This report describes the dynamics of the horizontal optokinetic response of the goldfish, and compares them with those of other species. Eye rotational velocity in response to step and sinusoidal rotations of the visual surround was tested using goldfish that had both eyes free to view the surround and to rotate with it. The step response was tested by switching on a visual surround display that was rotating at constant velocity, and then switching off the display, leaving the goldfish in the dark. The step onset response was characterized by rapid and gradual components; the latter rose with an almost linear trajectory for higher surround velocities. The response was more rapid at step-offset than at step-onset. The step-offset response overshoot baseline eye velocity for most goldfish and was oscillatory for others. The steady-state response increased with constant velocity surround rotation within the range ±40 deg/sec but saturated outside that range. Steady-state response gain was higher for nasally-directed than for temporally-directed surround rotations. The frequency response was essentially low-pass, with gain decreasing from about 0.9 and phase lag increasing from zero to 90 deg as surround rotational frequency increased from 0.01 to 3.0 Hz. Sinusoidal response gain decreased as a function of surround peak acceleration. The results indicate that the horizontal optokinetic response of the goldfish is nonlinear and resembles in many respects that of mammals. Models developed to simulate the dynamics of the optokinetic response of mammals can be applied to that of goldfish and reproduce its nonlinear features.

Introduction

Among sensorimotor systems, the vestibular-optokinetic system is one of the best understood, both in its performance under normal circumstances and in its plasticity as it adapts to abnormal circumstances. Most of the work to date on the performance and plasticity of the vestibular-optokinetic system has been carried out using mammals as subjects [Wilson and Melvill Jones, 1979]. For example, classic work using humans has shown that the performance of the vestibular-ocular reflex can change dramatically when the normal relationship between rotation of the head and the apparent rotation of the visual surround is changed [Gonshor and Melvill Jones, 1976]. Similar experiments have been carried out using other mammalian species such as cats [Robinson, 1976] and monkeys [Miles and Eigmy, 1980]. Recent experiments, in which plastic changes in vestibular-ocular reflex performance were produced by altering the normal relationship between head rotation and visual surround rotation, have been carried out using goldfish as sub-
jects [Schairer and Bennett, 1986; Pastor et al., 1992]. This work demonstrated that the speed and extent of vestibular-ocular reflex modification is much greater for goldfish than for any mammal studied to date. The goldfish has therefore become an important subject in the study of the mechanisms of vestibular-ocular reflex plasticity.

All of these experiments involve an interaction between the vestibular-ocular reflex, which stabilizes gaze by producing eye rotation that counterbalances head rotation, and the optokinetic response, which stabilizes gaze by matching eye rotation to the rotation of the visual surround. Therefore, a consideration of the dynamics of the optokinetic system is necessary in order to design and evaluate vestibular-ocular reflex modification experiments. The dynamics of mammalian optokinetic systems have been studied for many years [e.g. Collewijn, 1969; Cohen et al., 1977; Maioli and Precht, 1984; Hess et al., 1985]. Although the goldfish optokinetic system has been studied [Easter, 1972; Dieringer et al., 1992], a description of its dynamics is not available. The purpose of this paper is to describe the dynamics of the horizontal optokinetic system of the goldfish.

Previous work has shown that the behavior of the optokinetic system in mammals is highly nonlinear. Nonlinear features include saturation in the responses to constant velocity and sinusoidal surround rotations. Our results show that the behavior of the horizontal optokinetic system in goldfish is similar to that in mammals, particularly with regard to response nonlinearities. A model that combines features of previous models of the optokinetic system in mammals [e.g. Collewijn, 1972; Lisberger et al., 1981; Maioli, 1988] also describes the nonlinear and dynamic behavior of the horizontal optokinetic system in the goldfish.

Materials and Methods

Experiments were conducted on ten comet goldfish (Carassius auratus), approximately 16 cm in length. Each goldfish was wrapped in gauze and restrained in an experimental tank using contoured body supports. Its mouth was opened over a plastic tube and secured to it with a loop of string. The goldfish was artificially respirated with fresh water that was pumped through the tube. A small coil of Teflon-insulated copper wire (20 turns, 5.3 mm external coil diameter) was attached to the outer covering of the left eye, concentric with the pupil, using ophthalmic suture (6-0 monofilament). All procedures involving goldfish were approved by the University of Illinois Laboratory Animal Care Advisory Committee under protocol number B3R085, in accordance with the Public Health Service Policy on Humane Care and Use of Laboratory Animals.

The tank was placed within an apparatus that was equipped with magnetic field generating coils. Eye rotational position was transduced using the magnetic search-coil technique [Robinson, 1963; Remmel, 1984]. After each experiment, the eye coil was detached, repositioned in the magnetic field, and calibrated with a protractor. Positive voltages represent clockwise eye rotations, which are nasally directed for the left eye.

The optokinetic response was elicited by rotation of the visual surround. The surround display was produced by a hollow sphere, 10.0 cm in diameter, into which were drilled holes subtending either 2.8 or 5.7 deg. The holes were distributed randomly at a density of 35%. The experimental tank was cylindrical and had an opaque wall. The sphere was suspended above the center of the tank and illuminated from the inside using a 20 W halogen light-bulb. The goldfish had an unobstructed view of the projected random-dot pattern, from the center of the tank, of ±150 deg horizontally and ±15 deg vertically. The display light provided the only illumination in the experimental apparatus, so the goldfish was in the dark when it was extinguished. Illumination was monitored electronically using a comparator circuit that detected current flow through the bulb.

The sphere was rotated using a servo-controlled motor either at constant velocity or sinusoidally. The constant velocities ranged between ±100 deg/sec. Single sinusoidal rotations ranged in frequency from 0.01 to 3.0 Hz, with peak amplitudes ranging from 5 to 100 deg/sec. The servomotor tachometer signal was calibrated during constant velocity rotations by measuring the time intervals between sync pulses that occurred once per revolution. Positive voltages represent clockwise surround rotations, which are nasally directed for the left eye. Rotation of the random-dot surround elicited optokinetic nystagmus, which consisted of alternating slow- and fast-phases.

The eye position and surround velocity (tachometer) signals were antialias filtered at 25 Hz and digitized at 50 Hz for all constant velocity and sinusoidal data below 1.0 Hz, and filtered at 150 Hz and digitized at 300 Hz for sinusoidal data at 1.0 Hz and above. The illumination signal from the comparator circuit was digitized directly at 50 Hz without pre-filtering. Digitized data were stored on hard disk and tape for off-line analysis. Analysis of the data was performed in the MATLAB programming environment (The MathWorks, Inc.). The eye position data were digitally differentiated using a modification of the approach described by Bahlill and McDonald [1983]. A five-point central difference estimator was applied to the eye position data, and the resulting eye velocity data were low-pass filtered (single-pole, non-causal) at 12.5 Hz for constant velocity data and sinusoidal data below 0.10 Hz, and at 0.07 Hz for sinusoidal data above 1.0 Hz. The entire procedure introduced minimal phase distortion and gain attenuation.

The fast-phases were edited out of the eye velocity data using an automatic procedure following threshold setting by the user, leaving only the slow-phase portion of the response. Slow-phase eye velocity, either between spontaneous successades in the dark or during the steady-state response to constant velocity surround rotation, was measured by computing the mean over a 30-sec stretch of data. A least-squares routine was used to fit sinusoids to the sinusoidal response data (no fewer than five cycles of data were fit at any frequency). This provided estimates of the parameters of the sinusoidal responses, which were distorted due to nonlinearities in the optokinetic system. Gain (peak slow-phase eye velocity/peak surround velocity) and phase difference (slow-phase eye velocity phase - surround velocity phase) were computed using the fitted parameters. Eye velocity, gain, or phase were averaged over all goldfish tested at each surround rotation. Mean values are reported along with the standard error of the mean (SEM = SD/n).

A combined linear/nonlinear model of the horizontal optokinetic system of the goldfish was constructed using the SIMULINK dynamic system simulation program (The MathWorks, Inc.). Due to nonlinearities in the model, the simulated eye velocity response to
Fig. 1. Typical step-onset response of the goldfish horizontal optokinetic system. The inverted, open triangle marks the moment at which a light switches on, revealing a random-dot surround that was rotated in the nasal direction for the left eye (clockwise) at a constant velocity of 20 deg/sec. Left horizontal eye position, shown in A, was digitized and eye rotational velocity, shown in B, was computed from eye position (see Methods). Every tenth point is plotted. Before stimulus onset, the goldfish made spontaneous saccades in the dark (A, positive deflections correspond to clockwise eye rotations which are nasally directed for the left eye), and eye velocity (B) was roughly zero. Stimulus onset evoked optokinetic nystagmus (A), in which the nasally directed slow-phases that followed the surround were interrupted by temporally directed fast-phases. Slow-phase eye velocity (B, fast-phases removed) increased rapidly during the first few seconds and then continued to rise more gradually until the rotational velocity of the eye roughly matched that of the surround.

sinusoidal surround rotations was distorted. For this reason, a least-square routine was also used to fit sinusoids to the simulated sinusoidal data, and gain and phase difference were computed using the fitted parameters, as for the real data.

Results

Rotation of the visual surround elicited the optokinetic response in goldfish. The visual surround consisted of a random-dot display that became visible to the goldfish when the light in the display was switched on (see Methods). The goldfish was in the dark when the display was switched off. The head of the goldfish was situated at the center of the display, which was rotated around it in the horizontal plane (about an earth-vertical axis). All recordings were made from the left eye. In all cases, the horizontal optokinetic system of the goldfish was tested in the normal, closed-loop situation where both eyes were free to view the surround and to rotate with it.

A typical example of the horizontal eye rotations in a goldfish, in the dark and immediately after the random-dot display rotating at a constant velocity of about 20 deg/sec was switched on, is shown in figure 1A (eye position) and B (eye velocity). Goldfish make spontaneous, saccadic eye rotations in the dark (positive deflections represent clockwise eye rotational positions or velocities, which are nasally directed for the left eye). The eye tends to drift nasally during the intersaccadic intervals. Slow-phase eye velocity during intersaccadic intervals in the dark was measured in ten goldfish, and the mean (± SEM) was 0.45 ± 0.05 deg/sec. The optokinetic response was elicited when the display
Fig. 2. Typical step responses of the goldfish horizontal optokinetic system. Data were taken from the same goldfish as in figure 1. The inverted, open triangle marks the moment at which a light switched on revealing a rotating random-dot surround, and the inverted, filled triangle marks the moment at which the light switched off again leaving the goldfish in the dark. The surround was rotated nasally at various constant velocities as indicated and the slow-phase eye velocity of the response is shown (A–D). At stimulus onset (light-on), a rapid initial rise followed by a more gradual rise to the steady-state response was apparent at all surround velocities. The gradual rise appeared to be roughly exponential for the lower surround velocities (less than 40 deg/sec) but became almost linear for the higher surround velocities (40 deg/sec or greater). The fall in slow-phase eye velocity was rapid following the offset (light-off) of all stimuli.
was switched on (open, inverted triangle) and was nystagmic, consisting of slow-phases that follow the rotating visual surround and fast-phases that quickly rotate the eye in the opposite direction (fig. 1A). The eye position range was reduced and shifted in the fast-phase direction during optokinetic nystagmus. Slow-phase eye velocity rose rapidly at first and then continued to rise more gradually until the rotational velocity of the eye roughly matched that of the surround (fig. 1B).

**Step Response of the Horizontal Optokinetic System of the Goldfish**

The step response of the horizontal optokinetic system of the goldfish was tested by rotating the random-dot surround display at constant velocity and switching it on for a period of up to three minutes and then switching it off again. Therefore, step-onset and step-offset coincided with the moment at which the light in the display was switched on and switched off, respectively. During steps, the goldfish viewed the surround display rotating at constant velocity when the display light was on. However, since the visual surround display light provided the only illumination in the experimental apparatus, the goldfish was in the dark when the display light was off.

The optokinetic system functions in negative-feedback to minimize retinal-slip error, which is the difference between eye and surround rotational velocity [Collewijn, 1972]. The optokinetic system is driven by retinal-slip error only when the surround is visible, as it is in the light. In the dark, when the surround becomes invisible, retinal-slip error is no longer available to drive the optokinetic system, and it switches into another configuration as it relaxes from its previously driven state [Maioli, 1988]. The step and step-offset optokinetic responses have traditionally been tested in the light and dark, respectively, and have been referred to as optokinetic nystagmus (OKN) and optokinetic after-nystagmus (OKAN), respectively.

The step-onset (light-on) response consisted of an initial rapid component and a more gradual component for all goldfish tested. A typical example of the step response for nasally-directed, random-dot surround rotations at various constant velocities is shown in figure 2A through D (data in fig. 1 and 2 are from the same goldfish). Following the onset of the step stimulus (open, inverted triangle) slow-phase eye velocity rose rapidly to about 15 deg/sec and then more gradually until it reached steady-state.

For lower surround velocities (less than 40 deg/sec), both the rapid and gradual components appear roughly exponential with shorter and longer time constants, respectively (fig. 2A, B). For higher surround velocities (40 deg/sec or greater), the gradual component is not exponential but appears to rise almost linearly, and the time to reach steady-state is prolonged (fig. 2C, D). For example, the mean time to steady-state for ten goldfish increased from about 26 sec for surround rotation at 20 deg/sec to about 69 sec for surround rotation at 80 deg/sec. Dependency of the dynamics and duration of the gradual component upon surround velocity indicates that the horizontal optokinetic response of the goldfish is nonlinear.

The step responses for nasally- and temporally-directed surround rotations are qualitatively similar but differ in gain. The slow-phase eye velocity responses to random-dot surround rotations at various constant velocities within the range ±100 deg/sec were measured after the response had reached steady-state. Mean responses computed for four goldfish are shown, along with the SEM (error bars), in figure 3A. Steady-state eye velocity increases with constant velocity surround rotation within the range ±40 deg/sec but saturates outside that range, indicating nonlinearity. Steady-state response gain was calculated (E/S, eye velocity/surround velocity) and is plotted against surround velocity in figure 3B. The steady-state response gain is higher for nasally-directed (positive) than for temporally-directed (negative) surround rotations.

In contrast to the step-onset (light-on) response, which increases in duration as surround velocity increases, the step-offset (light-off) response is rapid regardless of the velocity of the preceding surround rotation. For each of the step responses shown in figure 2, slow-phase eye velocity fell rapidly following the offset of the stimulus (filled, inverted triangles) and slightly overshot baseline eye velocity. The offset response following the 20 deg/sec surround velocity step (fig. 2B) is reproduced in figure 4A. Such an overshooting step-offset response was observed in 70% of the goldfish tested. In the other 30% the offset-response could oscillate about baseline eye velocity for a full cycle or more, and the most pronounced example, also following the offset of a 20 deg/sec surround velocity step, is shown in figure 4B. For goldfish in which they occurred, there was some tendency for the oscillations to be more pronounced following the offset of midrange (10–40 deg/sec) surround velocity steps.

**Frequency Response of the Horizontal Optokinetic System of the Goldfish**

The frequency response of the horizontal optokinetic system of the goldfish was tested by rotating the random-dot surround sinusoidally at various frequencies and peak velocities. An example of the optokinetic response to a sinusoidal stimulus is shown in figure 5. The random-dot sur-
Fig. 3. Steady-state eye velocity and gain of the goldfish horizontal optokinetic system in response to constant velocity, random-dot surround rotation. Slow-phase eye velocity was measured in steady-state (see Methods). Each point in A represents the mean eye velocity response of four goldfish. Error bars represent the standard error of the mean (SEM = SD/n). The steady-state response increased with surround rotational velocity within the range ±40 deg/sec but saturated outside that range. The mean (±SEM) steady-state gain (ES, eye velocity/surround velocity) is plotted as a function of surround velocity in B. Gain was higher for nasally-directed (positive) than for temporally-directed (negative) surround rotational velocities.

Fig. 4. Step-offset responses of the goldfish horizontal optokinetic system. The inverted, filled triangle marks the moment at which the random-dot surround was switched off, leaving the goldfish in the dark. The surround was rotated nasally at a constant velocity of 20 deg/sec (A and B). The step-offset (light-off) response typical of most goldfish slightly, but not significantly, overshoed baseline (A, data were taken from the same goldfish as in fig. 1, 2). However, some goldfish showed an oscillatory step-offset response (B).

round was rotated at 0.05 Hz with a peak velocity of approximately 20 deg/sec, and the response is from the same goldfish that provided the data for figures 1 and 2. In response to a sinusoidally rotating surround, the goldfish optokinetic system produced slow-phase eye velocities that were also roughly sinusoidal and at the same fundamental frequency as the stimulus. There was some tendency for the waveform to appear distorted due to the nonlinearities in the optokinetic system.

Despite waveform distortions, sinusoids were fit to the data (see Methods) for the purpose of estimating gain and phase at eight single sinusoidal surround rotations ranging in frequency from 0.01 to 3.0 Hz. The peak velocity of the sinusoidal surround rotations was chosen to be 20 deg/sec, because this value is typical of the peak velocities that are used in vestibular-ocular reflex modification experiments.
on goldfish [e.g. Schairer and Bennett, 1986; Pastor et al., 1992]. The response at each frequency was tested for ten goldfish and the mean (+ SEM) gain and phase is plotted versus log frequency in figure 6A and B, respectively. The phase characteristic is roughly that of a linear, low-pass element, in that phase lag increases from zero to 90 deg as frequency increases from 0.01 to 3.0 Hz. However, gain begins to decrease (from about 0.9) at a frequency much lower than expected on the basis of the phase characteristic.

This discrepancy in gain-phase behavior could be due to nonlinearity in the goldfish optokinetic system.

To further explore the nonlinear behavior of the optokinetic frequency response, it was tested at two midrange frequencies (0.05 and 0.5 Hz) over a range of peak velocities (5 to 100 deg/sec) of sinusoidal random-dot surround rotation. Peak slow-phase eye velocity was measured at each frequency and peak surround velocity for ten goldfish, and the mean (+ SEM) is plotted in figure 7A. Eye velocity is
Fig. 6. Frequency response of the goldfish horizontal optokinetic system. The random-dot surround was rotated sinusoidally at eight single frequencies (0.01, 0.03, 0.05, 0.1, 0.3, 0.5, 1.0, and 3.0 Hz) with a peak velocity of about 20 deg/sec. The gain (E/S, peak eye velocity/peak surround velocity) and phase difference (eye velocity phase - surround velocity phase) of the response were estimated at each frequency (see Methods) and are plotted versus log frequency. Each point represents the mean (±SEM) for the gain (A) and phase (B) of ten goldfish. The frequency response was low-pass.

higher at the lower (0.05 Hz) than at the higher (0.5 Hz) frequency for each surround velocity, due to the predominantly low-pass characteristics of the optokinetic system. But the response saturates at both frequencies, and saturation occurs at lower surround velocities for the higher (0.5 Hz) than for the lower (0.05 Hz) frequency. Gain was com-

Fig. 7. Dependency of gain on stimulus amplitude of the goldfish horizontal optokinetic response. The random-dot surround was rotated sinusoidally at 0.05 or 0.5 Hz with peak velocities ranging from 5 to 100 deg/sec. Each point in A represents the mean (±SEM) peak velocity of the optokinetic response of ten goldfish. The optokinetic response saturated at both frequencies, with saturation being more pronounced at the higher (0.5 Hz) than at the lower (0.05 Hz) frequency (A). The mean gain (E/S) of the optokinetic response was calculated at each frequency and amplitude and is plotted versus peak surround acceleration on log-log axes in B. Gain curves for the two frequencies touch and show a nonlinear decrease with surround acceleration.
puted at each frequency and surround velocity and is plotted against peak surround acceleration on log-log axes in figure 7B. The curves for the two frequencies touch, and gain decreases as the peak acceleration of the surround increases in a nonlinear fashion.

**Modeling the Horizontal Optokinetic System of the Goldfish**

The foregoing results indicate that the behavior of the horizontal optokinetic system of the goldfish is nonlinear in many respects. For the purpose of gaining insight into this behavior, a combined linear/nonlinear model was constructed that reproduced qualitatively many of the dynamic and nonlinear features of the results. This model, schematized in figure 8, is a simplified merging of previous models of the optokinetic system of mammals [CollieMin, 1972; Robinson, 1977; Raphan et al., 1979; Lisberger et al., 1981; Maioli, 1988]. Because the values of most of the model parameters are not known for the goldfish, they were set so that the model would qualitatively simulate the results. Therefore, rather than try to provide an accurate fit to the data, the purpose of the model is to illustrate that the general principles that apply in describing the dynamic and nonlinear behavior of the optokinetic system in mammals apply also to that in the goldfish.

The model of the goldfish optokinetic system is essentially a negative-feedback servomechanism. Its function is to reduce retinal-slip error ($\hat{e}$) by matching eye velocity ($\hat{E}$) to surround velocity ($\hat{S}$). Retinal-slip error is calculated as $\hat{e} = \hat{S} - \hat{E}$, and it is simply the velocity with which the image of the surround sweeps over the retina. A switch (D/L switch) controls the retinal-slip input to the model. Retinal-slip is available to drive the optokinetic system only in the light, when the surround is visible (D/L switch closed).

The model consists of three first-order, linear low-pass elements and three static nonlinear elements connected in series, parallel, and feedback. The dynamics of the linear elements are described in Laplace notation, where $s$ stands for complex frequency ($s = j\omega$, where $j = \sqrt{-1}$ and $\omega$ is frequency in rad/sec). In order to simulate both the rapid and
the more gradual components of the step-onset response, the model consists of a parallel arrangement of fast and slow pathways. Each pathway consists of a retinal-slip input from the visual system, which is modeled as a static nonlinearity, and an eye-velocity command generator, which is modeled primarily as a first-order, linear, low-pass element. The low-pass element of the fast pathway was assigned a time constant (τf) of 1 sec and a gain constant (Gf) of 1. The low-pass element of the slow pathway was assigned a time constant (τs) of 50 sec, which represents velocity storage [Robinson, 1977; Raphan et al., 1979], and a gain constant (Gs) of 6.

The main nonlinear elements in the model represent the retinal-slip inputs to the slow and fast pathways from the visual system [Collewijn, 1972]. The retinal-slip input to the fast pathway is linear (slope of 1) within the range ±15 deg/sec but saturates outside that range. The retinal-slip input to the slow pathway is linear (slope of 1) within the range ±10 deg/sec, but it goes linearly from ±10 deg/sec to zero at ±180 deg/sec (reversing-slope nonlinearity). Additionally, a nonlinear element was inserted at the output of the slow pathway, which is linear (slope of 1) within the range ±40 deg/sec but saturates outside that range. The output of the fast pathway is not limited.

An additional low-pass element was placed in a loop that negatively feeds back the output of the slow pathway eye-velocity command generator to its input [Maioili, 1988]. The purpose of this loop is to simulate the rapid step-offset (light-off) response, by quickly discharging the eye-velocity command that has been stored in the slow-pathway command generator. By appropriately setting the parameters in the feedback discharge element, the step-offset response can be made to overshoot or oscillate. An additional switch (L/D switch) controls the velocity-storage discharge loop. To simulate the differences in step-onset (light-on) and step-offset (light-off) dynamics, the discharge loop is closed only in the dark (L/D switch closed). Thus, the optokinetic system model switches from the light-on configuration, in which the retinal-slip input signal is available (D/L switch closed) and the velocity-storage discharge loop is open and inactive (L/D switch open), to the light-off configuration in which the retinal-slip input is not available (D/L switch open) and the discharge loop is closed and active (L/D switch closed).

The model reproduces both the rapid initial rise and the more gradual rise to steady-state of the step-onset (light-on) response of the goldfish horizontal optokinetic system. The eye velocity step responses of the model to nasally-directed surround rotations of various velocities is illustrated in figure 9. Simulation artifacts at 20 and 140 sec (due to the relatively coarse temporal resolution of the step response simulations) indicate the times at which the light in the model was switched on and off, respectively.

The rapid component of the simulated step-onset response is due primarily to the fast pathway. Because of the saturation of the visual input to the fast pathway, it can never reduce retinal slip by more than ±15 deg/sec, and it never contributes more than ±15 deg/sec eye velocity. The gradient component of the simulated step-onset response is due to the slow pathway which, because of the nonlinearity of its visual input, is linear only for retinal slips in the range ±10 deg/sec. For inputs in its linear range, the slow pathway produces a long, exponential step-onset response (time constant ~50 sec) that slowly changes eye velocity and reduces retinal slip. For larger slips the input to the slow pathway from the visual system gradually diminishes until it becomes zero at ±180 deg/sec. Because of this reversing-slope nonlinearity, the amount of retinal slip that the slow pathway can reduce decreases as slip increases beyond ±10 deg/sec. However, as the slow pathway does produce this limited amount of retinal-slip reduction, its input from the visual system increases and, consequently, the amount of retinal slip it can further reduce also increases. This mechanism allows the slow pathway to gradually produce more retinal slip reduction and, as the step response continues, eye velocity increases gradually and rises with an almost linear trajectory. This mechanism can also account for the finding that the time to steady-state increases as surround velocity increases.

The steady-state eye velocities of the model in response to simulated surround rotations at various constant velocities were measured and are plotted in figure 10. As for the real horizontal optokinetic system of the goldfish, the steady-state eye velocity of the model increases with constant velocity surround rotation within the range ±40 deg/sec but saturates outside that range. Unlike the real system, however, the output of the model is symmetrical for nasally- and temporally-directed surround rotations. It easily could be made asymmetrical by making the slopes of the static nonlinearities different for nasally- and temporally-directed retinal slips but, in the interest of keeping the model simple, this was not done. The saturation of the steady-state eye velocity response of the model is due to saturating nonlinearities, both of the visual input of the fast pathway and at the output of the slow pathway.

Switching the light off in the model both removes the retinal-slip input and closes the internal loop that discharges the eye-velocity command that has been stored in the slow pathway. Simulated step-offset (light-off) responses following nasally-directed steps of 20 deg/sec surround velocity.
Fig. 9. Simulated step responses of the goldfish horizontal optokinetic system. The simulation artifacts at 20 and 140 sec mark the moments at which the light in the model was switched on and off, respectively. Simulated slow-phase eye velocity is shown (A-D) in response to nasal surround rotations at various velocities as indicated. As for the real data, step onset evokes a rapid initial rise and a more gradual rise to the steady-state response. The gradual rise appears to be roughly exponential for the lower surround velocities (less than 40 deg/sec) but becomes almost linear for the higher surround velocities (40 deg/sec or greater). The fall in slow-phase eye velocity is rapid following the offset of all steps.
Fig. 10. Simulated steady-state eye velocity of the goldfish horizontal optokinetic system in response to constant velocity surround rotation. As for the real data, the simulated steady-state response increases with surround rotational velocity within the range ±40 deg/sec but saturates outside that range.

are shown in figure 11. With a gain constant for the discharge element ($G_d$) of 4 sec and a time constant ($\tau_d$) of 1 sec, the discharge loop produces the slightly overshooting step-offset response observed for most goldfish. Increasing the discharge time constant ($\tau_d$) to 4 sec makes the system more underdamped and decreases its natural frequency [Maioli, 1988]. This reproduces the oscillatory step-offset response observed in some goldfish.

To simulate the nonlinearity in the gain of the sinusoidal response of the goldfish horizontal optokinetic system, the model was run with sinusoidal surround rotations of 0.05 and 0.5 Hz and peak velocities ranging from 5 to 100 deg/sec. The gain of the model for each combination of frequency and peak velocity is plotted against peak surround acceleration on log-log axes in figure 12. The gain curves for the two frequencies touch, and gain decreases as surround acceleration increases, as for the real system. This behavior is due to nonlinearities in the model. If the model (and the real system) were linear, then the gain at each frequency would be independent of stimulus acceleration. Then the curves in figure 12 (and fig. 7B) would be straight horizontal lines, and the gain at 0.05 Hz would be higher.

Fig. 11. Simulated step-offset responses of the goldfish horizontal optokinetic system. The simulation artifact at 140 sec marks the moment at which the light was switched off in the model. The simulated surround was rotated nasally at a constant velocity of 20 deg/sec. The simulation was run with the discharge element gain constant ($G_d$) set at 4, and the time constant ($\tau_d$) set at either 1 or 4 sec, as indicated. The solid curve ($\tau_d = 1$) models the step-offset response typical of most goldfish, which slightly overshoots baseline, while the dashed curve ($\tau_d = 4$) models the oscillatory step-offset response observed in some goldfish.

Fig. 12. Simulating the dependency of gain on stimulus acceleration of the goldfish horizontal optokinetic response. The simulated surround was rotated sinusoidally at 0.05 or 0.5 Hz with peak velocities ranging from 5 to 100 deg/sec, and the gain ($E/S$) of the simulated optokinetic response was calculated at each frequency and amplitude and plotted versus peak surround acceleration on log-log axes. As for the real data, gain curves for the two frequencies touch and show a nonlinear decrease with surround acceleration.
than the gain at 0.5 Hz, due to the low-pass characteristics of the optokinetic system. However, the nonlinearities cause both curves to turn down as surround acceleration increases. The nonlinearities in the slow pathway affect the response more at 0.05 Hz, while the fast pathway nonlinearity affects the response more at 0.5 Hz. The simulated curves turn down more sharply than those for the real data, because the nonlinearities are piece-wise linear in the model but would be smooth curves in the real system. However, the limits on piece-wise linear functions were easier to set, and so they were retained to keep the model simple.

Discussion

The horizontal optokinetic system has been studied in a variety of species, including the goldfish and other teleost fishes [Easter, 1972; Dieringer et al., 1992], frogs [Dieringer and Precht, 1982], turtles [Dieringer et al., 1983], pigeons [Gioanni, 1988], rats [Hess et al., 1985], rabbits [Collewijn, 1969; Collewijn et al., 1980; Collewijn, 1981], cats [Godaux et al., 1983; Maioli and Precht, 1984], and monkeys [Cohen et al., 1977; Lisberger et al., 1981; Paige, 1983]. Our results extend previous findings [Easter, 1972; Dieringer et al., 1992] and reveal that the horizontal optokinetic system of the goldfish shares many features in common with that of other species.

Comparing the Horizontal Optokinetic Step Response between Species

In all mammalian and avian species studied, the step-onset (light-on) response of the horizontal optokinetic system consists of two components: a rapid initial rise and a more gradual rise to steady-state. The rapid component is more prominent for monkeys [Cohen et al., 1977; Paige, 1983] and cats [Maioli and Precht, 1984] than for rabbits [Collewijn, 1969], rats [Hess et al., 1985], and pigeons [Gioanni, 1988]. The goldfish horizontal optokinetic response also has a prominent rapid component. It appears that the rapid component of the optokinetic response of monkeys is mediated by the vestibulocerebellum, because it is impaired by lesions of the flocculus [Zee et al., 1981; Waespe et al., 1983]. The vestibulocerebellum may also mediate the rapid component of the horizontal optokinetic response of the goldfish. The trajectory of the gradual component is more linear than exponential at higher surround velocities for the goldfish, and this is also the case for pigeons [Gioanni, 1988], rats [Hess et al., 1985], rabbits [Collewijn, 1969], cats [Maioli and Precht, 1984], and monkeys [Cohen et al., 1977].

Even under binocular viewing conditions, the horizontal optokinetic system of the goldfish is asymmetrical, in that its response for either eye is stronger for nasally directed than for temporally directed surround rotations [Easter, 1972]. The response of the horizontal optokinetic system, under binocular viewing conditions, was tested in a survey of 20 species of marine and fresh-water teleost fishes [Dieringer et al., 1992]. It was found that some, like the goldfish, also have an asymmetrical optokinetic response, while other teleosts have a symmetrical optokinetic response. An optokinetic response asymmetry under binocular viewing conditions has also been observed for pigeons [Gioanni, 1988] but has not been described for any mammalian species. An asymmetry under binocular viewing conditions causes the two eyes to rotate at different velocities during an optokinetic response to the same surround rotation. It isn’t clear why such an eye velocity mismatch is tolerated in some species but not in others.

The steady-state response of the horizontal optokinetic system of the goldfish increased with surround velocity within the range ±40 deg/sec but saturated for surround velocities outside that range. This confirms a previous finding that the working range of the horizontal optokinetic response of the goldfish is limited to surround rotations between ±40 deg/sec [Easter, 1972]. In comparison, the working range limits of the horizontal optokinetic response are roughly ±1 deg/sec for frogs and turtles [Dieringer and Precht, 1982; Dieringer et al., 1983], ±10 deg/sec for rats and rabbits [Collewijn, 1969; Hess et al., 1985], ±20 deg/sec for pigeons [Gioanni, 1988], at least ±60 deg/sec for cats [Maioli and Precht, 1984], and ±100 deg/sec for monkeys [Cohen et al., 1977; Lisberger et al., 1981; Paige, 1983]. This comparison lends support to the contention that goldfish and other teleost fishes possess a well developed optokinetic response, upon which they rely for gaze stabilization during self-propulsive or environmental movements that may be species specific [Dieringer et al., 1992].

The step-offset (light-off) response of the horizontal optokinetic system in the goldfish appears underdamped, and as such it can be described as a sinusoidal oscillation with an exponentially decaying amplitude [Maioli, 1988]. In most goldfish (70%) the amplitude decayed fast enough that the step-offset response just slightly overshot baseline eye velocity before returning to it. In some goldfish (30%) the step-offset response oscillated about baseline eye velocity for a full cycle or more before finally settling to it. Similar overshooting step-offset responses, and oscillatory responses less typically, have also been observed for avian and mammalian species [pigeons, Gioanni, 1988; rats, Hess et al., 1985].
1985; cats, Maioli and Precht, 1984; monkeys, Cohen et al., 1977]. Rabbits provide a notable exception, as their step-offset response has a linear trajectory which does not appear to oscillate or even to overshoot baseline eye velocity [Collewijn et al., 1980].

For monkeys [Waespe and Henn, 1978] and cats [Clément et al., 1981], the step-offset response becomes more underdamped as the optokinetic system habituates to prolonged or repeated surround rotation stimulation. In a survey of 20 species of teleost fishes [Dieringer et al., 1992], the step-offset response of the horizontal optokinetic system could oscillate, undershoot, or return to baseline without undershooting, depending upon the species and presumably also upon the state of habituation. The total duration of the step-offset response for the various species of teleost fishes ranged from zero to 22 seconds, and was about 12 seconds on average for the goldfish [ibid.]. This value is in the range of total durations for the step-offset responses described here (e.g. fig. 4).

Comparing the Horizontal Optokinetic Frequency Response between Species

The frequency response of the horizontal optokinetic system of the goldfish is essentially low-pass in that its gain decreases and its phase lag increases as the frequency of surround rotation increases. Similar low-pass characteristics are exhibited by the horizontal optokinetic systems of all species for which it has been examined [pigeons, Gioanni, 1988; rats, Hess et al., 1985; rabbits, Collewijn, 1969; cats, Godaux et al., 1983; Maioli and Precht, 1984; monkeys, Paige, 1983]. For the horizontal optokinetic frequency response of the goldfish, for example, gain decreases from almost 0.9 at 0.01 Hz to less than 0.3 at 1.0 Hz. Similarly, phase lag increases from about zero at 0.01 Hz to more than 45 deg at 1.0 Hz. It would be of interest to determine the consequences, if any, of these differences in optokinetic gain and phase lag on visual modification of the goldfish vestibular-ocular reflex at different frequencies.

The relationship between peak eye velocity and the peak velocity of sinusoidal surround rotations is nonlinear for the goldfish horizontal optokinetic response. A similar dependency of gain upon surround peak velocity has been observed for rabbits [Collewijn, 1981] and cats [Godaux et al., 1983; Maioli and Precht, 1984]. As for the rabbits and cats, the gain of the horizontal optokinetic response of the goldfish decreases as the peak acceleration of sinusoidal surround rotation increases. This is thought to be due primarily to nonlinearities in the visual inputs to the optokinetic system.

Modeling the Horizontal Optokinetic System

The model used to simulate the horizontal optokinetic response of the goldfish was derived from previous models that were designed to simulate various aspects of the optokinetic behavior of mammals. The model by Collewijn [1972] introduced the concept of the optokinetic system as a negative-feedback servomechanism, the function of which was to minimize retinal-slip error. This model contained two static nonlinear elements, one saturating and one reversing-slope, that represented retinal-slip inputs from the visual system. It also contained two linear low-pass elements in series and explained how the gradual rise of the optokinetic response could be due both to the low-pass characteristics and the reversing-slope nonlinearity. The low-pass elements served other functions as well. One low-pass element was used to convert the eye velocity signal into an eye position command. The other was needed to prevent instabilities in the negative-feedback mechanism which, due to its high gain and pure time delay, was prone to oscillate.

The second low-pass element was later identified in monkeys as the velocity-storage mechanism [Raphan et al., 1979]. It is possible that the function of velocity storage is to insure stability in the real optokinetic system also. Neurophysiological studies suggest that the velocity-storage mechanism may reside in the vestibular nucleus. Vestibular nucleus neurons respond to visual surround rotation and are active during the optokinetic response of monkeys [Waespe and Henn, 1977, 1979; Boyle et al., 1985], cats [Keller and Precht, 1979], rats [Cazin et al., 1980], frogs and turtles [Dieringer et al., 1983], and goldfish [Dichgans et al., 1973; Allum et al., 1976]. They can have activity related to both the rapid and gradual components of the optokinetic response. The response related to the gradual component indicates the involvement of the velocity-storage mechanism. In the goldfish model, the low-pass elements in the fast and slow (velocity-storage) pathways represent vestibular nucleus neurons, which generate the eye velocity commands for the optokinetic response.

The velocity-storage mechanism was modeled either as a low-pass element that had its time constant at a positive feedback [Robinson, 1977], or as a leaky integrator in parallel with a direct (and more rapid) pathway [Raphan et al., 1979]. In the goldfish model, the velocity-storage element (in the slow pathway) was modeled simply as a low-pass element with a time constant \( \tau_s = 50 \text{ sec} \) that was arbitrarily set to be long in comparison with that of the fast-pathway low-pass element \( \tau_r = 1 \text{ sec} \). The velocity-storage models [Robinson, 1977; Raphan et al., 1979] predicted that the optokinetic step-onset (light-on) response should be
more rapid than the step-offset (light-off) response. However, it was demonstrated recently that, compared with the optokinetic step-onset (light-on) response, the step-offset (light-off) response is more rapid and underdamped [Maio1, 1988]. This was modeled by placing an additional low-pass element in a negative-feedback loop around the velocity-storage mechanism that is closed whenever the optokinetic response is not driven by an appropriate retinal-slip input [Ibid]. That occurs, for example, when the light is switched off during an ongoing optokinetic response, as for the step-offset (light-off) response reported here. This negative-feedback loop discharges the velocity-storage mechanism at step offset and, with appropriate values for the discharge element gain and time constant, produces underdamped responses.

All of these features have been incorporated into the model of the horizontal optokinetic system of the goldfish (fig. 8), with the addition of a nonlinearity that was placed at the output of the slow pathway. A similar, saturating nonlinearity was included at the output of the slow pathway in a model of the optokinetic system in monkeys [Lisberger et al., 1981]. The saturating nonlinearity at the output of the slow pathway represents a limitation on the maximum firing rate of vestibular nucleus neurons. Although no attempt was made to precisely fit the model to the data, it provides a qualitative reproduction of the dynamic and nonlinear features of the results. Because the model was developed to describe data from mammals, its ability also to describe the present data attests to the similarity of the optokinetic mechanisms of mammals and goldfish.

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References


